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Research paper

Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species

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Spring phenology of temperate forest trees is optimized to maximize the length of the growing season while minimizing the risk of freezing damage. The release from winter dormancy is environmentally mediated by species-specific responses to temperature and photoperiod. We investigated the response of early spring phenology to temperature and photoperiod at different stages of dormancy release in cuttings from four temperate tree species in controlled environments. By tracking bud development, we were able to identify the onset of bud swelling and bud growth in *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Quercus petraea* (Mattuschka) Liebl. and *Picea abies* (L.) H. Karst. At a given early stage of dormancy release, the onset and duration of the bud swelling prior to bud burst are driven by concurrent temperature and photoperiod, while the maximum growth rate is temperature dependent only, except for *Fagus*, where long photoperiods also increased bud growth rates. Similarly, the later bud burst was controlled by temperature and photoperiod (in the photoperiod sensitive species *Fagus, Quercus* and *Picea*). We conclude that photoperiod is involved in the release of dormancy during the ecodormancy phase and may influence bud burst in trees that have experienced sufficient chilling. This study explored and documented the early bud swelling period that precedes and defines later phenological stages such as canopy greening in conventional phenological works. It is the early bud growth resumption that needs to be understood in order to arrive at a causal interpretation and modelling of tree phenology at a large scale. Classic spring phenology events mark visible endpoints of a cascade of processes as evidenced here.

Keywords: day length, deciduous trees, development, phenology, warming.

Introduction

Trees in temperate and boreal climates undergo a period of dormancy and enhanced freezing resistance to withstand the harsh climate conditions during winter. The phenological events that coincide with induction and release of dormancy (bud set and bud burst) are finely tuned to the seasonality of the tree's environment, minimizing the risk of potentially fatal freezing damage in autumn and spring, while maximizing the length of the growing season. A well-timed phenology is crucial for long-term survival, successful reproduction and species persistence (Larcher 2003).

Plant dormancy is characterized by suspension of growth and development (Samish 1954), that is, suppressed cell division and a strongly reduced metabolism. Three different states of dormancy are distinguished (Lang et al. 1987): (i) endodormancy, an internal (genetically controlled) set state of inactivity; (ii) ecodormancy, a state of inactivity imposed by unfavourable environmental conditions; and (iii) paradormancy, a state of specific bud dormancy maintained due to physiological factors outside the dormant meristems (e.g., correlative inhibition and apical dominance). The phenological changes that occur when plants perceive the environmental signals for the induction and release of dormancy are associated with physiological

responses including phytohormones, phytochromes and carbohydrates (Chao et al. 2007). The gradual transitions between the different phases of dormancy involve numerous genetic, biochemical, physiological and anatomical alterations (Faust et al. 1997, Rinne et al. 1997, Horvath 2010, Cooke et al. 2012). During the winter months, bud scales may grow minutely (Perry 1971) and cell division in the apical meristems may continue at low rates, but elongation growth is absent due to an inhibition of the sub-apical tissue (Romberger 1963).

In humid extra-tropical climates, the induction and release of seasonal dormancy are triggered by environmental signals, mainly temperature and photoperiod. In most temperate and boreal trees, dormancy is induced by the decreasing length of the photoperiod in autumn and cool temperatures, resulting in the cessation of growth and the formation of winter buds (Wareing 1956, Vaartaja 1959, Thomas and Vince-Prue 1997). The astronomically defined photoperiod serves as a reliable environmental signal for the progression of the season and may thus indicate the period with a higher risk of freezing events in autumn before trees are actually exposed to such temperatures. Photoperiod and low temperature may induce dormancy through independent pathways (Welling et al. 2002) and in a few species, low temperatures alone seem to be sufficient to induce endodormancy (Heide and Prestrud 2005, Heide 2011).

Once established, endodormancy ensures that growth will not be resumed during warm spells in winter. In tree species adapted to cool climates, endodormancy is generally released after sufficiently long exposure to cool, non-freezing temperatures ('chilling'; Perry 1971, Sarvas 1974). Yet, the actual range of effective temperatures for chilling is only vaguely known for forest trees, and cool, non-freezing temperatures up to 10 °C, most likely between 2 and 4 °C, are expected to be most effective (Battey 2000). Higher temperatures may even negate previous chilling (Perry 1971), while lower (sub-zero) temperatures are generally considered to be ineffective for the fulfilment of the chilling requirement, presumably because very low temperatures prevent a physiological integration of signals (too low metabolic activity). Once the chilling requirement is fulfilled, metabolic activity increases, hydrolytic enzymes are activated and carbohydrate reserves gradually become mobilized. As a first visually identifiable clue, the onset of bud swelling indicates that the transition from endodormancy to ecodormancy has occurred (Saure 1985, Pallardy 2008). The bud water content rises (Essiamah and Eschrich 1986) and the buds become increasingly susceptible to freezing. The subsequent release of ecodormancy is modulated by favourable environmental conditions. Bud burst of many short-lived and pioneer species is then mediated by warm temperatures only and bud burst occurs when the accumulated temperature sum exceeds a genotype-specific threshold (forcing requirement; degree-days; Nienstaedt 1967, Perry 1971). Photoperiod sensitivity is most pronounced in *Fagus sylvatica* L. (Klebs 1914, Wareing 1953, Heide 1993*b*), but has also been observed in other tree species (Heide 1993*a*, Partanen et al. 1998, Caffarra et al. 2011, Basler and Körner 2012). One hundred and twenty years ago, Jost (1894) had already observed a failure or major delay of bud burst in *Fagus* on twigs subjected to complete darkness in situ. Photoperiod controls of spring phenology were adopted mainly by long-lived, late successional tree species (Caffarra and Donnelly 2010, Körner and Basler 2010). Photoperiod may interact at different stages of dormancy release, e.g., long photoperiods are likely to substitute for a lack of chilling (Downs and Borthwick 1956, Wareing 1969, Heide 1993*a*) and decrease the thermal requirement for bud burst (Myking and Heide 1995, Caffarra et al. 2011). However, photoperiodic responses in spring phenology are highly species dependent and still not widely acknowledged, mostly due to the fact that species commonly operate within a photoperiod 'window' in which temperature has an overwhelming effect, particularly in cool years (Körner 2007). In a nutshell, the three potential environmental drivers (chilling, photoperiod and temperature) of spring phenology interact in complex, species-specific ways that are as yet to be clearly disentangled.

