



Photoperiod sensitivity of bud burst in 14 temperate forest tree species

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ARTICLE INFO

Article history:

Received 3 April 2012

Received in revised form 1 June 2012

Accepted 6 June 2012

Keywords:

Spring phenology

Daylength

Temperature

Development

Season

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

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