Review

Photoperiod constraints on tree phenology, performance and migration in a warming world

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ABSTRACT

Increasing temperatures should facilitate the poleward movement of species distributions through a variety of processes, including increasing the growing season length. However, in temperate and boreal latitudes, temperature is not the only cue used by trees to determine seasonality, as changes in photoperiod provide a more consistent, reliable annual signal of seasonality than temperature. Here, we discuss how day length may limit the ability of tree species to respond to climate warming *in situ*, focusing on the implications of photoperiodic sensing for extending the growing season and affecting plant phenology and growth, as well as the potential role of photoperiod in controlling carbon uptake and water fluxes in forests. We also review whether there are patterns across plant functional types (based on successional strategy, xylem anatomy and leaf morphology) in their sensitivity to photoperiod that we can use to predict which species or groups might be more successful in migrating as the climate warms, or may be more successfully used for forestry and agriculture through assisted migration schemes.

Key-words: bud burst; bud set; carbon uptake; chilling; climate change; day length; dormancy; photosynthesis; senescence.

INTRODUCTION

The continuing rise in atmospheric CO_2 concentrations due to fossil fuel burning and anthropogenic land use change is expected to increase global mean temperature by 2 to 5 °C within the next 85 years (Collins *et al.* 2013), but this average conceals important patterns. Warming will not be distributed equally across the globe: higher latitude regions will warm more than equatorial regions, with mean annual temperatures in arctic regions predicted to warm by 8.3 °C and summer temperatures in boreal regions by 5 °C under the highest emission scenario by the year 2100 (Collins *et al.* 2013; IPCC 2013). Experimental warming results indicate that these increases in temperature will affect tree growth through direct effects on plant physiology, with predominantly positive effects on deciduous species and more negative effects on evergreen species (Way & Oren 2010).

These direct effects may be compounded in natural settings as warming should also expand the period where temperatures are conducive to growth in these regions: earlier springs and later autumns will alter tree phenology and physiological activity, and are expected to increase the length of the growing season. A longer growing season could, in turn, increase annual forest productivity (Keenan *et al.* 2014), or offset reductions in mid-summer carbon uptake caused by increasing heat and drought stress (Stinziano & Way 2014).

However, temperature is not the only seasonal cue for organisms: photoperiod, or day length, is another critical signal that indicates the progression of the seasons in a given location. Photoperiod will not change as the climate warms, leading to potential asynchrony in these functionally paired cues (Hänninen & Tanino 2011). For example, as the climate warms at a specific location, the day of year when the risk of spring frost ceases or autumn frost risk appears will have a shorter photoperiod than it does currently (Fig. 1, compare panels b and c), provided the risk of extreme events is unaltered by climate change (Wang *et al.* 2014). Organisms that rely on photoperiodic cues for sensing the arrival of spring and the approach of winter may have constrained responses to warming, which would limit expected extensions of the growing season in mid- and high latitude forests (Saikkonen *et al.* 2012). This is a critical process to understand, since a longer growing season in these systems, as is widely predicted under climate warming, can increase tree height and diameter growth (Oleksyn *et al.* 2001; Heide 2003) and forest ecosystem productivity (Richardson *et al.* 2009, 2010; Dragoni *et al.* 2011; Keenan *et al.* 2014; but see Piao *et al.* 2008). Moreover, changes in phenology associated with climate warming of mid- and high latitude forests will have direct impacts on regional and global carbon, water and energy cycling. A difference of approximately a week in the timing of canopy development can account for over 20% of the inter-annual variability in forest net photosynthetic production (Myneni *et al.* 1997), while uncertainties in predicting the timing of bud burst across years in a temperate forest generated uncertainties of over 9% in annual modelled gross primary productivity (GPP) and over 3% in annual evapotranspiration in a forest stand (Migliavacca *et al.* 2012). Accounting for photoperiod effects on both forest phenology and photosynthetic activity is therefore important for improving models that predict the seasonality of forest

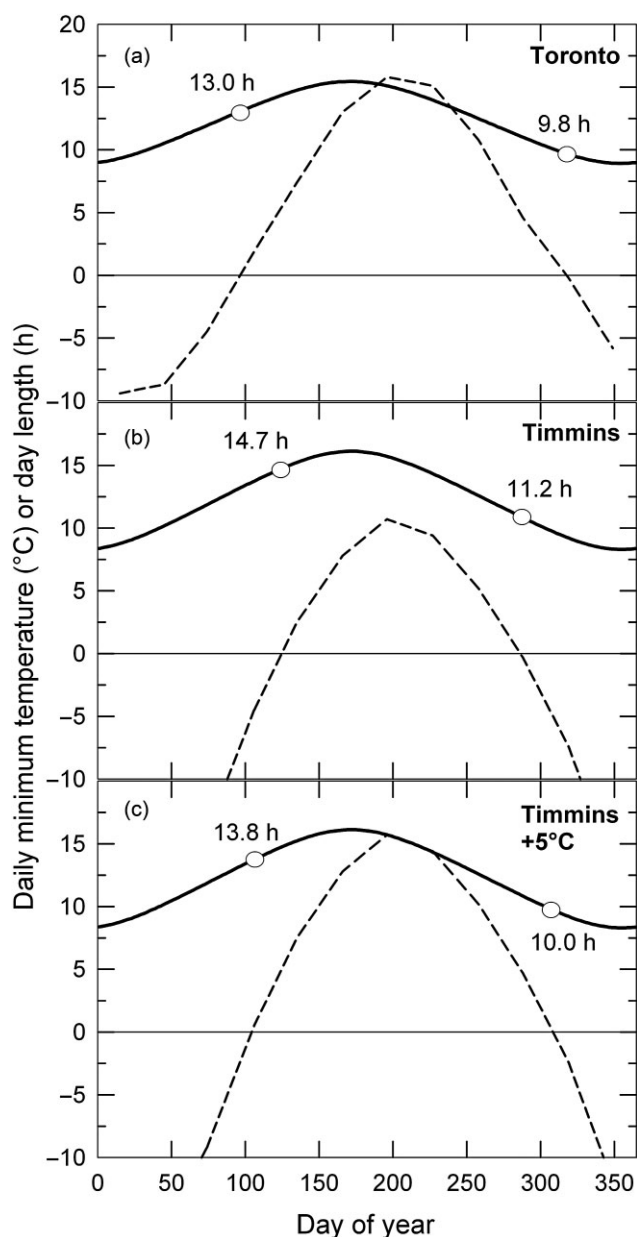*Correspondence: D. A. Way. e-mail: dway4@uwo.ca*

