

Early leafout leads to cooler growing seasons in woody species

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Abstract

Recent results have challenged the assumption that longer growing seasons increase plant growth, but struggled to explain how. Using rarely available plant-level phenology from a common garden of 18 woody species, we found earlier leafout led to earlier growth cessation (budset) and lower thermal growing seasons, especially for early-leafing species. These results challenge our fundamental understanding of controls on budset and suggest why apparently longer seasons do not increase growth.

Terrestrial forests are a major mitigation pathway for climate change, sequestering 20% of greenhouse gas emissions (1). Most models of climate change assume warming will drive longer seasons, more tree growth and, thus, more carbon storage (Fig: 1a), following decades of evidence from ecosystem-scale studies (2; 3). However, recent findings from observations of individual trees have questioned this assumption (4; 5). At the same time new experiments on saplings have suggested that plants may adjust their end of season timing dynamically such that longer seasons do not increase total productivity (Fig: 1b), though the mechanism—and prevalence—of this effect is unclear (6; 7; 8),

These results suggest fundamental gaps in our understanding of how early-season events and the environment of the growing season shape end-of-season events, but addressing these gaps requires working across plant strategies and varying definitions of a growing season. Because the timing of leafout and senescence are critical to plant growth strategies they vary strongly across species (9). Within species, populations also vary (10), especially because end-of-season events are usually locally adapted (e.g. budset 11; 12). Increasing evidence also suggests local climate may define narrow periods of growth for many species, with most significant growth earlier in the growing season (13; 8). These results suggest the calendar growing season (i.e., the number of days between the start and end of the growing season) may be less informative to predicting growth than estimates that directly incorporate environmental conditions (14).

The thermal growing season—a period of favorable meteorological conditions for plant growth (14)—offers an alternative to the calendar growing season. It is also widely used, most commonly in the metric of growing degree days, a temperature derived measure of time that accumulates when temperatures are above a certain minimal threshold (15; 16; 17). Because plant photosynthetic rates increase with temperature (18) the thermal growing season is mechanistically related to primary productivity, and thus may be a better proxy than calendar time for relating growing season length to carbon gain. Yet we generally lack plant-level phenological data for the start and end of season to examine how the calendar and thermal seasons of species and populations compare across years.

Here, we use rarely available plant-level data from three years of a multi-species, multi-population common garden to test how variation in start and end of season events drive shifts in calendar and thermal growing seasons. Our results leverage phenological observations of leafout and growth cessation

(budset) at the individual tree-level to understand how growing seasons scale across populations, species and communities, and may thus improve our understanding of ecosystem measures to improve forecasting.

Across three years and 13 co-occurring species (Tab: 2) collected from four populations across a 4.5 latitudinal gradient (Fig:S1), our common garden (located in Boston, Massachusetts) captured high variation in the timing of both start (leafout) and end of season (budset) events (Figure 2a,b). Resulting calendar and thermal growing seasons varied almost two-fold across individual trees (2.1x and 1.8x respectively), with earlier leafout leading to longer calendar growing seasons (Fig: 1c,d), as routinely seen with anthropogenic climate change (19; 20).

Longer calendar growing seasons did not lead to higher thermal growing seasons, as generally assumed; instead early calendar growing seasons led to lower (cooler) thermal growing seasons (Fig: 1c,d, this and other results were similar when we determined the length the growing season length with leaf coloration instead of budset, Figure S4). This result was driven by an apparent relationship between leafout and budset at the individual level combined with differences in thermal conditions of the early season during leafout and later in the season during budset. When plants leafed out earlier in the spring they stopped growth (budset) earlier, but the additional days of growth in the spring—when temperatures were cool—were rarely offset thermally by the days lost in the later season to earlier budset, which occurred in warmer months (July-August, Figure 2c).

Differences between thermal and calendar growing seasons were strongest in the earlier-leafout species, which leaf out during the coolest part of the spring (Fig: 1-2). For later leafing species, earlier leafout did not substantially reduce their thermal growing season, likely because their earlier leafout still occurred in thermally favorable times of the season. Species was also the a major predictor of variation in leafout, budset and growing season length ($\sigma_{species}$ days for leafout: : 8.12UI₉₀[5.54,11.56], days for budset: 9.73 UI₉₀[6.99,13.57], days for season length: 14.45, UI₉₀[10.34,19.9]).

