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Latitudinal population transfer reduces temperature sum requirements for bud burst of European beech

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Abstract The phenology of many woody plants is controlled by an interaction of chilling requirements, photoperiod and temperature forcing. Predictions of leaf unfolding and connected ecosystem processes in global warming should thus consider not only increasing temperatures but also require a thorough understanding of the cumulative effects of daylength and temperature. In the present study, bud burst of six populations of European beech was assessed at two provenance trial sites across a latitudinal gradient of 6° within two consecutive years. Significant differences in bud burst were found among populations, trial sites and observation years. If flushing was related to the temperature forcing at trials sites, populations at the southern trial required similar temperature sums in both observation years, though the average flushing date differed by 6 days. At the northern trial site, bud burst occurred approximately 14 days later, but here

the trees required 43 % degree days less to reach the same flushing state. This indicates a significant effect of the photoperiod on the temperature requirement for bud burst. The flushing sequence among populations was stable across trial sites and observation years, suggesting that similar genetic pathways regulate bud burst throughout the beech distribution. Also, it indicates that the environment of the trial location rather than the genetic origin of the populations determines its reaction to increase spring temperatures in climate change. Significant interactions of the velocity of flushing were observed between populations and trial sites, but not between populations and observation years at the same site. Together with the high variation among populations, this points to local adaptations to specific temperature-photoperiod regimes, however, adaptations to local temperature forcing seem stronger than to the light conditions.

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Introduction

Climate change is predicted to alter the distribution of species and ecosystems significantly (e.g. Sykes et al. 1996; Guisan and Thuiller 2005). The future distribution of forest trees is of particular interest, because trees often dominate and shape complete ecosystems,

thereby guaranteeing ecosystem functioning, carbon storage (Stümer et al. 2010) and various benefits for the human population, including recreation and wood production (Mantau et al. 2001; Hanewinkel et al. 2013). Natural processes that would allow trees to track the changing environment are so far considered too slow to capture the speed of the human-caused warming. For example, the natural migration of northern hemisphere tree species is far below the expected speed of climate change according both, combined fossil/DNA studies (Petit et al. 2008) or modelling expertise (Nathan et al. 2011). Also adaptation through natural selection takes last too long (Savolainen et al. 2007) and may have undesirable side-effects such as higher tree mortality (Kuparinen et al. 2010), although trees generally harbour high genetic diversity and large population sizes (Petit and Hampe 2006). Therefore, assisted migration has been suggested as a management measure to adapt forests to future conditions and to conserve tree species or populations threatened by climate change (McLachlan et al. 2007; Aitken et al. 2008; Leech et al. 2011). To develop transfer schemes for species or populations requires profound knowledge on the interaction between climate conditions and traits responsible for the survival, growth and reproduction. In particular, traits that regulate the timing of growth, i.e. bud burst and leaf colouring, were found to be important as they determine growth and productivity (Keeling et al. 1996; Kramer et al. 2000) as well as the distribution of species (Chaine and Beaubien 2001). These traits also show the strongest signals of local adaptation (Savolainen et al. 2007) because the optimal flushing respectively leaf colouring time is a trade-off between the avoidance of late and early frost events and the maximal utilisation of the vegetation period for photosynthesis and growth (Leinonen and Hänninen 2002; Gömöry and Paule 2011). However, phenological traits are not only controlled by temperature conditions, but also by photoperiodic constraints (daylength, light quality) of the latitude (Saikkonen et al. 2012) and thus raised debates on whether photoperiodic effects should be integrated into predictions of climate change effects (Körner and Basler 2010a, b; Chaine et al. 2010).

For European beech (*Fagus sylvatica* L.), one of the most important deciduous tree species in central Europe, bud burst and its connection to environmental conditions has been addressed in numerous studies

using field observations and phytotron experiments on the individual, the population and the species level (e.g. Heide 1993; Kramer 1994; von Wühlisch et al. 1995; Falusi and Calamassi 1996; Liesebach M. et al. 1999; Jazbec et al. 2007; Robson et al. 2011; Wolf 2011; Kreyling et al. 2012). However, the conclusions of these studies are somewhat contradictory: while physiological studies in climate chambers revealed strong effects of both photoperiod and temperature forcing (Heide 1993; Falusi and Calamassi 1996), observations in natural populations (Kramer 1994) and field experiments (Gömöry and Paule 2011) suggest that mainly temperature signals determine the flushing course. For population transfers, both approaches might be insufficient, because neither artificial long-day treatments (e.g. 24 h in Heide 1993) nor experiments on single sites (Gömöry and Paule 2011; but see Wolf 2011 for multiple field tests) or experimental warming studies (e.g. Kreyling et al. 2012) are able to mimic the putative range shifts which should be facilitated by assisted migration.

