Contents lists available at ScienceDirect



Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Research Paper

Temporal photoperiod sensitivity and forcing requirements for budburst in temperate tree seedlings



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ARTICLE INFO

Keywords: Chilling sum Forcing sum Dormancy depth Day length Ecotype Intraspecific variation Interspecific variation Budburst prediction Winter climate change Phenology

ABSTRACT

Phenological responses to winter and spring warming in trees alter growing season length and can influence productivity. An improved mechanistic understanding of phenology, including temporal changes in budburst forcing requirements (BFR) and photoperiod sensitivity, could improve projections of phenological shifts and changes in tree species composition in response to climate warming. We investigated changes in BFR and photoperiod sensitivities at high temporal resolution from mid-winter to spring in seedlings of eight common deciduous and coniferous temperate tree species. Eight provenances of *F. sylvatica*, a dominant European species, also were included to examine variability in bud dormancy patterns within a species. Tree seedlings were overwintered in a common garden and transferred weekly into climate chambers at forcing temperatures (+20 °C) from December to April. Budburst was observed under 16 and 8 h photoperiods. Across species, as chilling unit sums accumulated, BFR and photoperiod sensitivity decreased. Functions relating chilling and forcing unit sums explained ambient spring budburst accurately. BFR differed strongly among species, but not among provenances of *F. sylvatica* from similar latitudes. Overall, our results indicate that a precise tracking of BFR and photoperiod sensitivity helps explain species-specific differences in phenotypic sensitivities, which can improve species-specific projections of phenological responses to climate warming.

1. Introduction

Changes to the start of the growing season in trees impact primary productivity (Richardson et al., 2010) and can have wide reaching implications for plant-animal interactions due to potential changes in the timings of foraging and pollination (Both et al., 2009). In Europe, the growing season advanced on average by 11 days from the 1960s to the 21 st century, mostly due to earlier leaf emergence (Linderholm, 2006; Menzel et al., 2006). The timing of spring growth plays a vital role in influencing biomass production by modifying the growing period, with budburst dates influencing carbon assimilation and tree energy budgets (Kindermann et al., 1996). For example, a 20% extension in the growing season can increase the annual net ecosystem productivity of a deciduous forest by as much as 50% (Dragoni et al., 2011), although carbon sequestration may not necessarily increase due to higher respiration rates (Piao et al., 2008). Nevertheless, the tradeoff of earlier leaf flushing is an increased risk of late spring frost damage

(Gömöry and Paule, 2011; Mimura and Aitken, 2010).

Evidence shows that budburst can be altered by modifying the temperature (Fu et al., 2012) and photoperiod (Myking and Heide 1995) after bud set; therefore, abiotic environmental changes likely drive variability in spring budburst dates. Observed advancements in spring phenology have been species-specific (Cleland et al., 2007; Laube et al., 2014; Menzel et al., 2006; Willis et al., 2008), largely due to species-specific requirements for the breaking of bud dormancy. Temperature and photoperiod are the most important factors controlling phenology in dominant tree species outside the tropics (Körner, 2007).

Bud phenology is driven mechanistically by changes in (or the absence of) bud dormancy. In many temperate deciduous trees, endodormancy or "the inability of a bud to burst at normal growth temperatures in long days" (Sogaard et al., 2008), is released by a required chilling period (Laube et al., 2014). Once endo-dormancy is completely released, trees enter eco-dormancy, where the buds become

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http://dx.doi.org/10.1016/j.agrformet.2017.09.011

Received 19 December 2016; Received in revised form 8 May 2017; Accepted 20 September 2017 0168-1923/ © 2017 Elsevier B.V. All rights reserved.

Table 1

Geographical and climatic characteristics of the seed origins of the tree seedlings used in the experiment, and the respective tree seedling ages at the start of experiment.

Species	Latitude °N	Longtitude °E	Elevation	Sowing date	age (years)
Acer pseudoplatanus L.	49.89	11.05	409–537	2012 (April)	2
Picea abies L.	49.90	10.50	445–450	2010 (May)	4
Fagus sylvatica L.	50.04	11.85	800-920	2013 (May)	1
Abies alba Mill.	49.96	11.04	325–379	2009 (October)	4
Sorbus torminalis L.	49.84	10.38	270	2011 (June)	2
Larix decidua Mill.	50.08	9.25	440	2012 (May)	2
Tilia cordata Mill.	49.45	11.14	330	2011 (June)	2
Quercus robur L.	49.52	11.06	307–311	2013 (May)	1

increasingly responsive to warm forcing temperatures (Harrington and Gould, 2015; Kramer, 1994). Short photoperiods can prevent premature dormancy release when the chance of frost still may be high (Häkkinen et al., 1998; Heide, 1993a), while long photoperiods can compensate for insufficient winter chilling temperatures by reducing budburst sensitivity to warmer temperatures (Häkkinen et al., 1998; Heide, 1993b; Sanz-Pérez et al., 2009). Budburst sensitivity to photoperiod is of particular importance for assessing tree growth responses to climate warming (Heide, 1993b; Schaber and Badeck, 2003; Vitasse et al., 2009), because photoperiod plays a role in bud dormancy release and budburst (Basler and Körner, 2014; Partanen et al., 1998; Zohner and Renner, 2015), and can limit the sensitivities of some tree species to warmer winter and spring temperatures (Way and Montgomery, 2014).