These results suggest that some of the apparently conflicting recent findings of whether longer seasons increase growth or productivity may be due to different scales of observation, including the different species they integrate over. Our result that individual trees appear to accelerate their end of season events with earlier start of season events supports other studies conducted on a small number of species (though using alternative metrics of senescence, 21; 6). Thus, we may expect that studies of individual

trees could find little relationship between earlier leafout and growth (22; 23; 6), which could be driven by currently unstudied shifts in the thermal seasons. Additionally, because differences between thermal and calendar growing seasons were species-dependent, previous findings may depend on the species studied, consistent with other work comparing across smaller sets of species (22; 23). This variation also likely scales up to affect ecosystem-level estimates which generally have one measure of the start of season—for the earliest leafout species—and one for the end of season, likely capturing the later-leafout species.

Beyond species-level variation, we found high variation across years in both leafout and budset. We expected large differences across years in leafout (σ_{year} : 10.65 days UI_{90} [4.88, 20.86], Fig: 2b), because it varies strongly with local climatic conditions—one of the reasons it is the most consistent biological indicator of anthropogenic climate change (24). In line with this, we also found little variation across populations in leafout ($\sigma_{population}$: 0.57, UI_{95} [0.04, 1.77], Fig: 2a). Yet our finding of up to 15 days of variation across years in budset was surprising (σ_{year} : 15.02 days, UI_{90} [6.44, 30.84], Fig: 2b) because budset is generally thought to be strongly locally adapted and controlled by photoperiod, which does not vary year to year (12; 10). We did find evidence of local adaptation ($\sigma_{population}$: 2.34 days, UI_{90} [0.4, 6.13], Fig 2a), with populations from the site with the fewest frost free days (FFD, Figure S3) setting buds approximately two days before the site with next fewest FFD. These differences, however, were weak (Figure 2a) and 6X and 4X smaller than the variation due to year and species (respectively).

The shift in budset with earlier leafout suggests a potential pathway to better understand and predict recent findings, given additional research. While most work on budset has stressed the role of photoperiod (12), other studies have found evidence of temperature control (25; 26). Our results suggest an additional potential role of leafout timing, which could be confounded with temperature. Teasing apart these potential cues appears an important next step. Testing these relationships for other end of season events could also help resolve connections between start and end of season events with growth. While we found similar findings using leaf coloring, there are many ways that plants transition from growth to dormancy each year—generally at different times for different events (26)—with different implications for carbon gain (14).

Our multi-species common garden study showed that for early-leafing species, earlier leafout does not extend their thermal growing season—a proxy for potential carbon uptake period—despite extending

the calendar growing season. Given that photosynthesis is limited by cold temperatures in early spring, earlier leafout appears to provide limited opportunity for substantial growth, yet may deprive plants of fully using late-season warmth. This may explain why multiple studies have failed to find correlations between longer seasons and increased plant growth (27; 4; 5). Our results suggest little advantage from a carbon or primary productivity perspective for leafing out too early in the season, as thermal conditions are not favorable for photosynthesis and assimilation. Varying light availability over the early season combined with different plant strategies may alter this equation, however, potentially explaining why some species leafout during these thermally unfavorable conditions. Supporting this, we found understory species often showed the strongest relationship, suggesting that leafing out in thermally poor conditions before the upper canopy closes and reduces light may be a successful strategy.

The link between earlier leafout and lower thermal seasons was driven by variation across years at the individual and species levels—scales that are not always well studied in phenology research (19). While satellite observations can document intriguing trends (e.g., 8), observations that include far more species at a finer scale are likely critical for mechanistic understanding. Sampling across species of different leafout and growth strategies appears especially important, alongside studies of how different communities and climates may shape the relationship between calendar and thermal growing seasons. Understanding whether the thermal responses are consistent across species with different strategies could also inform how the thermal season varies over time and space, improving our ability to accurately model biological carbon fluxes.