Figure 1. The link between photoperiod and seasonal temperatures at (a) a lower latitude site (Toronto, Canada; 43° 42'N 79° 24'W) and (b) a higher latitude site (Timmins, Canada; 48° 28'N 81°20'W) ~700 km north of Toronto. Solid lines indicate day length, dashed lines represent mean minimum daily temperature and circles illustrate the photoperiod where the minimum temperature crosses the freezing threshold. The high latitude site (Timmins) has a shorter growing season, but bud burst cannot occur until a relatively long photoperiod, compared with the lower latitude site (Toronto). Northwards migration of trees from Toronto to Timmins will expose the individuals to a different photoperiod × temperature regime. (c) Photoperiod by temperature conditions in a 5 °C warmer climate for the higher latitude site (Timmins). Day length remains constant, but minimum temperatures increase, lengthening the potential growing season, but creating another set of photoperiod × temperature regimes for the trees that remain *in situ* as the climate warms (Climate data from Environment Canada).

ecosystem carbon and water fluxes (Hunter & Lechowicz 1992; Migliavacca *et al.* 2012; Melaas *et al.* 2013) that feedback onto the climate system.

Genetic adaptations to a local photoperiod and temperature regime may constrain the ability of species to respond to climate change (Bradshaw & Holzapfel 2007). Trees are expected to migrate polewards as the climate warms, but this geographic movement will induce a mismatch between the thermal environment and the day length signals of the new site in comparison with the site of origin (compare Fig. 1a,b). Depending on the degree of phenotypic plasticity exhibited in response to temperature and photoperiod, and the extent to which a species relies on day length cues for determining phenology, trees may not be able to migrate as far as is currently predicted under a climate-envelope model approach.

The ability of forest systems to respond to the rapid increases in temperature predicted for coming decades can therefore be divided into *in situ* responses of existing trees, migration potential for future populations and evolutionary responses (e.g. Aitken *et al.* 2008). For the vegetation that remains in place while the climate changes around it, the ability to acclimate to the new thermal environment will be critical for stand productivity and survival, and we will spend the first part of the review discussing how temperature and photoperiod interact with regard to *in situ* phenology and physiology. In response to rising temperatures, tree species are also expected to migrate polewards so that the populations remain in a similar climate as their current distribution, and the second part of this review will concentrate on how photoperiod may constrain the movement of tree populations, either through natural migration or via human-assisted migration. Lastly, although tree species will surely adapt to climate change, the long lifespan of trees and the rapid rate of climate change will limit the ability of evolution to offset the threat to forests over the next century (Jump & Peñuelas 2005). The role of evolution in tree responses to warming has been recently reviewed (Alberto *et al.* 2013) and we therefore will not extensively discuss the role of adaptation in this review.

PHOTOPERIOD CONSTRAINTS ON PHENOLOGY

In seasonally cold climates, plant developmental systems have evolved to match a seasonal climate cycle that shifts annually from favourable to unfavourable periods for growth and survival. Woody plants with perennial aboveground structures must enter dormancy prior to the onset of temperatures that are lethal to active buds and other tissues. In addition, trees have evolved to resume growth at a time that minimizes the risk of frost damage but maximizes growing season length. However, temperature is a fickle cue: variation in the onset and cessation of frost risk from year to year varies considerably. In the early 1900s, Coville made seminal observations that plants from northern, seasonally cold climates do not break bud in spring when moved into warm greenhouses in late summer (Coville 1920). This provided early evidence of the complex cues that plants in seasonally cold environments use to sense the seasons and respond

appropriately, and established the critical importance of exposure to near freezing temperatures for dormant buds to gain the physiological ability to resume growth (c.f. Olmsted 1951 for *Acer saccharum*; Perry & Wang 1960 for *Acer rubrum*).

Over the ensuing decades, much progress was made, resulting in a general understanding that the degree of warming in spring, the onset of cold temperatures in fall, the duration of winter chilling and the photoperiod all provide important cues for tree phenology (e.g. Chandler & Tufts 1934; Campbell & Sugano 1979; Cannell & Smith 1983; Hunter & Lechowicz 1992; Oleksyn *et al.* 1992; Hänninen 2006; Linkosalo *et al.* 2006; Morin *et al.* 2009; Vitasse *et al.* 2009, 2011). The molecular and genetic bases for either temperature-based or photoperiodic regulation of tree phenology and physiology are still relatively unknown, although the topic has attracted considerable attention now that the poplar genome has been sequenced (Tuskan *et al.* 2006). The results point to important roles for phytochromes, the genes, CONSTANS (CO) and FLOWERING LOCUS T (FT), and regulators of the circadian clock in controlling seasonal bud burst, growth cessation and dormancy (e.g. Bohlenius *et al.* 2006; Gyllenstrand *et al.* 2007; Hsu *et al.* 2011; Cooke *et al.* 2012; Karlgren *et al.* 2013). Further study on the mechanisms linking photoperiod and seasonal phenology in trees is needed before we can use this understanding to predict future responses of forests in a changing climate.

