

Photoperiod sensitivity of bud burst in 14 temperate forest tree species

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ABSTRACT

The timing of spring phenology of trees reflects a trade-off between a longer growing season and a lower risk for damage by late freezing events. Temperature is driving rates of development directly, but given the high inter-annual variability in weather, it is a poor environmental cue for the progression of the season and thus, the period with low freezing risk. In contrast, photoperiod is a reliable and weather independent signal of the progression of the season. Using growth chamber experiments we assessed the photoperiod sensitivity of bud burst under artificial spring conditions in cuttings of 14 common European tree species that belong to different life-strategy types (pioneers or exotic species vs. native late-successional species; 3 conifers/11 broadleaved). Fully chilled twigs were sampled from populations along two elevational gradients in the Swiss Alps. Applying realistic contrasts in photoperiod, short photoperiods delayed bud burst in five late successional species to variable degree, whereas no distinct photoperiod sensitivity was observed in early successional species. In *Picea abies*, the photoperiod response was additionally influenced by elevation of origin, whereas in *Quercus petraea* and *Abies alba* regional differences in the photoperiod response were observed. For late successional species, photoperiod is thus an important environmental signal that will constrain responses to climatic warming because rising temperatures will drive phenology toward the species specific photoperiod threshold.

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1. Introduction

The precise timing of phenological events (bud burst, flowering, bud set) is a key factor for long-term survival, successful reproduction and species establishment (Larcher, 2003). To survive the harsh winter conditions in high latitude seasonal climates, trees go through a period of dormancy and enhanced freezing resistance during winter. The timing of the induction and the release from dormancy is closely linked to three components of local climate conditions, with the amount of low temperatures experienced (chilling), photoperiod and (forcing) temperature acting as the main environmental drivers in humid extra tropical regions (Körner, 2007).

The autumnal growth cessation and the induction of dormancy, including freezing resistance, is largely a photoperiodic response to the longer nights (shorter daylength) in autumn (Klebs, 1903, 1914; Vaartaja, 1959; Thomas and Vince-Prue, 1997), although, concurrent temperatures are modulating this response (Heide, 2003; Kalcsits et al., 2009). Unlike actual weather, the astronomically defined photoperiod is a most reliable indicator for the progression of the season and thus, the photoperiodic

induction of dormancy ensures that trees are ready to cope with freezing temperatures well before the first freezing events occur (Körner, 2007). The period of dormancy may then be separated into the three main phases (1) predormancy, (2) endodormancy, and (3) ecodormancy, based on the depth of silencing of metabolic activity (Samish, 1954). The transition from endodormancy to ecodormancy is jointly controlled by the fulfillment of chilling requirement and by photoperiod, where chilling temperatures describe a rather vaguely defined range of cool, non-freezing temperatures below 10 °C (Battey, 2000), with the range of 2–5 °C being the most effective for most species (Cannell, 1989). During ecodormancy (warm) temperatures accelerate bud development until bud burst marks the start of a new growing season. The transitions between the different phases of dormancy are gradual, with species or even genotypes differing in their requirements for these environmental triggers (Perry, 1971).

The timing of dormancy induction and its release always reflect a trade-off between the length of the active period ('growing season') and the risk of damage by freezing temperatures, both in early autumn and in spring (Larcher, 2003; Bennie et al., 2010). The dissimilar phenological responses of different species may thus be linked to the species life-history. While opportunistic pioneer species adopt a more 'risky', often even temperature-only driven dormancy release, late successional species generally show a more 'conservative', more complex response, with a large chilling requirement and enhanced photoperiod sensitivity

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(Körner, 2007; Caffarra and Donnelly, 2010; Körner and Basler, 2010). Also nutrition influences this trade-off, with species that have high nutrient access, such as *Alnus* sp. (with N₂-fixing symbionts) employing a more risky foliage life history than species operating at more restricted nutrient supply (Tateno, 2003). Within species, genetic adaptation to local climate conditions, such as the differentiation into latitudinal and elevational ecotypes, is common (Morgenstern, 1996; Thomas and Vince-Prue, 1997).

The warming temperatures in the last decades are facilitating a longer growing season, especially an earlier onset of spring, which has been observed across many scales and taxa (Parmesan and Yohe, 2003; Menzel et al., 2006). However, such a response will follow a nonlinear trend in an even warmer future, given that some species will hit their genetically fixed photoperiod or chilling constraints as warmer temperatures facilitate potential earlier leafing (Körner and Basler, 2010; Morin et al., 2010). Thus, photoperiod sensitivity of bud burst may prevent some species from tracking the earlier onset of warm weather in spring as the climate gets warmer. As the timing of bud burst has a strong heritable component (Engler, 1905; Burger, 1926; Morgenstern, 1996), a re-adaptation may take several generations (Langlet, 1971; Nienstaedt, 1974), which means centuries in the case of trees.

Photoperiodic responses of spring phenology were assessed in several tree species, most prominently in *Fagus sylvatica* (Wareing, 1953; Falusi and Calamassi, 1990; Heide, 1993b; Caffarra and Donnelly, 2010), but also in a few other tree species (e.g. Nienstaedt, 1967; Worrall, 1975; Heide, 1993a; Myking and Heide, 1995; Caffarra et al., 2011). However, these results are often contradictory or challenging to interpret, given the complex interactions of the three drivers, chilling photoperiod and actual temperature forcing. In addition, genotypes (provenances) of a species may also differ in their photoperiod responses, as was observed in *Betula* (Heide, 1993b; Myking and Heide, 1995).

