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

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

19 question this assumption.

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

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

We found unexpected trade-off between early calender growing seasons and thermal growing seasons, in which later leafout in calendar time resulted in a longer thermal growing season, though this relationship was strongest in earlier leafing species. At the community level, earlier leafout was correlated with earlier

which later leafout in calendar time resulted in a longer thermal growing season, though this relationship
was strongest in earlier leafing species. At the community level, earlier leafout was correlated with earlier
budset, resulting in a relatively stable calendar growing period over the three years—though later leafing
individuals tended to have shorter growing periods. Earlier leafout may have little advantage to the thermal
growing season because early lower temperature are less favorable for photosynthesis, and the correlation
between leafout and budset suggest early individual will miss out on later season conditions more favorable
for photosynthesis. This relationship may explain some of the contrasting results of how climate change affects
growing season length and productivity. This study shows linking phenological growing seasons to carbon
storage requires integrating existing ecosystem measures with phenological variation at multiple scales, and
that progress will require more efforts to understand and model species-level shifts in phenology.

## 2 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

- 42 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;
- 44 Keenan et al., 2014). Current findings, however, have called this critical assumption into question. Recent
- 45 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.,
- <sup>47</sup> 2020; Norby, 2021a; Zohner *et al.*, 2023).
- 48 Some of this uncertainty may stem from the fact that there are multiples ways to measure the growing season.
- 49 The most common and intuitive way to measure the growing season is to use calendar time (i.e., the number
- 50 of days between the start and end of the growing season). Observations have found that calendar growing
- seasons have lengthened with climate change (Menzel & Fabian, 1999; Liu et al., 2010), but other studies
- base found that earlier leafout is often correlated with earlier end-of-season events (Zani et al., 2020; Liu
- <sup>53</sup> et al., 2016; Keenan & Richardson, 2015).
- An alternative to the calendar growing season is the thermal growing season, defined here as the period of
- favorable meteorological conditions for plant growth (Körner et al., 2023). The thermal growing season is
- measure in thermal time, or growing degree days, a temperature derived measure of time that accumulates
- when temperatures are above a certain minimal threshold (Chuine, 2000; Moore & Remais, 2014; Yang et al.,
- <sup>58</sup> 1995). Because plant photosynthetic rates increase with temperature increases (Farquhar et al., 1980) from
- the cool spring to warm summers in the temperate zone , the thermal growing season is mechanistically
- $_{60}$  related to primary productivity, suggesting it may be a better proxy for relating growing season length to
- 61 carbon gain than calendar time. Importantly, depending on the temperature over the course of a growing
- 62 season, years with substantially different calendar growing seasons can have very similar thermal growing
- 63 seasons, or vice versa.
- Recent work has suggested early, increased productivity in the calendar growing seasons drives early senes-
- cence (Zani et al., 2020), and proposed that plants adjust mid-season based on a combination of growing season
- temperature and daylength (Zohner et al., 2023), this maintaining a consistent thermal growing season. Such

studies, however, are based generally on large-scale satellite measurements and small-scale single species pot 67 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 end-of-season events. While results from satellites (e.g., using NDVI) show a correlation between the star and end of the season, the signature that is 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 startof-season events, these trends may importantly vary across populations (Aitken & Bemmels, 2016). Such 76 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 deter-82 mine 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 how this relates to the thermal growing season, 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.

