Early spring leads to longer but cooler growing seasons for woody species

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1 Abstract

It is currently unclear if longer growing seasons due to climate change increase carbon storage, because plants may adjust their growth period based on their carbon-sink capacity. Using rarely available plant-scale phenological measurements from a common garden experiment, we found a correlation between earlier leafout

and budset, which resulted in shorter thermal growing seasons—when leafout was early—a relationship that was strongest in early-leafing species.

Terrestrial forests are a major mitigation pathway for climate change, sequestering 20% of greenhouse gas emissions annually (1; 2). Most models of climate change assume sequestration may increase as warming drives longer seasons, more tree growth and, thus, more carbon storage, following decades of evidence from ecosystem-scale studies (3; 4; 5). However,recent findings that earlier leafout and warmer seasons do not increase productivity or tree growth (6; 7; 8; 9), have called this assumption into question.

These results suggest fundamental gaps in our understanding of how early-season events and the environmental conditions of the vegetative period shape end-of-season events. This discrepancy could be related to differences in the scale of observation, which affects how the start and end of the season are measured (10; 11). Often findings of a correlation between season length and growth have utilized ecosystem-scale estimates of productivity (**?** 5; 12) and the start and end of season that blur across species and individuals. In contrast, recent findings of a disconnect have come often from observations of individual trees on one or a few species (13; 8; 14) and experiments on juvenile trees of one to species (6; 7; 9). These experiments have suggested that plants adjust their end of season timing dynamically such that longer seasons do not increase total productivity, but the mechanism—and prevalence—of this effect is unclear (6; 7; 9).

The timing of leafout and senescence are critical to plant growth strategies (15) and thus likely vary across species. Within species, populations may also vary (16), especially because end-of-season events are usually more locally adapted than start-of-season events (e.g. budset 17; 18). Increasing evidence also suggests local climate may define narrow periods of growth, with most significant growth earlier in the growing season (19; 9). These results suggests 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 (10).

The thermal growing season—a period of favorable meteorological conditions for plant growth (10)—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 (20; 21; 22). Because plant photosynthetic rates increase with temperature (23) 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. Importantly, depending on the interannual temperature variation, years with substantially different calendar growing seasons can have very similar thermal growing seasons, or *vice versa*, but 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-scale data—phenological observations over three years from a multi-species common garden study—to test correlations between leafout and budset in different species from four populations across a 4.5 latitudinal gradient. We examine how start-of-season events (i.e., leafout) may affect end-of-season events (i.e., budset) to determine the length of both the calendar and thermal growing seasons. Our results leverage observations of leafout and growth cessation at the individual tree-level to understand how these processes scale to populations, species and communities and may thus improve our understanding of ecosystem-scale measures to improve forecasting.

2 Results & Discussion

Across three years and 18 co-occuring species from four populations, our common garden captured high variation in the timing of both start and end of season events (Figure 2). Resulting calendar and thermal growing seasons varied almost two-fold across individual trees (2.10x and 1.84x respectively), with earlier leafout leading to longer calendar growing seasons (Fig: 1a,b), as routinely seen with anthropogenic climate change (24; 25). However, longer calendar growing seasons did not lead to higher thermal growing seasons, as generally assumed.

Insteadearly calendar growing seasons led to lower thermal growing seasons (Figure 1c,d, this and other results were similar when we determined the length the growing season length with leaf coloration instead of budset, Figure S3). 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 3a,b).

The differences between thermal and calendar growing seasons was strongest in the earlier-leafout species, which leaf out during the coolest part of the spring (Figure 1-3). For later leafing species, earlier leafout did not substantially reduce their thermal growing season. This is likely because for later species an earlier leafout still occurred in thermally favorable times of the season, and a relatively small advance in calendar time resulting in a proportionately larger gain in thermal sums. Species was also the a major predictor of variation in leafout, budset and growing season length ($\sigma_{species}$ days for leafout: : 8.12UI$_{90}$[5.54,11.56], days for budset: 9.73 UI_{90}[6.99,13.57], days for season length: 14.45, UI_{90}[10.34,19.9l Figure 2a-b).

These results suggest that some of the current apparently conflicting findings of whether longer seasons increase tree 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 hasten their end of season events with earlier start of season events supports other studies finding a similar correlation (though using alternative metrics of senescence, 26; 6), but found this varied by species. Thus, we may expect that studies of individual trees—and for certain species—could find little relationship between earlier leafout and growth (**?** 6), which could be driven by currently unstudied shifts in the thermal seasons. Additionally, because differences between thermal and calendar growing seasons were strongly species-dependent, previous findings may depend strongly on the species studied, consistent with other work comparing across smaller sets of species (27; 28). 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 given the correlations we found between start and end of season events. Thus, by integrating across species some studies may find stronger correlations between productivity and earlier seasons.