Spring phenological responses to warming do not appear to be strongly constrained by photoperiod under current climate conditions. The advancement of spring phenology by recent climate warming has been confirmed on a global scale via field data and remote sensing (Walther *et al.* 2002; Menzel *et al.* 2006). On a smaller scale, experimental, observational and modelling studies suggest that bud burst in both deciduous and evergreen species is usually more strongly temperature-dependent than day length-dependent (e.g. Wareing 1956; Barr *et al.* 2004; Rollinson & Kaye 2012; Laube *et al.* 2014). For example, balsam poplars (*Populus balsamifera*) grown in two common gardens with the same photoperiod but different temperatures broke bud 6 weeks earlier in the warmer climate than the cooler site despite shorter day lengths at the time of bud burst (Soolanayakanahally *et al.* 2013). Similarly, experimental warming advanced bud burst by almost 2 weeks in *Picea mariana* (Bronson *et al.* 2009). However, even though leaf unfurling is linked to spring temperatures, the response may not be linear: warming treatments ranging from 1 to 6 °C continuously advanced bud burst in *Betula pendula*, but *Quercus robur* and *Fagus sylvatica* saplings had weaker responses of leaf unfurling to warming greater than 4 °C than to temperatures below this threshold (Fu *et al.* 2013). When photoperiod is directly manipulated, it affects the accumulated temperature sum needed to burst bud in some species, but temperature cues are still the dominant factors controlling bud burst timing (Laube *et al.* 2014). Other spring phenological phenomena, such as flowering, are also tightly correlated with spring temperature, and flowering in a number of mid- to high latitude tree species is being advanced by warming (e.g. *Populus tremuloides*, Beaubien & Hamann 2011; *Prunus jamasakura*, Primack *et al.* 2009).

Further evidence supporting the dominance of temperature as the primary cue for spring phenology is that process-based models relying solely on temperature tend to fit historical time-series as well as (or even better than) those based on both temperature and photoperiod (Hunter & Lechowicz 1992; Linkosalo *et al.* 2006; Vitasse *et al.* 2011; Kalvāns *et al.* 2014). Most models currently used to estimate the spring onset of bud burst or carbon uptake in temperate and boreal forests rely on temperature, although the manner of accumulating thermal units and the role of chilling requirements varies (Hunter & Lechowicz 1992; Migliavacca *et al.* 2012). However, incorporating information on photoperiod can improve model performance, indicating some role for day length cues in these processes. Adding a day length parameter improved the ability to capture spring CO_2 and water fluxes (as compared with eddy flux measurements) and canopy development (as measured by remote sensing), particularly in plots dominated by deciduous species (Melaas *et al.* 2013). The model that best captured 20 years of spring bud burst data at the Harvard Forest experiment included photoperiod (Migliavacca *et al.* 2012). And using both temperature-related data and calendar date (as a potential proxy for photoperiod) improved estimates of bud break timing in *B. pendula* compared with a temperature-only approach (Häkkinen *et al.* 1998).

While many studies suggest that photoperiod may not be the dominant cue in spring, these results could be due to the fact that under current conditions, trees are robust to some variation in vernal cues: the control system has 'built-in' flexibility to cope with the inevitable vagaries of inter-annual climate fluctuations. For example, there is phenotypic plasticity within a single genotype to respond to different photoperiod × temperature cues (Kramer 1995), but genotypes from harsher environments, such as high altitude or latitude sites, can have less plasticity than genotypes from more moderate sites, likely reflecting the severe consequences on fitness of a mistake in phenology in these environments (Vitasse *et al.* 2013). This begs the question: as climate change moves the combinations of chilling, warming and photoperiod outside of historical conditions, will stronger photoperiodic control of spring bud burst be exposed? The best evidence for the potential of photoperiod to grow in importance in a warming world comes from studies that manipulate winter chilling, spring warming and photoperiod. In studies across a range of species, a consistent photoperiod effect has been seen on insufficiently chilled buds. Specifically, when buds receive less chilling (as they will under climate change, where winters are expected to warm faster than other seasons), seedlings forced in long photoperiods burst bud before those exposed to short photoperiods (Nienstaedt 1967; Worrall & Mergen 1967; Campbell & Sugano 1975; Falusi & Calamassi 1990; Caffarra & Donnelly 2011; Laube *et al.* 2014). This suggests that warmer winters will make plants less responsive to warming at the shorter photoperiods expected in warmer, earlier springs, which may constrain the expansion of the growing

season. There is also evidence for direct photoperiodic sensitivity of bud burst in some species (e.g. *F. sylvatica*; Heide 1993a): at shorter photoperiods, it takes longer for buds to burst than at long photoperiods, indicating that long photoperiods enhance dormancy release (Heide 1993a,b). Tree species that fall into this category are likely to be strongly limited in their ability to respond to warmer springs by breaking bud earlier.