1 Figures

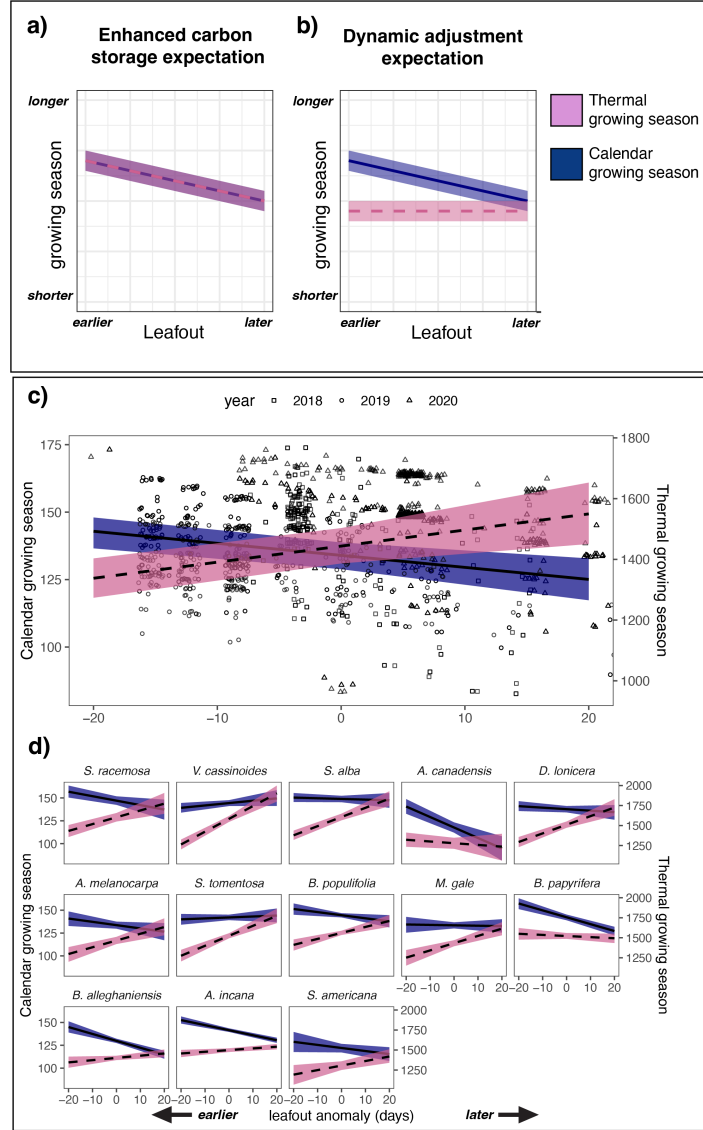


Figure 1: The relationship between leafout timing and growing season length differs between the calendar growing season and the thermal growing season. Panel (a) conceptually demonstrates the expected relationship between leafout timing, and both calendar and thermal growing season length under the expectation that longer growing seasons lead to increased carbon storage. Panel (b) conceptually demonstrates the expected relationship between leafout timing, and both calendar and thermal growing season length under the expectation that plant dynamically adjust the end of their growing season such that longer growing seasons do not increase carbon storage. In our study, later leafout resulted in a shorter calendar growing season (median estimated effect: -0.45 days, $UI_{90}[-0.68, -0.21]$) (c) and this pattern was consistent across species in our study (d). In contrast, an increasing later leafout resulted in a longer thermal growing season (median estimates effect: 5.3 growing-degree days, $UI_{90}[2.12, 8.44]$) (d) though this effect was stronger for species that typically leafout earlier in the season—panels in c) display in the typical order of leafout among species. The black trend lines represent the median effect of leafout timing on growing season length and shaded region 90% uncertainty intervals. Points in c) represent the raw data (per individual tree per year).