Any experimental research targeted at revealing mechanisms of tree phenology, is facing severe methodological constraints, since whole trees cannot be undertaken photoperiod manipulation in situ (e.g. shortening daylength while simulating warming). Seedlings or cuttings (cut twigs) of mature trees may be used as substitute in growth chambers, however the phenology of seedlings is known to differ from that of mature trees, whereas cuttings are per se disconnected from (potential) whole-tree signals affecting bud burst. The way experimental treatments are performed, using different fixed rather than fluctuating temperatures (Campbell and Sugano, 1975; Erez and Couvillon, 1987; Myking, 1997; Partanen et al., 1998; Saxe et al., 2001) and constant vs. gradually lengthening photoperiods (Partanen et al., 1998), may further influence bud burst.

Given the diverse results in the literature, and aware of potential methodological limitations we made an effort to assess the basic photoperiod sensitivity of bud burst in a multi-species approach, including elevationally separated populations from geographically distinct regions. We conducted growth chamber experiments with cuttings of 14 temperate forest tree species, including species with differing leaf duration (deciduous vs. evergreen), whole tree life strategy (early- vs. late successional), bio-geographic origin (native vs. exotic), and in some species, different provenances from populations along two elevational gradients in the Swiss Alps. To our knowledge, no study has yet assessed the contemporary photoperiod sensitivity of bud burst in a wide range of temperate forest tree species after extensive chilling during winter under dynamic photoperiods. Given the above mentioned limitations, results will be conservative, that is, we may not be able to detect the full strength of in situ photoperiod control under such experimental conditions. Distinct photoperiod sensitivity is expected in late successional species.

2. Methods

2.1. Study sites

Three distinct sampling sites were defined along each of the two elevational gradients in the region of Chur (46°51' N/9°32' E, hereafter named 'eastern transect') and Lavey (46°12' N/7°02' E, 'western transect'), Switzerland. Temperature loggers (TidBit v2, Onset Computer Corporation, Bourne, MA, USA) were placed at the three different sites along each transect inside the forest in order to track the local air temperatures (2 m above ground, shaded) and to provide a link to long term temperature records from nearby weather stations. 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. Both slopes are facing west and are covered by near natural forest stands (historical management could not be excluded).

2.2. Sampling

Sampling of the cuttings took place on 2 and 3 March 2009: according to species distribution along the gradients, each species was sampled from two out of the three sites per gradient, a high and a low elevation site (Table 1). The elevational difference between the high and low sampling sites was between 400 and 500 m, which corresponds to a mean temperature difference of around 3 K. On each sampling site, dormant twigs of five individual trees per occurring species were sampled from the lower canopy (5–6 m above ground; 4 twigs per tree) using a 4 m tree pruner (Fiskars, Helsinki, Finland). The twigs were immediately labeled, watered, and transported to the Institute of Botany within 6 h where they were stored at 2 °C in the dark until the start of the experiments, once all samples had been collected (i.e. after 2 days, 4 March 2009). *Tilia cordata* and *Prunus avium* were sampled on the western transect only (no suitable trees in the eastern transect). Additionally, we sampled (as a reference) two exotic ornamental tree species, horse chestnut (*Aesculus hippocastanum*) and lilac (*Syringa vulgaris*), which are known to be photoperiod insensitive and thus, are closely tracking temperature (Defila and Clot, 2001; Larcher, 2007; both species sampled from low elevation only). In the following we refer to species by their genus name.

2.3. Sample treatment

Before the start of the experiment, the sampled twigs were re-cut to a length of around 30–40 cm. The number of buds per twig was species dependent and ranged from 2 in *Aesculus* up to around 40 buds in *Larix*. The twigs were then half dipped into a disinfectant sodium hypochlorite solution for 30 s (200 ppm active chlorine), re-cut a second time underwater at a steep angle using a sterile hand pruner, and finally placed into 0.5 l glass bottles filled with 0.4 l cool tap water. For *Fraxinus* and *Quercus*, the water was additionally treated with the broad-spectrum antibiotics gentamicin sulfate (40 µg/l; Sigma-Aldrich, Germany; Larcher et al., 2010) since the xylem of these ring-porous species tends to become jammed by growing bacteria. During the experiment, the water was changed weekly and at the same time twigs were re-cut another 1–3 cm in order to assure good water supply.

2.4. Growth chamber conditions

The photoperiod sensitivity of spring phenology in a future climate was assessed with the assumption that warm temperatures will occur earlier in the season and thus, will coincide with a shorter photoperiod. Hence, we programmed fully automatic phytotron units to match such realistic dynamic climate scenarios. We

Table 1

Species and number of sampled trees per species along two elevational gradients in the Swiss Alps. Each species was sampled from a high and a low elevation site per gradient, according to species distribution along the gradient. A total of 960 twigs were cut from 240 trees.

	Western transect			Eastern transect		
	500 m	1000 m	1450 m	700 m	1100 m	1520 m
Early successional native species						
<i>Acer pseudoplatanus</i> L.		5	5		5	5
<i>Betula pendula</i> Roth	5	5			5	5
<i>Corylus avellana</i> L.	5	5		5	5	
<i>Fraxinus excelsior</i> L.	5	5		5	5	
<i>Larix decidua</i> Mill.		5	5		5	5
<i>Prunus avium</i> (L.) L.	5	5				
<i>Sorbus aucuparia</i> L.	5	5		5		5
Late successional native species						
<i>Abies alba</i> Mill.	5	5		5	5	
<i>Fagus sylvatica</i> L.	5	5		5	5	
<i>Picea abies</i> L.		5	5		5	5
<i>Quercus petraea</i> (Mattuschka) Liebl.	5	5		5	5	
<i>Tilia cordata</i> Mill.	5	5		–	–	
Exotic, ornamental species						
<i>Aesculus hippocastanum</i> L.	5	–		5	–	
<i>Syringa vulgaris</i> L.	5	–		5	–	