In contrast to spring phenological responses, cues for autumn phenological responses, including adjustments of leaf biochemistry and physiology for the upcoming winter season, often include both declining photoperiod and temperatures (Hänninen & Tanino 2011). As is the case in the spring, autumn temperatures are a much less consistent seasonal cue than day length across years, and the ability to respond to rising temperatures will be limited by local adaptation that links photoperiod and temperature cues to seasonality for a given provenance and location. In general, warmer autumns are expected to delay leaf senescence, a trend that has been seen in several experiments (e.g. Gunderson *et al.* 2012; Reyes-Fox *et al.* 2014; Montgomery *et al.* unpublished data) and has been detected in remote sensing data across large geographical regions (Jeganathan *et al.* 2014). However, this is not always the case. In poplars grown in common gardens with the same photoperiod but different temperatures, the trees at the warmer site initiated spring growth 6 weeks earlier than at the cooler site, but only extended their total growing season by 2 weeks, since autumn phenological events also occurred earlier, despite the warm late season weather (Soolanayakanahally *et al.* 2013). This echoes the coupling recently found by Fu *et al.* (2014) between earlier leaf flushing caused by winter and spring warming and earlier autumn leaf senescence, even though both control and warmed plants received similar summer and autumn temperatures. Earlier leaf drop in warmer years and sites has been seen in a range of other tree species, including *B. pubescens* and *Populus canescens*, and when combined with only a small advancement of spring leaf out, this can actually cause a shorter growing season in warmer years in species such as *Larix decidua* and *Q. robur* (Kramer 1995). As well, several studies suggest that leaf senescence in poplars is mainly photoperiodically cued (Barr *et al.* 2004; Pudas *et al.* 2008; Fracheboud *et al.* 2009), often occurring on the same day every year at a given site despite annual temperature variation. In contrast, a warming experiment in Northern Minnesota, USA has found that growing season extension because of warming was equal or greater in the autumn than in the spring for a number of species, including *Populus tremuloides* (Montgomery *et al.* unpublished data), and remote sensing-derived measures of growing season length have found that delayed autumn senescence contributes more to recent extensions of the growing season length than earlier spring leaf out in many parts of Europe (Garonna *et al.* 2014).

There is considerable evidence that photoperiod is the dominant cue for growth cessation and bud set in many temperate and boreal trees (e.g. *Populus* species, Howe *et al.* 1995; Keller *et al.* 2011; *Pinus sylvestris*, Oleksyn *et al.* 2001; *B. pendula*, Li

et al. 2003; *Picea abies*, Chen *et al.* 2012), although temperature has been shown to impact these processes in some species (e.g. *Picea abies*, Heide 1974; *Populus* species, Kalcsits *et al.* 2009; Rohde *et al.* 2009; members of the *Rosaceae*, Heide & Prestrud 2005; Heide 2008; Heide 2011). Bud set represents a major shift in developmental pathways that starts the process of dormancy induction prior to winter (Howe *et al.* 1995). The genetic components of the signalling pathway for bud set and growth cessation because of shortening photoperiods have attracted considerable attention in recent years (e.g. Howe *et al.* 1995; Bohlenius *et al.* 2006; Gyllenstrand *et al.* 2007; Chen *et al.* 2012; Karlgren *et al.* 2013; for a recent review see Petterle *et al.* 2013).

Most evidence for photoperiodic control of growth cessation and bud set comes from provenance trials (Howe *et al.* 1995; Oleksyn *et al.* 2001; Luquez *et al.* 2008; Keller *et al.* 2011) or controlled chamber experiments (e.g. Howe *et al.* 1995; Chen *et al.* 2012). Keller *et al.* (2011) showed significant divergence among balsam poplar (*Populus balsamifera*) populations in bud set when grown in a common garden, and this divergence was beyond that expected because of neutral processes, suggesting strong selection for this phenological trait. Phenotypic variance in bud set is strongly related to region of origin, with northern populations setting bud earlier than southern ones, consistent with the role of photoperiod as a major control on bud set (Li *et al.* 2003; Luquez *et al.* 2008; Keller *et al.* 2011; Chen *et al.* 2012). Generally, trees from lower latitudes have a shorter critical photoperiod to induce growth cessation or bud set (Li *et al.* 2003; Luquez *et al.* 2008; Chen *et al.* 2012). Thus if moved poleward, they tend to set bud later and achieve higher growth than local genotypes. Similarly, when populations are moved towards the equator, they tend to set bud and cease growth earlier as they have longer critical photoperiods (Li *et al.* 2003; Luquez *et al.* 2008). Differences among individuals and years in when growth cessation and bud set occur have important implications for forest and ecosystem productivity. The timing of growth cessation has been linked to differences in total growth in a number of species, with trees that halt growth earlier growing less overall: for example, the timing of growth cessation explained 42–86% of variation in growth among Scots pine (*Pinus sylvestris*) provenances across a range of common gardens (Oleksyn *et al.* 2001).

These kinds of responses have implications for trees exposed to warming temperatures *in situ*, as well as for both natural and assisted migration of forest species. Photoperiod will likely serve to restrain responses to warming *in situ* because trees will continue to set bud at a particular day length despite the lengthening of the favourable period for growth after that critical photoperiod. In contrast, a short critical photoperiod could extend growth under climate change if southern provenances move northward naturally or via assisted migration, provided frost damage is avoided. Thus, unlike spring phenology, which is largely temperature driven, bud set and growth cessation processes that are significantly linked to photoperiod will be much less likely to respond to climate warming. Over time, new locally adapted combinations of temperature tolerance and critical

photoperiod for bud set will be established in populations that migrate (Savolainen *et al*. 2011), but this evolutionary response is unlikely to occur quickly in long-lived trees.

While we often recognize that the effects of warming on spring phenology and physiology will carry over into summer and autumn performance of an individual or stand in the same year, the effects of autumn and winter warming can also affect plant performance the following spring (Heide 2003; Søgaard *et al*. 2008; Hänninen & Tanino 2011; Way 2011). Most studies focus on either spring or autumn phenology, discussing them as if they were separate phenomena, and the effects of warming are rarely linked over a year or more. But these legacy effects can be substantial. In a recent paper, Fu *et al*. (2014) found that an early season warming treatment advanced spring bud burst in *Q. robur* and *F. sylvatica*, but that even without any further warming, the earlier leaf unfurling was correlated with earlier autumn senescence and bud burst the following spring, implying a carry-over effect that did not require external forcing from the environment. Warmer winters will also mean that chilling requirements are less likely to be fulfilled, such that trees that experience climate change over coming decades may need even greater heat sums to force bud burst. There is thus a pressing need to study warming in an integrated way across the seasons that accounts for legacy effects from one growing season to the next, across the winter period and over years, rather than concentrating solely within a single growing season (Williams *et al*. 2014). Moving towards a more complete annual or multiyear framework for thinking about the effects of climate change on tree phenology should therefore be a priority to promote our ability to capture the complex effects of temperature changes across many seasons and their interactions with photoperiod.