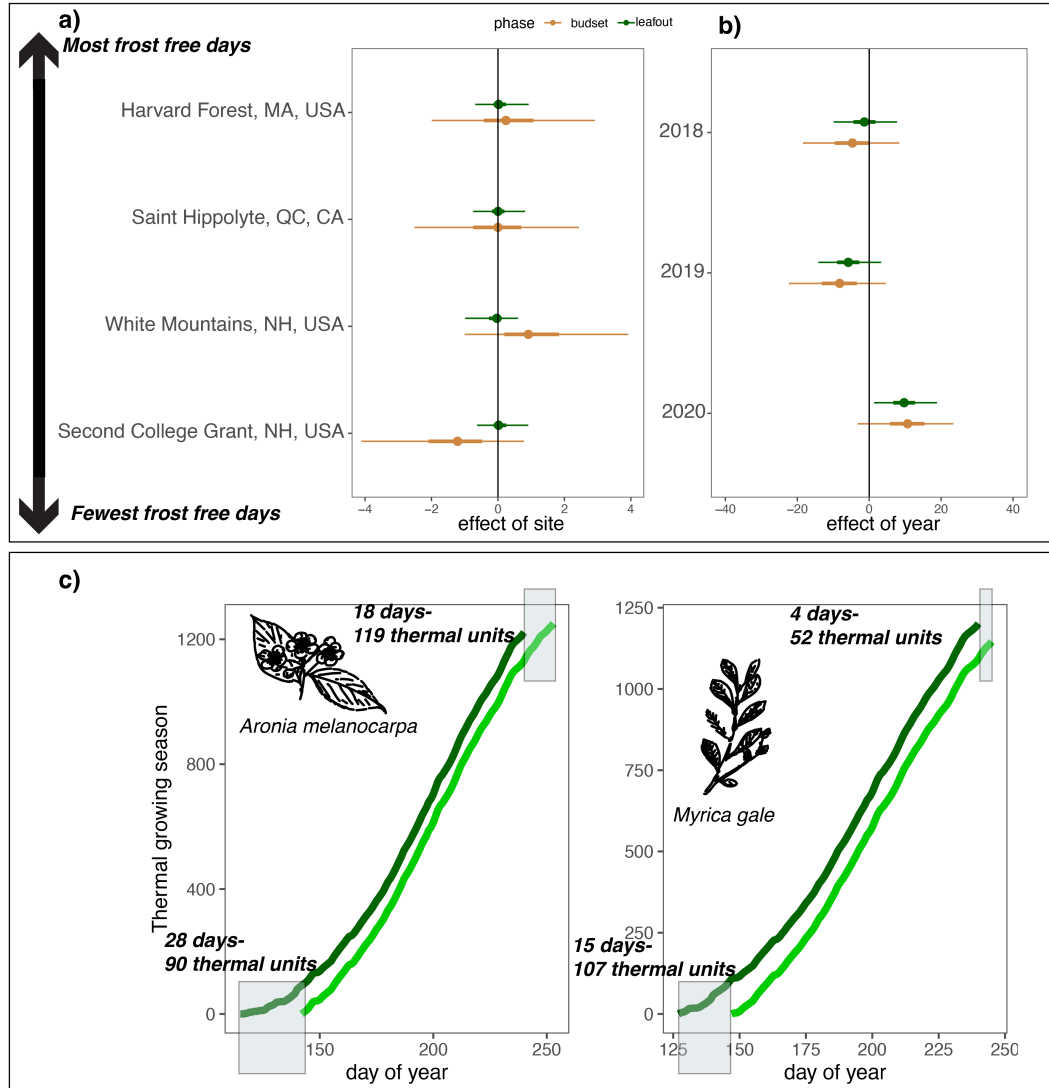


Figure 2: Difference in leafout and budset (in days) partitioned populations (a) and years (b). Point represent the median effect size estimate, and thick and thin bars the 50% and 90% uncertainty intervals, respectively. Panel (c) demonstrates how thermal conditions can vary across the calendar growing season and can generate a complex relationship between the calendar and thermal growing seasons by depicting the relationship between individuals of two shrub species with similar life-history strategies. Despite the fact the the early individual (light green line) of *Aronia melanocarpa* leafs out 28 days before it's later con-generic (dark green line) and only sets bud 18 days before it (i.e., it has a 10 day longer calendar growing season) it's thermal growing season is shorter because most of its growth advantage takes place in the unfavorable early spring. In contrast for *Myrica gale* where both the early (light green) and later (dark green) individual leaf out later in the spring, the 15 day head start and 4 day earlier finish of the earlier individual (11 day longer calendar growing season) results in a longer thermal growing season.

References

- [1] Roe, S., Streck, C., Beach, R., Busch, J., Chapman, M., Daioglou, V., Deppermann, A., Doelman, J., Emmet-Booth, J., Engelmann, J., Fricko, O., Frischmann, C., Funk, J., Grassi, G., Griscom, B., Havlik, P., Hanssen, S., Humpenöder, F., Landholm, D., Lomax, G., Lehmann, J., Mesnildrey, L., Nabuurs, G.-J., Popp, A., Rivard, C., Sanderman, J., Sohngen, B., Smith, P., Stehfest, E., Woolf, D., and Lawrence, D. Land-based measures to mitigate climate change: Potential and feasibility by country. *Global Change Biology* **27**(23), 6025–6058 (2021).
- [2] White, M. A., Running, S. W., and Thornton, P. E. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern us deciduous forest. *International Journal of Biometeorology* **42**(3), 139–145 (1999).
- [3] Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., O’Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., and Richardson, A. D. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**(7), 598–604 (2014).
- [4] Dow, C., Kim, A. Y., D’Orangeville, L., Gonzalez-Akre, E. B., Helcoski, R., Herrmann, V., Harley, G. L., Maxwell, J. T., McGregor, I. R., McShea, W. J., et al. Warm springs alter timing but not total growth of temperate deciduous trees. *Nature* **608**(7923), 552–557 (2022).
- [5] Silvestro, R., Zeng, Q., Buttò, V., Sylvain, J.-D., Drolet, G., Mencuccini, M., Thiffault, N., Yuan, S., and Rossi, S. A longer wood growing season does not lead to higher carbon sequestration. *Scientific reports* **13**(1), 4059 (2023).
- [6] Zani, D., Crowther, T. W., Mo, L., Renner, S. S., and Zohner, C. M. Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. *Science* **370**(6520), 1066–1071 (2020).
- [7] Norby, R. J. Comment on “increased growing-season productivity drives earlier autumn leaf senescence in temperate trees”. *Science* **371**(6533), eabg1438 (2021).