Closest weather station data (1981–2010; provided by MeteoSwiss, the Swiss Federal Office of Meteorology and Climatology): West (Aigle, 381 m a.s.l.): 1010 mm annual precipitation, 10.1 °C mean annual T, duration of the growing season ($T_m > 5$ °C) 262 d. East (Chur 556 m a.s.l.): 860 mm annual precipitation, 9.7 °C mean annual T, duration of the growing season ($T_m > 5$ °C) 255 d.

defined two similar temperature treatments in combination with either long or short photoperiods (9.5 h at start of experiment resp. 11 h at start of experiment; Fig. 1). Temperature was set to cycle ± 5 K around the daily mean temperature, which was increased by 0.5 K every five days, simulating temperatures increase as spring progresses. The photoperiod in all treatments consisted of 8 h high intensity light from metal halide lamps (MF400LS/U, EYE Iwasaki Electric Co., Japan) providing $506 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD (photosynthetically active photon flux density; Red:Far Red 4.2) at plant level and a low intensity extensions using incandescent lamps (Classic A 100 W, Osram AG, Munich, Germany) providing $42 \pm 6 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD (Red:Far Red 0.8). The length of the photoperiod was extended daily using time switches, set to follow the natural (astronomical) daylength extension at the sampling latitude ($\sim 47^\circ$ N) of around 3–4 min per day. The short photoperiod treatment thereby corresponded to the daylengths from February

to April at this latitude, whereas the long photoperiod treatment simulated daylengths of March to May. The two treatments were replicated and randomly assigned to four of these computer controlled growth cabinets (each $253 \text{ cm} \times 120 \text{ cm} \times 195 \text{ cm}$, Weiss Klimatechnik GmbH, Germany).

Every second day sample positions within each chamber were randomized and every 5 days the samples and photoperiod treatments were switched between the chambers, to minimize potential chamber effects. The chambers were constantly well ventilated to maintain a homogenous temperature distribution within the chamber. The set point temperature during the light period was adjusted to compensate for the heat emission of the lamps. Temperature, humidity as well as light conditions at plant level were monitored using data loggers (HOBO Temperature/RH resp. HOBO Light On/Off, Onset Computer Corporation, Bourne, MA, USA).

2.5. Observations

Given the large number of samples (in total 960 twigs of 240 trees; 4 twigs per tree; Table 1), observations had to be split over two day (on each day, half of the cuttings were visually inspected for bud development). The status of the uppermost buds was rated using a four stage scale, as defined by (Murray et al., 1989): (1) bud dormant, (2) bud swollen, (3) bud burst (first green leaf tip showing), (4) leaf unfolding (leaf stalk visible). For efficient observation, each bottle was bar-coded and the bud status was assigned by a bar-coded reference table using a barcode-reader.

2.6. Statistical analysis

Bud burst data was analyzed using split-split plot ANOVAs for each species. The two replicates were used as blocking factor, the photoperiod treatment was applied to whole plots (chambers), and the cuttings within each chamber were treated as elevational samples nested in their region of origin.

Temperatures at the sampling sites (elevations) before sampling were calculated using the linear regressions of the temperature data logged on-site after sampling with temperatures from nearest weather stations (R^2 always > 0.95 , weather station data provided by the Swiss Federal Office of Meteorology and Climatology

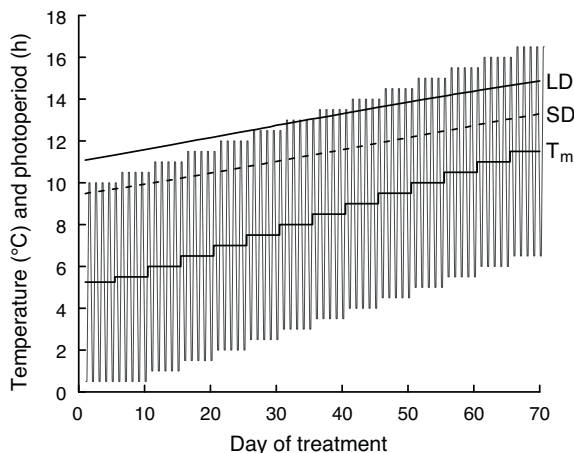


Fig. 1. Experimental variation of photoperiod and temperature during the simulated late winter/spring conditions. Long day (LD; starting daylength as of 1 March) and short day (SD; starting daylength as of 1 February) treatments were continuously adjusted to simulate progression of season at a distance of ca. 90 min. Both photoperiod treatments were combined with similar stepwise-increases in temperature (T_m for daily mean) in order to simulate the natural progression of spring weather at 47° N.

Table 2
Results of the split–split plot ANOVAs for the number of days to bud burst in the 14 tree species included in the experiment. The table shows *p*-values of *F*-tests, bold values are statistically significant (*p* < 0.05).

Species	Photoperiod	Region	P × R	Elevation	P × E	R × E	P × R × E
Early successional native species							
<i>Acer</i>	0.468	0.001	0.621	0.001	0.731	<0.001	0.961
<i>Betula</i>	0.322	0.082	0.243	<0.001	0.381	0.459	0.315
<i>Corylus</i>	0.344	0.032	0.152	0.009	0.451	0.344	0.514
<i>Fraxinus</i>	0.182	0.893	0.256	0.016	0.346	0.242	0.242
<i>Larix</i>	0.758	0.146	0.184	<0.001	0.203	0.020	0.203
<i>Prunus</i>	0.617	–	–	0.075	0.563	–	–
<i>Sorbus</i>	0.732	0.003	0.809	<0.001	0.371	0.005	0.557
Late successional native species							
<i>Abies</i>	0.034	0.222	0.027	0.002	0.316	0.089	0.206
<i>Fagus</i>	0.032	0.047	0.061	0.007	0.499	0.252	0.126
<i>Picea</i>	0.045	0.066	0.160	0.002	0.006	0.770	0.684
<i>Quercus</i>	0.050	0.006	0.016	0.127	0.352	0.027	0.406
<i>Tilia</i>	0.064	–	–	0.076	0.315	–	–
Exotic, ornamental species							
<i>Aesculus</i>	0.818	0.220	0.617	–	–	–	–
<i>Syringa</i>	0.927	0.090	0.763	–	–	–	–

P: photoperiod, R: region, E: elevation.