The objective of the present study was to analyse the effect of a latitudinal population transfer on the flushing course of European beech. Growing conditions at different latitudes mimic the effect of different photoperiods and temperature forcings. To consider genetic variation and putative local adaptations, six beech populations from a wide range of the natural range were selected. Repeated observations in two consecutive years accounted for varying weather conditions in spring. ANOVA and mixed model analysis were used to identify effects of population, trial site and observation year and to evaluate the consequences of population transfers.

Materials and methods

Experimental setup

Observations of flushing were done on two common garden experiments of the European provenance trial series 1993/1995 for European Beech (e.g. von Wühlisch 2007) located at Gablitz, Austria and Schaedtbek, Germany (Table 1). The trial sites were established in 1995 with 2-year-old seedlings, where from each population in total, 150 seedlings were planted within three randomised blocks. For the present study, six populations (Liesebach M. 2012a)

Table 1 Geographic location, climate and soil characteristics of the two field trials

	Gablitz	Schaedtbek
Coordinates	48°15'N; 16°07'E	54°18'N; 10°18'E
Altitude (m)	350	40
Mean annual temperature (°C) ^a	8.8	8.3
Mean temperature in vegetation period (°C) ^a	16.6	14.6
Annual precipitation (mm) ^a	729	729
Precipitation in vegetation period (mm) ^a	395	354
Soil characteristics ^a	Waterlogged soil (Stagnosol) derived from sandstone with average nutrient and water supply, located at uphill depletion zone	Moderately moist site. Soil is mottled in deeper layers and has stagnic properties near the surface

^a More details on climate and soil conditions can be found in Liesebach M. (2012a) and Müller (2012)

were selected for detailed investigations of bud break (Table 2). The number of remaining trees per population ranged from 88 to 116.

Monitoring of flushing

Bud break was studied by monitoring each single individual on two to nine observation dates in approximately weekly intervals. Intervals were adjusted to the present state of bud break: during fast changes, the intervals were reduced to three days. On each date, the state of flushing was recorded for each tree in the upper third of the crown according to a 7-phase flushing scheme (Malaisse 1964; Schueler et al. 2012): 1—dormant buds; 2—buds swollen and elongated; 3—buds begin to burst, first green visible; 4—folded and hairy leaves begin to appear; 5—leaves are spread out; 6—leaves unfolded, but still fan-shaped, pale scales present and 7—leaves unfolded, smooth and bright. At the trial site Schaedtbek,

flushing was monitored in spring 2005 and 2006, at the trial site Gablitz in 2006 and 2007 (Fig. 1).

Data loggers to monitor temperature and precipitation were installed at Schaedtbek in 2005 and in Gablitz in 2006. Since the climate monitoring in Gablitz started at April 2006, temperature data of the neighbouring climate station Mariabrunn of the Central Institute for Meteorology and Geodynamics of Austria (aerial distance ~10 km) were used to reconstruct missing data, by comparing temperature data between 2006 and 2008. For each site and year, temperature sums (given as degree days) were calculated starting with the first day above a mean temperature of 5 °C and summing up all daily mean temperatures above the forcing threshold of 10 °C (Kramer 1994).

Statistical analysis

In order to compare the flushing course among populations, sites and years, the monitoring data were

Table 2 Geographic origin, altitude and the number of individual trees per populations that were monitored within the present study. Populations are shown in increasing latitude

Pop. No.	Pop. name	Country	Longitude	Latitude	Altitude (m asl)	Gablitz N	Schaedtbek N
5	Anguiano	Spain	02°45'W	42°15'N	950	88	89
146	Beius-Bihor	Romania	22°16'E	46°41'N	295	107	96
109	Neuberg-Mürzsteg	Austria	15°28'E	47°45'N	1,050	109	98
110	Kladská	Czech Republic	12°37'E	50°02'N	690	103	99
44	Oderhaus	Germany	10°50'E	51°40'N	710	92	116
46	Gransee	Germany	13°10'E	53°00'N	70	100	96

Populations are shown in increasing latitude

N number of survived individual trees that were analysed in the present study; Further details are available in Liesebach M. (2012a, b)

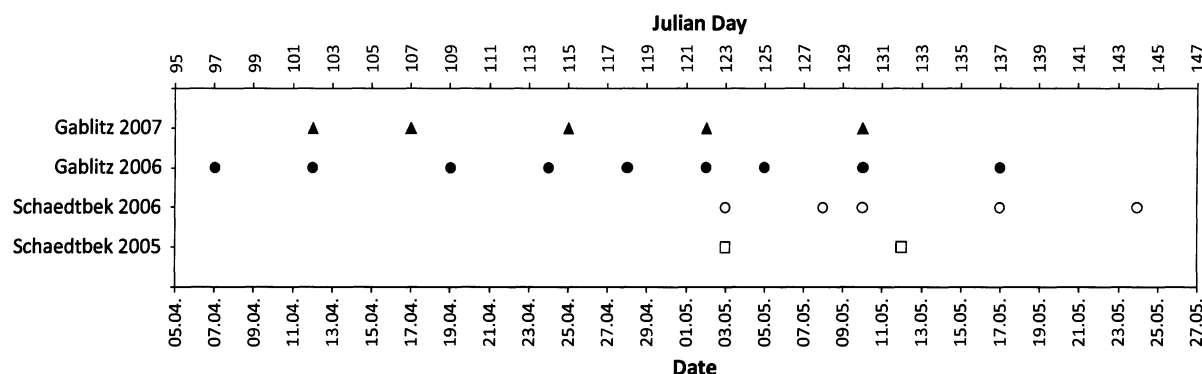


Fig. 1 Monitoring schedule at the two experimental sites within the different observation years. The monitoring days are marked by filled (site Gablitz) and open (site Schaedtbek) symbols