In photoperiod-sensitive species, a delayed bud burst under short photoperiods may relate to a later onset of bud development or to slower rates of bud development. In this study, we assessed the responses of early spring phenological phases (bud swelling and bud burst) to photoperiod at different temperatures during release from endodormancy in three photoperiod-sensitive species (European beech *F. sylvatica*, sessile oak *Quercus petraea* (Mattuschka) Liebl. and Norway spruce *Picea abies* (L.) H. Karst.) and an assumingly photoperiod-insensitive species (sycamore maple *Acer pseudoplatanus* L.). We conducted growth chamber experiments using cuttings from mature trees after three consecutive sampling dates (presumed states of dormancy release) in late winter and early spring. To account for possible ecotypic differentiation, we sampled each species in populations from two elevations and across two regions. We expected an earlier dormancy release and bud burst in warm temperatures and a distinct delay of bud burst under shorter photoperiods in the late successional species (*Fagus, Quercus* and *Picea*) assessed here.

Materials and methods

Sampling region

High- and low-elevation sampling sites were defined along two elevational gradients in the region of Chur (46.51°N/9.51°E, hereafter named 'eastern transect') and Lavey (46.12°N/7.02°E, 'western transect'), Switzerland (for further details, see Basler and Körner 2012). The elevational difference between the high and low sampling sites was ~500 m, which corresponds to a mean temperature difference of ~3 K on both transects. In the

year preceding the experiment, temperature loggers (TidBit v2, Onset Computer Corporation, Bourne, MA, USA) were placed at the sampling sites inside the forest in order to track the local air temperatures (2 m above ground, shaded). The two regions were treated as replicates of the elevational sampling for all further analysis (no climatic contrast based on our records). In order to avoid confusion between temperatures (°C) and temperature differences, we join other authors in adopting K (for Kelvin) for all differences in temperature.

Sampling

During late winter/early spring 2010, cuttings of four species (*A. pseudoplatanus*, *F. sylvatica*, *Q. petraea* and *P. abies*; hereafter we refer to species by their genus name) were sampled three times (26/27 January, 1/2 March, 30/31 March) on each of the four sampling sites. On each site, dormant twigs of five individual trees per species were sampled from the lower canopy (5–6 m above ground, five twigs per tree) using a 4-m tree pruner (Fiskars, Helsinki, Finland). The twigs were immediately labelled, watered and transported to the Institute of Botany within 6 h where they were stored at 2 °C in the dark until sample preparation on the following day (28 January, 3 March, 1 April).

Sample treatment

Sample preparation was done according to the method described in Basler and Körner (2012): the twigs were cut to a length of 30–40 cm, the lower part dipped into a disinfectant chlorine solution, were re-cut the second time under water at a steep angle using sterile branch scissors and placed into 0.5-l glass bottles filled with 0.4-l cool, chlorine-free tap water. During the experiment, the water was changed weekly and at the same time the twigs were re-cut another 1–3 cm in order to assure good water supply.

Treatments

The treatments consisted of a fully reciprocal design of two temperature treatments (6 °C versus 9 °C daily mean temperature with a diurnal cycle with a 10-K amplitude, ±5 K day cycle) and photoperiods (initially 9.2 h (short day length, SD) versus 10.8 h (long day length, LD), increased daily by the natural daily increase of photoperiod at 46.5°N) assigned to four computer controlled growth cabinets (each 253 × 120 × 195 cm, Weiss Klimatechnik GmbH, Reiskirchen-Lindenstruth, Germany). The initial photoperiod resembled the natural photoperiod of 25 January (SD) and 25 February (LD) at the sampling sites. The photoperiod in all treatments consisted of 8-h high-intensity light from metal halide lamps (MF400LS/U, EYE Iwasaki Electric Co., Tokyo, Japan) providing 506 ± 30 µmol m^{-2} s^{-1} PFD (Red:FarRed 4.2) at plant level and a low PFD intensity extension period using incandescent lamps (Classic A 100W, Osram AG, Munich, Germany) providing 42 ± 6 µmol m^{-2} s^{-1} PFD (Red:FarRed 0.8). This low PDF extension to the desired photoperiod should prevent a confounding between the photoperiod and the dose of photon flux received (Wareing 1953). An additional set of cuttings was placed in a warm greenhouse (>21 °C) with long day length (16 h) provided by metal halide lamps to determine the time to bud burst under warm forcing conditions.

Visual bud census

Bud development was observed at 2-day intervals, using a four-stage scale for bud development (dormant, swollen, bud burst, leaf unfolding). Bud burst was defined by the appearance of the first green leaf tip. Due to the large number of samples (1200 twigs after the third sampling), we used a customized barcode system to efficiently accomplish the bud observations: the samples were identified by a barcode label and the visually determined bud status was stored directly in a spreadsheet using a bar-coded scale for the state of bud development.

Tracking bud swelling and image analysis

Bud development until bud burst was tracked using image time series made by scanning the twigs every 3–4 days using a commercial flatbed scanner (CanoScan LiDe 200, Canon, Tokyo, Japan; scanned at 300-dpi resolution). Bud width, length and projected area were then extracted from the individual bud images using a custom-designed semi-automatic software (by the author, written in python; www.python.org). A total of 960 time series (~10,000 images) was assembled; however, 234 time series had to be excluded from further analysis, as no continuous observation of the same bud on the twig was possible or the observed bud failed to burst.