MeteoSwiss). The degree-days at bud burst were calculated from the reconstructed daily mean temperatures at the sampling site (from 1 January until sampling) and the daily mean treatment temperatures (from sampling until bud burst), using 0 °C as base temperature for degree-day accumulation, as recommended by Heide (1993a). Chilling days were calculated according to Murray et al. (1989) and reflect the number of days since 1 November with daily mean temperature ≤5 °C. Since species differ in their individual temperature response, the absolute degree-day value calculated here should assist in explaining the influence of the climatic conditions before sampling and possible ecotypic responses.

For all data processing, statistical analysis and graphics R 2.11.1 (R Development Core Team, 2010) were used. All the values mentioned are mean ± standard deviation, unless noted otherwise.

3. Results

3.1. Climatic conditions

The twigs were sampled as late as early March, to ensure trees were sufficiently chilled. Naturally, buds from lower elevation will have experienced less chilling and consequently also warmer temperatures during the previous winter than those from high elevation (Fig. 2). According to the degree-days and the number of chilling days, the winter before the experiment was slightly warmer along the eastern transect than along the western transect, however the thermal differences among the three sampling sites per transect were quite similar on both transects.

During the experiment, the temperatures among the four chambers were similar, with only minute deviations between chambers (SD of daily mean temperatures always ≤0.3 K). Mean relative humidity inside the chambers was kept constant at 71 ± 8%.

3.2. Sequence of bud burst among species

We observed bud burst under our experimental conditions on all cuttings until the end of the experiment after 70 days (100% bud burst). The bud burst in all cuttings, even under the shorter photoperiods, is thus an indication of successful chilling, given that lack of chilling would have significantly reduced the fraction of bursting buds or delayed bud burst in cuttings (Heide, 1993a). The species required different time to bud burst and were following approximately the natural order of early to late flushing species, as commonly found by field observations in Switzerland (Defila,

1991). The earliest species, *Prunus*, started to flush already after 17 days, followed by *Larix*, *Sorbus*, *Betula*, *Aesculus*, *Syringa*, *Corylus*, *Acer*, *Fraxinus*, *Fagus*, *Picea*, *Quercus*, *Abies* in that sequence, and finally after more than 60 days of exposure to the treatment conditions, *Tilia*. The general order of species' bud burst remained similar in both photoperiod treatments. Within-population variation in the time of bud burst was generally low.

3.3. Photoperiodism

Photoperiod affected the timing of bud burst by delaying bud burst in short photoperiods in cuttings of five out of the 14 tested species, namely in the late successional species *Abies*, *Fagus*, *Picea*, *Quercus* and *Tilia* (Table 2), the species belonging to the late bud burst group, with the effect in *Tilia* only marginally significant (5.2 ± 2.7 days). In three of the species which show a clear photoperiod effect, we observed a significant interaction between

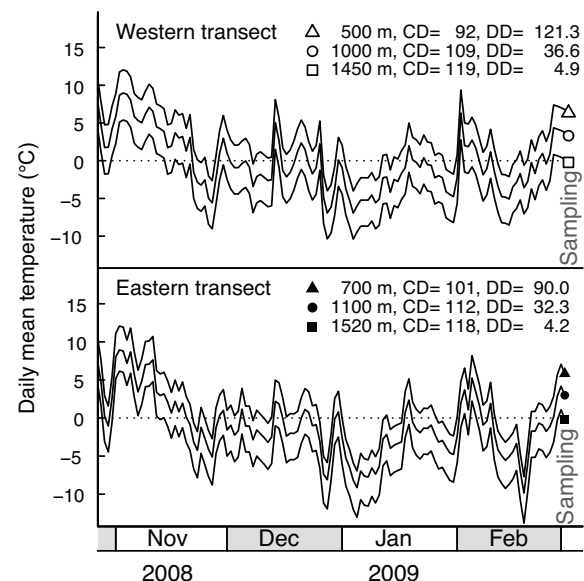


Fig. 2. Daily mean temperatures at the sampling sites in the winter before sampling the cuttings from adult trees. CD indicate number of chilling days since 1 November with daily mean temperature ≤5 °C and DD degree-days > 0 °C since 1 January until sampling.