WHICH SPECIES ARE MOST LIKELY TO BE CONSTRAINED BY PHOTOPERIOD IN THEIR *IN SITU* RESPONSES TO WARMING?

Although we have a general understanding that winter chilling, spring warming and photoperiod all interact to influence tree leafing phenology, our understanding of species-specific cues and how they differ among co-occurring species is poor (Vitasse *et al*. 2009; Laube *et al*. 2014; Körner & Basler 2010). There are hints that the phenology of different tree functional types may respond differently to recent climate warming: high latitude regions dominated by deciduous conifers (i.e. *Larix*) have seen the greatest advances of spring growth, while regions dominated by broad-leaved deciduous trees show the greatest delays in autumn senescence (Jeganathan *et al*. 2014). Bud burst in seedlings may be less sensitive to photoperiod than adult trees, as they need to take advantage of understory light availability before canopy closure occurs (Vitasse 2013). But the generality of these responses is unknown, and a lack of understanding of the relative importance of these cues for different forest tree species hinders our ability to predict phenological responses and their ecological impacts on forest ecosystems under future climate scenarios.

While spring phenology is less sensitive to photoperiod than autumn phenological events, there has been considerable research on the effect of photoperiod on bud burst in a range of species. In a recent study, Basler & Körner (2012) found that short photoperiods delayed bud burst in late-successional species, such as *Picea abies* and *Abies alba*, but that bud burst in early-successional tree species (e.g. *Larix decidua*) was not photoperiod-limited, confirming earlier work on *Picea abies* (Partanen *et al*. 1998). However, Caffarra & Donnelly (2011) found that bud burst was affected by photoperiod in all the species examined, including late-successional *F. sylvatica* and *Tilia cordata*, as well as early-successional *B. pubescens* and *Salix x smithiana*. Short days have little impact on the timing of bud burst in *Pinus sylvestris* (Hänninen 1995) or in *Sorbus* spp. (Heide 2011), while changing the photoperiod from 16 to 8 h had no effect on dormancy release in six species of *Ulmus* (Ghelardini *et al*. 2010). There are also interactions between day length and temperature on phenology: photoperiod can alter the spring temperatures needed for bud burst in a range of species, where longer days reduce the temperature needed to induce leaf development (e.g. *Liquidambar styraciflua*, Farmer 1968; *Pseudotsuga menziesii*, Campbell & Sugano 1975; *Q. petraea*, Nizinski & Saugier 1988). But not all species respond the same way: exposing cuttings to long days decreased the heat sum necessary for bud burst in *B. pubescens*, *Alnus incana*, *Alnus glutinosa* and *Populus tremula*, but not in *Sorbus aucuparia* or *Rubus idaeus* (Heide 1993b). As discussed earlier, photoperiodic sensitivity of bud burst may only be seen in a range of tree species when sufficient chilling has been achieved (Laube *et al*. 2014).

Modelling work also reveals that the phenology of some tree species is strongly responsive to photoperiod and less so in others. Schaber & Badeck (2003) found that accounting for photoperiod was more important in modelling species that burst bud late in the spring (*F. sylvatica* and *Q robur*) than in those developing earlier (*B. pendula*, *Larix decidua* and *Aesculus hippocastanum*). Separately, Hunter & Lechowicz (1992) found photoperiodic cues appeared less important in models predicting bud burst date in some species (such as *Populus tremuloides* and *Acer saccharum*) than others (such as *Q. alba* and *Fraxinus americana*), and suggested that bud break may be less responsive to photoperiod in diffuse-porous xylem trees that develop their canopy early in the spring and are less damaged by freeze-thaw events compared with ring-porous species that leaf out later and are more vulnerable to cavitation by freeze-thaw damage (Sperry & Sullivan 1992).

We compiled the results from a range of studies that examined photoperiodic sensitivity of spring leaf-out phenology in tree species. We did not conduct a similar analysis for autumn leaf phenology or growth cessation/bud burst because of a lack of data for the former and the fact that in nearly all tree species the latter is sensitive to photoperiod (with exceptions in the *Rosaceae*; Heide & Prestrud 2005; Heide 2008; Heide 2011). We added information on the successional strategy employed by the species and the xylem anatomy type to investigate these hypotheses, using data from a range of sources, including Burns & Honkala (1990),

the InsideWood database (http://insidewood.lib.ncsu.edu), the earlier categorizations in Laube *et al.* (2014) and primary literature on individual species as needed. In this classification, a photoperiod-sensitive species shows an effect of photoperiod on modulating bud burst in every study, photoperiod-insensitive species never show an effect of photoperiod on phenology and equivocal species have mixed results. We analysed whether there were differences in ecological strategy or anatomy between photoperiod sensitive and insensitive species, using a nominal logistic model (JMP Pro 10.0.0, SAS Institute, Cary, NC, USA). When examined across a broad range of species, patterns in photoperiodic sensitivity of bud burst do not follow successional niche (as suggested by Basler & Körner 2012), xylem anatomy groupings (as suggested by Hunter & Lechowicz 1992) or evergreen/deciduous leaf type divisions ($0.25 < P < 0.74$; Table 1). While results for some species (such as *Fagus sylvatica*) are repeatable across studies, for others (such as *Picea abies*), the categorization of photoperiodic sensitivity is inconsistent among studies. As elegantly demonstrated in the recent work of Laube *et al.* (2014), determining whether bud burst is sensitive to photoperiod requires accounting for the degree of chilling the plant has received, which likely accounts for the differing results in the literature for a given species. As well, the effect of ontogeny on photoperiodic sensitivity of phenological processes has only been recently discovered (Vitasse 2013), which may also contribute to the diverse results in the literature. The discovery of an underlying ecological or physiological scheme that differentiates between photoperiodically sensitive and insensitive tree species would be useful for facilitating predictions of tree phenology in a future climate, but unfortunately there is currently no evidence for such a system. Experiments that aim to ascertain whether bud burst is photoperiod-sensitive should therefore ensure that chilling requirements have been met, but a clearer understanding of how rapidly warming winters at high latitudes will affect bud burst timing through changes in chilling requirements and photoperiod should also be a research priority. Lastly, it should be noted that while photoperiod can affect spring phenological events in trees, half of the species examined in Table 1 are photoperiod-insensitive, emphasizing the importance of temperature cues over those of day length in bud burst.