The onset of bud swelling (λ) and thus, the duration of the bud swelling period under our controlled temperature treatments were determined as the nonlinear least-squares estimates of a partially linear model fitted to the individual bud measurement time series $y(t)$:

$$\log(y(t)) = \begin{cases} y_o & (t < \lambda) \\ \mu_{max}(t - \lambda) + a & (t \geq \lambda) \end{cases} \quad (1)$$

where t denotes time, y_o is the fitted size of the dormant bud and μ_{max} the fitted maximal bud growth rate. The parameter a is given as

$$a = y_{max} - \log\left(e^{\mu_{max}(t-\lambda)} + e^{y_{max}-y_o} - 1\right) \quad (2)$$

where y_{max} is a theoretical asymptote fitted to allow decelerated growth prior to bud burst. In cases where growth deceleration before bud burst was very low or absent, the fitting procedure failed to converge using Eq. (2) in Eq. (1). Therefore, a reduced model with parameter a set to $a = y_o$ (as Eq. (2) approaches y_o for large values of y_{max}) was additionally fitted

to the bud measurement time series and the model resulting in a lower residual sum of squares was used for the determination of λ (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). The model was derived from bacterial growth models with a lag phase (e.g., Buchanan et al. 1997, Baty and Delignette-Muller 2004). Our adaptation of the lag-exponential model was found to be more versatile to fit our data and provides more stable estimates of the onset of bud swelling (λ) than a logistic or Gompertz model with a lag phase. Time series consisting of less than four valid bud measurements or where bud swelling was assumed to have started before the first measurement of the time series (where a simple exponential model, without the initial linear period, provided a better fit) were excluded from further analysis. The bud size at bud burst was determined using the parameters derived from the above equations. The scanned bud images were also used to double check the visually determined bud burst dates assessed during the experiment.

Statistics

Effects of sampling date (prolonged exposure to in situ temperatures) and elevation of origin on bud size at sampling and depth of dormancy (days to bud burst during warm >21 °C, long-day conditions 16 h) were tested using analyses of variance (ANOVAs), followed by post hoc (Tukey's HSD) to test for individual differences between treatments.

Effects of temperature, photoperiod and, for bud burst only, elevation of origin, including all their interactive effects on the onset of bud swelling, bud growth rate and bud burst, were tested by fitting linear models with restricted maximum likelihood using the sampling date nested in site as random factor. All statistical analyses and figures were done using R 2.15.0 (R Development Core Team 2010).

Results

Field conditions/treatments

The local winter temperatures in 2009/2010 on both sampling sites before sampling corresponded closely to the long-term average, with the exception of a warm spell in November 2009. The temperatures on the eastern transect were slightly warmer than on the western transect, while the temperature difference between the high and low sampling sites was ~3 K on both transects. The period between the first and second sampling dates was dominated by cool temperatures with daily means well below 5 °C and occasional freezing spells. Between the second and third sampling, the trees experienced an additional period of sub-zero temperatures before the temperatures started to rise with daily means >5 °C in the second half of March (Figure 1).

In the growth chambers, the treatment temperatures could be maintained near the set points with overall mean temperatures

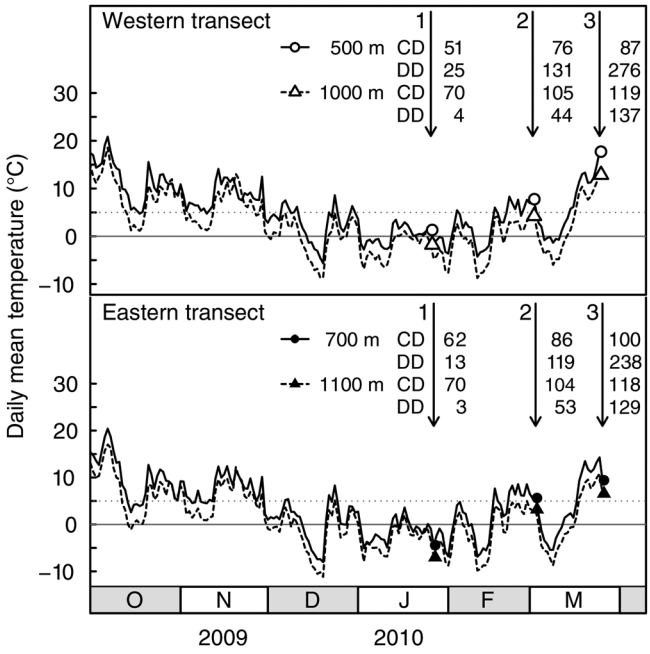

Figure 1. Daily mean temperatures at the sampling sites in the winter before the experiment and between the three consecutive sampling dates. CD indicates the number of chilling days from 1 November with daily mean temperature <5 °C and DD degree-days >0 °C from 1 January until sampling.

of 8.7 ± 2.3 °C (SD) and 8.7 ± 2.6 °C (LD) in the warm treatments, and 5.6 ± 2.2 °C (SD) 5.7 ± 2.1 °C (LD) in the cool treatments. During the whole experiment (96 days), temperature sums were 829 degree-days (SD) and 822 degree-days (LD) in the warm treatments, and 530 (SD) and 548 (LD) degree-days in the cool treatments. In the warm greenhouse, the mean temperature of the additional long day forcing treatment was 22.6 ± 2.8 °C (2158 degree-days).

Development of bud size and dormancy on sampling sites

In situ bud size during late winter and early spring was influenced by elevation of origin and sampling date (26/27 January, 1/2 March, 30/31 March). At the first sampling date at the end of January, all sampled buds appeared to be fully dormant. Significantly larger buds were observed only at the last sampling at the end of March, indicating that bud swelling had already started under the local weather conditions at the sampling sites (Figure 2). A significant increase of bud length, width and projected area at the last sampling was found in all four species, although in the absence of an increase of bud width in *Quercus*. Against expectation, we also observed elevational differences in two species: buds from higher elevations were consistently larger than from lower elevations at all three sampling dates in *Acer*, while *Picea* showed the opposite pattern.