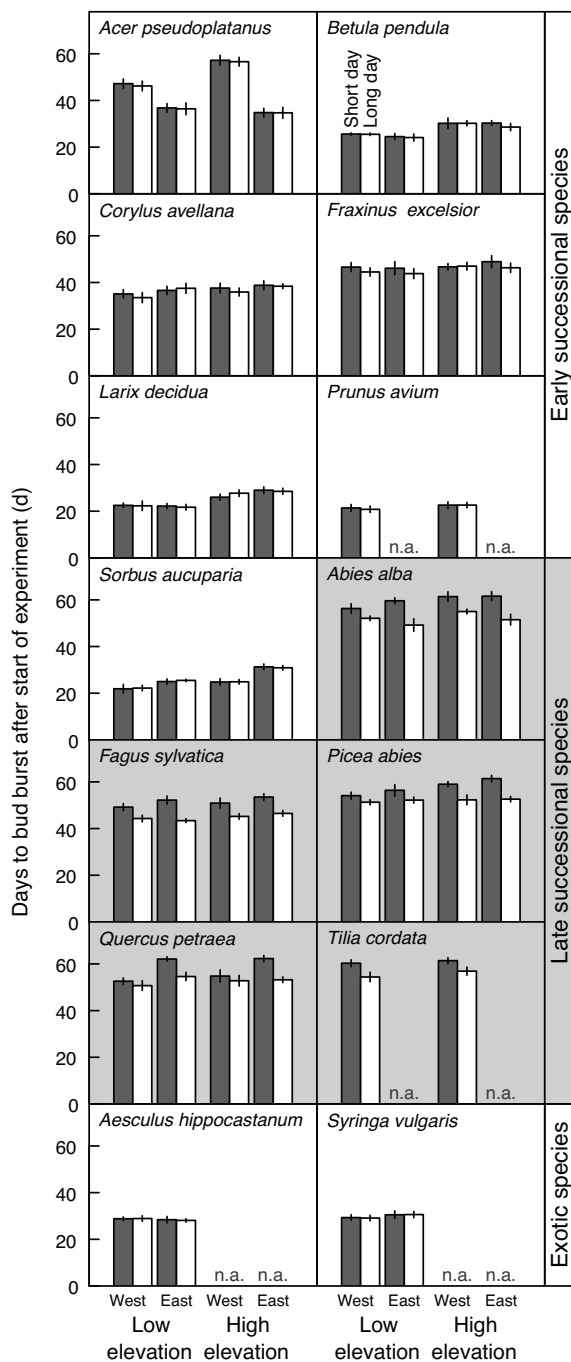


Fig. 3. Mean date (\pm SD) of bud burst under short and long photoperiod treatments in cuttings sampled from high and low elevation mature trees along two elevational transects (East and West; Swiss Alps) under similarly increasing temperatures.

photoperiod and either region or elevation of origin (Fig. 3 and Table 2): in *Abies*, and even more prominently in *Quercus*, the delay of bud burst in short photoperiods was larger in the cuttings sampled from the eastern transect than from those sampled from the western transect (*Abies*: 10.3 ± 3.3 vs. 5.3 ± 3.8 days; *Quercus* 8.3 ± 2.0 vs. 2.0 ± 3.4 days). Finally, in *Picea* the delay of bud burst in short photoperiods was influenced by elevation: the delay was more pronounced in samples from high (7.8 ± 2.4 days) compared to low elevation (3.5 ± 2.7 days). No photoperiod effect was observed in the cuttings early successional species (*Acer*, *Betula*, *Corylus*, *Fraxinus*, *Larix*, *Prunus* and *Sorbus*) and in the two ornamental, exotic species *Aesculus* and *Syringa*.

3.4. Ecotypic responses

Irrespective of photoperiod, the elevation of cutting origin had an delaying effect on the time of bud burst in almost all studied species (Fig. 3 and Table 2): except for *Abies* sampled on the western transect, and *Acer* sampled on the eastern transect, we observed significantly earlier bud burst in the cuttings from low elevation than in those from high elevation. However, this effect was quite small, mostly two to four days. In most of these species, this elevational delay of bud burst was additionally influenced by the cutting's region of origin, although the direction of the region effect was not consistent: in *Larix*, *Sorbus* and *Quercus*, the elevational delay of bud burst was larger in the cuttings from the eastern transect, whereas in *Abies* and *Acer* this difference was larger in the samples from the western transect. In four species (*Acer*, *Corylus*, *Quercus*, *Sorbus*) the regional differences found were fairly consistent: cuttings sampled at the eastern transect flushed a few days later than those originating from the western transect, although a significant region effect, in the absence of an interaction with elevation, was only present in *Corylus*.

3.5. Degree-days until bud burst

In the five photoperiod sensitive species, longer photoperiods accelerated bud burst and thus, we also found reduced degree-days at bud burst under longer photoperiods (Table 3 and Fig. 4). Additionally, the degree-days at bud burst were influenced by elevation and/or region of cutting origin in all species assessed here. As described in the preceding section, bud burst of high elevation cuttings was, with few exceptions, later than in cuttings from low elevations under our simulated spring temperatures. Consequently, the high elevation cuttings experienced more degree-days until bud burst during the experiment. However, by including the pre-sampling temperatures since 1 January at the sampling sites into the degree day calculation, we found that the high elevation cuttings of all species (except *Acer* and *Larix*) opened their buds after less degree-days than the low elevation cuttings. No clear elevational pattern was found in *Acer*, which exhibited opposite responses to elevation among regions, both, in terms of days to bud burst and degree-days at bud burst. In *Larix*, elevation of origin had no significant effect on the degree-days at bud burst, despite the highly significant effect on the time of bud burst. Similarly, the regional differences in the time of bud burst in *Corylus* were not reflected in the degree-days at bud burst of this species. Should the different populations have similar thermal requirements for bud burst, the differences in the time of bud burst observed are thus most likely associated with the pre-sampling in situ temperatures.

4. Discussion

This screening for interactive responses of bud burst to photoperiod, temperature and provenance, using cuttings of adult trees revealed both, genetic as well as environment induced effects. Applying as realistic as possible combinations of dynamic temperature and photoperiod conditions, the study permitted a clear ranking of species in terms of photoperiod control of spring development (as opposed to temperature-only control). In the following we will discuss the observed photoperiod and non-photoperiod related responses and their implication for phenology in a warmer climate in future.

4.1. Photoperiod sensitive species

A delayed bud burst in response to a short photoperiod was observed here in the five late successional species *A. alba*, *P. abies*, *F. sylvatica*, *Q. petraea* and *T. cordata*. In these species, photoperiod

Table 3
Results of the split-split plot ANOVAs for the degree-days until bud burst (temperature sum >0 °C since 1 January) for the 14 tree species included in the experiment. The table shows *p*-values of *F*-tests, bold values are statistically significant (*p* < 0.05).

