

¹ Early spring leads to longer but cooler growing seasons for woody
² species

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¹⁴

¹⁵ **1 Abstract**

¹⁶ The extension of the growing season in the spring in temperate regions is one the most prominent biological
¹⁷ indicators of climate change. Most models of carbon storage assume that earlier growth will result in longer
¹⁸ seasons and thereby enhance forest carbon storage, however current findings have challenged this assumption.

¹⁹ A recent hypothesis that has gained support in the literature is that plants dynamically adjust the end of their
²⁰ growing season based on their carbon-sink capacity, such that longer seasons do not increase total productivity.

²¹ If this is the case, variation in the calendar growing season (number of days) should be independent of
²² variation in the thermal growing season (i.e., the period of favorable meteorological conditions for plant
²³ growth), which should remain relatively stable across years. We tested this prediction using rarely available
²⁴ plant-scale phenological measurements from a three year common garden experiment. The garden included
²⁵ 18 woody species, native to the Eastern United States from four populations of origin.

²⁶ We found that at the community level, earlier leafout was correlated with earlier budset, resulting in a
²⁷ relatively stable calendar growing period over the three years. Because thermal conditions were lower at the
²⁸ start than end of the season, the relationship between earlier leafout and budset resulted in shorter thermal
²⁹ growing seasons when leafout was early—a relationship that was strongest in early-leaving species.

³⁰ This relationship may explain some of the contrasting results of how climate change affects growing season
³¹ length and productivity—if early leaf out results in earlier budset, as a whole plant are active for a pro-
³² portionately large period of time where thermal conditions are less thermally optimal for photosynthesis.

³³ This study shows linking phenological growing seasons to carbon storage requires integrating existing ecosys-
³⁴ tem measures with phenological variation at multiple scales, and that progress will require more efforts to
³⁵ understand and model species-level shifts in phenology.

³⁶ 2 Introduction

³⁷ Terrestrial forests are a major mitigation pathway for climate change, sequestering 20% of greenhouse gas
³⁸ emissions annually (Shanley *et al.*, 2024; Roe *et al.*, 2021). Most models of climate change assume this storage
³⁹ may increase as warming drives longer seasons, more tree growth and, thus, more carbon storage, following
⁴⁰ decades of evidence from ecosystem-scale studies (Churkina *et al.*, 2005; White *et al.*, 1999; Keenan *et al.*,
⁴¹ 2014). Recent findings that earlier leafout and warmer seasons do not increase productivity or tree growth

⁴² (Zani *et al.*, 2020; Norby, 2021a; Dow *et al.*, 2022; Zohner *et al.*, 2023), however, have called this assumption
⁴³ into question.

⁴⁴ 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
⁴⁵ differences in the scale of observation, which also affects how the start and end of the season are measured
⁴⁶ (Körner *et al.*, 2023*in press*; Wolkovich *et al.* *in press*). Many findings of a correlation between season length
⁴⁷ and growth have focused on ecosystem-scale estimates of productivity (?Keenan *et al.*, 2014; Norby, 2021b)
⁴⁸ and the start and end of season, where the signatures that are measured schmear across species and individuals.
⁴⁹ In contrast, recent findings of a disconnect have come often from observations of individual trees on one
⁵⁰ or a few species (Camarero *et al.*, 2022; Dow *et al.*, 2022; Silvestro *et al.*, 2023), experiments on juvenile trees
⁵¹ of one to species (Zani *et al.*, 2020; Norby, 2021a; Zohner *et al.*, 2023). These experiments have suggested
⁵² that plants adjust their end of season timing dynamically such that longer seasons do not increase total
⁵³ productivity, but the mechanism—and prevalence—of this effect is unclear (Zani *et al.*, 2020; Norby, 2021a;
⁵⁴ Zohner *et al.*, 2023).

