Tree seasonality in a warming climate

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Climate warming has increased researchers' interest in plant phenology and its modelling. Although the main focus is on projections of accelerated springtime phenological events, also a further extension of the growing season by delayed growth cessation is often projected. However, ecophysiological studies indicate that, for boreal and temperate trees, such generalisations are precluded owing to differential climatic conditions and inter- and intraspecific genetic differences. The annual cycle of these trees is an integrated system, where one phase affects subsequent phases, resulting in delayed impacts, which are only partially addressed in current ecophysiological models. Here, we outline an updated integrated conceptual model of the annual cycle by identifying ecophysiological phenomena that are particularly significant under climate warming.

Neglected impacts of the annual cycle

Climate warming has increased the attention paid to plant phenology and the duration of the growing season [1–4]. Changes in the phenological patterns caused by climatic warming can have major implications for both the global carbon cycle [5] and the ecology of plants [6] and their herbivores [7]. The main research focus has been on the acceleration of springtime phenological events of plants (e.g. bud burst in boreal and temperate trees), which can be caused by climate warming [8–11]. Such acceleration will have considerable implications for both the risk of frost damage [12–15] and the photosynthetic production [5,16,17] of the trees, with the photosynthetic production also feeding back to the climate system [2]. Somewhat less attention has been paid to the effects of climate warming on the growth cessation and senescence of plants in autumn; mainly, a prolongation of the growing season is often projected [2,10,18].

However, as emphasised recently, because of genetic interactions with chilling temperatures and photoperiod, climate warming will not accelerate the bud burst and growth onset in all boreal and temperate tree species [3]. A recent transplantation study carried out with three European *Quercus* species suggested that, even when bud burst and growth onset are accelerated by climatic warming, the acceleration response can be nonlinear, so that the acceleration levels off with increased levels of warming [19]. Furthermore, a recent review reveals that warming causes acceleration, rather than a delay, of growth cessation in many tree species, ecotypes and cultivars [20]. The projections of the effects of climate warming are further complicated by intraspecific genetic variation in the environmental regulation of the annual cycle, which is related to the large geographical distribution areas of many boreal and temperate tree species [20,21]. Owing to these differences, not only the intensity, but also the direction of the response to warming can vary among ecotypes, so that warming accelerates the growth cessation in some and delays it in other ecotypes of a given species. To our knowledge, such differences among ecotypes have not been addressed in global change modelling.

It has been known for a long time that the annual cycle of growth and dormancy in boreal and temperate trees forms an integrated system, where one phase in the cycle affects the subsequent phases, so that environmental factors have several delayed impacts [22–28]. Many of these delayed impacts have been addressed in process-based ecophysiological simulation models [29,30] often used in scenario studies [6,13,14,31–33], but many remain unaddressed. Here, we outline an updated integrated conceptual model for the annual cycle of boreal and temperate trees by identifying phenomena of particular significance under climate warming.

Bud burst and growth onset

Cell division and growth in the buds are temperature dependent, so that the rate of development towards bud burst and growth onset increases with rising air temperatures [26,27]. This is the physiological basis of the common projection of accelerated springtime phenological events in plants, often deduced in computer simulations by the accumulation of day degrees or other types of temperature sum (Figure 1) [12–14,31–33].

Glossary

Chilling: exposure to low non-freezing temperatures required for rest break (see below) in both vegetative and reproductive buds.
Dormancy: general term indicating the opposite of growth; that is, a condition where no visible growth is observable in the bud.
Fixed growth habit: height growth pattern where growth consists entirely of the lengthening of the primordia formed in the bud during the previous growing season.
Free growth habit: height growth pattern where the lengthening of new primordia developed during the same growing season also contributes to height growth.
Process-based model: a simulation model where the development of a plant or an entire ecosystem is described by explicitly addressing physiological and biophysical phenomena.
Rest: special case of dormancy where growth is arrested by physiological conditions in the bud, so that the bud remains dormant regardless of the environmental conditions.
Rest break: removal of the growth-arresting physiological conditions in the bud, caused in most cases by the accumulation of chilling. After rest completion, the bud can remain dormant for several months if the air temperatures remain low.