Species	Photoperiod	Region	P × R	Elevation	P × E	R × E	P × R × E
Early successional native species							
<i>Acer</i>	0.410	0.001	0.526	0.880	0.732	<0.001	0.963
<i>Betula</i>	0.404	0.001	0.239	<0.001	0.344	<0.001	0.286
<i>Corylus</i>	0.316	0.212	0.157	<0.001	0.411	0.011	0.510
<i>Fraxinus</i>	0.171	0.036	0.250	<0.001	0.346	0.006	0.244
<i>Larix</i>	0.961	0.483	0.177	0.061	0.224	0.008	0.196
<i>Prunus</i>	0.451	–	–	0.001	0.534	–	–
<i>Sorbus</i>	0.907	0.018	0.846	<0.001	0.400	0.003	0.537
Late successional native species							
<i>Abies</i>	0.034	0.018	0.029	<0.001	0.208	0.090	0.207
<i>Fagus</i>	0.033	0.094	0.061	<0.001	0.612	0.002	0.142
<i>Picea</i>	0.043	0.094	0.139	0.032	0.005	0.651	0.585
<i>Quercus</i>	0.048	0.018	0.014	<0.001	0.347	0.252	0.420
<i>Tilia</i>	0.062	–	–	0.003	0.365	–	–
Exotic, ornamental species							
<i>Aesculus</i>	0.588	0.003	0.607	–	–	–	–
<i>Syringa</i>	0.783	0.011	0.761	–	–	–	–

P: photoperiod, R: region, E: elevation.

influenced bud burst despite a high degree of preceding chilling. Our results thereby confirm the photoperiod sensitivity of fully chilled buds, as was previously evidenced only in seedlings and cuttings of *Fagus* (Kramer, 1936; Wareing, 1953; Heide, 1993b; Caffarra and Donnelly, 2010) and seedlings of *Picea* (Partanen et al., 1998), while such photoperiod sensitivity has not yet been described in *A. alba* and *Q. petraea*. In *Quercus*, photoperiod sensitivity was observed previously in seedlings of the deciduous *Q. faginea*, but not in the co-occurring, evergreen *Q. ilex* subsp. *ballota* in Spain (Sanz-Perez et al., 2009). In *Tilia*, the marginally significant trend to earlier bud burst of fully chilled buds under our dynamic long photoperiods, challenges the earlier finding that photoperiod sensitivity of this species is limited to insufficiently chilled plants, as was observed in rooted cuttings under constant long photoperiod (16 h vs. 8 h; Caffarra and Donnelly, 2010).

4.2. Photoperiod insensitive species

As expected, neither of the two species of exotic origin, *Aesculus* and *Syringa*, was found to be photoperiod sensitive. Also cuttings of early successional (*Acer*, *Betula*, *Corylus*, *Larix*, *Prunus*, *Sorbus*) and intermediate successional species (*Fraxinus*) revealed no measurable photoperiod response. Our finding for *Sorbus* are consistent with those by Heide (1993a) and suggest a general, photoperiod independent control of dormancy for this species, given that this species also shows a weak photoperiod influence on autumnal dormancy induction (Wareing, 1956; Heide, 2011). In the fully chilled cuttings of *Betula*, the absence of a photoperiod effect under our treatment conditions matches observations by Myking and Heide (1995) and Caffarra et al. (2011). These authors reported photoperiod sensitivity in *Betula* when chilling was incomplete. Our findings in *Corylus*, also belong to the *Betulaceae*, and *Prunus* however, are inconsistent with previous observations: in cuttings of *Corylus*, a 24 h photoperiod advanced bud burst by 2–3 days compared to an 8 h photoperiod, even after extensive chilling until mid March and treatment conditions of 21 °C, which may be considered as rather extreme test conditions (Heide, 1993a). In *Prunus*, a 16 h photoperiod advanced bud burst in rooted cuttings from mature trees compared to seedlings, whereas no such difference was found in a 12 h photoperiod (Besford et al., 1996). We were not able to detect a photoperiod effect under our realistically small contrasts in photoperiod (ca. 90 min only), indicating that such an effect, is too weak to materialize under daylength and temperature conditions as they actually occur at our sampling latitude in spring. However, it cannot be excluded that our initial short photoperiod

of 9.5 h was already beyond a potential short photoperiod threshold to break endodormancy under the temperatures employed, nor exclude that cuttings do not reveal the full response (Section 4.5).

4.3. Ecotypic responses

4.3.1. Ecotypic photoperiod responses

Strong heritability of the timing of dormancy release and a considerable variation among provenances of a species under common growing conditions, as observed here, has been frequently evidenced in broad forest tree transplant experiments (e.g. Engler, 1905; Burger, 1926, but see reviews by Langlet, 1971; Morgenstern, 1996 and references therein). In contrast, some common garden (Vitasse et al., 2009b)/modeling studies (Chuine et al., 2000) arrived at similar temperature sensitivity of spring phenophases in seedlings of geographically separated populations from low temperate latitudes (southern France), which led the authors to conclude that local adaptation plays only a minor role for phenology under climate warming.