- [8] Zohner, C. M., Mirzaghali, L., Renner, S. S., Mo, L., Rebildaine, D., Bucher, R., Palouš, D., Vitasse, Y., Fu, Y. H., Stocker, B. D., and Crowther, T. W. Effect of climate warming on the timing of autumn leaf senescence reverses after the summer solstice. *Science* **381**(6653), eadf5098 (2023).
- [9] Grime, J. P. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**(982), 1169–1194 (1977).
- [10] Aitken, S. N. and Bemmels, J. B. Time to get moving: assisted gene flow of forest trees. *Evol Appl* **9**(1), 271–90 (2016).
- [11] Bauerle, W. L., Oren, R., Way, D. A., Qian, S. S., Stoy, P. C., Thornton, P. E., Bowden, J. D., Hoffman, F. M., and Reynolds, R. F. Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling. *Proceedings of the National Academy of Sciences* **109**(22), 8612–8617 (2012).
- [12] Soolanayakanahally, R. Y., Guy, R. D., Silim, S. N., and Song, M. Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*populus balsamifera* l.). *Plant, cell & environment* **36**(1), 116–127 (2013).
- [13] Zweifel, R., Sterck, F., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Häni, M., Peters, R. L., Walther, L., Wilhelm, M., et al. Why trees grow at night. *New Phytologist* **231**(6), 2174–2185 (2021).
- [14] Körner, C., Möhl, P., and Hiltbrunner, E. Four ways to define the growing season. *Ecology Letters* **26**(8), 1277–1292 (2023).
- [15] Chuine, I. A unified model for budburst of trees. *Journal of Theoretical Biology* **207**(3), 337–347 (2000).
- [16] Moore, J. L. and Remais, J. V. Developmental models for estimating ecological responses to environmental variability: Structural, parametric, and experimental issues. *Acta Biotheoretica* **62**(1), 69–90 (2014).
- [17] Yang, S., Logan, J., and Coffey, D. L. Mathematical formulae for calculating the base temperature for growing degree days. *Agricultural and Forest Meteorology* **74**(1), 61–74 (1995).

- [18] Farquhar, G. D., von Caemmerer, S., and Berry, J. A. A biochemical model of photosynthetic co₂ assimilation in leaves of c₃ species. *Planta* **149**(1), 78–90 (1980).
- [19] Menzel, A. and Fabian, P. Growing season extended in europe. *Nature* **397**(6721), 659–659 (1999).
- [20] Liu, B., Henderson, M., Zhang, Y., and Xu, M. Spatiotemporal change in china’s climatic growing season: 1955–2000. *Climatic Change* **99**(1), 93–118 (2010).
- [21] Liu, Q., Fu, Y. H., Zhu, Z., Liu, Y., Liu, Z., Huang, M., Janssens, I. A., and Piao, S. Delayed autumn phenology in the northern hemisphere is related to change in both climate and spring phenology. *Global Change Biology* **22**(11), 3702–3711, 2024/12/03 (2016).
- [22] Cuny, H. E., Rathgeber, C. B., Lebourgeois, F., Fortin, M., and Fournier, M. Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east france. *Tree physiology* **32**(5), 612–625 (2012).
- [23] Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., and Damesin, C. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree physiology* **32**(8), 1033–1045 (2012).
- [24] Pörtner, H. O., Roberts, D. C., Tignor, M., Poloczanska, E. S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., and Rama, B. *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, (2022).
- [25] Rohde, A., Bastien, C., Boerjan, W., and Thomas, S. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiology* **31**(5), 472–482, 05 (2011).
- [26] Michelson, I. H., Ingvarsson, P. K., Robinson, K. M., Edlund, E., Eriksson, M. E., Nilsson, O., and Jansson, S. Autumn senescence in aspen is not triggered by day length. *Physiologia Plantarum* **162**(1), 123–134 (2018).
- [27] Čufar, K., De Luis, M., Prislan, P., Gričar, J., Črepinšek, Z., Merela, M., and Kajfež-Bogataj, L. Do

variations in leaf phenology affect radial growth variations in *Fagus sylvatica*? *International journal of biometeorology* **59**, 1127–1132 (2015).