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Commentary

Tree phenology responses to warming: spring forward, fall back?

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Some of the strongest evidence that organisms are already responding to climate change is the lengthening of the growing season at mid- to high latitudes (Menzel and Fabian 1999, Menzel et al. 2006, Ibáñez et al. 2010). Earlier spring bud burst and later autumn senescence have lengthened the growing season by ~11 days since the 1960s (Menzel and Fabian 1999). This response could help mitigate climate change if a longer growing season increases carbon sequestration, since this would provide a negative feedback on rising atmospheric CO_2 concentrations by increasing the terrestrial carbon sink.

However, while elevated temperatures can delay autumn senescence, temperature is an unreliable cue of when the sequence leading to dormancy should be initiated; late summer and early fall temperatures do not necessarily correlate with the timing of the first frost. Trees need to have completed a series of processes, including growth cessation, bud set and leaf senescence, before the first frost arrives or risk physical damage (see Figure 1). Thus, in many species, day length is used as a signal to begin growth cessation, the first step towards reaching winter dormancy (Wareing 1956). The importance of temperature and day length cues in determining the cessation of tree growth varies between species, with some groups thought to rely exclusively on photoperiod (Pauley and Perry 1954, Wareing 1956, Howe et al. 1996). This dependence on a day length signal has implications for forests in a warming world: while temperatures may increase over time, day length will remain unchanged, limiting the ability of photoperiod-controlled tree species to extend their growing season.

In this issue, Rohde et al. (2011) show that, across a latitudinal range of field sites, temperature alters the timing of growth cessation in *Populus*, a genus where photoperiod alone is often thought to determine the end of the growing season (Pauley and Perry 1954, Howe et al. 1996, Bohlenius et al. 2006, Fracheboud et al. 2009). While warmer temperatures delayed the onset of growth cessation in hybrid poplar, so did cold nights, implying that there was an optimum temperature sum for rapid growth cessation (Rohde et al. 2011). Temperature also affected the time between growth cessation and bud set, with warmer temperatures hastening the process of bud development (Rohde et al. 2011), consistent with results from growth chamber experiments (Mölmann et al. 2005). This work joins other recent studies (Mölmann et al. 2005, Fracheboud et al. 2009, Tanino et al. 2010) that demonstrate that even in trees thought to be photoperiod controlled, temperature can modify the timing of key phenological events.

Based on the findings of Rohde et al. (2011), rising temperatures would delay growth cessation in poplar, but accelerate bud development. Other studies in hybrid poplar have found that while treatments with warmer days can indeed delay growth cessation, some combinations of elevated day and night temperature treatments instead led to earlier growth cessation (Kalcsits et al. 2009). While it is therefore unclear whether climate warming will delay or accelerate growth cessation, these differences between studies indicate that the balance between changes in day and night temperature may be critical for predicting changes in tree phenology. Night temperatures appear to have a greater impact on growth cessation and bud set than day temperatures (Kalcsits et al. 2009, Tanino et al. 2010), and since increases in night temperatures are expected to be greater than those in day temperatures, climate warming may alter these processes more rapidly than experiments based on average temperature changes would predict.

Temperature can also influence other late season phenological events, including senescence and dormancy. Higher temperatures slowed the speed of chlorophyll degradation during leaf senescence in *Populus tremula* (Fracheboud et al. 2009). In hybrid poplar, warm nights and low day–night temperature differences promoted deeper winter dormancy and cold hardiness (Kalcsits et al. 2009), implying that the temperature changes predicted by global climate models might enhance dormancy.