While common garden experiments are excellent tools to assess overall provenance responses under a common climate, it remains difficult to separate thermal responses from photoperiodic responses because both may be ecotypic. For the induction of dormancy, photoperiod ecotypes have been evidenced in many species (Klebs, 1914; Vaartaja, 1959; Thomas and Vince-Prue, 1997; Li et al., 2003; Böhlenius et al., 2006), hence, photoperiod ecotypes may also be expected in dormancy release, although the controls of dormancy release are much more complex. However, among the photoperiod sensitive species examined here, such an ecotypic photoperiod effect with elevation was found in *Picea* only. This species showed later bud burst under short photoperiods in the high elevation cuttings compared to those from low elevation. In the cuttings of *Abies* and *Quercus* the more pronounced photoperiod responses in the eastern provenances may relate to selective effects of the extreme ‘foehn’ wind in this area, causing exceptionally warm episodes in late winter/early spring, often followed by late freezing. In *Fagus* and *Tilia* however, we found a similar photoperiod effect across the different regions and elevations. For *Fagus*, this is in agreement with the similar responses to photoperiod in four latitudinal ecotypes (47–59° N) observed by Heide (1993b), who tested cuttings sampled from four regions in mid March with constant photoperiods between 8 and 16 h and under a warm 21 °C temperature regime. Given that *Fagus* has been shown to have a very large chilling requirement (Murray et al., 1989), the actual

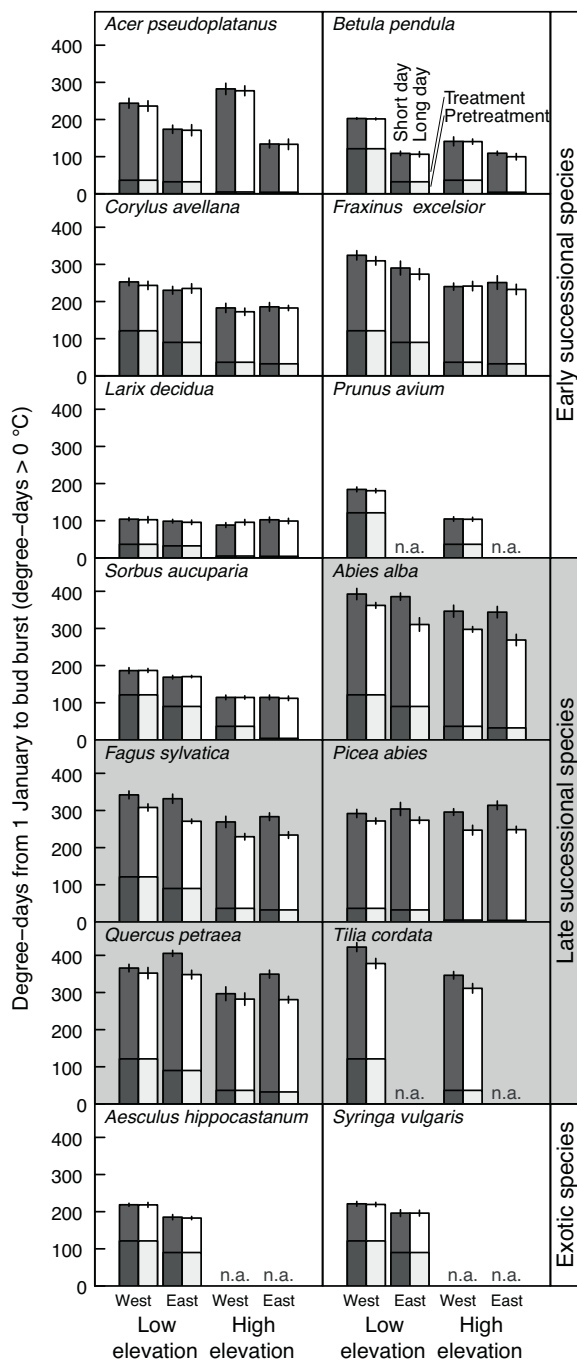


Fig. 4. Degree days until bud burst in 14 tree species under short and long photoperiod treatments simulating future spring conditions (mean \pm SD). The degree-days experienced the sampling sites before sampling at high and low elevation sites along two elevational gradients (East and West; Swiss Alps) is indicated.

weight of photoperiod and chilling for the response to follow-up warm temperatures may depend on local weather conditions.

4.3.2. Ecotypic thermal responses

Besides photoperiod ecotypes, provenances may also exhibit heritable thermal responses, the current experiment was not primarily designed to assess. Such provenance-specific thermal responses are most prominently demonstrated by the remarkable elevation-independent (and hence temperature-pre-history independent) variation of bud burst observed here in the photoperiod insensitive species *Acer pseudoplatanus* (Fig. 4), a species

known for its strong provenance variation in the time of bud burst (Engler, 1905; Vitasse et al., 2009a). In most other species assessed here, the high elevation cuttings opened their buds later than the low elevation cuttings under similar temperature and photoperiod conditions (Fig. 3). However, contrary to classical common garden experiments, the cuttings used here have not experienced the whole period of dormancy under similar climatic conditions, hence our results may also reflect the contrasting natural pre-history in the field. Obviously, the low elevation trees have experienced higher temperatures before sampling than the high elevation trees (Fig. 2). Although the buds appeared dormant (unswollen) at sampling, buds from low elevation might still have been at a slightly advanced developmental stage, in favor of an earlier bud burst. Hence, similar responses under the same controlled conditions under otherwise substantially different natural pre-history may mask differences that might have been seen when provenances had been exposed to an identical pre-history, as irrelevant this would be from an ecological point of view.