The assessment of dormancy state at sampling as measured by the number of days to budburst under a warm, long day treatment (>21 °C/16 h photoperiod) revealed that the

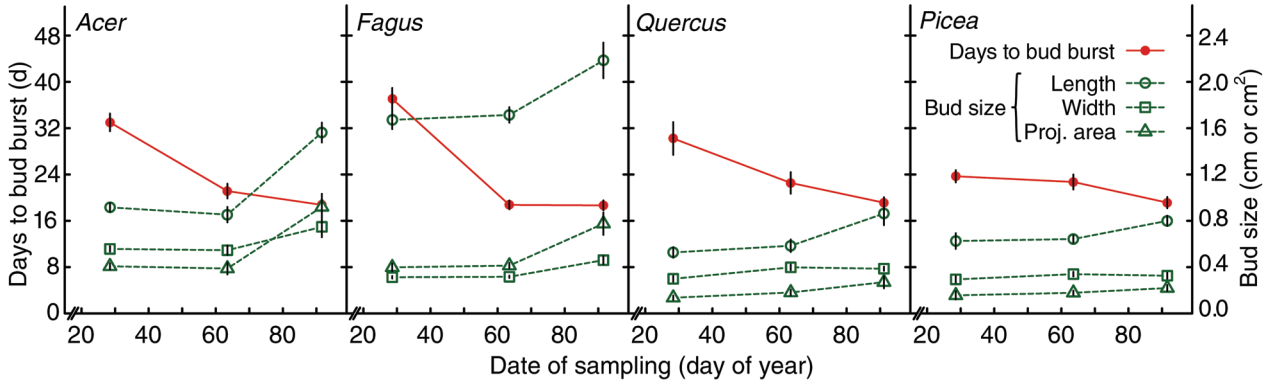

Figure 2. Mean (±SE) days to bud burst under forcing conditions (>21 °C/16 h photoperiod) and bud size in four species at three consecutive sampling dates during winter/spring 2010. The figure shows pooled data over four sampling sites.

initial dormancy at the first sampling in January was deeper in the broad-leaved species (*Acer*, *Fagus* and *Quercus*) than in the needle-leaved *Picea* (Figure 2). In all the four species, the depth of dormancy decreased with later sampling dates, until only ~16 forcing days were required (at >21 °C) for bud burst after the last sampling by the end of March (Figure 2). In *Fagus* and *Quercus*, elevation of origin influenced the decrease of dormancy with later sampling dates. In *Fagus*, high-elevation cuttings exhibited a deeper initial dormancy than low-elevation cuttings, while no distinct elevational pattern in dormancy state across the three sampling dates was present in *Quercus* (Table 1). In all species, days to bud break shortened despite no signs of bud swelling.

The influence of temperature and photoperiod on bud development

Photoperiod and temperature treatments resulted in species-specific responses of bud swelling and bud burst.

Bud swelling As the projected bud area measurement is likely to provide the best general representation of bud size and correlates well with bud length (coefficients of determination R^2 *Acer* 0.96, *Fagus* 0.83, *Quercus* 0.88, *Picea* 0.89) and, to a lesser extent, with bud width (R^2 *Acer* 0.76, *Fagus* 0.83, *Quercus* 0.61, *Picea* 0.67), we report projected bud area data only. No a priori difference in initial (dormant) bud size was present between the individual treatments (Table 2). Bud swelling started 27–61 days after sampling for the first sampling cohort, 21–39 days after sampling for the second sampling cohort (Figure 3) and had already started under in situ conditions before the third sampling date (hence, this sampling cohort was excluded from the analysis of bud swelling). Bud swelling was mainly influenced by temperature and, to a lesser extent, by photoperiod (Figure 3). Thereby, warm temperatures significantly advanced the onset of bud swelling and increased the maximum rate of bud growth in all four species (Table 2). Long photoperiods also advanced the onset of bud swelling and increased the maximum bud growth rates, but only in *Fagus*. However, the total duration of bud swelling until bud burst was affected by temperature and photoperiods in all species, with the exception of *Acer*, where it was controlled by temperature only. In all species, bud swelling started earlier under our treatment conditions in the second sampling cohort, while the time of sampling had no effect on maximum bud growth rates or on the duration of bud swelling until bud burst. Still, later sampling reduced the temperature effect on the onset of bud swelling in *Acer* and the photoperiod effect on the onset of bud swelling in *Picea*. Later sampling also decreased the influence of temperature

Table 1. Effects of date of sampling (26/27 January, 1/2 March, 30/31 March) and elevation of origin on bud size at the time of sampling and the days to bud burst after a subsequent transfer to forcing conditions (>21 °C/16 h photoperiod) in four species. The table shows results of ANOVA as *P*-values of *F*-tests, bold values are statistically significant ($P < 0.05$).

	Bud dimensions			Dormancy
	Length	Width	Projected area	Days to bud burst
Acer pseudoplatanus				
Sampling (*S*)	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Elevation (*E*)	**<0.001**	**<0.001**	**<0.001**	0.503
S × *E*	0.126	0.73	0.185	0.081
Fagus sylvatica				
Sampling	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Elevation	0.500	0.393	0.53	**0.019**
S × *E*	0.23	**0.003**	**0.021**	**0.019**
Quercus petraea				
Sampling	**<0.001**	0.336	**<0.001**	**<0.001**
Elevation	0.461	0.462	0.274	0.967
S × *E*	0.840	**0.042**	0.531	**0.002**
Picea abies				
Sampling	**0.018**	0.069	0.122	**0.028**
Elevation	**<0.001**	**0.003**	**<0.001**	0.503
S × *E*	0.368	**0.017**	0.109	0.456

Table 2. Effects of temperature, photoperiod and sampling date (26/27 January, 1/2 March; reflecting increased natural chilling) on the initial bud size (projected area; BS_i), bud size before bud burst (BS_{BB}), onset (λ) and duration (t_{BS}) of bud swelling and maximum growth rate (μ_{max}). The table shows results of ANOVA as *P*-values of *F*-tests, bold values are statistically significant ($P < 0.05$).