⁵⁶ The timing of leafout and senescence are critical to plant growth strategies (Grime, 1977) and thus likely
⁵⁷ vary across species. Within species, populations may also vary (Aitken & Bemmels, 2016), especially because
⁵⁸ end-of-season events are usually more locally adapted than start-of-season events—with populations using
⁵⁹ unique photoperiods to cue growth cessation depending on the local climate (e.g. budget Bauerle *et al.*, 2012;
⁶⁰ Soolanayakanahally *et al.*, 2013). Increasing evidence also suggests local climate may define narrow periods of
⁶¹ growth, with most significant growth earlier in the growing season Zweifel *et al.* (2021); Zohner *et al.* (2023).
⁶² These results suggests the calendar growing season (i.e., the number of days between the start and end of
⁶³ the growing season) may be less informative to predicting growth than estimates that directly incorporate
⁶⁴ environmental conditions (Körner *et al.*, 2023).

⁶⁵ The thermal growing season—a period of favorable meteorological conditions for plant growth (Körner *et al.*,
⁶⁶ 2023)—offers an alternative to the calendar growing season. It is also widely used, most commonly in the

67 metric of growing degree days, a temperature derived measure of time that accumulates when temperatures
68 are above a certain minimal threshold (Chuine, 2000; Moore & Remais, 2014; Yang *et al.*, 1995). Because
69 plant photosynthetic rates increase with temperature (Farquhar *et al.*, 1980) the thermal growing season
70 is mechanistically related to primary productivity, and thus may be a better proxy than calendar time for
71 relating growing season length to carbon gain. Importantly, depending on the temperature over the course of
72 a growing season, years with substantially different calendar growing seasons can have very similar thermal
73 growing seasons, or *vice versa*, but we generally lack plant-level phenological data for the start and end of
74 season to examine how the calendar and thermal seasons of species and populations compare across years.

75 Here, we use rarely available plant-scale data—phenological observations over three years from a multi-
76 species common garden study—we test how correlated leafout and budset are in different species from four
77 populations across a 4.5 latitudinal gradient. We examine how start-of-season events (i.e., leafout) may affect
78 end-of-season events (i.e., budset) to determine the length of both the calendar and thermal growing seasons.
79 Our results scale from observations of leafout and growth cessation at the individual tree-level to understand
80 how these processes scale to populations, species and communities and may thus improve our understanding
81 of ecosystem-scale measures to improve forecasting.

82 **3 Results & Discussion**

83 Across three years, our multi-population and multi-species common garden captured high variation in the
84 timing of both start and end of season events (Figure 1). Resulting calendar and thermal growing seasons
85 varied almost two-fold across individual trees (ADD INFO), with earlier leafout leading to longer calendar
86 growing seasons (Fig: 2a,b), as routinely seen with anthropogenic climate change (Menzel & Fabian, 1999;
87 Liu *et al.*, 2010). However, longer calendar growing seasons did not lead to higher thermal growing seasons,
88 as generally assumed.

89 Instead, we found an apparently fundamental—and unexpected—trade-off where early, longer calendar grow-

ing seasons led to lower thermal growing seasons (Figure 2c,d, this and other results were similar when we determined the length the growing season length with leaf coloration instead of budset, Figure ??). This result was driven by an apparent relationship between leafout and budset at the individual plant-level combined with the generally poor thermal conditions of the early season during leafout relative to the more favorable thermal conditions 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 are often very 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 trade-off between thermal and calendar growing seasons was strongest in the earlier-leafout species, which leaf out during the coolest part of the spring (Figure 2-3). 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 ($\sigma_{species}$ for leafout: : 8.22UI₉₅[5.28,12.61], for budset: 9.84 UI₉₅[6.68,14.46], for season length: 14.54, UI₉₅[9.81,21.25] Figure 1a-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, Liu *et al.*, 2016; Zani *et al.*, 2020), but found this was strongest for certain species. Thus, we may expect that studies of individual trees—and for certain species—could find little relationship between earlier leafout and growth (?Zani *et al.*, 2020), which could be driven by currently unstudied shifts in the thermal seasons. Additionally, because the trade-off between thermal and calendar growing seasons was strongly species-dependent, what previous studies find may depend strongly on the species studied, consistent with other work comparing across smaller sets of species (Cuny *et al.*, 2012; Michelot *et al.*, 2012).