Beyond species-level variation, our results also found high variation across years in both leafout and budset. Differences across years in leafout were high (σ_{year}:10.65 days UI_{90}[4.88,20.86], Figure 2) and expected, as leafout is highly plastic, varying with local climatic conditions—one of the reasons it is the most consistent biological indicator of anthropogenic climate change (29). In line with this, we also found almost no variation across populations in leafout ($\sigma_{population}$:0.57, UI_{95}[0.04,1.77], Figure 2b). Yet the finding of strong variation across years in budset was surprising (σ_{year}:15.02 days UI_{90}[6.44,30.84], Figure 2), given budset is generally thought to be strongly locally adapted and controlled by photoperiod, which does not vary year to year (18; 16; 30). We did find evidence of local adaptation ($\sigma_{population}$:2.34 days, UI_{90}[0.4,6.13], Figure 2). Populations from the Second College Grant (the site with the fewest frost free days; Figure S2) set buds approximately two days before those from the White Mountains (the site with the next fewest frost free days). These differences, however, were weak (Figure 2b) and 6X and spVpopX 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, but will require a new approaches to how we view and study budset and other end of season events. Most work on budset in broadleaf species comes from one genus (*Populus spp.*) and has stressed the major control of photoperiod limiting responses to anthropogenic warming. Yet some studies have found evidence of temperature (31; 32; 33), contrasting with this prediction. Teasing apart effects of temperature from intrinsic correlations between start and end of season events appears an important next step. Doing so across additional species may be especially helpful, as a focus on single species may not always predict broad scale trends (34), and our results suggest important variation across species.

Budset represents the stop of primary growth and generally correlates strongly with the stop of radial growth (18), but it is only one of many ways that plants begin to transition from growth to dormancy each year—generally at different times for different events (33). While the need to better understand which metrics of end of season events correlate best with growth and carbon gain has been often discussed (35; 10), our results suggest we also need to study how these events shift with earlier and warmer years. Studies of leaf longevity have begun to examine this, but more work across different metrics of end of season and across many more species is critical.

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 (36; 13; 8; 14). Our results show that there may be little advantage from a carbon or primary productive perspective for leafing out too early in the season, as thermal conditions are not favorable for photosynthesis and assimilation. Many of the species that are most phenologically sensitive to climate change are already among the earliest species to leaf out in temperate plant communities (37; 38), implying there may be little to gain from a carbon perspective.

This trade-off between earlier leafout and the thermal season was driven by variation across years at the individual and species levels—scales that are not always studied closely in phenology research, where many long-term records from natural systems were not collected on specific individuals and satellite observations integrate over species in an ecosystem (24; 39; 40). Our results raise questions about why some species leafout early during these unfavorable conditions, and why species tracking spring warming due to climate change have increased performance relative to non-trackers (41). In our study we only evaluated the thermal conditions that may affect photosynthesis, rather than photosynthesis itself, which also depends strongly on light availability. In forest systems, light availability is strongly dependent on canopy conditions. In our study, the species that leafed out the earliest are understory shrubs, for whom access to light becomes severely limited later in the growing season as canopy trees leaf out. It may be that for these species, the light availability early in the season necessitates leafing out in sub-optimal thermal conditions (42).

Our findings suggest that linking phenological growing season to primary productivity requires accounting for phenological variation at multiple scales (individual, species level, multiple phases). Progress will require more efforts to understand and model species-level shifts in phenology. While satellite observations can document intriguing trends (e.g., 9), 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 as we found later-leafout species did not exhibit a strong trade-off. Whether this is consistent across other communities of species—and other climates is an important question. Understanding whether the thermal responses are consistent across species with different leafout and growth strategies could also inform how the thermal season varies over time and space, improving our ability to accurately model biological carbon fluxes.