	Bud swelling				
	BS_i	λ	μ_{max}	BS_{BB}	t_{BS}
Acer pseudoplatanus					
Temperature *(T)*	0.605	**<0.001**	**<0.001**	0.109	**<0.001**
Photoperiod (*P*)	0.971	0.690	0.201	0.308	0.265
Sampling (*S*)	0.516	**0.004**	0.232	0.328	0.375
T × *P*	0.520	0.165	0.600	0.689	0.237
T × *S*	0.314	**0.002**	0.154	0.835	**0.019**
P × *S*	0.699	0.450	0.411	0.250	0.266
Fagus sylvatica					
Temperature	0.338	**0.017**	**<0.001**	0.543	**<0.001**
Photoperiod	0.309	**0.013**	**0.001**	0.921	**<0.001**
Sampling	0.052	**<0.001**	0.938	0.303	0.225
T × *P*	0.370	0.083	0.216	0.086	**0.050**
T × *S*	0.269	0.098	0.734	0.175	0.065
P × *S*	0.164	0.943	0.901	0.266	0.316
Quercus petraea					
Temperature	0.373	**<0.001**	**<0.001**	0.076	**0.001**
Photoperiod	0.869	0.235	0.320	0.682	**0.001**
Sampling	0.911	**0.005**	0.728	0.693	0.061
T × *P*	0.144	0.131	0.117	0.959	0.703
T × *S*	0.238	0.332	0.442	0.750	**0.013**
P × *S*	0.621	0.595	0.525	0.728	0.993
Picea abies					
Temperature	0.830	**<0.001**	**<0.001**	0.059	**<0.001**
Photoperiod	0.353	0.240	0.079	0.683	**<0.001**
Sampling	0.282	**0.029**	0.445	0.411	**0.029**
T × *P*	0.856	0.067	0.685	0.680	0.637
T × *S*	0.363	0.110	0.808	0.626	**0.013**
P × *S*	0.143	**0.024**	0.301	0.356	0.540

on the duration of bud swelling in all species but *Fagus*. No significant differences were observed for the bud size at bud burst in either species.

Bud burst In all treatments and for all three sampling dates, some buds randomly failed to burst and desiccated before the end of the experiment. In general, we observed higher bud burst percentages in the diffuse porous species *Acer* (92%) and *Fagus* (98%) and lower percentages in the ring porous *Quercus* (79%) and the coniferous *Picea* (80%). In the latter species, bud burst failed most likely due to conduit failure in cuttings' xylem during the experiment, despite our precautional re-cutting and exchange of water.

The time of bud burst, the most striking phenological event in spring, was significantly influenced by date of sampling, temperature and photoperiod. Here again, later sampling dates, warmer temperatures and longer photoperiods consistently decreased the time to bud burst under our treatment conditions (Figure 4).

With later sampling dates, and thus shorter exposure to the contrasting treatment conditions, the treatment effects generally weakened (Figure 4, Table 3). The strongest temperature effect on bud burst was found in *Picea*, although the effect was only slightly weaker in *Acer* and *Quercus*. *Fagus* was least responsive to temperature (Table 3). The photoperiod effect on the time of bud burst was strongest in *Fagus* and *Picea*, only relatively weak in *Quercus* and absent in *Acer*.

In all species except *Picea*, the time of bud burst was additionally influenced by the cutting's elevation of origin on at least one of the three sampling dates (Tables 3 and 4): in *Acer* and *Fagus*, we observed earlier bud burst on low-elevation cuttings compared with high-elevation cuttings, irrespective of temperature, when sampled at the first sampling date. With later sampling dates, this effect disappeared in *Acer* and was reversed in *Fagus*. A reversed pattern, that is, bud burst of high-elevation cuttings preceding those of low-elevation cuttings, was observed in *Quercus*, but only for the first two sampling dates, while no such effect of elevation of origin was found for the third sampling date.

Furthermore, a significantly larger photoperiod effect was found under warm temperatures than under cool temperatures for the first two sampling dates in *Picea* and for the second

sampling in *Fagus*, whereas no significant photoperiod × temperature interaction was found in the other species. Finally, in *Picea* cuttings of the second sampling date, the photoperiod effect was significantly stronger in cuttings from high elevations than in those from low elevations and we also observed a slightly stronger response to temperature in the low-elevation samples than in those from high elevations.

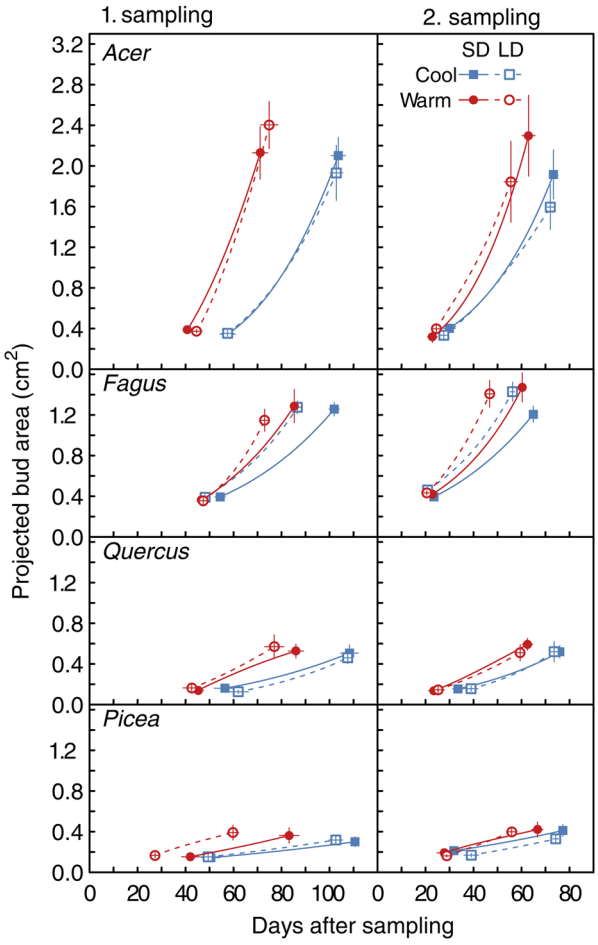

Figure 3. Average bud growth from the onset of bud swelling until bud burst under different temperature and photoperiod conditions of two consecutive sampling dates (26/27 January, 1/2 March). The underlying parameters were obtained by fitting a lag-exponential function to the individual bud size time series (see the Materials and methods section). Error bars represent ±SE. The figure shows pooled data over four sampling sites.