115 This variation also likely scales up to affect ecosystem-level estimates which generally have one measure of
116 the start of season—for the earliest leafout species—and one for the end of season, likely capturing the later-
117 leafout species given the correlations we found between start and end of season events. Thus, by integrating
118 across species some studies may find stronger correlations between productivity and earlier seasons.

119 Beyond species-level variation, our results also found high variation across years in both leafout and budset.
120 Differences across years in leafout were high ($\sigma_{year}:10.62\ UI_{95}[4.39,25.23]$, Figure 1) and expected, as leafout
121 is highly plastic and varies strongly depending on local climatic conditions—one of the reasons it is the most
122 consistent biological indicator of anthropogenic climate change (Pörtner *et al.*, 2022). In line with this, we
123 also found almost no variation across populations in leafout ($\sigma_{population}:0.61,\ UI_{95}[0.02,2.6]$, Figure 1b). Yet
124 the finding of strong variation across years in budset was surprising ($\sigma_{year}:15.13\ UI_{95}[5.66,37.54]$, Figure 1),
125 given budset is generally thought to be strongly locally adapted and controlled by photoperiod, which does
126 not vary year to year (Soolanayakanahally *et al.*, 2013; Aitken & Bemmels, 2016; Vico *et al.*, 2021). We did
127 find evidence of local adaptation ($\sigma_{population}:2.35,\ UI_{95}[0.22,8.2]$, Figure 1). Populations from the Second
128 College Grant (the site with the fewest frost free days; Figure ??) set buds approximately two days before
129 those from the White Mountains (the site with the next fewest frost free days). These differences, however,
130 were weak (Figure 1b) and 6X and 4X smaller than the variation due to year and species (respectively).

131 The shift in budset with earlier leafout suggests a potential pathway to better understand and predict recent
132 findings, but will require a new approaches to how we view and study budset and other end of season events.
133 Most work on budset in broadleaf species comes from one genus (*Populus spp.*) and has stressed the major
134 control of photoperiod limiting responses to anthropogenic warming. Yet some studies have found evidence of
135 temperature (Olsen *et al.*, 2014; Rohde *et al.*, 2011; Michelson *et al.*, 2018), contrasting with this prediction.
136 Teasing apart effects of temperature from intrinsic correlations between start and end of season events appears
137 an important next step. Doing so across additional species may be especially helpful, as a focus on single
138 species may not always predict broad scale trends (Morales-Castilla *et al.*, 2024), and our results suggest
139 important variation across species.

¹⁴⁰ Budset represents the stop of height growth and generally correlates strongly with the stop of radial growth
¹⁴¹ (Soolanayakanahally *et al.*, 2013), but it is only one of many ways that plants begin to transition from growth
¹⁴² to dormancy each year—generally at different times for different events (Michelson *et al.*, 2018). While the
¹⁴³ need to better understand which metrics of end of season events correlate best with growth and carbon gain
¹⁴⁴ has been often discussed (Gallinat *et al.*, 2015; Körner *et al.*, 2023), our results suggest we also need to study
¹⁴⁵ how these events shift with earlier and warmer years. Studies of leaf longevity have begun to examine this,
¹⁴⁶ but more work across different metrics of end of season and across many more species is critical.

¹⁴⁷ 3.1 Ecological and forecasting implications

¹⁴⁸ Our multi-species common garden study showed that for early-leaving species, earlier leafout does not extend
¹⁴⁹ their thermal growing season—a proxy for potential carbon uptake period—despite extending the calendar
¹⁵⁰ growing season. Given that photosynthesis is limited by cold temperatures in early spring, earlier leafout
¹⁵¹ appears to provide limited opportunity for substantial growth, yet may deprive plants of fully using late-season
¹⁵² warmth. This may explain why multiple studies have failed to find correlations between longer seasons and
¹⁵³ increased plant growth (Čufar *et al.*, 2015; Camarero *et al.*, 2022; Dow *et al.*, 2022; Silvestro *et al.*, 2023). Our
¹⁵⁴ results show that there may be little advantage from a carbon or primary productive perspective for leafing
¹⁵⁵ out too early in the season, as thermal conditions are not favorable for photosynthesis and assimilation. Many
¹⁵⁶ of the species that are most phenologically sensitive to climate change are already among the earliest species
¹⁵⁷ to leaf out in temperate plant communities (Shen *et al.*, 2014; Geng *et al.*, 2020), implying there may be little
¹⁵⁸ to gain from a carbon perspective.