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4 Figures

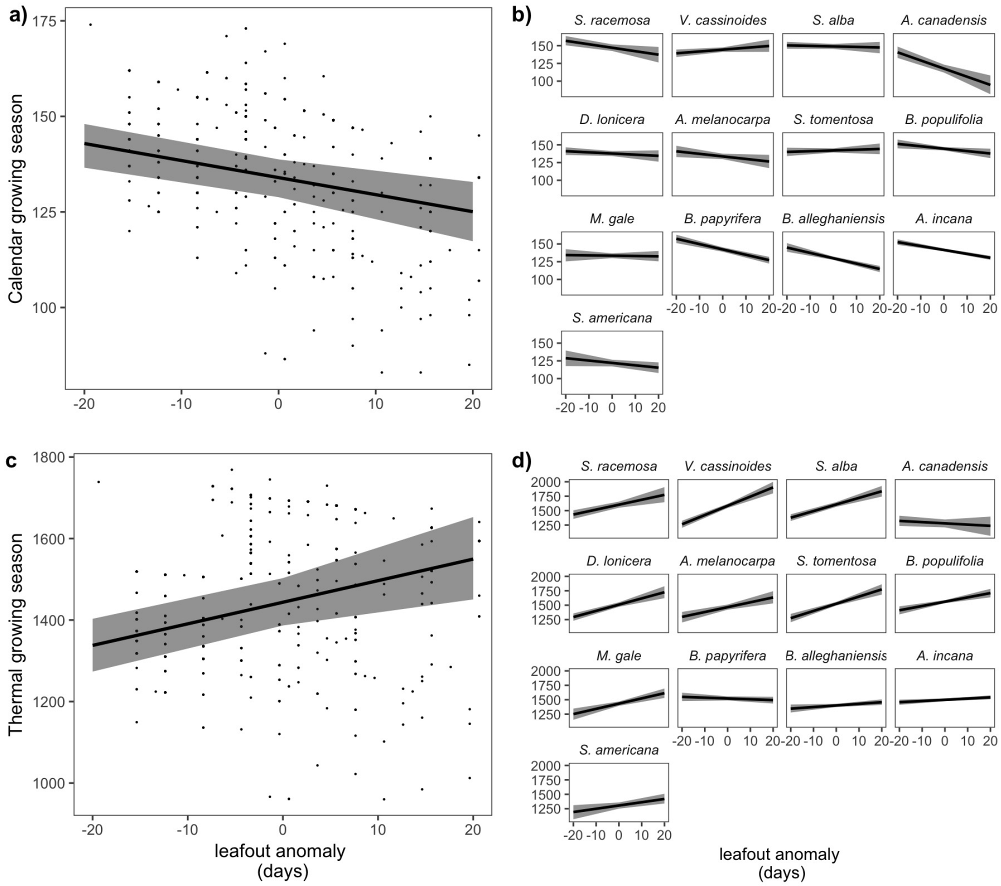

Figure 1: The relationship between Start of Spring (calendar day of leafout) and growing season length differs between the calendar growing season and the thermal growing season. Later leafout resulted in a shorter calendar growing season (median estimated effect: -0.45 days, $UI_{90}[-0.68, -0.21]$) (a) and this pattern was consistent across species in our study (b). In contrast, an increasing later leafout resulted in a longer thermal growing season (median estimates effect: 5.3 growing-degree days, $UI_{90}[2.12, 8.44]$) (c) 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 a), and c) represent the raw data (per individual tree per year).

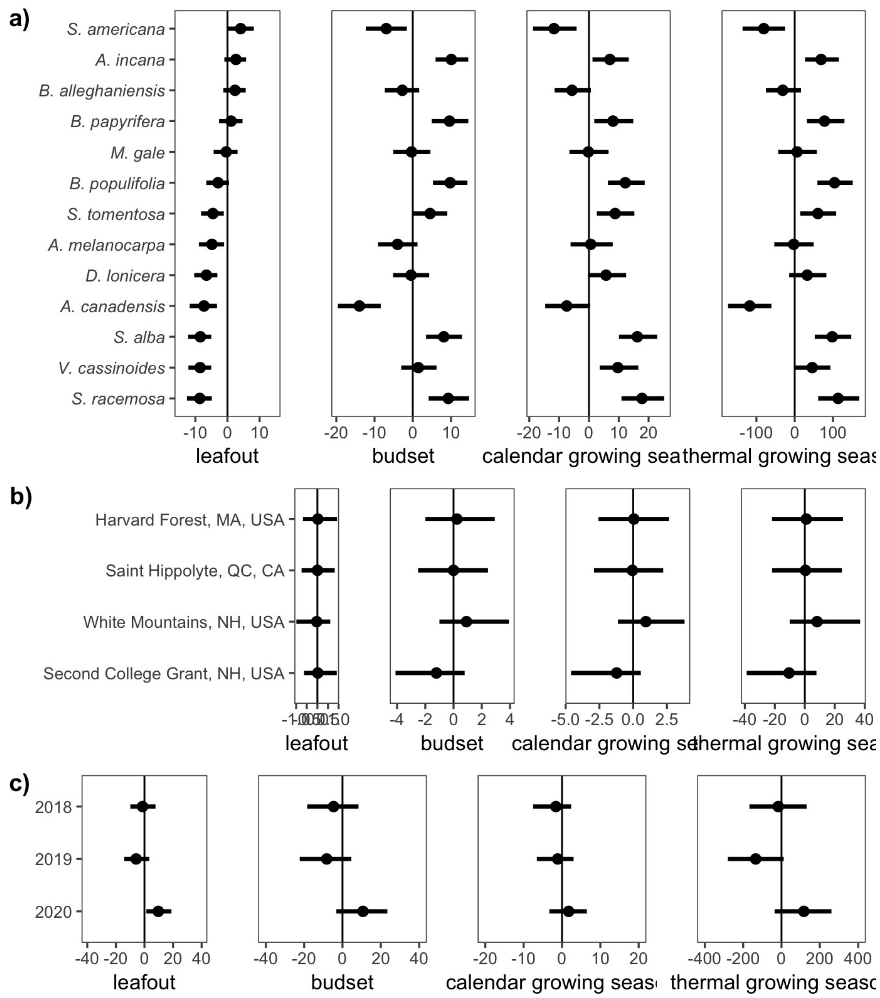

Figure 2: Difference in leafout, budset and growing season length (in days) partitioned between species (a) populations (b) and years (c). Point represent the median effect size estimate, and bars the 90% uncertainty intervals.