Under our treatment conditions, high elevation cuttings open their buds later, however, at less of degree-days than low elevation cuttings (degree-days in situ since 1 January to sampling and treatment degree-days until bud burst; Fig. 4). Similarly, a lower thermal requirement for bud burst of high elevation provenances has also been found in common gardens experiments with *Fagus* (Hjelmqvist, 1940; von Wuehlisch et al., 1995; Chmura and Rozkowski, 2002; Vitasse et al., 2009a) and *Picea* (Engler, 1905; Burger, 1926; Worrall, 1983) and some other species (Acevedo-Rodriguez et al., 2006). Consequently, a lower thermal threshold for bud burst, as was also observed here, was suggested for high elevation provenances of these species (Worrall, 1983; von Wuehlisch et al., 1995). In *Picea* however, seemingly inconsistent results have been found in common garden experiments: Burger (1926) observed consistent earlier bud burst of young trees (9–15 years) from high elevation grown at 380 m, 670 m and 1880 m a.s.l., with a more pronounced difference in higher elevation gardens. In a large provenance trial at low elevation (226 m a.s.l.) however, no such trend were observed in *Picea* seedlings, whereas even a reversed trend was observed in young trees (>9 years; Holzer and Nather, 1974). These differences may have been introduced by the enhanced photoperiod sensitivity of the high elevation ecotypes of this species as observed here. The reverse trend, that is earlier bud burst of low elevation provenances (and thus at less degree-days) was also found in seedlings of *P. avium* (Besford et al., 1996) and *Q. petraea* (Vitasse et al., 2009a; Alberto et al., 2011). Our observed opposite elevational pattern in the degree-days at bud burst in these species may also have been caused by species specific temperature thresholds for the progression of development, which may be higher than the 0 °C daily base temperature used here for degree-day calculation. Higher thresholds would reduce the weight of the mostly cool pre-sampling temperatures in situ (Fig. 2) and may thus counterbalance the elevational effects on the degree-days observed here. However, also in common garden studies the presence or direction of elevational trends of bud burst under similar climatic conditions seems to be strongly species specific and may be influenced by age of the plant material used (seedling vs. mature tree) and climate (elevation) of the garden. Furthermore, ecotypic elevational trends may be missing because of high within-population variance of bud burst or because elevation is confounded with latitude in the different studies.

4.4. Ecological advantage of photoperiod sensitivity

The obvious ecological advantage of photoperiod sensitivity is the reduced risk of freezing damage in new, but premature tissue. Thus, species specific differences are likely to be related to seasonal freezing risk in the species' natural habitat and to the species'

life history. In contrast to the photoperiod sensitive late successional species, early successional species commonly reach bud burst as soon as temperatures permit, without pronounced chilling and photoperiod requirements. This opportunistic behavior will lengthen the active growing season, while enhancing the risk of freezing damage. In the photoperiod sensitive species however, photoperiod seems to be modulating the response to concurrent warm temperatures guiding bud burst into a 'safer' period. Longer photoperiods may thus either decrease the thermal requirement for bud burst, or (more likely) speed up development at a given temperature. The generally late bud burst of ring-porous species however, as observed here in photoperiod insensitive *Fraxinus* (holding an intermediate successional position), but also in the late successional *Quercus*, may be additionally associated with a slower reactivation of water supply by a new layer of xylem before bud burst, given that these species lose most of the hydraulic conductivity through embolism during winter (Sperry et al., 1994).

4.5. Methodical considerations

Photoperiod experiments with trees face two problems related to tree size and the known differences between young life stages compared to older life stages (Ununger et al., 1988; Besford et al., 1996; Partanen et al., 2001). In situ photoperiod manipulation on mature trees, without affecting thermal conditions and allowing for appropriate replication, is constrained by tree size and the dose-independency of the photoperiod signal which would require absolute light-tight darkening of whole trees during the early/late parts of the day, should the effect of warmer temperature be tested at shorter photoperiods. Alternatively, growth chamber experiments are always limiting plant size, such that only small saplings or cuttings (cut twigs) of mature trees can be used. While saplings, in contrast to mature trees, are known to exhibit a more opportunistic behavior concerning bud burst (understory trees flush before canopy trees, utilizing light before the canopy closes; Uemura, 1994; Augspurger and Bartlett, 2003; Richardson and O'Keefe, 2009), cuttings are, per definition, disconnected from whole-tree (hormonal) signals potentially affecting bud burst. In some tree species cuttings may respond quite autonomously and thus, can serve as an appropriate substitute for mature trees in growth chamber studies, whereas in other (unknown) cases, cuttings will not reflect whole tree responses. The direction of artifact is unpredictable, but delays in phenology may be expected in processes related to xylem pressure and tissue turgor and root plus whole crown hormonal signals. We assume that the sum of these limitations leads to a conservative picture of photoperiod signals in cuttings compared to whole tree responses. Hence many of the observed patterns may indicate direction, rather than the full signal strength that would only be seen in a whole tree approach.

5. Conclusions

The observed photoperiod sensitivity in late successional tree species, demonstrates that spring phenology of most of the observed late successional tree species is not driven by temperature alone, even after experiencing substantial (natural) chilling. In a future climate with warmer springs, photoperiod will become an increasingly important factor for constraining the timing of spring phenology when warmer weather conditions are accelerating development (earlier bud burst) toward genetic photoperiod thresholds. Combined with reduced chilling in milder, low elevation winters, some late successional species are likely not to continue tracking the actual (warmer) temperatures as they currently still do. Our results evidence the considerable photoperiod influence on bud burst at otherwise weak indications for ecotypic

differentiation. Our results suggest that photoperiod plays only a minor role in early successional species. Since phenology of trees can be expected to have been selected for efficient use of the growing-season, different photoperiod and temperature sensitivities among species or genotypes are likely to affect the success of species in a warmer climate. The selection for new photoperiod genotypes will take several tree-generations (>100 years). The results obtained here in cuttings of adult trees are likely to underestimate the actual significance of photoperiod for spring phenology. Taken together, the experimental evidence for spring phenology presented here, warns at scaling trends observed in the recent past into a warmer future by accounting for temperature only. Such extrapolations need to account for temperature–photoperiod interactions in mature, late successional trees.

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