¹⁵⁹ This trade-off between earlier leafout and the thermal season was driven by variation across years at the
¹⁶⁰ individual and species levels—scales that are not always studied closely in phenology research, where many
¹⁶¹ long-term records from natural systems were not collected on specific individuals and satellite observations
¹⁶² integrate over species in an ecosystem (Menzel & Fabian, 1999; Pettorelli *et al.*, 2005; Davies *et al.*, 2013).

¹⁶³ Our results suggest that linking phenological growing season to primary productivity requires accounting for

¹⁶⁴ phenological variation at multiple scales (individual, species level, multiple phases). Progress will require
¹⁶⁵ more efforts to understand and model species-level shifts in phenology. While satellite observations can
¹⁶⁶ document intriguing trends (e.g., Zohner *et al.*, 2023), observations that include far more species at a finer
¹⁶⁷ scale are likely critical for mechanistic understanding. Sampling across species of different leafout and growth
¹⁶⁸ strategies appears especially important as we found later-leafout species did not exhibit a strong trade-off, but
¹⁶⁹ whether this is consistent across other communities of species—and some of the latest leafout species, which
¹⁷⁰ are often difficult to grow in common gardens (given their slow growth)—and other climates is an important
¹⁷¹ questions. Understanding whether the thermal responses are consistent across species with different leafout
¹⁷² and growth strategies could also inform how the thermal season varies over time, and by species.

¹⁷³ Our results raise questions about why some species leafout early during these unfavorable conditions, and why
¹⁷⁴ species tracking spring warming due to climate change have increased performance relative to non-trackers
¹⁷⁵ (Cleland *et al.*, 2012). In our study we only evaluated the thermal conditions that may affect photosynthesis,
¹⁷⁶ rather than photosynthesis itself, which also depends strongly on light availability. In forest systems, light
¹⁷⁷ availability is strongly dependent on canopy conditions. In our study, the species that leafed out the earliest
¹⁷⁸ are understory shrubs, for whom access to light becomes severely limited later in the growing season as canopy
¹⁷⁹ trees leaf out. It may be that for these species, the light availability early in the season necessitates leafing
¹⁸⁰ out in sub-optimal thermal conditions (AUGSPURGER *et al.*, 2005).

¹⁸¹ 4 Methods

¹⁸² 4.0.1 The Common Garden

¹⁸³ In 2014-2015, we collected seeds of 18 species woody plants from multiple parent plants at four field sites
¹⁸⁴ in eastern Northern America spanning approximately a 3.5 degree latitudinal gradient. The four field sites
¹⁸⁵ included Harvard Forest (42.55°N , 72.20°W), the White Mountains (44.11°N , 52.14°W), Second College
¹⁸⁶ Grant of Dartmouth College (44.79°N , 50.66°W), and St. Hippolyte, QC, CAN (45.98°N , 74.01°W). We

187 transported all seeds back the the Weld Hill Research Building at the Arnold Arboretum in Boston MA
188 (42.30°N, 71.13°W) where we germinated seeds following standard germination protocols, and grew them to
189 seedling stages in the research greenhouse. In the spring of 2017 we out-planted seedlings to establish the
190 Common garden (Table ??).

191 Plots were regularly weeded and watered throughout the duration of the study and were pruned in the fall
192 of 2020. Survival of *Acer spicatum*, *Acer pensylvanicum*, *Vaccinium myrtilloides* *Quercus alba*, and *Quercus*
193 *rubra* was limited and these species are therefore not included in the following analyses. Based on survivorship
194 in the common garden, our subsequent analyses are based on 2-31 individuals per species (Tab. ??). Our
195 statistical analyses account for the unbalanced design that is frequently occurs in common gardens and other
196 provenance trials (CITE).