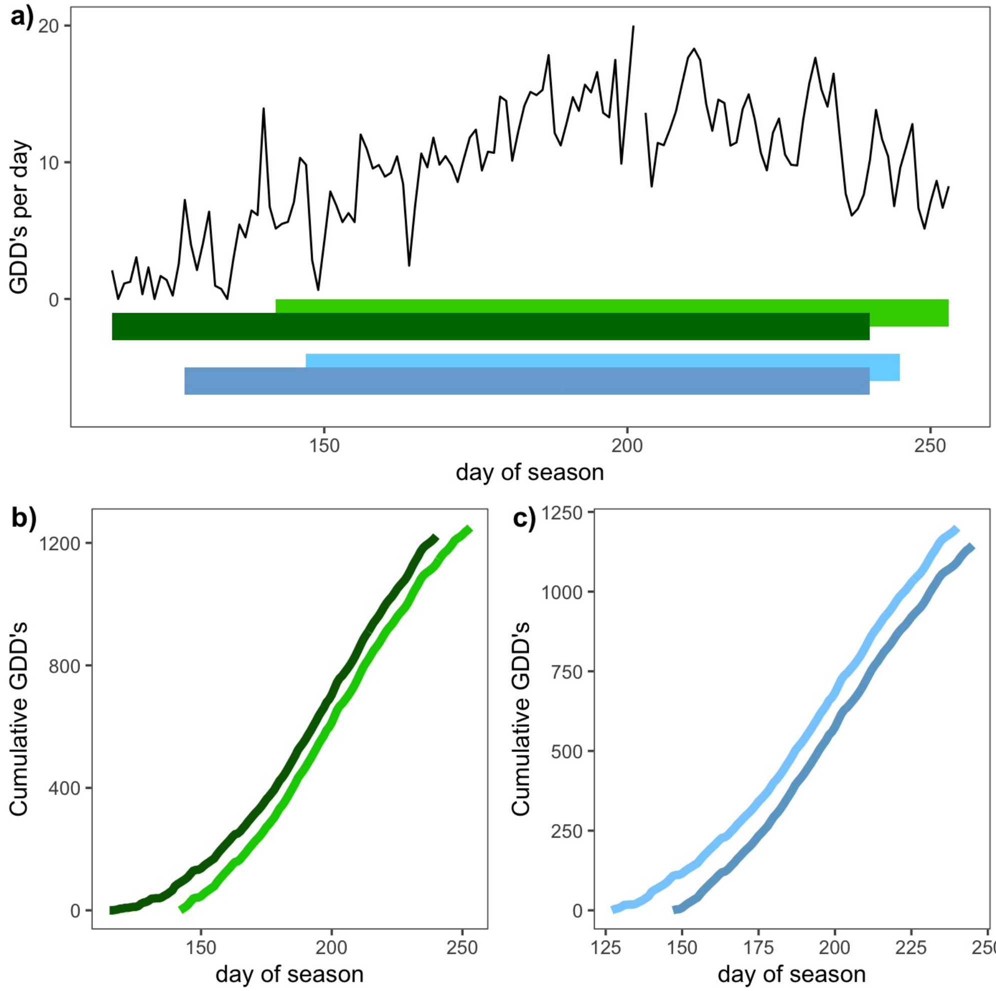

Figure 3: Thermal conditions vary across the calendar growing season, which can generate a complex relationship between the calendar and thermal growing seasons. Panel a) depicts the daily heat sums at the Weld Hill Research Building in 2019 and the calendar growth season of early and late leafing individuals of *Aronia melanocarpa* (green bars) and *Myrica gale* (blue bars). Despite the fact the the early individual of *A. melanocarpa* leafs out 24 days before it's later con-generic and only sets bud 13 days before it (i.e., it has a 14 day longer calendar growing season) it's thermal growing season is shorter (panel b) because most of its growth advantage (explain this better) takes place in the unfavorable early spring. In contrast for *M. gale* where both the early and late individual leaf out later in the spring, the 20 day head start and 5 day earlier finish of the earlier individual (15 day longer calendar growing season) results in a longer thermal growing season for it as well (panel c)

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