Phenological differences among species explain why early leafout extends the calendar but not thermal growing season

Dan, Cat, Deidre and Lizzie

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1   Introduction

Terrestrial forests currently sequester 20% of greenhouse gas emissions annually (Shanley *et al.*, 2024; Roe *et al.*, 2021), providing a significant mitigation pathway for climate change. In mid and high latitudes, net carbon uptake is primarily determined by the length of the growing season (White *et al.*, 1999). Most models of carbon storage assume that earlier spring leafout with climate change will drive longer seasons and increased carbon storage, in part offsetting future warming (Churkina *et al.*, 2005; White *et al.*, 1999; Keenan *et al.*, 2014). Recent findings, however, have called this critical assumption into question.

Recent research has 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 (Zani *et al.*, 2020; Norby, 2021a; Zohner *et al.*, 2023). Observations have found that calendar growing seasons have lengthened with climate change (Menzel & Fabian, 1999; Liu *et al.*, 2010), but other studies have found that earlier leafout is often correlated with earlier end-of-season events (Zani *et al.*, 2020; Liu *et al.*, 2016; Keenan & Richardson, 2015). Recent work has suggested early, increased productivity in the growing seasons drives early senescence (Zani *et al.*, 2020), and proposed that plants adjust mid-season based on

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a combination of growing season temperature and daylength (Zohner *et al.*, 2023). Such studies, however, are based generally on large-scale satellite measurements and small-scale single species pot experiments, and contrast with findings from long-term large-scale CO_2 enrichment studies (Norby, 2021b).

These contrasting results suggest fundamental gaps in our understanding of how early-season events (and thermal conditions of the vegetative period?) shape growing season length. How early-season events, such as leafout, affect end-of-season events is poorly understood. While results from satellites (e.g., using NDVI) show a correlation, what exactly is being measured for 'end of season' is not clearly tied to a plant-scale event. Yet any connections would likely start at the individual plant level, where we rarely if ever have good measures of start and end of season events together. Further, because end-of-season events are often more locally adapted—with plants using unique photoperiods to cue important events such as budset (Bauerle *et al.*, 2012; Soolanayakanahally *et al.*, 2013)—than start-of-season events, these trends may importantly vary across populations (Aitken & Bemmels, 2016). Such population-level studies, however, are based on a very limited number of species (Zeng & Wolkovich, 2024). Species generally vary strongly in their start-of-season phenology, with this being a major factor that can influence forecasts (Morales-Castilla *et al.*, 2024) and land surface models (Ma *et al.*, 2022). Results to date reporting correlation between start- and end-of-season events generally cannot differentiate between different species, populations or individuals, making our inference limited.

Here, we examine how start-of-season events, using leafout, may affect end-of-season, using budset, to determine the length of the growing season. We address this using rarely available plant-scale data—phenological observations over three years from a multi-species common garden study that can test how correlated leafout and budset are in different species across populations and examine which phenological event more strongly influences variation in growing season length. From this, we can understand how start- and end-of-season events together impact the calendar growing season, and its thermal conditions, which connect to potential productivity. This study offers insights into physiology that will allow us to scale from ecosystem level observations to individual mechanisms too, and improve forecasting.

2 Results & Discussion

We found an apparently fundamental—and unexpected trade-off—between early, longer calender growing seasons and the thermal growing season. In our common garden, earlier leafout led to earlier budset (Pearson's correlation coefficient of 0.32 $CI_{95}[0.25, 0.39]$) with implications for the total length of the growing season. Measured in calendar days, the growing season remained consistent over the three year study period (Figure 1c), despite substantial difference among years for leafout and budset. However, we found that a generally later leafout resulted in a longer thermal, or meteorological, growing season, defined here as the period of favorable meteorological conditions for plant growth (Körner *et al.*, 2023) (Figure 2c).

