

# Solstice optimizes thermal growing season

Victor Van der Meersch<sup>1</sup>, E. M. Wolkovich<sup>1</sup>

<sup>1</sup> Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall Vancouver, BC, Canada, V6T 1Z4.

---

**Abstract:** Recent research suggests that the summer solstice is an universal trigger for major plant physiological processes. While this would have strong implications for predicting forest and carbon cycle dynamics under climate change, the underlying mechanisms that could explain the emergence and importance of solstice as a cue still remain unclear. Here, we show that the solstice, on average, appears as a critical juncture for plants to optimally benefit from their growing season—yet, this subcontinental trend masks significant local variations and diverse trade-offs across different climates.

---

Plants use environmental cues to adjust the timing of major growth and reproductive events in response to variability within and between years. While we often know the proximate triggers—such as temperature and photoperiod—the fitness landscape shaping selection on these cues remain largely unknown for many events (Chuine and Régnière, 2017), leaving a critical gap in our understanding of how plants will respond and adapt to future climates.

Recently, summer solstice has been proposed as a universal trigger to modulate cues and initiate key physiological processes (Zohner et al., 2023; Journé et al., 2024)—an idea that builds on earlier suggestions of solstice-driven control of tree growth (Rossi et al., 2006). Plants may rely on the solstice as a signal to initiate the shift from growth to tissue maturation before winter and to prepare for reproduction in the following year through flower bud differentiation (Rossi et al., 2006; Zohner et al., 2023; Journé et al., 2024). This hypothesis suggests a fundamental new mechanism for how plants sense photoperiod (Gendron and Staiger, 2023), but recent results highlight that plants likely have multiple pathways to sense daylength (Wang et al., 2024)

This proposed photoperiod switch, if correct, could reshape predictions of forest responses to climate change. Using a fixed date like the solstice as a cue, however, could limit plasticity in how plants respond across their ranges, which span very different climates. Leaf unfolding, for example, can occur as late as early June in some parts of Europe where solstice has been proposed as a trigger (Zhang et al., 2022). In such regions, solstice seems a very early point in the full growing season (which can extend until late October; Liu et al., 2020) to shift growth investments for the year. Further, how stable solstice would be as a useful transition in a warmer future climate is unknown (Bonamour et al., 2019). Fixed cues with warming could drive forest declines, with significant implications for carbon storage (Green and Keenan, 2022)—raising important questions about the suitability for plants to rely on the solstice.

The timing of major plant transitions—such as the start of growth with leafout—should match development states with fitness opportunities, given no other constraints. In most environments, this involves a trade-off between increased opportunity for growth and reproduction (e.g. a longer window for growth) and increased susceptibility to climatic and biotic risks (e.g. a higher exposition to late frosts). Because plants cannot know the exact landscape of these

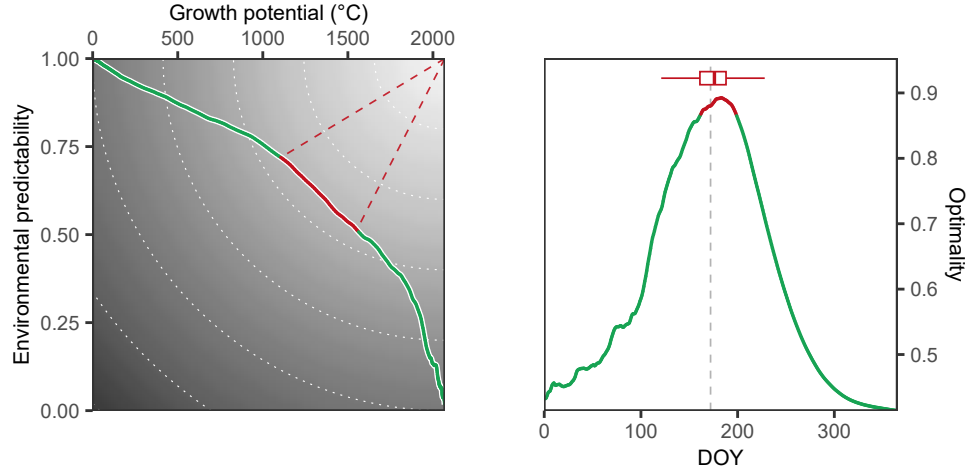
opportunities and risks in advance, they should rely on the most informative cues to accurately anticipate environmental conditions and optimize their chances for growth and reproduction (Chevin and Lande, 2015; Bonamour et al., 2019).