Discussion

The results show that bud burst of cuttings collected from mature trees during late winter and early spring respond differently to temperature and photoperiod, and these differences depended on minute differences in in situ stages of bud development. The origin of elevation as well as species identity influences responsiveness. The more advanced the endo- or ecodormancy release, the less the treatment conditions affected further bud development and the timing of bud burst. Hence, very early advances of bud development preset later phenology.

Chilling

In temperate climates, the release of endodormancy requires exposure to chilling temperatures before buds resume growth under warm temperatures. Insufficient chilling may delay bud burst or decrease bud burst percentage under warm forcing conditions (Samish 1954). Here, the initial dormancy in February was strongest in *Fagus*, intermediate in *Acer* and *Quercus* and surprisingly low in *Picea*. The remarkably low dormancy in *Picea* may arise from the fact that this species, in contrast to the others, seems to require less stringent chilling experience (Nienstaedt 1967, Worrall and Mergen 1967, Sogaard et al. 2008). The significant reduction in dormancy state observed between the first and second sampling cohorts (despite the lack of warm days at the field sites) may reflect the fulfilment of chilling requirements. The chill days as a measure for the degree of chilling as used here (days with mean temperature <5 °C) is only a rough approximation for the actual (unknown) dose-response to cool temperatures. Yet, there are no known physiological or molecular markers that indicate the fulfilment of the chilling requirement

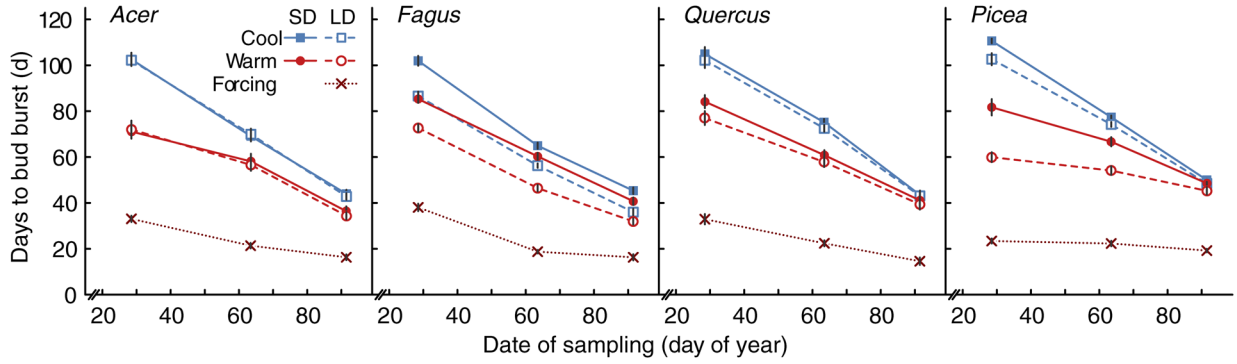

Figure 4. Mean days (±SE) to bud burst under different temperatures (6 versus 9 °C) and photoperiods [initially 9.2 h (SD) versus 10.8 h (LD), increased daily by the natural daily increase of photoperiod at 46.5° N] at three consecutive sampling dates during winter/spring 2010. Additionally, the bud burst under forcing conditions (>21 °C/16 h photoperiod, Figure 2) is shown. The figure shows pooled data over four sampling sites.

Table 3. Mean differences (±SD) in the days to bud burst between the temperature treatments (ΔBB (*T*), cold–warm) and photoperiod treatments (ΔBB (*P*); short–long) as influenced by elevation of origin and date of sampling.

Sampling date	Elevation	*Acer pseudoplatanus*		*Fagus sylvatica*		*Quercus petraea*		*Picea abies*	
		ΔBB (*T*)	ΔBB (*P*)	ΔBB (*T*)	ΔBB (*P*)	ΔBB (*T*)	ΔBB (*P*)	ΔBB (*T*)	ΔBB (*P*)
26/27 January	High	31.6 ± 14.5	−2.0 ± 27.1	17.4 ± 13.9	13.5 ± 16.0	19.9 ± 17.7	2.0 ± 22.7	38.1 ± 19.4	12.0 ± 32.9
	Low	29.9 ± 23.2	1.6 ± 31.8	13.2 ± 15.8	14.5 ± 15.2	27.4 ± 14.6	6.7 ± 24.3	32.9 ± 20.4	15.2 ± 29.4
1/2 March	High	16.8 ± 14.4	0.4 ± 18.8	9.3 ± 10.7	10.0 ± 10.4	15.1 ± 11.2	3.6 ± 15.6	16.5 ± 13.1	11.4 ± 15.5
	Low	7.4 ± 17.3	0.0 ± 18.0	5.1 ± 12.1	12.8 ± 8.6	14.3 ± 8.1	0.5 ± 13.4	14.3 ± 10.1	2.9 ± 14.5
30/31 March	High	9.8 ± 10.5	3.2 ± 12.4	4.0 ± 11.9	8.0 ± 10.8	2.0 ± 11.6	0.8 ± 11.7	2.5 ± 7.4	3.9 ± 7.1
	Low	6.1 ± 10.5	0.2 ± 11.4	4.1 ± 9.4	9.9 ± 6.8	4.8 ± 12.7	1.4 ± 13.7	2.5 ± 5.1	1.2 ± 5.4

Table 4. Analysis of variance of date of bud burst in response to temperature and photoperiod and elevation of origin in four species after three consecutive sampling dates (26/27 January, 1/2 March, 30/31 March) during winter/spring 2010. Significance level $P < 0.05$ (significant values in bold).

