Early leafout leads to cooler growing seasons in woody species

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Abstract

Recent results suggest earlier leafout does not always increase plant growth, but have struggled to explain why. Here, using rarely available plant-level phenology from a common garden of 13 woody species, we show that earlier leafout leads to earlier growth cessation (budset), and thus longer but cooler growing seasons, especially for early-leafing species. These results challenge fundamental assumptions about calendar versus thermal growing seasons with implications for carbon models.

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 (Figure 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 (Figure 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 (e.g., ruderal vs. competitive species) and varying definitions of a growing season. The timing of leafout and senescence are critical components of 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 (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 (13).

The thermal growing season—a period of favorable meteorological conditions for plant growth (13)—offers an alternative to the calendar growing season. It is widely used, most commonly in the metric of growing degree days, as a temperature-derived measure of time that accumulates when temperatures are above a certain minimal threshold (14; 15). Because plant photosynthetic rates increase with temperature (16) 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 enhance our understanding of ecosystem measures to improve forecasting.

Across three years and 13 co-occurring species (Tab: 1) collected from four populations across a 3.5° latitudinal gradient (Figure 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 (Figure 1c,d), as routinely seen with anthropogenic climate change (17; 18).

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 (Figure 1c,d, this and other results were similar when we determined the growing season length with leaf coloration instead of budset, Figure S4). This was driven by a 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 (Figure 1-2). For later leafing species, earlier leafout did not substantially reduce their thermal growing season, bit it also did not increase it—suggesting thermal seasons do not increase with calendar growing seasons for any of our studied species. Species was the a major predictor of variation in leafout and budset($\sigma_{species}$ days for leafout: 8.1,UI$_{90}$[5.5, 11.6], days for budset: 9.7, UI_{90}[7, 13.6]).

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 (using alternative metrics of senescence, 19; 6). Thus, we may expect that studies of individual trees could find little relationship between earlier leafout and growth (20; 21; 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 (20; 21). This cross-species variation 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 interannual variation in both leafout and budset. We expected large differences across years in leafout (σ_{year}: 10.7 days, UI_{90}[4.9, 20.9], Figure 2b), because it varies strongly with local climatic conditions—one of the reasons it is the most consistent biological indicator of anthropogenic climate change (22). Similarly, we found little variation across populations in leafout ($\sigma_{population}$: 0.6 days, UI_{90}[0, 1.8], Figure 2a). Yet our finding of 15 days of variation across years in budset was surprising (σ_{year}: 15 days, UI_{90}[6.4, 30.8], Figure 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 ($\sigma_{population}$: 2.3 days, UI_{90}[0.4, 6.1], Figure 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 7X 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 ecosystem dynamics, given additional research. While most work on budset has stressed the role of photoperiod (12), other studies have found evidence of temperature control (23; 24). Our results suggest an additional potential role of leafout timing, which could be confounded with temperature. Teasing apart these potential cues while also testing these relationships for other end of season events could 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 (24)—with different implications for carbon gain (13).

Our multi-species common garden study showed that 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 and may especially deprive early-leafing species from fully using late-season warmth. While this may explain why multiple studies have failed to find correlations between longer calendar seasons and increased plant growth (4; 5), it generates a new question of why any species leafs out when thermal conditions are unfavorable. Varying light availability over the early season combined with different plant strategies may alter this equation, however, potentially making this a successful strategy for some species. Supporting this, we found understory species often showed the strongest relationship, suggesting they leaf out in thermally poor conditions to maximize access to light before the upper canopy closes.