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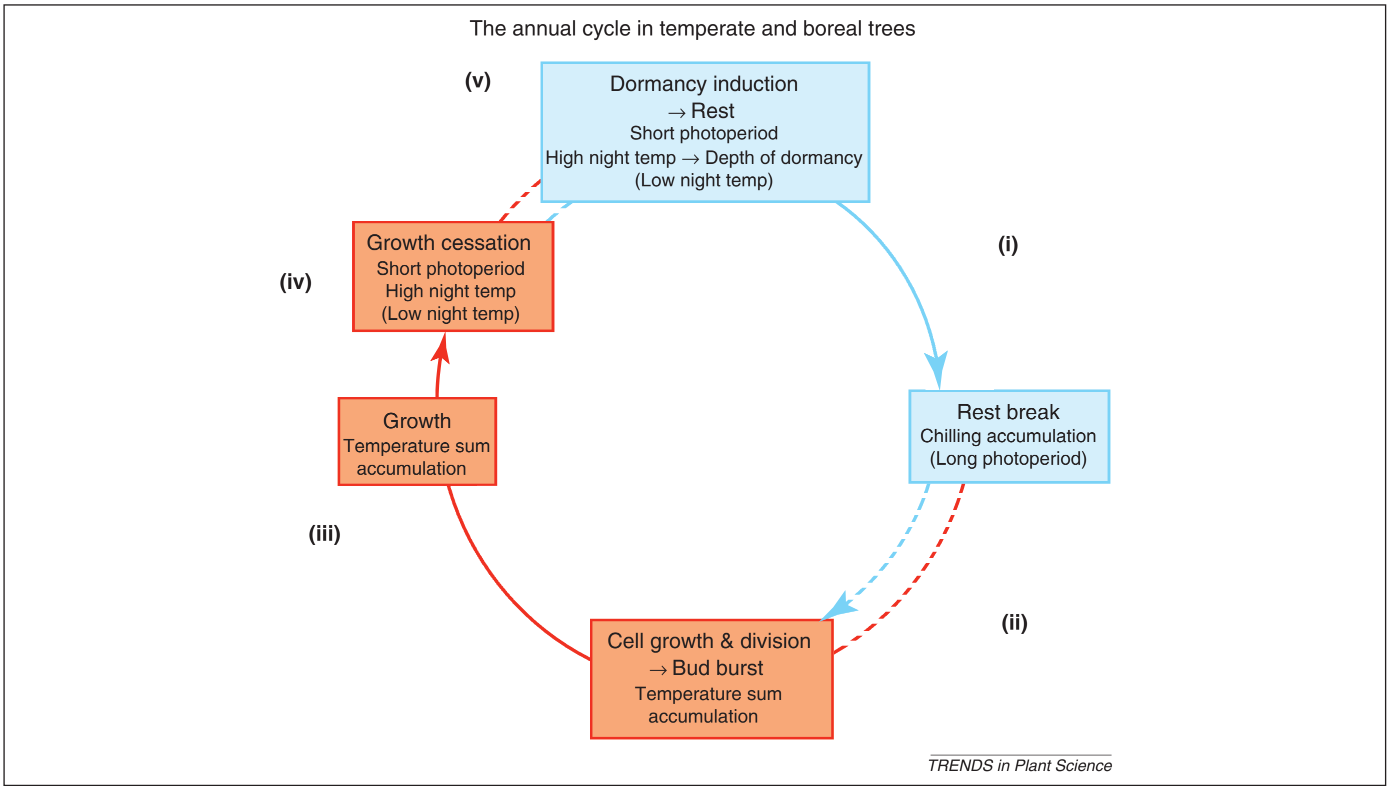