	1. Sampling		2. Sampling		3. Sampling	
	F	*P*	*F*	*P*	*F*	*P*
Acer pseudoplatanus	$F_{1,68}$		$F_{1,69}$		$F_{1,65}$	
Temperature (*T*)	79.90	**<0.001**	21.87	**<0.001**	19.61	**<0.001**
Photoperiod (*P*)	0.00	0.980	0.00	0.979	0.44	0.510
Elevation (*E*)	3.43	0.068	3.49	0.066	0.28	0.600
T × *P*	0.00	0.988	0.08	0.775	0.09	0.766
T × *E*	0.01	0.943	3.23	0.077	0.99	0.324
P × *E*	0.60	0.442	0.04	0.838	0.99	0.323
Fagus sylvatica	$F_{1,72}$		$F_{1,70}$		$F_{1,70}$	
Temperature	78.42	**<0.001**	34.78	**<0.001**	9.38	**0.003**
Photoperiod	66.65	**<0.001**	79.57	**<0.001**	44.02	**<0.001**
Elevation	9.63	**0.003**	4.49	**0.038**	9.33	**0.003**
T × *P*	0.00	0.957	6.80	**0.011**	0.02	0.897
T × *E*	0.71	0.403	2.53	0.116	0.07	0.787
P × *E*	0.40	0.531	0.79	0.376	0.03	0.862
Quercus petraea	$F_{1,58}$		$F_{1,53}$		$F_{1,55}$	
Temperature	114.97	**<0.001**	165.66	**<0.001**	15.35	**<0.001**
Photoperiod	8.84	**0.004**	7.00	**0.011**	2.20	0.144
Elevation	22.40	**<0.001**	17.14	**<0.001**	0.63	0.431
T × *P*	0.67	0.416	1.19	0.280	0.03	0.869
T × *E*	2.23	0.141	0.00	0.974	6.38	**0.014**
P × *E*	0.48	0.492	1.02	0.317	0.60	0.441
Picea abies	$F_{1,57}$		$F_{1,59}$		$F_{1,52}$	
Temperature	141.21	**<0.001**	81.08	**<0.001**	4.16	**0.046**
Photoperiod	30.32	**<0.001**	27.91	**<0.001**	5.07	**0.029**
Elevation	0.01	0.905	0.85	0.360	2.66	0.109
T × *P*	9.14	**0.004**	9.60	**0.003**	0.67	0.418
T × *E*	0.96	0.331	0.90	0.346	0.01	0.929
P × *E*	0.28	0.601	10.80	**0.002**	1.27	0.265

(Cooke et al. 2012). However, under our temperature and photoperiod test conditions buds can be assumed to have experienced sufficient chilling either by the cool in situ winter temperatures before sampling or later, under our rather moderate temperature treatments, with low night temperatures likely to have added to the fulfilment of chilling requests, if there was a need. The high bud burst percentage as well as the low thermal requirement under forcing conditions observed supports this assumption. Since the effective ranges of chilling and growth promoting temperatures may overlap, low temperatures within the upper range of potential chilling temperatures are also able to promote bud growth and induce bud burst, as was observed for example in experiments with *Betula pendula* Roth and *Betula pubescens* Ehrh. (Myking and Heide 1995), and *Sorbus aucuparia* L. (Heide 2011).

High-resolution data for actual field temperatures inside buds combined with histological observations in cut buds (Sutinen et al. 2009, 2012) or in situ automatic dendrometer-type

assessments of buds would help to identify the threshold temperatures for tissue growth in buds. From the results of studies in other tissues in cold-adapted plants, we expect a threshold near 5 °C (Alvarez-Uria and Körner 2007, Körner 2008, Rossi et al. 2008).

Bud swelling

Using individual bud image time series permitted us to accurately monitor the bud swelling period, which closely follows the transition from endo- to ecodormancy under our controlled conditions, together with an increase in metabolic activity, rise in bud water content and mobilization of storage reserves following dormancy release (Saure 1985, Pallardy 2008). Our data, for the first time, permitted not only the assessment of the responses of the onset of bud swelling to temperature and photoperiod, but also the estimation of bud growth curves of individual buds. Although the phenological phase of bud swelling is often part of observation protocols such as the widely used BBCH scale (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie; Meier 2001), the precise start of bud swelling is very difficult to ascertain over a multitude of buds at regular intervals. Thus, previous studies largely reported with more striking, later phenophases, such as bud burst or leaf unfolding, which also mark the start of the new growing season. Our results show that the onset and duration of bud growth are co-controlled by temperature and photoperiod in *Fagus* and *Picea* and to some extent in *Quercus,* but not in *Acer*, which appears to be temperature controlled only. These responses suggest further that although maximum bud growth rate is mainly driven by concurrent temperatures (with the exception of *Fagus*, where long photoperiods increase maximum growth rates), the duration of bud swelling is modulated by photoperiod in photoperiod-sensitive species.

The onset of bud swelling advanced in all species and treatment conditions with later sampling, which may be related to decreasing endodormancy in the later sampled cohorts and thus, likely linked to the additional natural chilling received in situ. Significant photoperiod effects on the onset of bud swelling, despite the sufficiently fulfilled chilling requirement (as indicated by the stable, low thermal requirement under forcing conditions), were present in *Fagus.* Still, with later sampling, and thus, advanced dormancy release, these photoperiodic effects decreased. Using calculated bud growth indices, chilling has been reported to affect the subsequent temperature response of bud growth in several species (Campbell and Sugano 1975, Cannell 1989, Battey 2000). We did not observe significantly different maximum bud growth rates or bud swelling duration with later sampling dates, suggesting again that the species were sufficiently chilled before bud swelling started or that such effects on bud growth rates may only be detected in stronger, less realistic temperature contrasts. Furthermore, our decreased duration of the bud swelling period in *Fagus, Quercus* and *Picea* under long photoperiods supports the conclusion that photoperiods may affect bud development also during ecodormancy release, as was reported for *B. pubescens* (Myking and Heide 1995, Caffarra et al. 2011), rather than substituting for a lack of chilling only (Downs and Borthwick 1956, Vegis 1964, Nienstaedt 1967, Cannell and Smith 1983).

Although the underlying physiological drivers of bud dormancy release are not yet completely understood, plant hormones, e.g., abscisic acid (ABA), gibberellic acid (GA), auxins (IAA) and cytokinins, are strongly involved in regulating bud dormancy (Wareing and Saunders 1971, Arora et al. 2003, Welling and Palva 2006, Chao et al. 2007, Meier et al. 2012). Among these, the levels of ABA and GA and IAA are affected by phytochrome, the plants sensory apparatus for perceiving day length (Olsen et al. 1997*b*, Sawada et al. 2008). While short-day induced ABA is mostly involved in dormancy induction (Rinne et al. 1994, Welling et al. 2002), a phytochrome-mediated increase in GA levels has been observed in *Salix pentandra* L. during dormancy release (Olsen et al. 1997*a*). Thus, the photoperiod responses observed here may reflect such plant hormonal effects, and these hormones may be candidates for further physiological research on plant dormancy release in photoperiod-sensitive late successional trees.