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 (17). 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 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

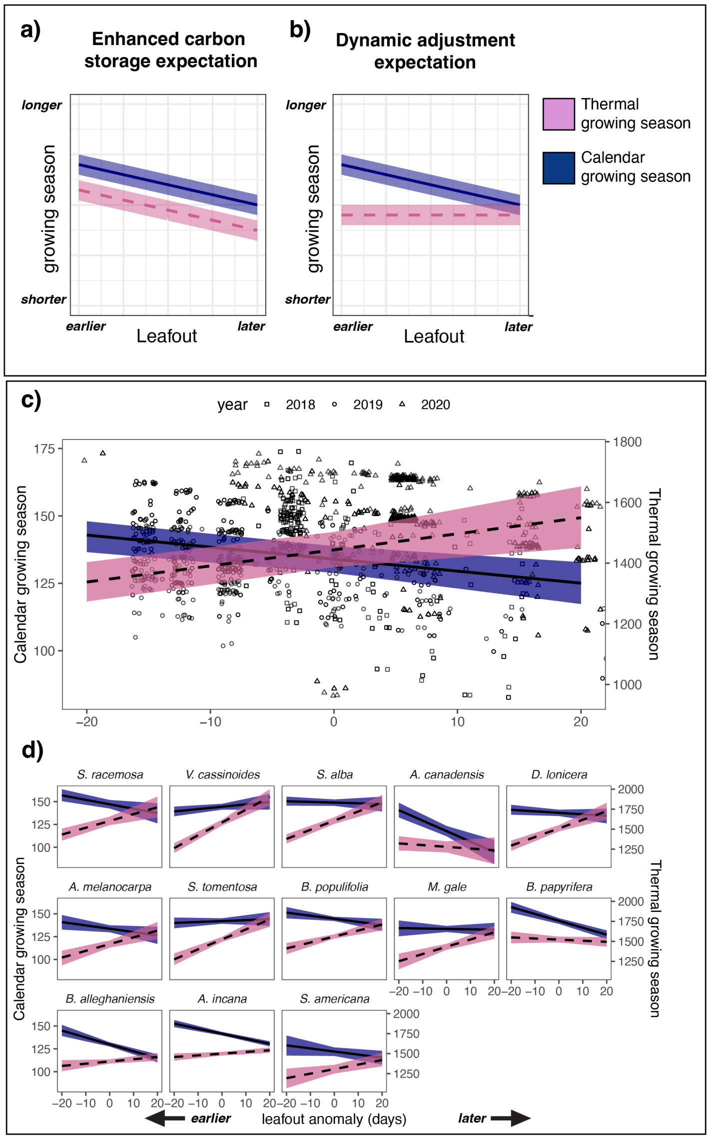

Figure 1: The relationship between leafout timing and growing season length differs between the calendar and the thermal growing seasons. Panels (a) and (b) conceptually demonstrate the expected relationships between leafout timing and both calendar and thermal growing seasons under two different expectations, with (a) showing the expectation that longer seasons lead to increased carbon storage, while panel (b) shows 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: -0.4 days, $UI_{90}[-0.7, -0.2]$) (c) and this pattern was consistent across species in our study (d). In contrast, later leafout resulted in a longer thermal growing season (median estimates effect: 5.3 growing-degree days, $UI_{90}[2.1, 8.4]$) (d), an effect that was stronger for species that typically leafout earlier in the season—panels in (d) 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).