transformed into five flushing parameters. All calculations were based on the change from flushing state 4 to 5, because this transition is the visually most distinct change and was found to have the most discriminatory power as revealed by the highest indices of Shannon's diversity calculated for each state across all observation days. These parameters include first, the average Julian date of change from state 4 to 5 (D_{4-5}), where the exact date of change was calculated by linear interpolation following Davi et al. (2011). Second, to relate leaf unfolding to temperature sums, the same linear interpolation was used to identify the temperature sums necessary for the change from state 4 to 5 (T_{4-5}). Third, the approximate daylength at the change from state 4 to 5 was calculated (L_{4-5}), because the length of the daily photoperiod has been suggested as another important factor for beech flushing in earlier studies (Heide 1993). Forth and fifth, the linear interpolations between state 4 and 5 were used to estimate the velocity of bud burst for individual trees and populations in relation to both the Julian day (V_D) and the temperature sums (V_T).

To test for the stability of flushing patterns, we calculated Pearson's correlation coefficient r between the various flushing parameters of different trials and years. For the correlations among years of the same site, we used data of single individuals to test for the stability within and among populations. The stability of flushing pattern among populations was tested by correlations of the average flushing variables among trial sites as well as among years.

To compare the flushing parameters and to estimate the effect of populations, blocks, years and sites, general linear models (GLM) were applied. First, for

each trial site and year, we tested for the effect of block and population using a GLM, where the population was considered as random effect. Second, comparison among sites and years was calculated by treating blocks as fixed and population/year, respectively, population/site as random variables. For multiple comparisons among populations, Scheffe's post hoc test was used. All statistical calculations were performed with Statistica 9.0 (Statsoft Inc.) using the modules GLM and variance components.

Results

The spring temperature forcing and the increase of daylengths at the two trial sites differ strongly (Fig. 2). Until March 19, days are longer at the southern trial site Gablitz; however, the increase in daylength is stronger at Schaedtbek and in the mid of May, when flushing was finished at all sites, days are already 40 min longer at Schaedtbek. Strong differences between sites and observation years were also observed for the course of temperature development. At the end of April, temperatures accumulated at Gablitz amounted to 235 and 310 degree days, in 2006 respectively 2007, whereas in Schaedtbek only 95 (2005) and 40 (2006) degree days were reached. The differences in environments and spring forcing among sites and years resulted in significant differences in bud break among trial sites and observation years (Fig. 3). Also, differences between populations were significant. In 2006, the average change from state 4 to 5 took place on May 2 in Gablitz and on May 8 in Schaedtbek. In 2007, the average bud break in Gablitz

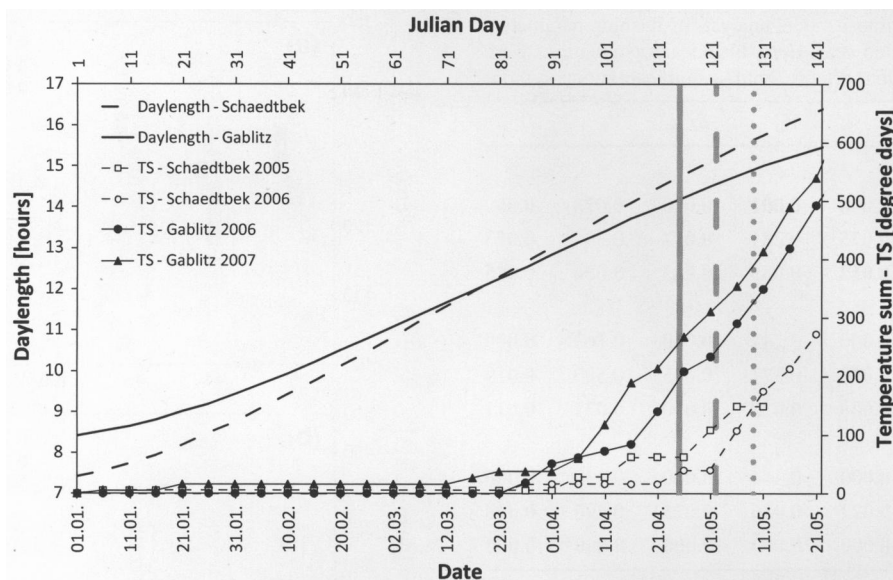


Fig. 2 Environmental conditions (daylength and temperature sum—TS) during bud burst at the two trial sites within the two observation years. The average bud burst dates (=transition from stage 4 to 5) of each site/year are indicated by vertical grey lines, where the full line shows the year 2006 at Gablitz, the dashed

line the year 2007 (Gablitz) and the dotted line the year 2006 at Schaetdbek. Data for bud burst in Schaetdbek 2005 are not shown, because no interpolation to the transition from state 4 to 5 was possible

