

Solstice optimizes thermal growing season

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Plants generally 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 larger mechanisms behind 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 proposed photoperiod switch, if correct, could reshape predictions of forest responses to climate change. It would also suggest a fundamental new mechanism for how plants sense photoperiod (Gendron and Staiger, 2023). Using a fixed date like the solstice as a cue, however, could limit plasticity and become less suitable in a warmer future climate (Bonamour et al., 2019). This may in turn drive forest declines, with significant implications for carbon storage (Green and Keenan, 2022), and thus raises important questions about the suitability for plants to rely on the solstice.

The timing of major plant transitions—such as 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 these exact 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, it is well established that plants respond primarily to integrated climate forcing, often measured as the accumulation of warm temperatures, in a given range—where metabolism is sufficient—and over a given period (growing degree-days or GDD; 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. Plants are thus expected 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).

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. Growth potential, on the other hand, is defined as the remaining GDD on day d (see Supplementary Methods and Supplementary Figure S1). 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. Plants are likely adapted to maximize growth during warmer years and to prepare for winter earlier in colder years. The earlier most of the variability in GDD accumulation occurs within the season, the earlier the optimal timing for transitions should be.

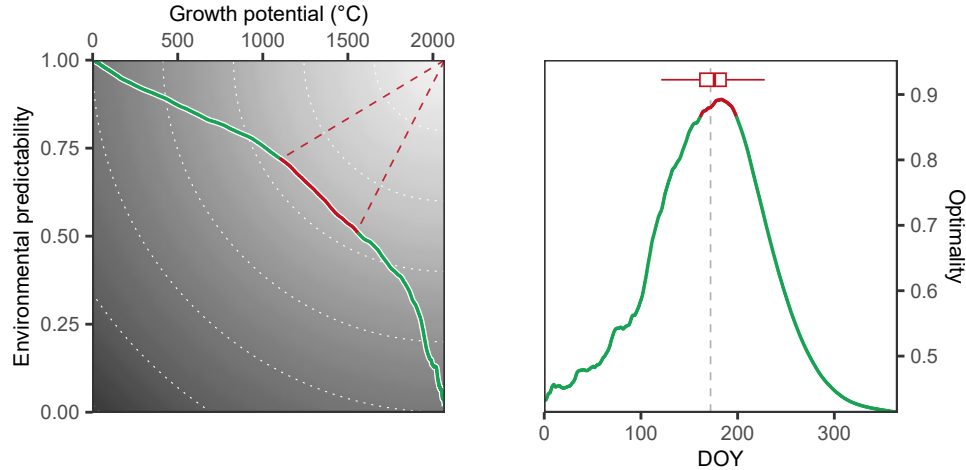


Figure 1: Solstice marks the average optimal trade-off between environmental predictability and growth potential across Europe (1951-2020). In the left panel, environmental predictability measures how well GDD by a given day predicts total yearly GDD (R^2 of a linear regression across years), while growth 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).

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 growth potential. If this specific day indeed represents a broad-scale optimum across different climatic conditions, plant 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 that it is challenging to disentangle 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 as well rely on a combination of both solstice and thermal cues to optimize growth and reproductive timing—which could 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 don’t 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.

Supporting the hypothesis of an alternative cue to the solstice, our results reveal substantial variation in the optimal timing across Europe (Figure 2). 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 plastic response in their specific environment. Leaf unfolding can occur as late as early June in some parts of Europe (Zhang et al., 2022), making solstice a potentially very early point in the full growing season (which can extend until late October in these regions; Liu et al., 2020) to shift growth investments for the year. 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.

Disentangling the role of the solstice as a cue for major growth and reproductive transitions is challenging, as plants have already started accumulating GDD several months before the solstice. Complex natural correlations in environmental data may generate spurious results (e.g. Gao et al., 2024), challenging us to test predictions from multiple avenues. Future research should explore which thermal cues might allow plants to track the optimal period, how these compare to a solstice-based cue, and whether they remain reliable in future climates (Supplementary Figures S4 and S5). To address this requires carefully designed experiments that decouple natural covariation between temperature and photoperiod (Buonaiuto et al., 2023; Elmendorf and Ettinger, 2020) and integrate new understanding of the multiple ways plants sense photoperiod (Wang et al., 2024). Beyond small-scale experiments, understanding local-scale trends and how they scale up to subcontinental scales could help inform what trends plants may leverage to predict their environments over time. Ultimately, a better understanding of how plant responses to photoperiod and temperature vary regionally will help clarify broader biological patterns.

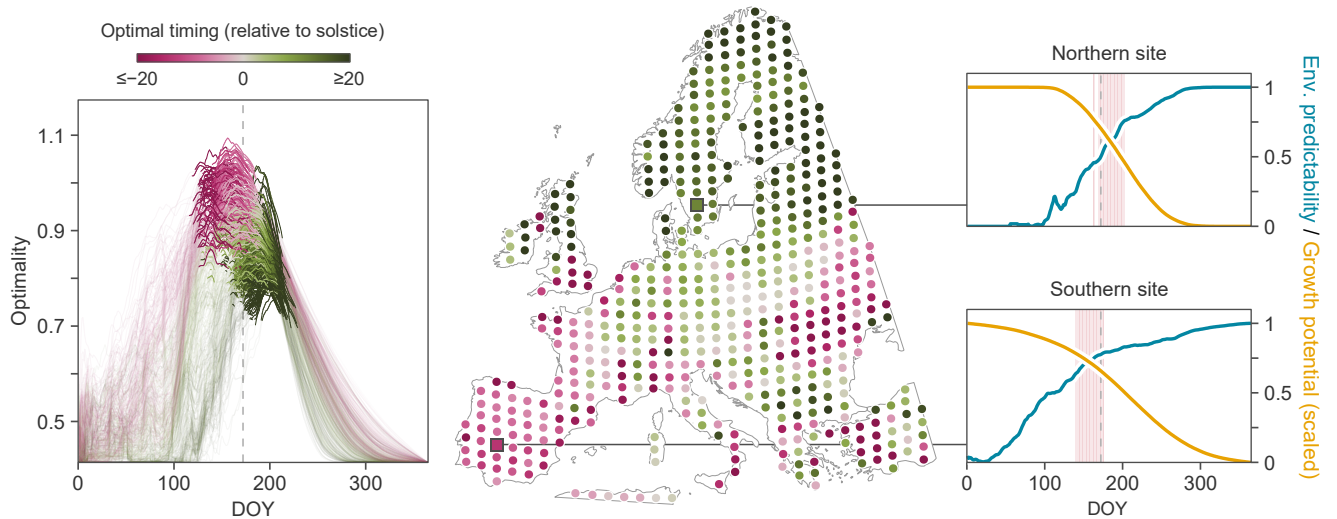


Figure 2: Variation in optimal timing reflects different climatic conditions across Europe (1951-2020). On the left panel, each curve shows the optimality for a given site. Sites are sampled on a regular grid across Europe, as shown on the central map. Colors indicate the timing—relative to the solstice—of 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.

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