The interplay between chilling requirements, forcing temperatures, and photoperiod in influencing budburst is species-specific (Vitasse et al., 2009); longer photoperiod and longer exposure to chilling temperatures reduce the thermal time to budburst in some species (Falusi and Calamassi, 1990; Heide, 1993b), but have no effect in others (Heide, 1993b; Schaber and Badeck, 2003). Required chilling temperature sums differ among Northern species (Farmer, 1968). For example, *Picea abies* requires four weeks of chilling at 3–6 °C to break dormancy (Dormling et al., 1968), whereas *Pinus monticola* requires 16 weeks of chilling at the same temperature (Steinhoff and Hoff, 1972). Tree species that advance their budburst dates the most typically have low forcing and chilling temperature requirements for budburst (Laube et al., 2014; Zohner and Renner, 2014)

Regarding changes in BFR and photoperiod sensitivity from winter to spring, photoperiod sensitivity has been shown to decrease in selected species as chilling requirements are fulfilled (Caffarra and Donnelly, 2011; Laube et al., 2014; Myking and Heide, 1995). With respect to changes in BFR, several studies have shown that the relationship between the accumulated chilling unit sum and BFR may be exponential, with BFR decreasing exponentially from midwinter to spring (Caffarra and Donnelly, 2011; Harrington et al., 2010; Heide, 1993b; Murray et al., 2014; Myking and Heide, 1995). Forcing requirements decrease as chilling units accumulate, until a point where they plateau and remain stable with additional chilling unit accumulation (Harrington et al., 2010; Harrington and Gould, 2015). When budburst dates have been analyzed in the context of hourly chilling and forcing sums, the required amount of forcing units needed for budburst could be explained by the specific amount of chilling units that had accumulated up to that point (Ford et al., 2016; Harrington et al., 2010). However, in order to test the generality of these relationships between exponential chilling unit sums vs. BFR, and the continuous decrease in photoperiod sensitivity, these need to be evaluated for multiple species at a fine resolution.

Phenological differences among tree populations from different longitudes, latitudes and elevations within single species also have been documented (Von Wuehlisch et al., 1995; Chmura and Rozkowski, 2002), and these within-species differences in bud phenology can at least in part be explained by genotypic variation (Campbell et al., 1989; Ekberg et al., 1991). Although environmental effects appear to explain much more variation in budburst dates than genetic differences (Vitasse et al., 2013), genetic control, which is observed down to the seed family level, enables budburst order in seedlings to be maintained across years with varying temperature (Li and Adams, 1993). Therefore, withinspecies variation in bud phenology should be considered whenever phenology is compared among species.

We used days to budburst under forcing conditions, a proxy for dormancy level (Li et al., 2005) to quantify changes in BFR from midwinter to spring in eight common European tree species known to differ in spring budburst dates (Kramer, 1995). Temporal changes in BFR and photoperiod sensitivity were then used to explain the spring budburst of each species in the field. We also explored variation in BFR within Fagus sylvatica, one of the most photoperiod sensitive (Kramer, 1994) and dominant tree species in Europe (Vitasse and Basler, 2013). We hypothesized that: 1) functions correlating changes in BFR with chilling unit sums would be exponential across species and would accurately predict the BFR at spring budburst, 2) higher mid-winter BFR and a slower rate of decrease in BFR would lead to later spring budburst dates both among species and among F. sylvatica provenances (due to adaptation to variation in climate at seed origin) and 3) photoperiod sensitivity would decrease continuously with chilling unit accumulation, and would differ more strongly among species than among F. sylvatica provenances (due to similar latitude at seed origin).

2. Materials and methods

Seven species of tree seedlings (*Abies alba* Mill., *Picea abies* L. H. Karst., *Quercus robur* L., *Acer pseudoplatanus* L., *Sorbus torminalis* L. Crantz, *Tilia cordata* Mill., *Larix decidua* Mill.) obtained from local German seed sources (Table 1) were grown in a tree nursery in the vicinity of Bayreuth, Germany (Bayerische Staatsforsten AöR – Pflanzgarten-Stützpunkt Bindlach), and delivered to the Ecological Botanical Garden in Bayreuth at the end of October 2013. Seedlings from all provenances and tree species were transplanted into 8 cm × 8 cm × 20 cm deep pots at the end of October using soil from the Ah and Bv horizons of a forest soil in Eberswalde, Germany, made up predominantly of 87.2% sand, 9.8% silt, 2.9% clay and < 0.5% humus.

We selected eight F. sylvatica provenances from seed sources in northern France, northern Germany and Poland to represent the potential variation in chilling requirements (due to differences in winter climate at their seed origins), while likely retaining similar photoperiod sensitivities among provenances (due to the seed origins stemming from similar latitudes (Table 2). The trees were cultivated from seed in greenhouses at the Thünen-Institute, Germany (Institute of Forest Genetics, Institute of Forest Ecosystems), with the exception of one provenance (Table 2 - Germany 3), which was cultivated together with the other tree species as described in the preceding paragraph. In late fall 2012, the two-year old seedlings were potted in 2 L pots (Hermann Meyer KG), and in the summer of 2013 they were delivered to the Bayreuth Ecological Botanical Garden and placed under a rainout shelter constructed of a steel frame (GlasMetall Riemer GmbH) and covered with a polyethylene sheet (0.2 mm, SPR5, Hermann Meyer GmbH), which permitted 90% of photosynthetic radiation to pass

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