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Spring phenology, phenological response, and growing season length

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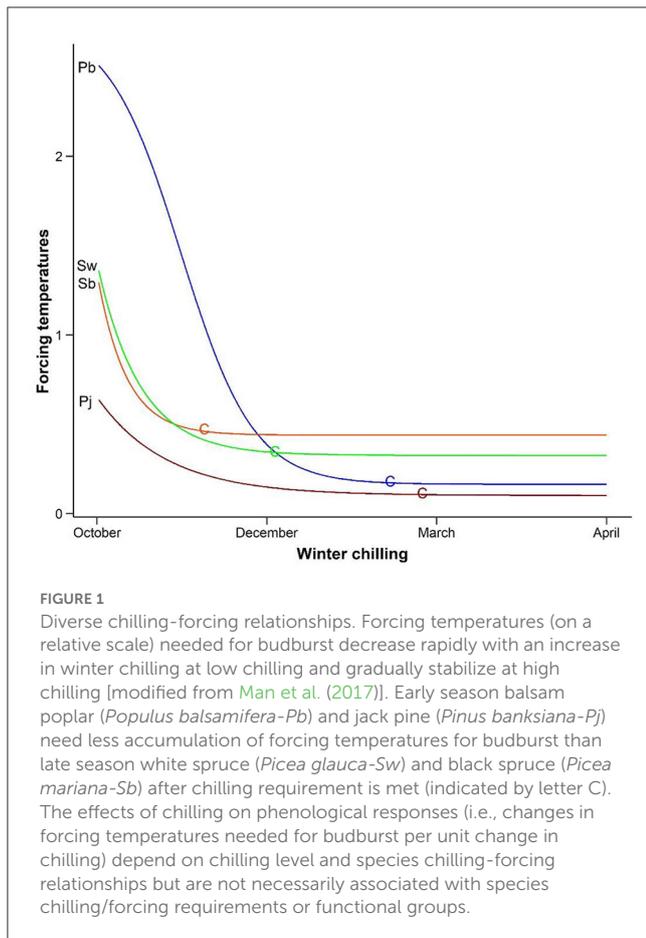
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Differential phenological responses

Plant phenology is shifting as a result of global warming (IPCC, 2019). General trends include advanced spring phenology (i.e., earlier budburst and leaf-out) and delayed leaf senescence, leading to an extended leaf-on period and possibly increased growth (Peñuelas et al., 2009; IPCC, 2019; Piao et al., 2019). However, responses vary among species, e.g., those with early spring phenology—referred to here as early season species—often show more pronounced advances in spring phenology (Abu-Asab et al., 2001; Beaubien and Hamann, 2011; Shen et al., 2014) than so called late season species. As global warming progresses, these among-species differences in leaf-on time or green-cover season may increase (Morin et al., 2009; Montgomery et al., 2020), leading to an expectation of possible changes in ecosystem structure and function (Polgar et al., 2014; Primack and Gallinat, 2016).

The annual development of plants in boreal and temperate regions is driven by the seasonal cycle of climatic conditions, although species-specific information about these changes is often lacking. Bud set, leaf senescence, and dormancy are induced by shorter daylength and lower temperatures in fall, while spring phenology is controlled primarily by temperatures, i.e., low chilling temperatures in fall and winter for dormancy release and high forcing temperatures for spring growth initiation (Chuine et al., 2016; Piao et al., 2019). As species chilling needs can be fulfilled long before spring arrives (see Figure 1), spring phenology is often not influenced by changes in cumulative winter chilling induced by global warming (Fu et al., 2015; Asse et al., 2018; Piao et al., 2019; Chu et al., 2021). Comparatively, early season species that need less accumulation of forcing temperatures (cumulative growing degree days or hours) to initiate spring growth are often more responsive or sensitive to rising temperatures (Abu-Asab et al., 2001; Beaubien and Hamann, 2011; Shen et al., 2014) than late season species. An early spring start is thought to help plants access resources and gain growth and competitive advantages (Polgar et al., 2014; Primack and Gallinat, 2016; Zettlemoyer et al., 2019; Montgomery et al., 2020). As early successional, exotic, and invasive species generally start growing early in spring, they are expected to benefit more from projected warming, resulting in proliferation of these species and therefore undesirable changes in ecosystems (Polgar et al., 2014; Zettlemoyer et al., 2019).

However, a recent study by Chu et al. (2021) suggests that this theory is not supported by plant thermal balance in spring. Shifts in spring phenology driven by global warming are associated with changes in both timing of spring growth and forcing temperatures, with the latter more indicative of plant development and growth (Chuine et al., 2016; Man et al., 2017; Piao et al., 2019). Due to cumulative effects of spring temperatures, early season species



gain fewer forcing temperatures from warming before growth initiation and more forcing temperatures after growth initiation than late season species. If warming-induced changes in forcing temperatures before and after growth initiation are both included, all plant species would equally benefit from warming in terms of total changes in forcing temperatures (Chu et al., 2021).

Factors influencing among-species differences

As shown by Chu et al. (2021), the more pronounced responses to global warming by early season species result largely from low temperatures in early and cold spring when these species leaf out, rather than their ability to track temperature changes. Although early season species resume growth early in spring and gain fewer forcing temperatures from their phenological shifts, at low temperatures they often need more time (or larger phenological advances) to accumulate forcing temperatures gained from warming. Therefore, leaf-out temperatures or spring phenology can strongly influence plant phenological responses to global warming. The effects of spring temperatures on phenological responses have occasionally been recognized (Shen et al., 2014), but never clearly elucidated. Depending on differences in the timing of spring growth and therefore leaf-out temperatures, early season

species could also have similar or smaller phenological changes than late season species in response to global warming (Chu et al., 2021).