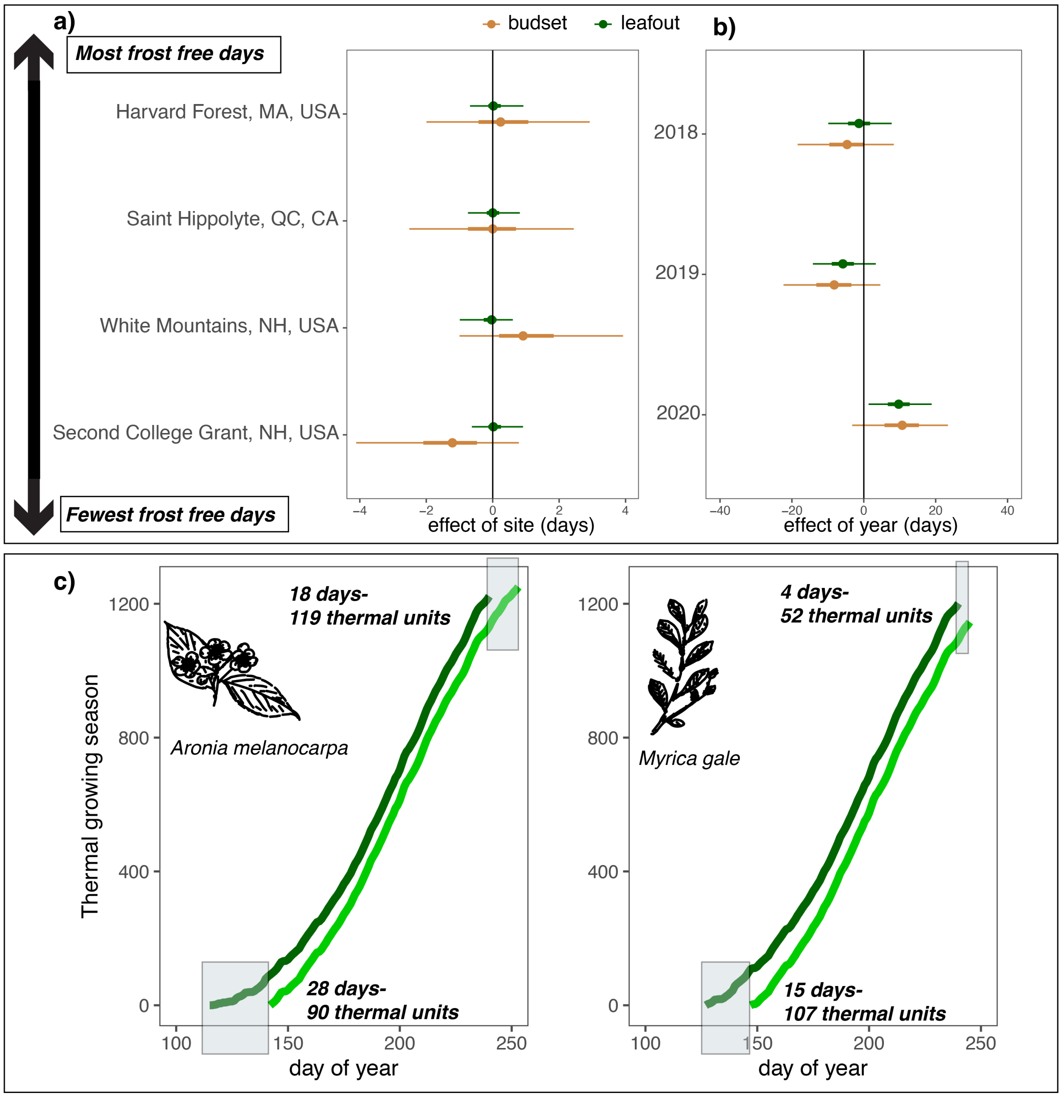

Figure 2: Differences in leafout and budset (in days) due to variation from populations (a) and years (b). Points represent the median effect size estimate, and thick and thin bars the 50% and 90% uncertainty intervals, respectively. Panel (c) shows how shifts in leafout and budset generate varying calendar and thermal growing seasons, contrasting two shrub species with similar life-history strategies. For *Aronia melanocarpa*, the earlier individual (dark green line) has a 10 day longer growing season (by leafing out 28 days earlier followed by setting bud 18 days earlier) than its the later leafing individual (light green line) but has a lower (cooler) thermal season because most of its early growth advantage takes place in the thermally unfavorable early spring. In contrast, for *Myrica gale*, both the early (dark green) and later (light green) individual leaf out later in the spring, such that the 11 day longer calendar growing season (from a 15 day leafout and 4 day earlier budset of the earlier individual) results in slightly warmer thermal season.

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