In particular, decades of research has established that plants respond to the accumulation of warm temperatures. These are often measured as ‘growing degree days’ (GDD), which aim to capture the temperature range (over a given period) that is sufficient for plant metabolism (Chuine and Régnière, 2017). This heat accumulation is a key factor in development and growth processes of both crops (e.g. Cross and Zuber, 1972) and wild plants (e.g. Hunter and Lechowicz, 1992). The number of GDD accumulated throughout the season directly impacts how quickly cells elongate to form new organs and how quickly a plant progresses through growth stages. Selection should drive plants to take full advantage of warmer years (with a high GDD accumulation) to maximize growth and set more flowers for the following season (Larcher, 1980), while also minimizing their risks of investing in growth and reproduction so late in the season that they lose tissue to frost or fail to ripen fruit.

Given the importance of GDD, plants should ideally time their transitions when their ability to predict the total GDD within the growing season is high while still having enough potential thermal energy to complete essential growth and reproductive processes. This trade-off means that there should be an optimal period when plants have accumulated enough GDD to reliably predict the total GDD by the end of the year—*environmental predictability*, while enough GDD still remains—which we call *growth potential*. Here, we define environmental predictability based on how well GDD accumulated by a day ( $d$ ) predicts the total GDD each year (measured as the  $R^2$  of a linear regression across years using 1 January to start accumulation). This measure directly relates to how plants accumulate information and gain predictive power through the season. In contrast, growth potential, which we define as the remaining GDD on day  $d$  (see Supplementary Methods and Supplementary Figure S1), aims to capture that plants must allow for enough remaining biological time before the end of the GDD season to complete key physiological processes (Zohner et al., 2023; Journé et al., 2024). This simple trade-off allows us to examine which window in the season appears optimal for plants to maximize growth and development while minimizing risks. This allows us to test if environmental predictability relative to remaining GDD is optimal at solstice, or if variability in GDD accumulation over the season pushes the optimal timing of transitions sooner or later in the year.

Using this trade-off framework, we found the optimal period to be near the summer solstice (Figure 1). Averaging across all of Europe, solstice appears as a critical juncture for the optimization of both environmental predictability and remaining growth potential. If this specific day indeed represents a broad-scale optimum across different climatic conditions, evolution towards a universal solstice trigger could make sense—especially since this optimum appears stable over the Holocene (Supplementary Figure S3).

Our results suggest solstice could act as a reliable marker but also highlight the challenges in disentangling the influence of the solstice from that of a thermal optimum cue. Given our metrics are based only a thermal season—i.e. we do not explicitly incorporate a photoperiod driver—our results suggest the existence of an understudied thermal cue that could give the same outcome. Plants could also rely on a combination of both solstice and thermal cues to optimize growth and reproductive timing—which would likely provide greater signal robustness to environmental change through partial redundancy between cues (Bonamour et al., 2019). Alternatively, this overlap could simply represent an emergent property of the climate system that plants do not necessarily use as a cue, since it would be costly for plants to closely track two different signals—i.e. to encode and decode both thermal and photoperiod information within their cells. In this case, solstice may merely represent a climatic reality that summer temperatures are relatively stable year-to-year over July and August, and thus average GDD