### $_{\scriptscriptstyle 10}$ 3 Results & Discussion

#### 91 3.1 Variation in leafout and budset

Our common garden captured high variation in both leafout and budset, allowing us to examine how the two correlate, but also providing important insights into how both vary across species, populations and years. Consistent with a high number of studies finding species and year-to-year environmental variation drive leafout variation (Delpierre et al., 2024; Donnelly et al., 2017; Polgar & Primack, 2011), we found high variance in leafout timing among species and years ( $\sigma_{species}$ :8.22  $UI_{95}$ [4.82,11.92],  $\sigma_{year}$ :10.62  $UI_{95}$ [3.63,21.6], Figure 1a,b). Population level variation was low ( $\sigma_{population}$ :0.61,  $UI_{95}[0,1.86]$ , Figure 1c). Sambucus racemosa was typically the first species to leafout in the spring, leafing out approximately two weeks before Sorbus americana the last species to leaf out (Figure 1a). There were no differences in leafout timing among the four populations included in our study (Figure 1b). Leafout was the earliest in 2019 and the latest in 2020 (Figure 1c). Spring phenological phases are reported to be more plastic than autumn ones (McKown et al., 2014; Aitken 102 & Bemmels, 2016; Vico et al., 2021), but we found that, relative to leafout, variance in budset timing was higher for species, years and populations ( $\sigma_{species}$ : 9.84  $UI_{95}$ [6.36,13.89],  $\sigma_{year}$ :15.13  $UI_{95}$ [4.36,31.39],  $\sigma_{nonulation}$ :2.35,  $UI_{95}$ [0,6.39], Figure 1), but followed similar relative contributions (highest variance in year, lowest in population). Budset was earliest for Amelanchier canadensis and latest for Alnus incana and Betula paperifera with more than three weeks between them (Figure 1a). Following trends leafout and our finding 107 that earlier leafout correlates with earlier budset, 2019 had the earliest budset and 2020 the latest (Figure 108 1a). 109 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 111 stable budset dates across years (?), (and find some review paper). Supporting this—and in contrast to 112 leafout—we found that populations did vary in their budset. Populations from the Second College Grant 113

set buds approximately three days before those from the White Mountains, but these differences statistically 114 weak (Figure 1b) and small. Our results suggest we need much more work on additional species, as results to 115 date have focused mainly on one genus (Populus) and more efforts to understand how environmental factors 116 beyond photoperiod may affect budset. Even for *Populus balsamifera*, the species suggested to be mainly 117 photoperiod-controlled, recent work suggests temperature may also play a major role (Michelson et al., 2018). 118 High variation across species in both their leafout and budset timing lead to species driving the most vari-119 ation in growing season length ( $\sigma_{species}$ :14.54,  $UI_{95}$ [9.32,20.28], with less variation among years ( $\sigma_{year}$ :4.53, 120  $UI_{95}[0.21,12.03]$ , Figure 1b) and little variation explained by population ( $\sigma_{population}$ :2.43,  $UI_{95}[0.6.4]$ , Figure 121 1). Due to it's early leafout and late budset S.racemosa had the longest calendar growing season of the species 122 in our study. A. canadensis and S. americana had the shortest growing seasons, though for A. canadensis 123 this was due to early budset and for S. americana late leafout (Figure 1a). Population level differences in 124 calendar growing season were determined by differences in budset, and followed the same pattern with the 125 Second College Grant populations marginally earliest and White Mountains latest, with high uncertainty. 126 (Figure 1b). 127

# 3.2 Comparing calendar to thermal growing seasons: why longer calendar seasons may result in increased primary productivity

Across all species, populations and years, later start of spring (i.e., leafout) in calendar time was associated with shorter growing seasons (mean estimated effect: -0.44,  $UI_{95}[-0.73, -0.16]$ ), and this associate was apparent to varying degrees in all species in our common garden (Fig. 2a,b). However when we controlled for species and population level differences, we found earlier leafout led to earlier budset (Pearson's correlation coefficient of 0.32  $CI_{95}[0.25, 0.39]$ ). resulting in a relatively stable calendar growing season 1c).

In contrast, we found an apparently fundamental—and unexpected trade-off—between early, longer calender growing seasons and thermal growing seasons. Across species, populations and years, a generally later leafout in calendar time resulted in a longer thermal growing season (mean estimated effect:  $5.49, UI_{95}[1.54, 9.23]$ ;

Figure 2c). These contrasting results—of a relatively stable growing season measured in calendar days at 138 the community scale, but one that is 'shorter' in thermal time with earlier leafout—may explain some of 139 the contrasting results of how climate change affects end-of-season events and productivity (Zani et al., 140 2020). Our results show that earlier leafout may have little effect on the thermal growing season because of 141 unfavorably low temperatures combined with the observed correlation between leafout and budset (Fig.,1). 142 Given that photosynthesis is temperature limited, earlier springs appear to provide limited opportunity for 143 substantial growth yet may deprive plants of fully using late-season warmth. This may explain why multiple 144 studies have failed to find correlations between longer seasons and increased plant growth (Cufar et al., 2015; 145 Camarero et al., 2022; Dow et al., 2022; Silvestro et al., 2023).