PHOTOPERIOD CONSTRAINTS ON PHYSIOLOGY

Although the role of day length in phenology has been extensively studied, the potential for photoperiod to direct impact tree physiology through non-phenological means has received little attention, although there are examples in the literature. Across a range of high latitude conifer genera (including *Picea*, *Pinus*, *Abies* and *Larix*), maximum growth of new wood occurs at the summer solstice and is more tightly linked to day length than to seasonal temperature patterns (Rossi *et al.* 2006). With regard to leaves, even if tree canopies develop earlier and are retained longer (in deciduous species), or become active earlier and dormant later (in evergreens) as

temperatures rise, this does not necessarily mean that trees will be physiologically active for that entire period of canopy retention. Other environmental factors, such as water availability, can clearly limit tree physiological capacity when green leaves are present in the canopy. Most researchers assume that a longer period with a green canopy equals more carbon uptake (e.g. Keenan *et al.* 2014), but it remains unclear whether photoperiod may likewise impose constraints on the physiology of fully developed leaves during relatively favourable temperature conditions.

While day length cues are likely to limit the duration of leaf presence in the canopy as described earlier, there is evidence that they can also regulate the physiological activity of those leaves. In temperate deciduous trees, seasonal variation in photosynthetic capacity is more closely correlated with photoperiod than with temperature (Bauerle *et al.* 2012): although leaves stayed green throughout the summer and early autumn, the capacity for photosynthetic carbon uptake had declined by over 80% before leaf senescence became visible, when compared with rates measured at the summer solstice. This is consistent with work showing that warm, short-day conditions reduce photosynthetic performance in *Pinus banksiana* seedlings, rather than enhancing carbon uptake (Busch *et al.* 2007). These effects can also be detected at a larger scale: incorporating a day length signal improves the ability to estimate forest and shrub-dominated stand productivity in a study of 385 site-years of eddy covariance data (Stoy *et al.* 2014). Photoperiodic constraints on photosynthetic capacity could help explain the asymmetric responses of photosynthetic activity in high latitude forests to spring versus autumn warming: climate change has advanced the onset of photosynthetic activity by approximately 6 d in the spring, where photoperiodic constraints on photosynthetic physiology are not expected to be strong, but only extended them by 3 d in the autumn (Barichivich *et al.* 2013). The need to account for a photoperiodic cue on tree carbon fluxes is therefore not limited solely to the role of day length in increasing the leaf-on period in a warming climate; it must also address the physiological activity of those leaves.

PHOTOPERIOD CONSTRAINTS ON MIGRATION

While warming will necessitate acclimation and phenotypic plasticity to new temperature regimes in existing trees, future individuals will theoretically be able to grow in more polewards locations as the climate warms. Indeed, the increases in temperature that have already occurred have shifted species distributions in a wide range of organisms (Parmesan & Yohe 2003). Unsurprisingly, our best evidence for these climate-related range shifts are in the more mobile species, which can respond fastest to changes in climate (Lenoir *et al.* 2008). In contrast, organisms such as trees are relatively slow in shifting their ranges as the climate warms since they are sessile and take many years (or even decades) to become reproductive, which can limit effective seed dispersal at the range edge; given these issues, evidence of tree migration in response to climate is easier to detect in

Table 1. Species grouped according to whether bud burst is sensitive or insensitive to photoperiod, and information on the successional dynamics, xylem anatomy and leaf habit of the species. Species with contrasting results are categorized as equivocal, with photoperiodic sensitivity of bud burst likely related to the degree of chilling used