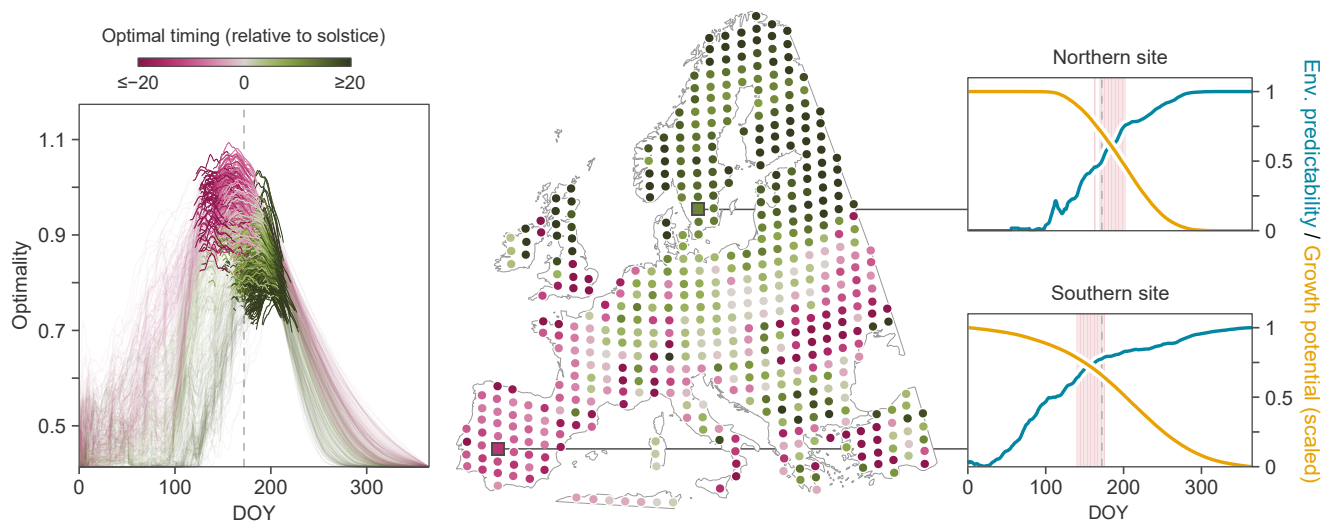


**Figure 1: Solstice marks the average optimal trade-off between environmental predictability and growth potential across Europe (1951-2020).** In the left panel, environmental predictability measures how well GDD by a given day predicts total yearly GDD ( $R^2$  of a linear regression across years), while growth potential represents the remaining GDD from that day onward. In the right panel, optimality is based on the Euclidean distance from the (unattainable) perfect point where both predictability and growth potential are maximized (illustrated by the red dashed lines and the gray gradient in the left panel). The red sections of the green curves represent days where optimality falls within the 90th percentile (i.e. top 10% most optimal days). GDD range was defined between 5°C and 35°C (see Figure S2 for 0-40°C).

predictability peaks in late June.

Supporting the hypothesis that solstice may not be a reliable cue, our results reveal substantial variation in the optimal timing when examined across Europe (Figure 2), as opposed to averaging over space (Figure 1). In warmer southern Europe, plants reach an optimum earlier in the season, whereas in northern regions, cooler temperatures delay this timing beyond the solstice. This regional variability suggests that plants should likely rely on cues that allow for a more plastic response in their specific environment than solstice would yield. From a parsimonious perspective, tracking primarily GDD-related cue might be more straightforward and aligned with the actual energy a plant needs to grow and reproduce—i.e. the cue would be sampled from a variable directly used by the plant. Whereas tracking the solstice is likely more complex. Indeed, plants would need to sense not just the photoperiod but also the variation in the rate of change of photoperiod over time—essentially, the second derivative.

Taken together, our results suggest solstice could be an optimal signal for plants to transition key physiological processes when averaged across space, and appears remarkably stable over past and potential future climates (Supplementary Figures S3 and S4), but is unstable at the local site-level (Figure 2, Supplementary Figure S5). Because selection operates on individuals, this disconnect between the local and continental scales makes it difficult to understand how solstice would evolve as a trigger, and suggests its importance in correlative analyses (such as ours, Zohner et al., 2023 and Journé et al., 2024) may appear due to natural correlations in environmental data that do not shape plant responses (e.g. Gao et al., 2024). Alternatively, our results could suggest an understudied role of solstice in how plants sense photoperiod with potentially deep evolutionary origins (Morales-Castilla et al., 2024). Disentangling these two hypotheses will require new experiments that decouple natural covariation between temperature and photoperiod (Buonaiuto et al., 2023; Elmendorf and Ettinger, 2020) to identify the cues plants use and more efforts to understand the fitness landscape of the growing season across space and time (Park and Post, 2022).