These contrasting results—of a relatively stable growing season measured in calendar days, but one that is 'shorter' in thermal time with earlier leafout—may explain some of the contrasting results of how climate change affects end-of-season events and productivity (Zani *et al.*, 2020). Our results show that earlier leafout may have little effect on the thermal growing season because of unfavorably low temperatures combined with the observed correlation between leafout and budset (Fig: 3a,1). Given that photosynthesis is temperature limited, earlier springs appear 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 (Čufar *et al.*, 2015; Camarero *et al.*, 2022; Dow *et al.*, 2022; Silvestro *et al.*, 2023).

This relationship was strongly species-dependent. with later leafout leading to longer thermal seasons most apparent in species that typically leaf out earlier in the spring relative to others. This included shrubs such as *Sambucus racemosa*, *Viburnum cassiodes*, *Spirea alba*, *Diervella lonicera*, *Aronia melanocarpa Spirea tomentosa* and the tree species *Betula populifolia*. Later-leafout species showed a weaker relationship)(*Betula papyrifera*, *Betula allegheniensis* and *Alnus incana*, Figure 2d).

We can see these dynamics play out by tracking the phenology of four individuals plants as an example. The earlier individual of *Aronia melanocarpa* depicted in Figure 3a, starts growing 24 days before a later

68 individual, but only ceases 13 days before it (i.e., it has a 14 day longer calendar growing season). However,

69 because the 24 day growth advantage it has occurs when thermal conditions are less favorable, it ends up

70 having a shorter thermal growing season (i.e., less change for carbon assimilation) than its later conspecific

71 (Figure 3b). This is not the case for the later leafing species *Myrica gale* where the both the earlier and later

72 leafing individual start growing under more optimal thermal conditions, so the 20 day "head start" the earlier

73 individual incurs results in a both a longer calendar and thermal growing season (Figure 3a,c).

74 *Variation in leafout and budset*

75 Our common garden captured high variation in both leafout and budset, allowing us to examine how the two

76 correlate, but also providing important insights into how both vary across species, populations and years.

77 Consistent with a high number of studies finding species and year-to-year environmental variation drive leafout

78 variation (Delpierre *et al.*, 2024; Donnelly *et al.*, 2017; Polgar & Primack, 2011), we found high variance in

79 leafout timing among species and years ($\sigma_{species}$:8.22 UI_{95}[4.82,11.92], σ_{year}:10.62 UI_{95}[3.63,21.6], Figure

80 1a,b). Population level variation was low ($\sigma_{population}$:0.61, UI_{95}[0,1.86], Figure 1c). *Sambucus racemosa*

81 was typically the first species to leafout in the spring, leafing out approximately two weeks before *Sorbus*

82 *americana* the last species to leaf out (Figure 1c). There were no differences in leafout timing among the

83 four populations included in our study (Figure 1c). Leafout was the earliest in 2019 and the latest in 2020

84 (Figure 1c).

85 Spring phenological phases are reported to be more plastic than autumn ones (McKown *et al.*, 2014; Aitken

86 & Bemmels, 2016; Vico *et al.*, 2021), but we found that, relative to leafout, variance in budset timing

87 was higher for species, years and populations ($\sigma_{species}$:9.84 UI_{95}[6.36,13.89], σ_{year}:15.13 UI_{95}[4.36,31.39],

88 $\sigma_{population}$:2.35, UI_{95}[0,6.39], Figure 1), but followed similar relative contributions (highest variance in year,

89 lowest in population). Budset was earliest for *Amelanchier canadensis* and latest for *Alnus incana* and *Betula*

90 *paperifera* with more than three weeks between them (Figure 1a). Following trends leafout and our finding

91 that earlier leafout correlates with earlier budset, 2019 had the earliest budset and 2020 the latest (Figure

92 1b).