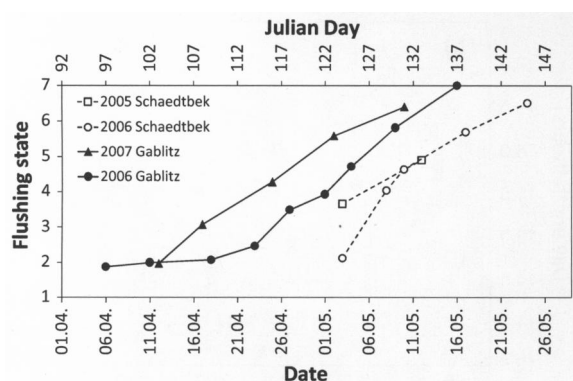


Fig. 3 Overview of the average flushing course at the two trial sites within the two observation years

occurred already on April 25. The flushing data of Schaetdbek in 2005 could not be transformed into the requested flushing parameters, because the two available observations did not covered the various flushing states of all trees and thus did not allow a linear interpolation of the transition between state 4 and 5. Therefore, these data were not considered for further analysis.

At both sites and within both observation years, the eastern alpine population “Neuberg-Mürzsteg” (No.

Table 3 Stability of flushing patterns among individuals and populations as revealed by correlations (Pearson’s correlation coefficient) between observation years and sites (bold—significant alpha < 0.05)

N	Among individuals		Among populations	
	GA 2006 vs. GA 2007	GA 2006 vs. GA 2007	GA 2006 vs. SB 2006	GA 2007 vs. SB 2006
556	6	6	6	6
D_{4-5}	0.847	0.977	0.979	0.933
V_D	0.026	0.438	−0.142	0.146
T_{4-5}	0.86	0.973	0.99	0.95
V_T	0.142	0.940	0.331	0.34
L_{4-5}	0.846	0.977	0.979	0.933

GA Gablitz; SB Schaetdbek; D_{4-5} Julian day of change from flushing state 4 to 5; T_{4-5} temperature sum necessary for the change from state 4 to 5; L_{4-5} daylength at the change from state 4 to 5; V_D velocity of bud burst in relation to Julian days; V_T velocity of bud burst in relation to temperature sums

109) was the first to reach state 5 and the northernmost population “Gransee” (No. 46) the latest. Generally, the flushing pattern of individual trees and populations showed a high stability (Table 3). The highest stability was obtained for the flushing state parameters D_{4-5}

Table 4 General linear model analysis of flushing parameters for each trial site and year. Here, blocks and populations were considered as random effects (bold—significant alpha < 0.05)

	D_{4-5}	V_D	T_{4-5}	V_T	L_{4-5}
Schaedtbek 2006					
Pop	0.000	0.001	0.000	0.028	0.000
Block	0.025	0.281	0.017	0.394	0.023
Pop × block	0.012	0.035	0.043	0.034	0.015
Gablitz 2006					
Pop	0.000	0.242	0.000	0.163	0.000
Block	0.020	0.377	0.045	0.580	0.019
Pop × block	0.008	0.028	0.000	0.031	0.011
Gablitz 2007					
Pop	0.000	0.344	0.000	0.138	0.000
Block	0.022	0.036	0.025	0.290	0.018
Pop × block	0.000	0.000	0.000	0.000	0.000