**Figure 2: Average optimal timing (Figure 1) hides variation in optimal timing across the different climatic conditions of Europe (1951-2020).** On the left panel, each curve shows the optimality for a given site. Sites are sampled on a regular grid across Europe, as shown on the central map. Colors indicate the timing—relative to the solstice—of the median optimal day. The two panels on the right show the trade-off between environmental predictability and growth potential (scaled to  $[0, 1]$ ) for two different sites. Days considered as optimal are highlighted in red.

## References

- Bonamour, S., L.-M. Chevin, A. Charmantier, and C. Teplitsky. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374:20180178.
- Buonaiuto, D. M., M. J. Donahue, and E. M. Wolkovich. 2023. Experimental designs for testing the interactive effects of temperature and light in ecology: The problem of periodicity. *Functional Ecology* 37:1747–1756.
- Chevin, L.-M., and R. Lande. 2015. Evolution of environmental cues for phenotypic plasticity. *Evolution* 69:2767–2775.
- Chuine, I., and J. Régnière. 2017. Process-Based Models of Phenology for Plants and Animals. *Annual Review of Ecology, Evolution, and Systematics* 48:159–182.
- Cross, H. Z., and M. S. Zuber. 1972. Prediction of Flowering Dates in Maize Based on Different Methods of Estimating Thermal Units. *Agronomy Journal* 64:351–355.
- Elmendorf, S. C., and A. K. Ettinger. 2020. Is photoperiod a dominant driver of secondary growth resumption? *Proceedings of the National Academy of Sciences* 117:32861–32864.
- Gao, X., A. D. Richardson, M. A. Friedl, M. Moon, and J. M. Gray. 2024. Thermal forcing versus chilling? misspecification of temperature controls in spring phenology models. *Global Ecology and Biogeography* 33.
- Gendron, J. M., and D. Staiger. 2023. New Horizons in Plant Photoperiodism. *Annual Review of Plant Biology* 74:481–509.
- Green, J. K., and T. F. Keenan. 2022. The limits of forest carbon sequestration. *Science* 376:692–693.
- Hunter, A. F., and M. J. Lechowicz. 1992. Predicting the timing of budburst in temperate trees. *The Journal of Applied Ecology* 29:597.
- Journé, V., J. Szymkowiak, J. Foest, A. Hacket-Pain, D. Kelly, and M. Bogdziewicz. 2024. Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants* 10:367–373.
- Larcher, W. 1980. *Plant Physiological Ecology*. Springer-Verlag.
- Liu, Q., S. Piao, M. Campioli, M. Gao, Y. H. Fu, K. Wang, Y. He, X. Li, and I. A. Janssens. 2020. Modeling leaf senescence of deciduous tree species in Europe. *Global Change Biology* 26:4104–4118.
- Morales-Castilla, I., T. Davies, G. Legault, D. Buonaiuto, C. J. Chamberlain, A. K. Ettinger, M. Garner, F. A. Jones, D. Loughnan, W. D. Pearse, et al. 2024. Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate Change* pages 1–7.
- Park, J. S., and E. Post. 2022. Seasonal timing on a cyclical earth: Towards a theoretical framework for the evolution of phenology. *PLOS Biology* 20:e3001952.
- Rossi, S., A. Deslauriers, T. Anfodillo, H. Morin, A. Saracino, R. Motta, and M. Borghetti. 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytologist* 170:301–310.

- Wang, Q., W. Liu, C. C. Leung, D. A. Tarté, and J. M. Gendron. 2024. Plants distinguish different photoperiods to independently control seasonal flowering and growth. *Science* 383:eadg9196.
- Zhang, H., I. Chuine, P. Regnier, P. Ciais, and W. Yuan. 2022. Deciphering the multiple effects of climate warming on the temporal shift of leaf unfolding. *Nature Climate Change* 12:193–199.
- Zohner, C. M., L. Mirzaghali, S. S. Renner, L. Mo, D. Rebindaine, R. Bucher, D. Palouš, Y. Vitasse, Y. H. Fu, B. D. Stocker, and T. W. Crowther. 2023. Effect of climate warming on the timing of autumn leaf senescence reverses after the summer solstice. *Science* 381:eadf5098.