197 **4.0.2 Phenological monitoring:**

198 For the years of 2018-2019, we made phenological observations of all individuals in the common garden twice
199 per week from February to December. In 2020 due to the COVID 19 pandemic, we monitored once per week
200 from March to November. We describe phenological stages using a modified BBCH scale (Finn *et al.*, 2007)
201 a common metrics for quantify woody plant phenological progression. We observed all major vegetative
202 stages (budburst BBCH 07, leafout BBCH 15, end of leaf expansion bbch 19, leaf coloration/drop BBCH 97,
203 reproductive phases flowering BBCH 60-65, fruiting BBCH 72-79 and fruit/cones fully ripe BBCH 89). We
204 added additional phases for budset and labelled full budset as BBCH 102.

205 **4.0.3 Data analysis**

206 To better understand the role that variation in leafout and budset phenology play in determining calendar
207 growing season length among species populations and years we fit a Bayesian hierarchical model with a
208 normal (Gaussian) probability distribution. We calculated growing season duration by subtracting the day
209 of leafout from the day of budset. We fit an intercept only model with phenophase timing (leafout, budset or

210 growing season duration) as the response variable and partial pooling across species, populations and years.

211 We only included observations with both budset and leafout observed on the same plant in this analysis ($n=$
212 595).

213 To assess the relationship between variation in leafout timing and calendar and thermal growing seasons we
214 fit two additional regression models with thermal or calendar growing season length as the response variable
215 and day of leafout as the main prediction. To account for species-level differences we included partially
216 pooling on the slope and intercept of species.

217 We define the thermal growing season as the cumulative growing degree day heat sums between the day of
218 leafout and the day of budset for each species. We calculated daily heat sums using the R package “pollen”
219 (Jakub Nowosad, 2019) using a 10 C base temperature with minimum and maximum daily temperature data
220 from the weld hill weather station.

221 All models were fit in the R package “brms” (Bürkner, 2018) on 4 chains with a 4000 iteration warm-up and
222 1000 sampling iterations on each chain for a total of 4,000 sampling iterations across all chains. We evaluated
223 model fit, with no divergent transitions, rhats less than 1.01 and high effective sample sizes. We performed
224 all analyses in R version 4.1.2 (R Core Team, 2021).