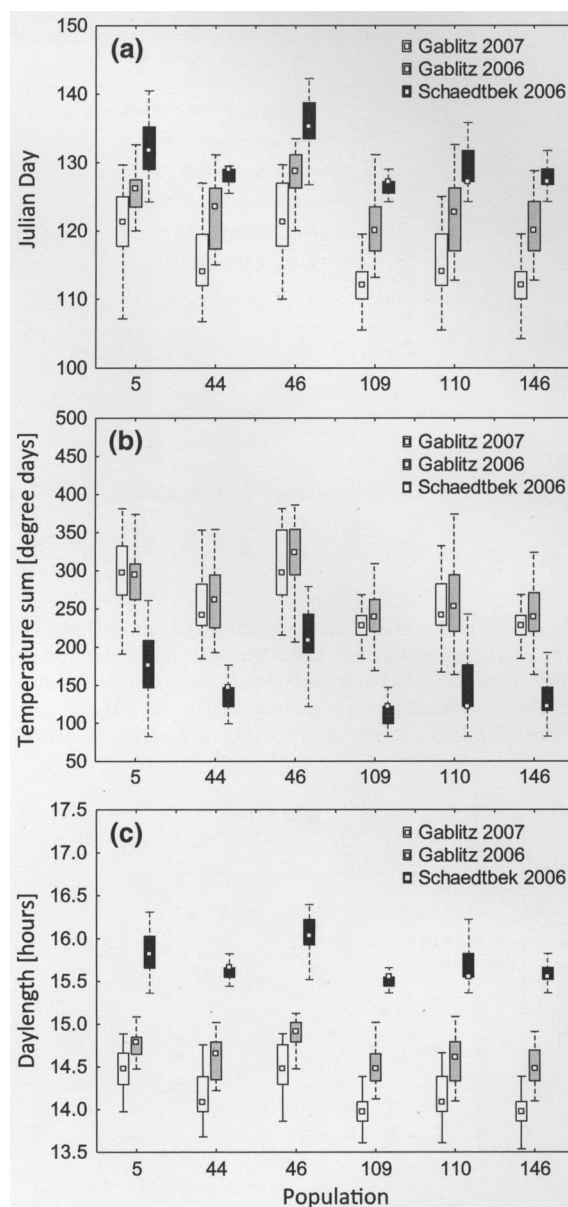
D_{4-5} Julian day of change from flushing state 4 to 5; T_{4-5} temperature sum necessary for the change from state 4 to 5; L_{4-5} daylength at the change from state 4 to 5; V_D velocity of bud burst in relation to Julian days; V_T velocity of bud burst in relation to temperature sums

Table 5 General linear model analysis of flushing parameters across years and trial sites. For these analyses, blocks were treated as fixed and populations/years respectively populations/sites as random variables (bold—significant alpha < 0.05)

	D_{4-5}	V_D	T_{4-5}	V_T	L_{4-5}
Gablitz: 2006 vs. 2007					
Year	0.000	0.000	0.043	0.000	0.000
Pop	0.000	0.173	0.000	0.001	0.001
Block	0.000	0.011	0.000	0.006	0.000
Year × pop	0.013	0.026	0.143	0.873	0.001
2006: Gablitz vs. Schaedtbek					
Site	0.000	0.836	0.000	0.012	0.000
Pop	0.000	0.580	0.000	0.258	0.000
Block	0.010	0.057	0.030	0.529	0.025
Site × pop	0.143	0.000	0.352	0.008	0.022

D_{4-5} Julian day of change from flushing state 4 to 5; T_{4-5} temperature sum necessary for the change from state 4 to 5; L_{4-5} daylength at the change from state 4 to 5; V_D velocity of bud burst in relation to Julian days; V_T velocity of bud burst in relation to temperature sums

(Julian day), T_{4-5} (temperature sum) and L_{4-5} (daylength). The velocity of flushing related to days (V_D) did not show any correlation among individuals or populations. However, when the velocity of flushing

**Fig. 4** Comparison of the average bud burst (=transition from stage 4 to 5) related to Julian days— D_{4-5} (a), the accumulated temperature sums— T_{4-5} (b) and daylength— L_{4-5} (c). Rectangles in boxes represent median, boxes represent lower and upper quartiles and whiskers represent extremes up to 1.5 of the interquartile range

was related to the increase of the temperature sum (V_T), significant correlations were obtained on the individual and the population level comparing the results of 2006 and 2007 in Gablitz. Correlations among sites on the population level were not significant also for V_T (Table 3).

(a) Gablitz: 2006 vs. 2007 – T_{4-5}						
Year	Pop	1	2	3	4	5
2007	109	X				
2007	146	X				
2006	109	X	X			
2006	146	X	X	X		
2007	110	X	X	X		
2006	110		X	X		
2007	44		X	X		
2006	44			X		
2006	5				X	
2007	5				X	
2007	46				X	X
2006	46					X

(b) 2006: Gablitz vs. Schaedtbek – T_{4-5}								
Site	Pop	1	2	3	4	5	6	7
SB	109	X						
SB	146	X						
SB	44	X						
SB	110	X						
SB	5		X					
SB	46			X				
GA	109				X			
GA	146				X	X		
GA	110				X	X		
GA	44					X		
GA	5						X	
GA	46							X

Fig. 5 Multiple comparison of the average bud burst date related to temperature sum T_{4-5} as post hoc analysis (Scheffe's test) of the GLM analysis. **a** Homogeneous groups of populations revealed

from the comparison of the two observation years at the site Gablitz. **b** Homogenous groups of populations for the comparison among the two trial sites in 2006 (SB Schaedtbek, GA Gablitz)

Comparisons of the flushing state for single sites and years revealed significant differences among populations and blocks for D_{4-5} , T_{4-5} and L_{4-5} (Table 4). At Schaedtbek, significant differences were also observed among populations for the velocity of flushing V_D and V_T . When the observation year and the trials site were added as additional fixed model effects, the differences among populations remained significant (Table 5).