Figure 1. An integrated conceptual model of the annual cycle of growth and dormancy in boreal and temperate trees, identifying the ecophysiological phenomena that determine the timing of growth onset and cessation. In addition to their short-term effects, air temperature and photoperiod have several delayed impacts on the timing of these phenological events. As depicted by the arrows for the periods of growth (red) and dormancy (blue), the delayed impacts are, in many cases, carried over for several months in the annual cycle. The alternation between growth and dormancy occurs gradually (dashed arrows). **(i)** Long-term accumulation of chilling during late autumn and early winter causes rest break (i.e. removal of the growth-arresting physiological conditions in the bud). In some cases, long photoperiods also affect rest break. **(ii)** After rest completion, growth onset (e.g. bud burst) is brought on by the cumulative effects of high temperatures, as described by temperature-sum models. **(iii)** Temperature sum accumulation regulates height growth and, in tree species with a fixed growth habit, also its cessation. **(iv)** In most species with a free growth habit, a short photoperiod is an essential environmental cue inducing growth cessation. However, several interactions with air temperature have been found, so that growth cessation might even be affected by earlier temperatures (i.e. those occurring before and during growth phase). In some species and ecotypes, growth cessation is induced by low night temperatures independently of the photoperiod. **(v)** Dormancy is induced by short photoperiods. High night temperatures during the induction increase the depth of dormancy by increasing the chilling requirement of rest completion and/or the temperature sum requirement of growth onset in some species. By contrast, low night temperatures advance dormancy in northern ecotypes under long photoperiods and in certain fruit cultivars that are insensitive to the photoperiod.

However, this projection might be complicated in several ways by dormancy (see Glossary), a typical feature of the buds of boreal and temperate trees [26,27,34–36]. Rest break, (i.e. the removal of growth-arresting conditions in the buds) requires prolonged exposure to chilling temperatures, typically several weeks (Figure 1). Trees with a low chilling requirement burst buds and commence growth in spring at an earlier date than do those with a high chilling requirement, the latter having a greater depth of rest [37,38]. This delayed effect of chilling temperatures on the timing of bud burst is projected to cause different acceleration responses to warming in boreal trees, depending on the chilling requirement: in trees with a low chilling requirement, warming accelerates bud burst more than in trees with a high chilling requirement [13,39].

In a few cases, the dormancy phenomenon and the related chilling requirement are projected to cause differences among trees in the timing of bud burst in terms of not only the intensity, but also the direction of the response to warming. The chilling required for bud burst will be delayed and, in milder climates, also reduced by climate warming. As shown by process-based ecophysiological modelling [12], this delaying effect of elevated air temperatures in autumn and winter can be carried over to the spring (Figure 1). In mild and maritime climates, warming is thus projected to delay bud burst in some species, such as balsam poplar (*Populus trichocarpa*) and common hawthorn (*Crataegus monogyna*) [31]. Furthermore, process-based modelling has revealed that the lack of chilling caused by climate warming can cause abnormal bud burst in some temperate species [33]. This aspect has also been demonstrated experimentally under controlled conditions by using artificial rest breaks at different stages of dormancy [40].

Recently, a delay of growth onset as a result of warm winters was also found in native meadow and steppe vegetation in natural conditions in the Tibetan Plateau of western China, and the delay was attributed to insufficient chilling [41]. These pioneering satellite-based observations suggest that the delay of growth onset caused by climatic warming in winter is not restricted to woody plants. The satellite observations from the Tibetan Plateau [41] mark the importance of experimental studies addressing the dormancy phenomena in herbaceous plants.

There is increasing experimental evidence that elevated air temperatures during dormancy induction in late summer and early autumn increase the depth of dormancy, so that more chilling is required for rest break and/or more accumulation of temperature sum for bud burst (Figure 1) [20,42–47]; some of the studies have made comparisons and found distinct ecotype- or cultivar-dependent responses. Thus, besides the impact of reduced chilling being carried over from the previous autumn and winter, the impacts of elevated air temperatures, with potentially delayed bud burst in spring, could be carried over from an even earlier time (i.e. from the previous summer; Figure 1). These phenomena and the differential ecotype- or cultivar-dependent responses are not addressed in current process-based ecophysiological models ([29,30]; however, see [48]).

Half a century ago, an experimental study revealed complicated interactions and delayed effects in the annual cycle of native sugar maple (*Acer saccharum*) [22]. The author concluded that the differential depth of dormancy was associated with the previous growing season and, in particular, the photoperiod prevailing after bud burst. When plants were grown in a 20-h photoperiod, a second flush of growth was produced, as opposed to only one flush in a 9-h photoperiod. The plants grown in the 20-h photoperiod with two flushes of growth over spring and summer subsequently evinced a greater depth of dormancy in the following autumn and winter than did those grown in the 9-h photoperiod. Although 20-h and 9-h photoperiods are extreme treatments, these results suggest a potentially complicated case of delayed interactive effects of temperature and photoperiod, which can affect the seasonality of the trees under climate warming. Accordingly, if springtime bud burst is advanced or delayed for some reason, photoperiod can interact to induce differential spring and summer growth patterns, which will then influence the subsequent rest during the autumn and winter and finally affect the timing of bud burst the next spring. These effects are not addressed in current process-based ecophysiological models [29,30] and, for the sake of simplicity, they are similarly not addressed in the conceptual model of Figure 1.