Species	Succession	Xylem	Leaf	Source
Photoperiod sensitive				
Abies alba	LS	T	E	Basler & Körner 2012; Laube *et al.* 2014
Alnus glutinosa	ES	DP	D	Heide 1993b
Alnus incana	ES	DP	D	Heide 1993b
Betula pubescens	ES	DP	D	Heide 1993b; Caffarra & Donnelly 2011
Cornus alba	ES	DP	D	Laube *et al.* 2014
Fagus sylvatica	LS	DP	D	Falusi & Calamassi 1990; Schaber & Badeck 2003; Caffarra & Donnelly 2011; Basler & Körner 2012; Basler & Körner 2014; Laube *et al.* 2014
Fraxinus americana	LS	RP	D	Hunter & Lechowicz 1992
Juglans regia	MS	RP	D	Laube *et al.* 2014
Liquidambar styraciflua	ES/MS	DP	D	Farmer 1968
Pinus strobus	MS	T	E	Laube *et al.* 2014
Pinus wallichiana	ES	T	E	Laube *et al.* 2014
Populus tremula	ES	DP	D	Heide 1993b; Laube *et al.* 2014
Prunus padus		DP	D	Heide 1993b
Quercus alba	LS	RP	D	Hunter & Lechowicz 1992
Quercus bicolor	MS	RP	D	Laube *et al.* 2014
Quercus petraea	LS	RP	D	Nizinski & Saugier 1988; Basler & Körner 2012; Basler & Körner 2014
Salix x smithiana	ES	DP	D	Caffarra & Donnelly 2011
Tilia cordata	LS	DP	D	Caffarra & Donnelly 2011
Photoperiod insensitive				
Abies homolepis	LS	T	E	Laube *et al.* 2014
Acer negundo	MS	DP	D	Laube *et al.* 2014
Acer saccharum	LS	DP	D	Hunter & Lechowicz 1992; Laube *et al.* 2014
Acer tataricum	ES	DP	D	Laube *et al.* 2014
Amorpha fruticosa	ES	RP	D	Laube *et al.* 2014
Carpinus betulus	LS	DP	D	Laube *et al.* 2014
Cornus mas	ES	DP	D	Laube *et al.* 2014
Fraxinus chinensis	MS	RP	D	Laube *et al.* 2014
Fraxinus excelsior	MS	RP	D	Basler & Körner 2012; Laube *et al.* 2014
Fraxinus pennsylvanica	MS	RP	D	Laube *et al.* 2014
Juglans ailantifolia	MS	RP	D	Laube *et al.* 2014
Juglans cinerea	ES	RP	D	Laube *et al.* 2014
Larix decidua	ES	T	D	Schaber & Badeck 2003; Basler & Körner 2012; Laube *et al.* 2014
Pinus nigra	ES	T	E	Laube *et al.* 2014
Pinus sylvestris	ES	T	E	Hänninen 1995; Laube *et al.* 2014
Populus tremuloides	ES	DP	D	Hunter & Lechowicz 1992
Prunus avium	MS	DP	D	Basler & Körner 2012; Laube *et al.* 2014
Prunus serotina	MS	DP	D	Laube *et al.* 2014
Quercus rubra	MS	RP	D	Laube *et al.* 2014
Robinia pseudoacacia	ES	RP	D	Laube *et al.* 2014
Rubus idaeus	ES		D	Heide 1993b
Sorbus aucuparia	ES	DP	D	Heide 1993b, 2011; Basler & Körner 2012
Sorbus intermedia	ES	DP	D	Heide 2011
Symphoricarpos albus	ES	DP	D	Laube *et al.* 2014
Ulmus glabra	LS	RP	D	Ghelardini *et al.* 2010
Ulmus macrocarpa	LS	RP	D	Ghelardini *et al.* 2010
Ulmus minor	LS	RP	D	Ghelardini *et al.* 2010
Ulmus parvifolia	LS	RP	D	Ghelardini *et al.* 2010
Ulmus pumila	LS	RP	D	Ghelardini *et al.* 2010
Equivocal				
Acer pseudoplatanus	LS	DP	D	IS = Basler & Körner 2012; Basler & Körner 2014; S = Laube *et al.* 2014
Aesculus hippocastanum	MS	DP	D	IS = Schaber & Badeck 2003; Basler & Körner 2012; S = Laube *et al.* 2014
Betula pendula	ES	DP	D	IS = Heide 1993b; Häkkinen *et al.* 1998; S = Schaber & Badeck 2003; Basler & Körner 2012; Laube *et al.* 2014
Corylus avellana	ES	DP	D	IS = Basler & Körner 2012; S = Laube *et al.* 2014
Picea abies	LS	RP	E	IS = Laube *et al.* 2014; S = Partanen *et al.* 1998; Ghelardini *et al.* 2010; Basler & Körner 2012; Basler & Körner 2014
Pseudotsuga menziesii	LS	T	E	IS = Laube *et al.* 2014; S = Campbell & Sugano 1975
Quercus robur	MS	RP	D	IS = Laube *et al.* 2014; S = Schaber & Badeck 2003
Syringa vulgaris	ES	DP	D	IS = Basler & Körner 2014; S = Laube *et al.* 2014

D, deciduous; DP, diffuse porous xylem; E, evergreen; ES, early successional; IS, photoperiod insensitive; LS, late successional; MS, mid-successional; RP, ring porous xylem; S, photoperiod sensitive; T, tracheids.

altitudinal studies, where distances are compressed, compared with latitudinal studies (Beckage *et al*. 2008). Despite this caveat, range expansions of some tree species related to climate warming have been noted over recent decades (Harsch *et al*. 2009; Vitasse *et al*. 2012).

How far will tree species need to move in coming decades? In the short-term, species that can maintain their climatic niche through phenotypic plasticity, acclimation of physiological processes and modification of phenology to align critical life history events (such as flowering) with the changing climate may not need to migrate to remain competitive (Amano *et al*. 2014). But perennial species, such as trees, appear to be less plastic in these traits (Amano *et al*. 2014), which likely necessitates greater migration distances than species that can significantly alter their physiology and phenology *in situ*. Using temperature predictions for the period from 2000 to 2100, Loarie *et al*. (2009) estimated that boreal forests would need to move 0.43 km per year and temperate forests by 0.35 km per year to remain in the same temperature niche. Models such as this indicate that the required rates of species movement may outstrip the capacity of trees to migrate. Evidence from fossil pollen in North America indicates that trees may have moved by as much as 1 km per year at the end of the last ice age (e.g. Davis 1981), which would be sufficient to match current predictions of temperature change in these areas. More recent work has greatly reduced this estimated maximum migration rate: genetic work has shown that low densities of trees north of the main populations of *Acer rubrum* and *Fagus grandifolia* facilitated migration, but at rates of less than 0.1 km per year (McLachlan *et al*. 2006). Iverson *et al*. (2004) also found that migration in a suite of North American tree species was much less likely for distances greater than 20 km over a 100-year time span than for shorter distances, and noted the importance of tree abundances at the range boundary to produce seed for uncolonized territory.