Significant differences in flushing state (for D_{4-5} , T_{4-5} , L_{4-5} and V_T) were found among the trial sites Gablitz and Schaedtbek in 2006 and among the observation years 2006 and 2007 at Gablitz (Table 5). However, when the average bud burst at Gablitz was related to Julian days and daylength (Fig. 4a, c), strong differences were found within and among populations, while the differences among populations were only minor when related to the temperature sums (Fig. 4b). For example, the average change from state 4 to 5 took place about 7 days later in 2006 (day 123) as compared to 2007 (day 126), while the required temperature sum up to this day differed only by 9 degree days (269 in 2006 and 260 in 2007). Indeed, Scheffe's post hoc test (Fig. 5a) did not reveal differences among the same populations in 2006 and 2007 for T_{4-5} .

Comparisons among the trial sites showed strong significant differences among populations also when the flushing state was related to temperature sums. Here, the post hoc test (Fig. 5b) did not show any correspondence between the same populations. Generally, in Schaedtbek, the trees required less than 60 %

of the temperature sum for bud burst as compared to Gablitz. If the flushing state was related to daylength (L_{4-5}), trees at Schaedtbek spread out leaves on days with 15.7 h on average, whereas they had only 14.6 h at Gablitz.

For the velocity of bud burst, significant differences were observed among years and sites when the velocity was related to temperature sums V_T (Table 5). When the velocity was related to Julian days V_D , significant differences were only observed between 2006 and 2007 in Gablitz. The plasticity of V_D and V_T at different years and on different sites is shown in Fig. 6a–d, respectively. The comparison between 2006 and 2007 in Gablitz demonstrates that the decrease of V_T and V_D was similar for all populations, while the comparison between Gablitz and Schaedtbek revealed unequal and partly opposite changes of the velocity of bud burst. For example, in population "Oderhaus" (No. 44) bud burst occurred at a similar rate in Gablitz and Schaedtbek, while other populations showed a lower velocity V_T in Schaedtbek.

Discussion

The present study provides strong evidence for the impact of photoperiodic signals in the control of bud burst of European beech in situ. In our comparison among trial sites with identical genetic material (progenies), we found that a latitudinal population transfer across 6° north reduced the temperature