When winter chilling is insufficient, changes in cumulative winter chilling by global warming can accelerate or delay phenological responses from what would be expected solely from changes in forcing temperatures (Chu et al., 2021). Besides different chilling and forcing needs and chilling–forcing relationships (see Figure 1) (Chuine et al., 2016; Man et al., 2017; Piao et al., 2019), plants may also differ in temperature use efficiency through different threshold temperatures for chilling and forcing accumulations, leading to diverse phenological responses to global warming (Zhang et al., 2018). The lack of sufficient winter chilling can be offset by more spring forcing without affecting spring growth (Chuine et al., 2016; Man et al., 2017). Relative to spring forcing, the accumulation of winter chilling is more complex and experimentally studied on few species (Chuine et al., 2016; Man et al., 2017). Spring phenology can be also adversely affected by freezing temperatures (Man et al., 2021) or moisture stress that may progressively develop and differentially affect species with differing spring phenology (Zettlemoyer et al., 2019). Interest in the influence of photoperiod on spring phenology is increasing (Körner and Basler, 2010). However, critical photoperiods have not been found, other than weak and variable compensation of insufficient chilling effects by longer photoperiod (Körner and Basler, 2010; Way and Montgomery, 2015; Zohner et al., 2016). The photoperiod effects reported in the literature are often concluded from growth timing differences, with differences in forcing temperatures ignored (Chu et al., 2021). In photoperiod experiments, longer photoperiods are often associated with more hours of daytime high temperatures (Chu et al., 2021), in addition to extra heating effects from artificial light sources (Mellor et al., 1964).

The common explanation that early season species need less chilling for dormancy release and are therefore less restricted by chilling deficiency induced by global warming (Morin et al., 2009; Polgar et al., 2014; Primack and Gallinat, 2016) seems true in some cases (Beaubien and Hamann, 2011). It may not apply in cases where reduced or delayed phenological responses occur in species of all spring phenology (Abu-Asab et al., 2001; Fitter and Fitter, 2002). In boreal tree species, black spruce and white spruce (*Picea mariana* and *Picea glauca*) are late flushing/late successional conifers but need substantially less chilling than some early flushing/early successional conifer or broadleaf tree species (Man et al., 2017; see also Figure 1). Similarly, in temperate forests of eastern Canada, early season tree species generally have more chilling needs than late season species (Man et al., 2020). High chilling needs are more ecologically meaningful to early season species than to late season species in minimizing risks of frost damage (Morin et al., 2009; Tao et al., 2021).

Growing season length

Regardless the causes of differential phenological responses among species, the use of phenological responses as an indication of changes in growing season length or growth potential is

misconceived and biased. First, the influence of daily temperatures on spring development increases during spring temperature recovery. Early season species could have longer leaf-on time from their phenological shifts but gain fewer forcing temperatures due to low leaf-out temperatures. The use of phenological responses to represent changes in growing season length (or growth potential) contradicts the convention that growing season is defined by temperatures for certain climatic conditions (Christiansen et al., 2011), not by leaf-on time for individual species. Second, in northern climate where spring development depends largely on temperatures, phenological models are generally based on the accumulation, rather than duration, of forcing temperatures (Chuine et al., 2016; Man et al., 2017; Piao et al., 2019). Forcing temperatures, a good predictor of plant development and growth, are used to estimate timing of spring growth, a poor predictor of plant development and growth; the latter is commonly used in discussing ecological implications of plant phenological changes, probably because it is comparable among different climatic conditions and connected to growing season length. Thus, changes in spring phenology do not necessarily represent changes in growing season length and alone would not be sufficient for understanding the ecological implications of plant phenological responses to global warming (Chu et al., 2021).

Conclusion

Temperatures at time of spring growth strongly influence plant phenological responses, with low temperatures associated with large responses and high temperatures with small responses (Prevéy et al., 2017; Chu et al., 2021; Wolkovich et al., 2021). Early season species start to grow at low spring temperatures and are often more advanced in spring phenology in response to warming. In the northern hemisphere, plant development and growth in spring is primarily restricted by low temperatures, rather than availability of light or soil moisture. Total changes in forcing temperatures from global warming do not differ among species with differing spring phenology (Chu et al., 2021). The use of phenological responses to represent changes in growing season length would include more early spring cold days and overestimate the potential benefits that may result from warming for early season species. Contrary to the suggestions by many

(Fitter and Fitter, 2002; Polgar et al., 2014; Shen et al., 2014; Primack and Gallinat, 2016; Zettlemoyer et al., 2019; Montgomery et al., 2020), early start in spring is not necessarily beneficial, particularly if frost risk increases with the advance of spring phenology into early spring and late winter (Morin et al., 2009; Man et al., 2013; Ma et al., 2019; Tao et al., 2021). Ecologists have been interested in sensitivity of spring phenology to changes in temperatures and comparison of among-species differences in phenological responses to global warming. These differences, however, are not as ecologically meaningful as is often suggested in understanding global change effects on ecosystem structure and function.

Author contributions

RM and Q-LD generated the ideas. XC, RM, and Q-LD contributed to the writing of the paper. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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