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228 **6 Figures**

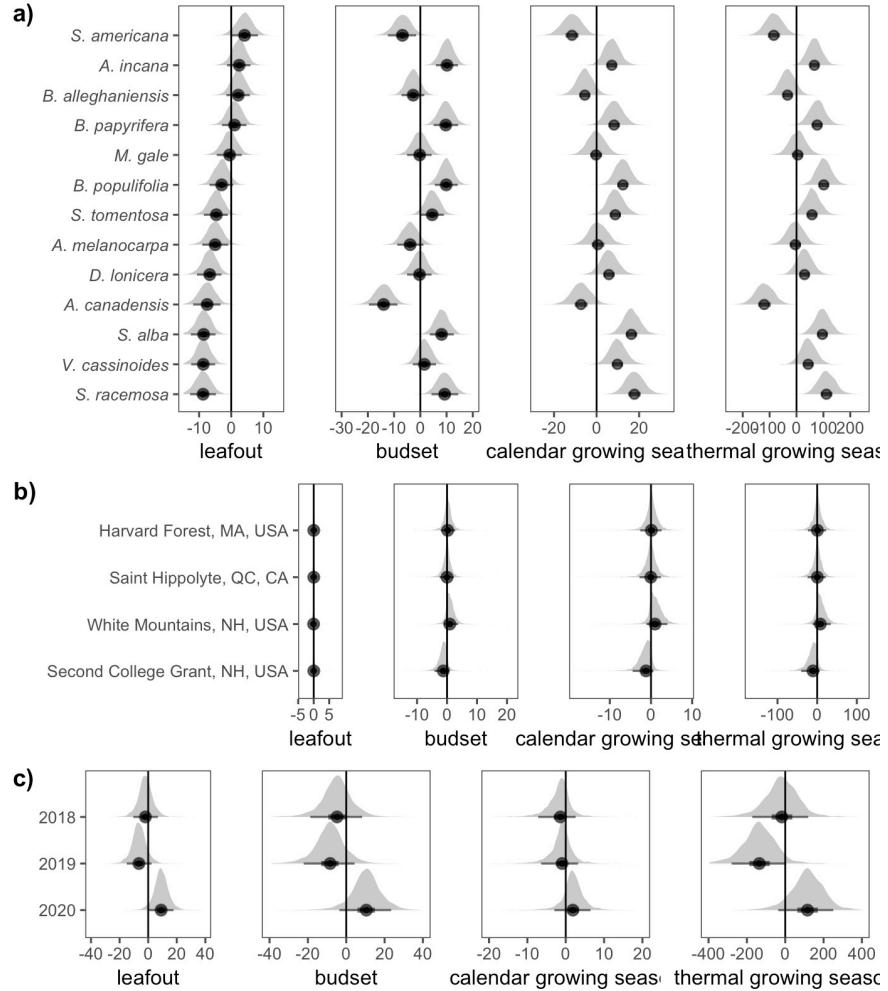


Figure 1: Difference in leafout, budset and growing season length partitioned between species (a) populations (b) and years (c). Point represent the median effect size estimate, and bars the 50% uncertainty intervals. The grey distribution depict the full uncertainty estimate around the estimate.

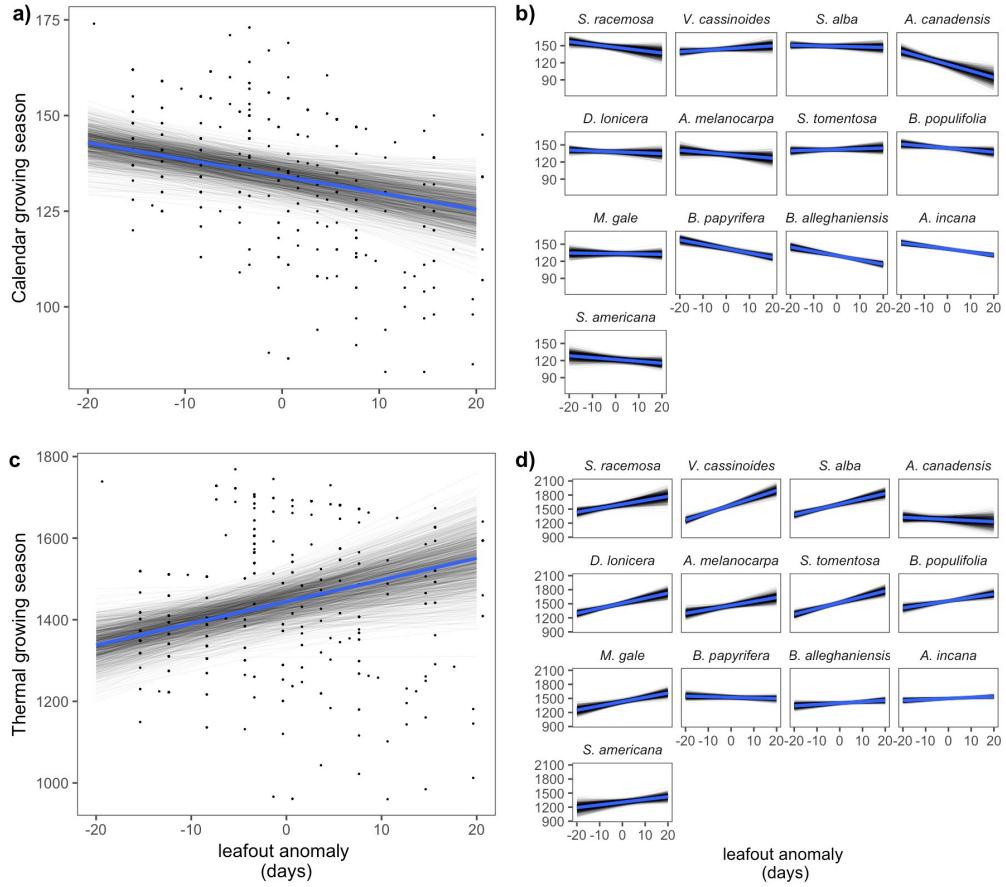


Figure 2: The relationship between Start of Spring (calendar day of leafout) and growing season length differs between the calendar growing season and the thermal growing season. Later leafout resulted in a shorter calendar growing season (a) and this pattern was consistent across species in our study (b). In contrast, an increasing later leafout resulted in a longer thermal growing season (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 blue trend lines represent the mean effect of leafout timing on growing season length and black lines represent 1000 draws from the posterior distribution as a measure of uncertainty. Points in a), and c) represent the raw data (per individual tree per year).