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These results are somewhat surprising as budset is commonly thought to be strongly dependent on population, with different populations requiring different critical photoperiods to trigger budset and leading to relatively stable budset dates across years (Soolanayakanahally2013, and find some review paper). Supporting this—and in contrast to leafout—we found that populations did vary in their budset. Populations from the Second College Grant set buds approximately three days before those from the White Mountains, but these differences statistically weak (Figure 1b) and small. Our results suggest we need much more work on additional species, as results to date have focused mainly on one genus (*Populus*) and more efforts to understand how environmental factors beyond photoperiod may affect budset. Even for *Populus balsamifera*, the species suggested to be mainly photoperiod-controlled, recent work suggests temperature may also play a major role (Michelson2018).

High variation across species in both their leafout and budset timing lead to species driving the most variation in growing season length ($\sigma_{species}$:14.54, UI_{95}[9.32,20.28], with less variation among years (σ_{year}:4.53, UI_{95}[0.21,12.03], Figure 1b) and little variation explained by population ($\sigma_{population}$:2.43, UI_{95}[0,6.4], Figure 1c). Due to it's early leafout and late budset *S.racemosa* had the longest calendar growing season of the species in our study. *A. canadensis* and *S. americana* had the shortest growing seasons, though for *A. canadensis* this was due to early budset and for *S. americana* late leafout (Figure 1a). Population level differences in calendar growing season were determined by differences in budset, and followed the same pattern with Grant marginally earliest and white mountains latest, with high uncertainty. (Figure 1b).

Ecological and forecasting implications

Our multi-species common garden study showed that for already 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. For early leafout species, delayed leafout resulted in a longer thermal growing season. This relationship was in part explained by positive correlations between leafout and budset where later leafing individuals also set buds later, extending their growth into that later part of the season when thermal conditions were more favorable. For later leafing species, earlier leafout did not substantially reduce their thermal growing season. This is likely because for them, even an earlier relative leafout still occurred

in thermally favorable times of the season, and a relatively small advance in calendar time resulting in a proportionately large gain in thermal sums.

Our results show that there is 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 (), implying there may be little to gain from a carbon perspective.

This result raises question 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 (). 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, is highly dependent on biotic interactions. In our study, the species that leafed out the earliest are under story 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 thermally bad conditions. In fact, some studies suggest that under story shrubs get all/most of their carbon before canopy closure (AUGSPURGER *et al.*, 2005).

This study shows linking phenological growing season to primary productivity requires account for phenological variation at multiple scales (individual, species level, multiple phases). These results suggest that progress will require more efforts to understand and model species-level shifts in phenology. While satellite observations can document intriguing trends (e.g., Zohner *et al.*, 2023), observations that include far more species at a finer scale are likely critical for mechanistic understanding. In particular our results suggest budset may be far more variable year to year than often suggested (Michelson *et al.*, 2018) but see(mckown2014, Vander2016). Recent work supports this, by highlighting an important role for temperature alongside photoperiod, in driving budset (Olsen *et al.*, 2014; **?**). Further, most work on budset in broadleaf species comes from one genus (*Populus spp.*) highlighting a critical gap, as a focus on single species may not always predict broad scale trends (Morales-Castilla *et al.*, 2024).

Of course, budset is just one of many ways that plants senescence each year – generally at different times for different events (Michelson *et al.*, 2018). Understanding which metrics of end of season events correlate best with growth and carbon gain are well-established critical needs (I don't have a ref for this but am sure someone has said it). 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

3   Methods

3.0.1   The common garden at Weld Hill

In 2014-2015, we collected seeds of 18 species woody plants from four field sites in eastern Northern America spanning approximately a 3.5 degree latitudinal gradient. The four field sites included Harvard Forest (42.55°N, 72.20°W), the White mountains (44.11°N, 52.14°W), Second College Grant of Dartmouth College (44.79°N, 50.66°W), and St. Hippolyte, CN (45.98°N, 74.01°W). We transported all seed back the the Weld Hill Research Building at the Arnold Arboretum in Boston MA (42.30°N, 71.13°W) where we germinated seeds following standard germination protocols, and grew them to seedling stages in the research greenhouse. In Spring of 2017 we planted them out to establish the common garden at Weld hill. Plantings were randomized between 16 plot blocks. Individuals that were too small to survive outside were maintained in the growth facilities for an additional year and out planted in the early spring of 2018. Plots were divided between tree plots which included species *Acer pensylvanicum, Amelanchier canadensis, Alnus incana, Betula papyrifera, Betula populifolia, Beluta alleghaniensis, Quercus alba*, and *Quercus rubra* and shrub plots which included the remaining species and shade cloth (Table 1). Plots were regularly weeded and watered throughout the duration of the study and were pruned in the fall of 2020.