There appears to be a mismatch between potential rates of tree movement and the rates predicted to be necessary to keep up with climate change (Loarie *et al*. 2009), indicating that tree species will likely have difficulty moving fast enough to keep pace with climate warming. In a recent study, Zhu *et al*. (2011) compared the spatial distributions of seedlings and trees with the same species and examined relationships between these distributions and 20th century climate; they found that only 19 out of 92 species showed a pattern consistent with northwards migration in response to warming. For forest species, this implies the need for assisted migration and/or assisted gene flow (Aitken & Whitlock 2013) to match appropriate genetic material, provenances and species in regions where the climate will be suitable for tree growth in coming decades. However, matching trees to a site for future productivity requires more than judging where a conducive temperature (and precipitation) regime will be found (e.g. Amano *et al*. 2014; see Savva *et al*. 2007); many other environmental factors, such as edaphic characteristics, are critical for determining the suitability of a site for tree growth. Of these remaining factors, photoperiod is likely to play a key

role in the ability of tree species and forests to respond to climate warming (Stinziano & Way 2014).

The phenology of most mid- to high latitude tree species is related to photoperiod through local adaptation (e.g. Howe *et al*. 1995), a process that likely also dictates chilling and forcing requirements (Beuker 1994). These genetic differences in growth and phenology across populations can be clearly seen in provenance studies, where individual trees from a large geographic range are grown together in a common garden scenario (e.g. Schmidtling 1994; Carter 1996; Oleksyn *et al*. 1998; Rehfeldt *et al*. 1999; Oleksyn *et al*. 2001). While most provenance trials were established to investigate which genotypes would be most productive in a given region, they also provide valuable data on how tree growth responds to different climates (temperatures and precipitation patterns) and photoperiods. In general, phenological traits such as bud burst, bud set and senescence are strongly associated with day length cues and local temperature patterns at the site of origin (Oleksyn *et al*. 1992, 2001; Howe *et al*. 1995; Li *et al*. 2003; Keller *et al*. 2011). While long distance gene flow or assisted gene migration might help high latitude populations adapt to warmer conditions within broadly distributed species (Kremer *et al*. 2012; Aitken & Whitlock 2013), the lower latitude genetic material that should include greater tolerance to warm growing temperatures will also include locally adapted genes for the photoperiod at the site of origin.

The successful migration of trees polewards as the climate warms will therefore depend on the extent to which the species uses photoperiodic cues to regulate phenology and physiology, and the match between seasonal temperatures and day lengths at the original and new sites. Migrations of short distances may not lead to substantial mismatches between temperatures conducive for growth and day length signals, and as seeds from warmer sites can have higher growth rates than seeds from the higher latitude local provenance, relatively short distance movements of seed could increase forest productivity (Rehfeldt *et al*. 1999; Savva *et al*. 2007), although tree growth can also be optimal at the local environment or in slightly colder regions (Schmidtling 1994; Carter 1996). But as described earlier, the distances trees must move to remain in their current thermal regime over the next century and beyond are likely to be quite large, leading to a shift in the link between seasonal temperatures and photoperiod. We illustrate this issue in Fig. 1, where a lower latitude site is depicted in Fig. 1a and a higher latitude site in Fig. 1b. At high latitudes, the risk of frost in the spring and autumn is lifted on a day with a longer photoperiod than at lower latitude sites. As such, if a genotype that relies on photoperiodic cues for phenology is transferred polewards, the tree would have a much higher risk of incurring severe frost damage by starting to grow too early in the season and ceasing growth too late in the autumn. The direct effects of low temperatures on preventing cell division and elongation via forcing requirements may moderate the effect of this in the spring, thus preventing premature bud burst. But if the sequence of events leading to senescence and dormancy is initiated too late during the summer because of the unexpectedly long

photoperiod during the growing season, two alternatives emerge. In a mild year, the tree could have a longer growing season than the individuals around it, which could facilitate greater growth and productivity (although an earlier growing season start may also deplete soil water reserves sooner and lead to earlier summer limitations on growth because of drought). In an average year, or a year with an early frost, the canopy will not have senesced before temperatures fall below freezing, reducing growth and productivity the following spring because of hindered reabsorption of nutrients from the leaves and possible frost damage to buds that may not have been sufficiently hardened. These scenarios are further complicated by the recent finding that earlier bud break can itself trigger earlier senescence (Fu *et al*. 2014), emphasizing the urgent need to elucidate the mechanism linking phenological events across seasons and years in perennial species.

CONCLUSIONS

Simple assumptions about how warming will impact high latitude forests often lead to predictions of increased growth and longer growing seasons. While this may occur in some sites (especially in the short term), elevated temperatures, especially when coupled with water limitations, have already been associated with reductions in tree growth and increases in tree mortality in boreal forests (Peng *et al*. 2011; Buermann *et al*. 2013). In addition to the well-known need to consider water and nutrient conditions in order to predict tree performance in a warmer climate, we emphasize the need to better understand how photoperiod will impact forest systems in a future world. A reliance on photoperiod as a seasonal cue for growth and physiological activity may either constrain forest productivity, via limitations on photosynthetic capacity, migration potential or growing season length, or permit longer growing seasons and greater tree growth in individuals that migrate to higher latitudes. Currently, there are no detectable patterns among species regarding their degree of photoperiodic sensitivity based on successional niche, leaf type or xylem structure, which precludes making broad predictions of which species will be most successful in migrating long distances, either naturally or through assisted migration or assisted gene flow schemes. Improving our knowledge of the mechanisms underlying photoperiodic control of tree phenology and physiology is critical for predicting how trees will respond to novel combinations of day length and temperature, especially when evolution is unlikely to keep pace with the rapidly changing climate.

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