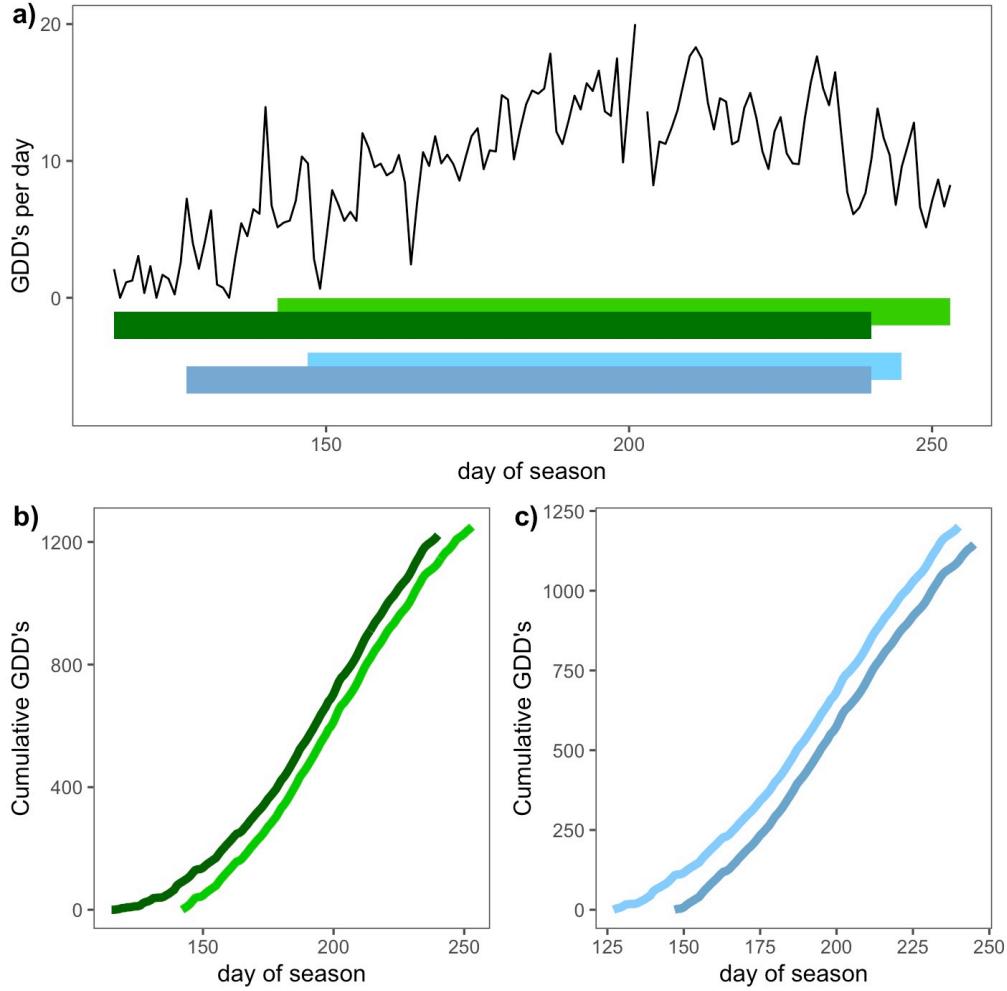


Figure 3: Thermal conditions vary across the calendar growing season, which can generate a complex relationship between the calendar and thermal growing seasons. Panel a) depicts the daily heat sums at the Weld Hill Research Building in 2019 and the calendar growth season of early and late leafing individuals 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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