Bud burst

As expected, warmer temperatures accelerated the final stages of bud development and resulted in earlier bud burst. With later sampling in the field, the temperature effects on bud burst diminished, indicating the gradually advancing dormancy release during late winter. While the buds of *Acer*, *Quercus* and *Picea* were about equally sensitive to temperature, generally lower temperature sensitivity was observed in *Fagus*. This finding is consistent with the generally lower temperature sensitivity of *Fagus* compared with other co-occurring species observed along elevational gradients (Dittmar et al. 2006, Migliavacca et al. 2008, Vitasse et al. 2009), and the findings of a common garden experiment along the same elevational gradients as used in this study, where a sensitivity to the mean temperature of the month of leaf unfolding of -2.6 ± 0.2 days K^{-1} in *Fagus*, and -4.0 ± 0.3 days K^{-1} in *Acer* was found (Vitasse et al. 2013). However, *Fagus* is the most photoperiod-sensitive species, and the photoperiod responses may have influenced these in situ 'temperature sensitivities' as well. By controlling for both temperature and photoperiod conditions, we obtained similar low temperature sensitivities in *Fagus* compared with the other species. Low temperature sensitivity and strong photoperiod sensitivity of bud development may lead to the low inter-annual variation reported for leaf unfolding in *Fagus* (Menzel et al. 2001, Studer et al. 2005, Vitasse and Basler 2013). The large delay of bud burst in *Picea* under our low temperature conditions, despite the low depth of dormancy, is likely to be related to the fact that this species exhibits a low, early fulfilled, chilling

requirement and these low temperatures may be close to the threshold temperature for bud development.

The observed photoperiod responses in the four species are in line with the results from a previous screening of 14 species for photoperiod influences on bud burst on the same elevational gradients (Basler and Körner 2012). For *Fagus,* the photoperiod effect on bud burst observed here confirms previous findings (Klebs 1914, Wareing 1953, Heide 1993*b*, Caffarra and Donnelly 2010).

The observed diminishing of photoperiod effects with later sampling dates may have been influenced either by longer exposure to chilling temperatures in situ or by the threshold nature of the photoperiod effect; once the critical photoperiod has been passed and developmental barriers are released, photoperiod may not exert any further influence. A diminishing photoperiod effect with increasing chilling has been described for several species (Worrall and Mergen 1967, Heide 1993*a*, Myking and Heide 1995, Partanen et al. 2005, Caffarra and Donnelly 2010), and these authors concluded that photoperiod was effective in insufficiently chilled buds only. Hence, following their reasoning, photoperiod could substitute chilling effects. Most of these studies assessed the effect of photoperiod after a controlled amount of chilling followed by rather high forcing temperatures (>20 °C), much warmer than the temperature ever would be in the field and much higher than the temperatures employed in our experiments.

Methodical considerations

Experiments such as the ones presented here may suffer from effects related to the disconnection of cuttings, and from potential whole-tree signals (e.g., hormonal signals produced outside the branchlet/bud), even though the phenology of adult trees seems to be well represented by that of cuttings (Vitasse and Basler 2014). For obvious reasons, however, in situ manipulation of photoperiod on adult trees was not an option and seedlings are not a good substitute to study the phenology of mature trees, due to ontogenic differences in phenology (Ununger et al. 1988, Besford et al. 1996, Partanen et al. 2001, Vitasse 2013). We assume that the use of cuttings' data leads to a conservative picture of photoperiod signals compared with whole-tree responses (see Basler and Körner 2012). Real-scale photoperiod reduction in mature forests is perhaps the most challenging type of any manipulation in global change research. It is the shortening of photoperiod in a warmer world (earlier thermal forcing) that matters, and no such experiment has ever been attempted on mature trees, and we doubt its feasibility, given the complete darkness (night extension) needed day by day. In-situ shortening of photoperiod has been conducted with saplings, e.g., Hänninen (1995) used 10–15 years old, 1.5–2 m tall saplings of *Pinus sylvestris* L. and found only a negligible effect of photoperiod on the timing of bud burst. Latitudinal transplant experiments seem more feasible, but in this case the temperature regime comes into play. Planting low-elevation northern provenances at high elevations in the south may be a possibility. Unfortunately, arboreta (or park trees) commonly hold no record of seed/plant origin.

Conclusions

We showed that photoperiod is involved in the release of bud dormancy in three out of four late successional tree species and we evidenced species-specific photoperiod effects on the onset of bud swelling and bud growth rates during the forcing period linked. Although recent climate warming caused a shift of spring phenology towards an earlier onset of the growing season in many plant species (Parmesan and Yohe 2003, Menzel et al. 2006), late successional, photoperiod-sensitive species are thus unlikely to fully track future warming at current rates, as photoperiodic cues become increasingly important. Warm temperatures in autumn (Heide 2003) or less chilling during winter (Morin et al. 2010) may delay bud burst even further in certain climates (e.g., mild costal climates). In consequence, the photoperiod-sensitive species may not profit from a substantially extended growing season in a warmer climate, especially as the autumn phenological events (growth cessation and bud set) are unlikely to become considerably delayed in a warming climate due to their strong photoperiodic control (Kramer 1936, Wareing 1956, Vaartaja 1959, Thomas and Vince-Prue 1997). Contrarily, in many tree species warm night temperatures in autumn have even been found to hasten growth cessation, except for photoperiod-insensitive species and a few northern ecotypes where low temperature alone has been found to induce growth cessation in autumn (as reviewed in Hänninen and Tanino 2011). Photoperiod thresholds are elevation specific (ecotypic) and photoperiod sensitivity commonly found in late successional tree species is a strategy to escape fatal freezing damage in immature, less robust tissue by delaying bud burst into low-risk periods, irrespective of actual weather.

Supplementary data

Supplementary material is available at *Tree Physiology* online.

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Conflict of interest

None declared.

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