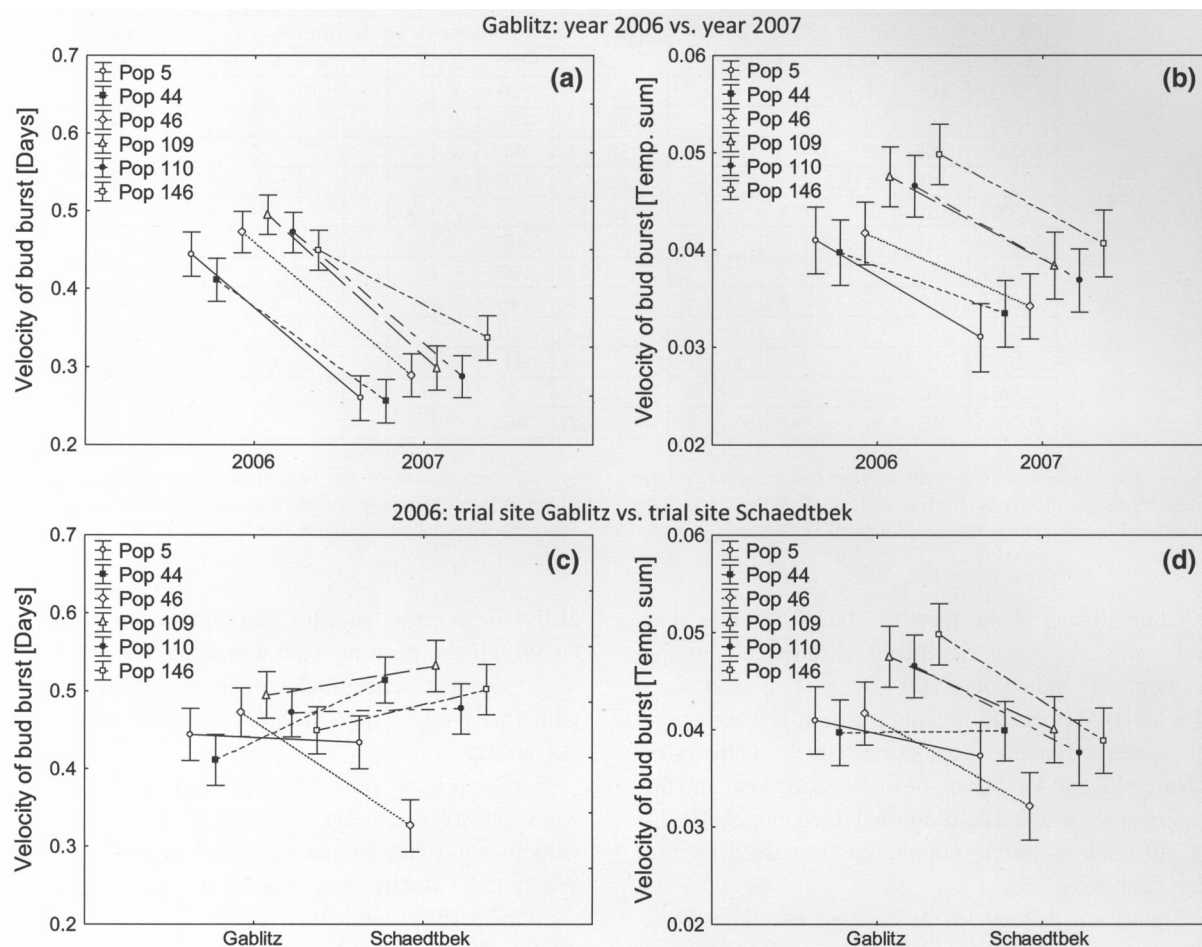


Fig. 6 Plasticity of the velocity of bud burst related to Julian day— V_D (a, c) and temperature sum— V_T (b, d) for comparisons between the observation years at the trial site Gablitz (a, b) and between the trial sites in 2006 (c, d)

requirement for bud burst of European beech to approximately 57 %, while interannual changes of the spring temperature forcing at a single site resulted in very similar temperature requirements. Thus, our field experiment supports earlier phytotron studies of Heide (1993) and Falusi and Calamassi (1996), which found that both photoperiod and temperature are crucial triggers of leaf phenology. Compared to the phytotron studies where long and short day treatments differed between 4 and 16 h, differences in the photoperiod are rather small among our trial sites (0–40 min during the main course of flushing). This suggests that the ultimate signal for the onset of flushing is initiated somewhere between 12 and 14 h. Also, if we compare the absolute variation in daylength across the entire distribution range of beech spanning approximately from 38° (e.g. Messina, IT) to 58° North (e.g.

Göteborg, SE), we find very similar daylengths in the mid-March (~12 h) that extend rapidly in the North but slower in the South (Fig. 7). In a recent review, Vitasse and Basler (2013) proposed two alternative models to account for the effect of photoperiod: either a fixed photoperiod threshold required for dormancy release, or through reduced temperature requirements with increasing daylength. Further studies at trial sites throughout larger latitudinal ranges would be required to finally resolve this question. Also, the phenological observations should be accompanied by physiological measures of cambial and bud activity prior to the appearance of leaves, since very likely, the vital environmental triggers of bud burst act weeks before leaf development can be assessed visually.

The low impact of temperature forcing on bud burst has also been demonstrated by recent analyses of bud

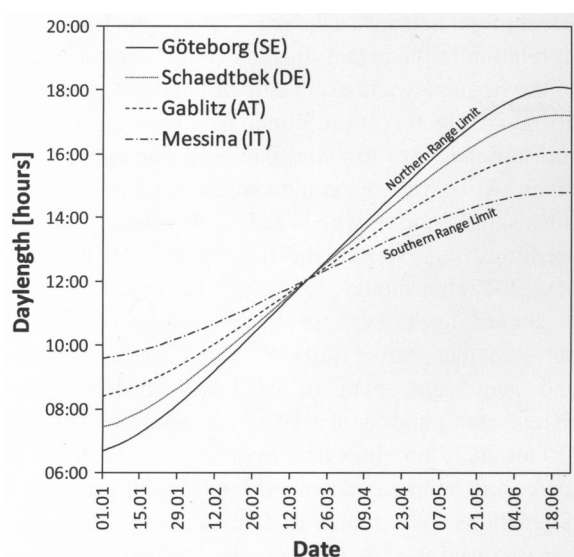


Fig. 7 Photoperiodic limitation of the daylength variation within the natural distribution of European beech. During mid of March (Julian day: 78), a similar daylength can be found all over the beech range

phenology across altitudinal gradients, where for European beech, the lowest sensitivity to spring temperatures has been found among several tree species (Vitasse et al. 2009; Davi et al. 2011). In contrast, field investigations of Gömöry and Paule (2011) and the analysis of phenological observations (Kramer 1994) attributed the flushing course mainly to the temperature signal. However, the latter studies were conducted within single trial sites (Gömöry and Paule 2011) or within small geographic ranges (Kramer 1994). Therefore, photoperiodic differences are likely small and negligible within these studies. Besides temperature and photoperiod, several earlier studies identified the number of chilling days during dormancy, i.e. days below a temperature threshold of 5 °C, as a significant factor in bud burst control (Murray et al. 1989; Heide 1993; Falusi and Calamassi 1990; Robson et al. 2011; Vitasse and Basler 2013). At the trial locations of the present study, a limited number of chilling days does not seem to play a crucial role, because the number of chilling days differed strongly between 2006 and 2007 at Gablitz (2006: 130 days; 2007: 55 days) but not among the trial sites (Schaedtbek 2006: 125 days). This suggests that at our trial sites—both located north of the Alps—the chilling threshold has been exceeded already with 55 days.