It has also been suggested that additional rest break requirements based on prevailing light conditions, such as the requirement of a long photoperiod, prevent or slow down the accelerating effects of springtime warming on bud burst even when the chilling requirement is met (Figure 1) [3,48–51]. With the exception of a few species such as beech (*Fagus sylvatica*) [52], however, the role of photoperiod in regulating the timing of bud burst remains unclear [4,30].

Growth cessation

Since the discovery of photoperiodism during the early 20th century [53], autumn growth cessation in boreal and temperate trees has generally been explained in terms of the attainment of a critical short photoperiod [24,54–57]. This notion suggests that climate warming should cause no change in the timing of growth cessation. Experimental evidence accumulated over several decades, however, points at interactive effects of photoperiod and air temperature on growth cessation in both coniferous and deciduous broad-leaved trees. In most cases, elevated night temperatures have induced earlier growth cessation (Figure 1) [20,42,44–47,58–64]. In tree species with a fixed growth habit, such as Scots pine (*Pinus sylvestris*), height growth cessation is regulated solely by temperature sum accumulation [65]. Furthermore, in many boreal tree species, an accelerated growth onset is followed by an accelerated growth cessation [65,66], suggesting that the accelerating impact of greater temperature sum accumulation in spring is carried over to the autumn (Figure 1). Collectively, these findings suggest that, contrary to the projection of a prolonged growing season in autumn [2,10,18], climate warming can accelerate growth cessation in many boreal and temperate trees. This scenario might be further substantiated by the observation that daily minimum temperatures have been increasing more than have daily maximums during the past few decades [67]. If this trend continues, then night temperatures will generally increase more than day temperatures; it is the high night temperatures in particular that have been shown to be an essential interactive factor accelerating tree growth cessation (Figure 1, see above).

In some trees, however, low night temperatures induce growth cessation (Figure 1). In most of these cases, growth cessation occurs in combination with a long photoperiod. This group of trees appears to consist of northern ecotypes and species whose dormancy induction is insensitive to the photoperiod. It is exemplified by northern ecotypes of Norway spruce (*Picea abies*), pubescent birch (*Betula pubescens),* red osier dogwood (*Cornus sericea*), laurel willow (*Salix pentandra*), and several species of the Rosaceae family [20,60,62,68–73]. In these species and ecotypes, climate warming is projected to cause an extension of the growing season in the autumn through delayed growth cessation. Furthermore, according to a recent modelling study, low temperatures accelerate the autumn colouration in three European broad-leaved tree species after the colouration has been induced by a short photoperiod [74]; thus, climatic warming is also projected to delay the autumn phenology of the trees in this case.

Concluding remarks

Climate warming is likely to accelerate bud burst and growth onset in most, but not all, boreal and temperate trees. Growth cessation might be either accelerated or delayed by warming, depending on the species and even on the ecotype. The differences among tree species, ecotypes and cultivars in their phenological responses to warming can have crucial impacts on the structure and functioning of boreal and temperate forest ecosystems, thus contributing to an overall multitude of ecological responses to climate change. The differences will also have important implications for practical forestry and horticulture, such as the need to reassess the suitability of a given tree provenance or cultivar used earlier in forest regeneration or fruit production.

The take-home message of the integrated conceptual model is that one part of the annual cycle impacts subsequent parts and that individual seasonal responses should not be examined in isolation without taking into account the history of the plant. Thus, because of several delayed impacts of environmental factors, any projections of the effects of climate warming on the phenology of boreal and temperate trees need to consider the entire annual cycle. Current process-based ecophysiological simulation models of the annual cycle [29,30] provide a useful tool for generating quantitative projections for the trees [14,31–33] and for scaling up these projections to higher organisational levels, ranging from stands and ecosystems to entire biogeographical areas [75–78]. For reliable projections of phenological changes, however, further species-, ecotype- and even cultivar-specific experimental data are needed in order to develop these models further and to better understand the underlying ecophysiology summarised in Figure 1.

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