3.0.2 Phenological monitoring:

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

3.0.3 Data analysis

To better understand the role that variation in leafout and budset phenology play in determining calendar growing season length among species populations and years we fit a Bayesian hierarchical with a Gaussian probability distribution. We calculated growing season duration by subtracting the day of leafout from the day of budset. We fit an intercept only model with phenophase timing (leafout, budset or growing season duration) as the response variable and partial pooling across species, populations and years. We only included observations with both budset and leafout observed on the same plant in this analysis ($n=595$).

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

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

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All models were fit in the R package brms on 4 chains with a 4000 iteration warm-up and 1000 sampling iterations on each chain for a total of 4,000 sampling iterations across all chains. We evaluated model fit, with no divergent transitions, rhats less than 1.01 and high effective sample sizes. All analysis were done in R.

4 Figures
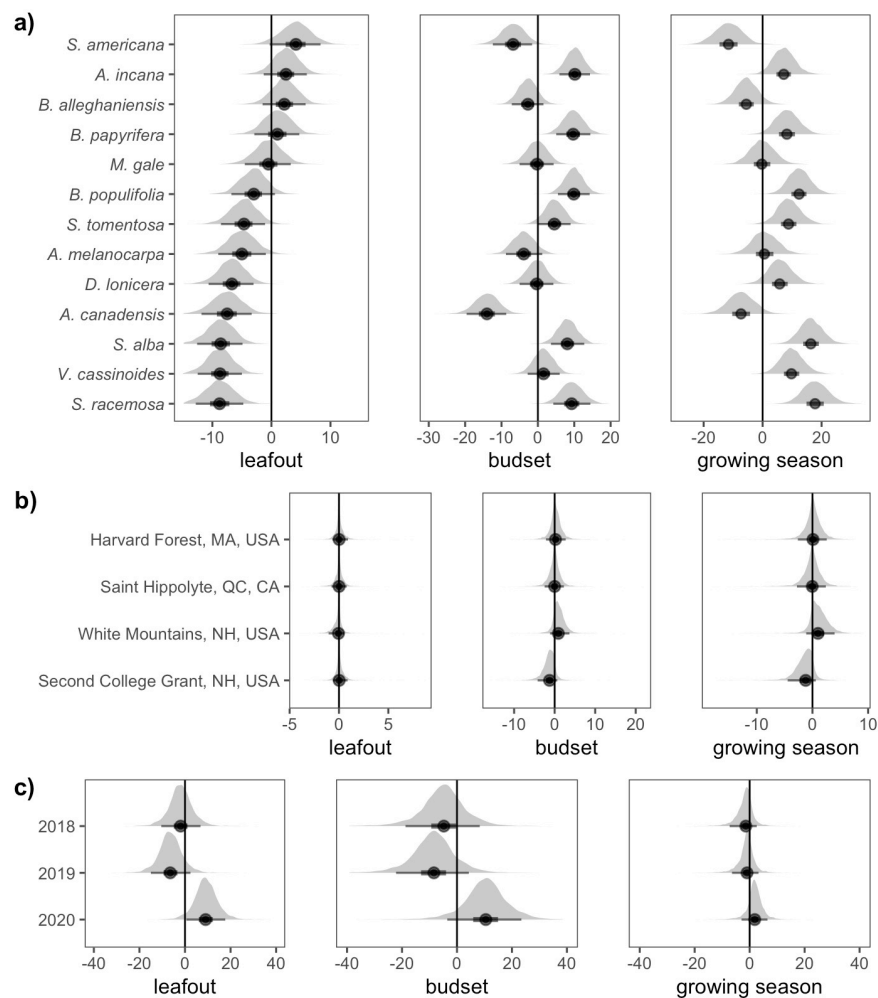

Figure 1: Difference in leafout, budset and calendar growing season length partitioned between species (a) populations (b) and years (c). Point represent the median effect size estimate, and bars the 50% uncertainty intervals. The grey distribution depict the full uncertainty estimate around the estimate.
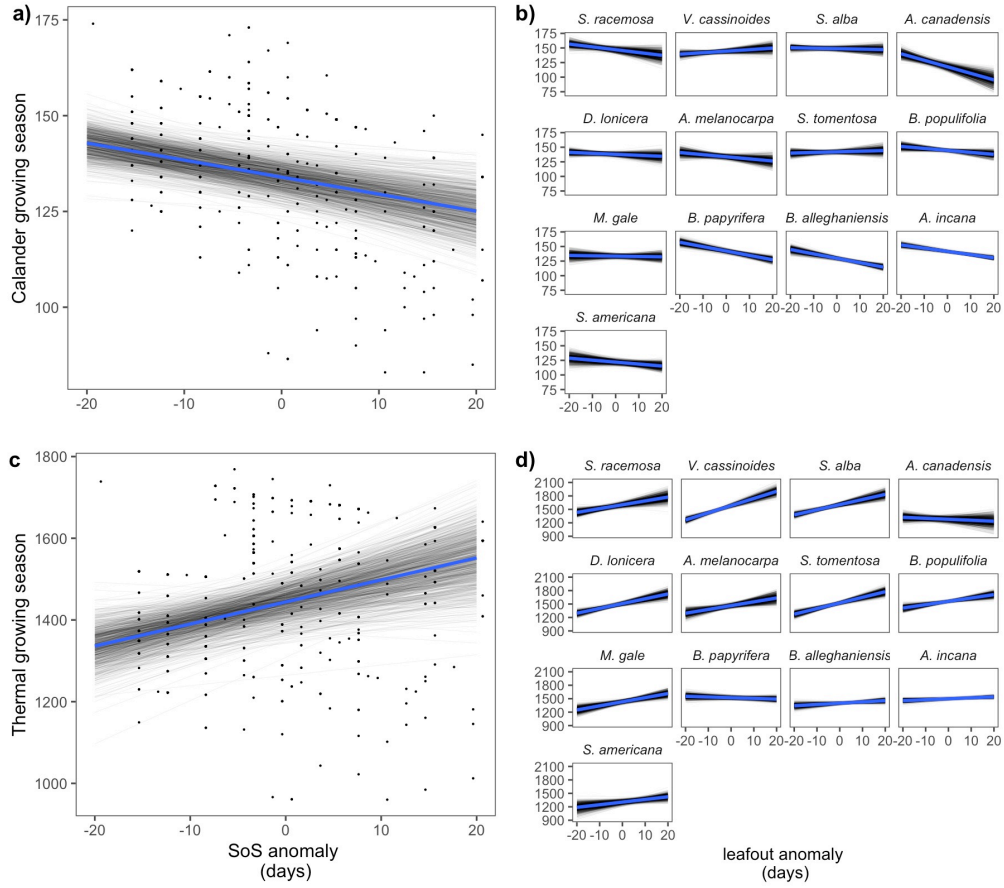
Figure 2: The relationship between Start of Spring (SoS; calendar day of leafout) and growing season length differs between the calendar growing season and the thermal growing season. An increasing later SoS resulted in a shorter calendar growing season (panel a) and this pattern was consistent across species in our study (panel b). In contrast, an increasing later SoS resulted in a longer thermal growing season (panel c) though this effect was stronger for species that typically leafout earlier in the season—panels in c) are display