The flushing course and velocity of individual trees within populations were highly stable in both observation years, confirming the strong genetic control of bud burst with heritabilities up to 0.7 (Billington and Pelham 1991; Howe et al. 2000). Also, the flushing sequence of populations was highly stable across trial sites, although the population transfer resulted in strongly reduced temperature requirements. This is in agreement with previous studies that observed significant earlier bud burst in populations from southeastern Europe and from higher elevations compared to populations from Western Europe and lower elevations (von Wühlisch et al. 1995; Chmura and Rożkowski 2002). It indicates that the control of bud burst through both photoperiod and temperature follows very similar genetic pathways across its entire distribution range, because our study included populations from a wide range of the natural distribution including different phylogeographic lineages (e.g. Magri et al. 2006; Liesebach H. 2012). This confirms the suggestion of Vitasse et al. (2009) that the population sensitivity to global warming is stable for given species, in spite of local adaptations. In our study, the high variation in temperature requirements among populations and the stable flushing sequence suggests that adaptations to local temperature regimes are much higher than adaptations to local light conditions. However, the analysis of flushing velocity in relation to temperatures revealed significant interactions between populations and trial sites and thus also points to local adaptations to specific photoperiod-temperature conditions. Hence, some populations seem to be able to utilise the different light regime better than others. This is in particular true for population “Oderhaus” (No. 44), which originates from a high altitude in northern Germany. “Oderhaus” shows a similar velocity of bud burst at both sites, while other populations from a comparable photoperiodic origin but different altitudes (e.g. Gransee, No. 46) or from a similar altitude but different photoperiodic origins (“Neuberg-Mürzsteg”, No. 109) showed lower flushing velocity at the northern trial site Schaedtbek (Fig. 4d). Insights into the interacting effects of photoperiod and temperature on regulating phenological traits and driving local adaptations are available from the annual herb *Arabidopsis thaliana*. Here, flowering time is regulated by four distinct but linked genetic pathways responsible for receiving and mediating light and temperature signals and

modulating flowering concertedly (e.g. Putterill et al. 2004). Since light and temperature signals are being detected and transmitted by separate pathways, natural selection is able to modify the response to a specific environmental variable independently from other environmental effects (Roux et al. 2006). The observed differences in the plastic response of beech populations could putatively be explained by similar regulatory networks.

The verification of photoperiodic effects in situ across a latitudinal transect has severe implications for the understanding and modelling of consequences of climate change for beech range expansions (Sykes et al. 1996) and for developing population transfer and assisted migration schemes in forestry (Kramer et al. 2010; Leech et al. 2011). Predictions of the future distribution range of European beech suggest range contractions mainly in southwestern Europe but beech expansion in north and northeastern Europe (e.g. Kramer et al. 2010). During these expansions, populations will eventually being exposed to other photoperiodic regimes. The present study suggests that beech generally owns robust regulations that enable a successful survival at higher latitudes, since all tested populations responded to changes of the photoperiod with reduced temperature requirements. Due to existing adaptations to local temperature and light regimes—however—significant differences in the length of the growing period and productivity can be expected for different populations. Successful beech forestry might therefore aim at transferring productive and early flushing populations from lower latitudes to utilise the vegetation period as much as possible (e.g. Chmura and Rożkowski 2002). Besides bud burst, Nielsen and Jørgensen (2003) also found higher adaptive potential to different soil water contents and better growth performance for populations of southern Europe and argued that such populations might be introduced also to Scandinavia. Such a population transfer does not necessarily need to imply higher susceptibility to frost events. For example, Višnjić and Dohrenbusch (2004) found high frost resistance also for populations of southeastern Europe, and Kreyling et al. (2012) observed the lowest late frost damage on the very early and the late flushing populations. In Kreyling's study, early flushing populations already had developed robust leaves that were able to withstand short nightly frost incidences. This suggests that the ultimate effect of a single late frost

event might depend on the exact date of the frost event in relation to the actual flushing state. Since forecasts of the frequency and exact date of late frost events are not available for future climates, so far, no specific recommendations to avoid late frost damages can be given. Also, final recommendations for forest plantations should not only be based solely on early tests of seedlings (e.g. Nielsen and Jørgensen 2003; Kreyling et al. 2012) but should also include field measurements at higher ages, because in beech the correlation between quantitative traits (e.g. height) at the juvenile and adult age seem to be lower than expected (Kleinschmit and Svolba 1996; Liesebach M. 2012b).

Our study provides new evidence for the effect of increasing temperatures on bud set of well-established populations. We found that an earlier temperature forcing was able to advance the budburst by about seven Julian days at our trial site Gablitz. A similar advance of bud burst with increasing temperatures has also been found by Čufar et al. (2012) and Vitasse and Basler (2013) for populations of higher altitudes but not for populations of lower sites. Thus, Vitasse and Basler (2013) suggest that populations at the colder boundary of beech distribution might be more sensitive to warmer spring temperatures than populations inhabiting lower altitudes and warmer climates. Because the reaction of the six tested populations in our comparison between 2006 and 2007 at Gablitz was very similar, we suggest that the environment of the trial locations rather than the genetic origin of the populations determines its reaction to increase spring temperatures.

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