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A similar result was seen across three deciduous, boreal tree species (*Betula pendula*, *Betula pubescens* and *Alnus glutinosa*), where elevated temperatures during short-day dormancy induction delayed bud burst the following spring, indicating that warmer temperatures had increased the depth of dormancy (Heide 2003), consistent with studies in *Picea abies* (Norway spruce) and *Acer platanoides* (Norway maple) (Heide 1974, Westergaard and Eriksen 1997, Granhus et al. 2009). As highlighted by Heide (2003), this greater dormancy and chilling requirement could be beneficial in a warmer climate, where milder winters and springs may otherwise promote early bud burst and therefore increase the risk of early spring frost damage. Recent work has shown that in grasslands, warm springs advance spring growth and lengthen the growing season, but warm winters delay spring growth; the net effect of regional climate warming has been an overall shortening of the growing season since 1996 due to the warm autumns and winters (Yu et al. 2010). However, dormancy depth is not always increased by exposure to warmer fall temperatures, making it difficult to assess whether something similar might occur in forests: low temperatures increased the depth of dormancy in northern ecotypes of *Cornus sericea* (red osier dogwood) (Svendsen et al. 2007). Thus, the degree to which warming will influence the timing and depth of winter dormancy in trees is still unclear, and may differ between species and ecotypes. To make predictions about how changes in temperature will affect the entire suite of autumn phenological responses and how that will then impact spring phenology will require thinking about these processes relative to each other, rather than studying spring and fall phenology separately (Figure 1).

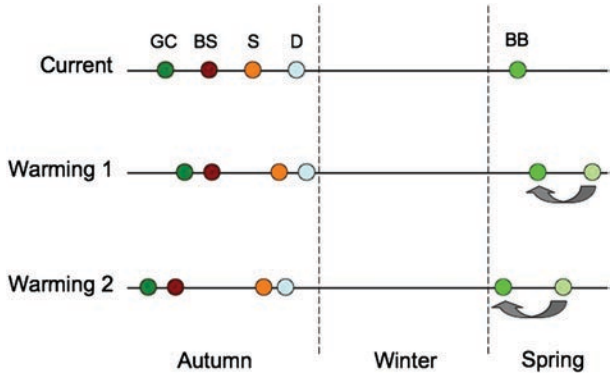

Figure 1. Potential changes in phenological events under current and elevated temperature climates. Growth cessation (GC), bud set (BS), senescence (S) and dormancy (D) must occur sequentially before winter; after chilling requirements are met in the winter, bud burst (BB) occurs in the spring (Current). In the Warming 1 scenario, elevated temperatures delay growth cessation (Rohde et al. 2011), reduce the time required for bud set, extend the duration of leaf senescence and hasten the onset of dormancy. Deeper winter dormancy and later dormancy onset delay bud burst in the spring compared with the Current scenario (pale green circle), but warmer spring temperatures encourage earlier bud burst (grey arrow), resulting in a slight delay in actual bud burst (bright green circle) compared with Current conditions. In the Warming 2 scenario, warmer temperatures accelerate growth cessation (Kalcsits et al. 2009), hasten bud set, slow senescence even more and greatly hasten dormancy development. Although the deeper winter dormancy induced in this scenario should also delay spring bud burst, warmer spring temperatures again encourage earlier bud burst, resulting in earlier than current bud burst in the tree. Many such scenarios can be arrived at by altering the time periods between phenological events, thus allowing large-scale signs of phenology shifts, such as leaf senescence and bud burst, to be delayed or hastened.

The effects of temperature need to be fully integrated into our models of how autumn phenology unfolds, particularly in those temperate and boreal trees where the early view of pure photoperiod control still predominates. But our current understanding of the molecular and physiological processes that trees use to sense and integrate environmental cues for growth cessation, bud set, senescence and dormancy is weak, despite the importance of these processes in determining the capacity of forests to extend their growing season in a warming climate (Olsen 2010). Some responses, such as accelerated bud development, may simply be direct effects of high temperatures on growth processes (Rohde et al. 2011). The importance of phytohormones in bud set and dormancy has been investigated for decades (e.g., Nitsch 1957, Lavender and Silim 1987), but their roles and those of other key physiological mechanisms (such as phytochrome-mediated signaling and the homologs of the *Arabidopsis* FLOWERING LOCUS T and CONSTANS genes) in determining the timing and rates of autumn phenology in trees are still not well understood (Howe et al. 1996, Bohlenius et al. 2006, Ruttink et al. 2007, Olsen 2010, Resman et al. 2010, Tanino et al. 2010). Greater insight into how these fine-scale mechanisms are affected by temperature and photoperiod may provide the key to explaining ecotypic and interspecific differences in how temperature affects phenology, and could improve our ability to predict how warming will alter both the length of the growing season and the carbon sequestration potential of mid- to high latitude forests.

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