in the typical order of leafout among species. The blue trend lines represent the mean effect of SoS 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. **to do: rename x-axis on b and d and write our the species names**
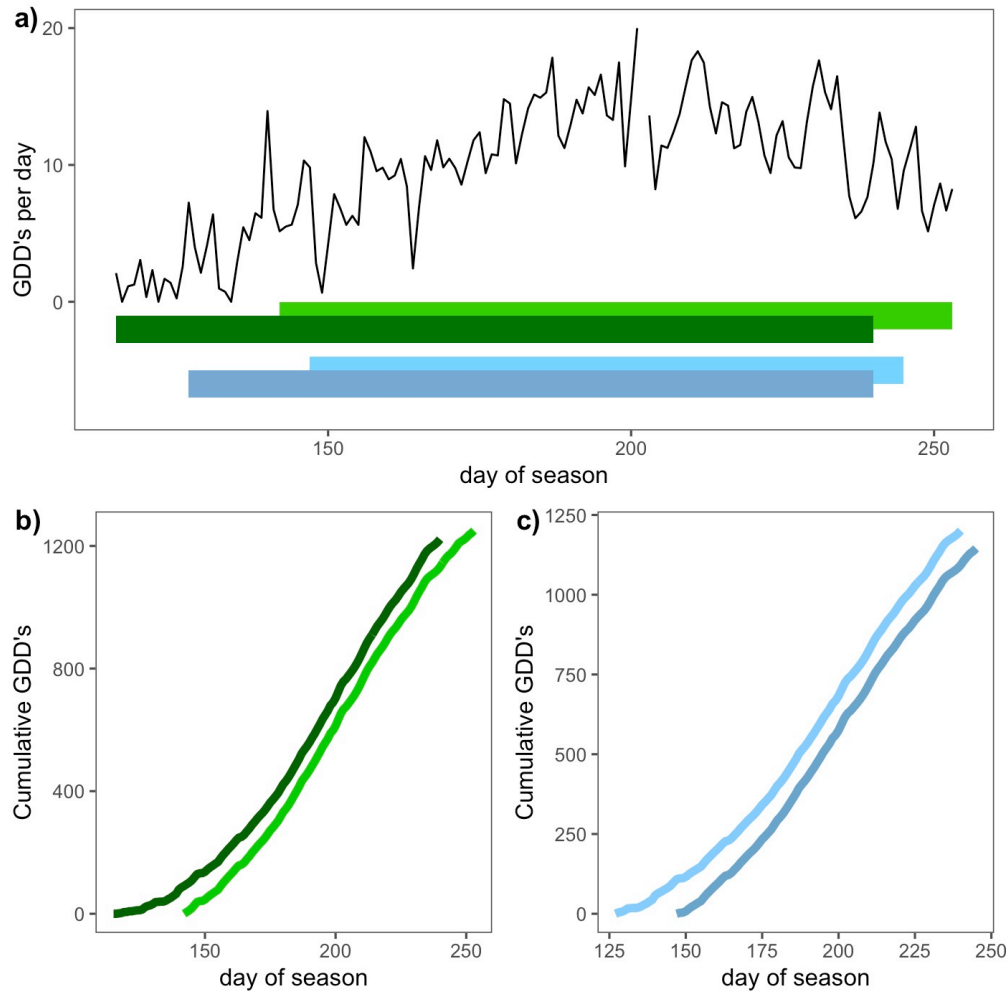
Figure 3: Thermal conditions vary across the calendar growing season, which can generate a complex relationship between the calendar and thermal growing seasons. Panel a) depicts the daily heat sums at the Weld Hill Research Building in 2019 and the calendar growth season of early and late leafing individuals 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)

Table 1: Species list

Species	functional group
Acer pensylvanicum	tree
Acer spicatum	tree
Alnus incana	shrub
Amelanchier canadensis	shrub
Aronia melanocarpa	shrub
Betula alleghaniensis	tree
Betula papyrifera	tree
Betula populifolia	tree
Diervilla lonicera	shrub
Myrica gale	shrub
Sambucus racemosa	shrub
Sorbus americana	shrub
Spiraea alba	shrub
Spiraea tomentosa	shrub
Viburnum cassinoides	shrub

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