This relationship was strongly species-dependent. Later leafout in calendar time lead to longer thermal seasons 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 (Figure 3, dark green bars) starts growing 24 days before a
later individual (light green bars), but only ceases 13 days before it (i.e., it has a 14 day longer calendar
growing season). However, because the 24 day growth advantage it has occurs when thermal conditions are
less favorable, it ends up having a shorter thermal growing season (i.e., less change for carbon assimilation)
than its later conspecific (Figure 3a,b). This is not the case for the later leafing species Myrica gale where
the both the earlier (dark blue bars) and later leafing individual (light blue bars) start growing under more
optimal thermal conditions, so the 20 day "head start" the earlier individual incurs results in a both a longer
calendar and thermal growing season (Figure 3a,c).

#### 3.3 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, 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.

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 (Shen et al., 2014; Geng et al., 2020), 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 176 species tracking spring warming due to climate change have increased performance relative to non-trackers 177 (Cleland et al., 2012). In our study we only evaluated the thermal conditions that may affect photosynthesis, 178 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 181 severely limited later in the growing season as canopy trees leaf out. It may be that for these species, the 182 light availability early in the season necessitates leafing out in suboptimal thermal conditions. In fact, some 183 studies suggest that under story shrubs get all/most of their carbon before canopy closure (AUGSPURGER 184 et al., 2005).

This study shows linking phenological growing season to primary productivity requires account for pheno-186 logical variation at multiple scales (individual, species level, multiple phases). These results suggest that 187 progress will require more efforts to understand and model species-level shifts in phenology. While satellite 188 observations can document intriguing trends (e.g., Zohner et al., 2023), observations that include far more 189 species at a finer scale are likely critical for mechanistic understanding. In particular our results suggest 190 budset may be far more variable year to year than often suggested (Michelson et al., 2018) but see 2014, 191 Vander 2016. Recent work supports this, by highlighting an important role for temperature alongside pho-192 toperiod, in driving budset (Olsen et al., 2014; ?). Further, most work on budset in broadleaf species comes 193 from one genus (Populus spp.) highlighting a critical gap, as a focus on single species may not always predict 194 broad scale trends (Morales-Castilla et al., 2024). Of course, budset is just one of many ways that plants begin to transition from growth to dormancy each year 196

Of course, budset is just one of many ways that plants begin to transition from growth to dormancy 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 (Gallinat

et al., 2015). 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.

### $_{202}$ 4 Methods

### 203 4.0.1 The Common Garden

In 2014-2015, we collected seeds of 18 species woody plants from multiple parent plants at 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 seeds 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 the spring of 2017 we outplanted seedlings to establish the Commmon 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 outplanted 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. Survival of *Acer spicatum*. *Acer pensylvanicum*, *Vaccinium myrtilloides Quercus alba*, and *Quercus rubra* was limited and as such these species are not included in the following analyses. Based on survivorship in the common garden, our subsequent analyses are based on offspring from 1-10 individual parent plants per field site.

#### 221 4.0.2 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.

#### $_{ m 29}$ 4.0.3 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" (Jakub Nowosad, 2019) using a 10 C base temperature with minimum and maximum daily temperature data from the weld hill weather station.
- All models were fit in the R package "brms" (Bürkner, 2018) 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. We performed all analyses in R version 4.1.2 (R Core Team, 2021).

# 5 Figures

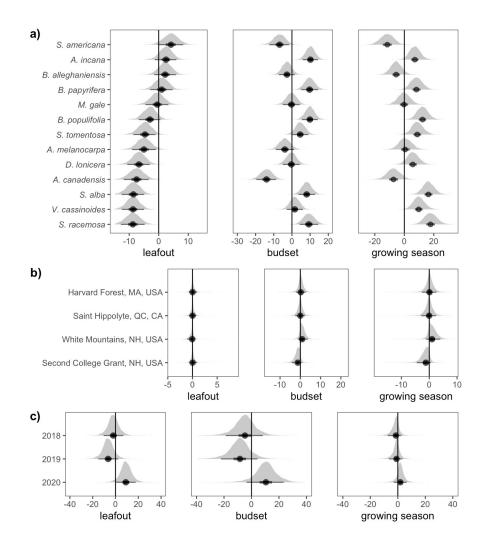


Figure 1: Difference in leafout, budset and calendar growing season length partitioned between species (a) populations (b) and years (c). Point represent the median effect size estimate, and bars the 50% uncertainty intervals. The grey distribution depict the full uncertainty estimate around the estimate.

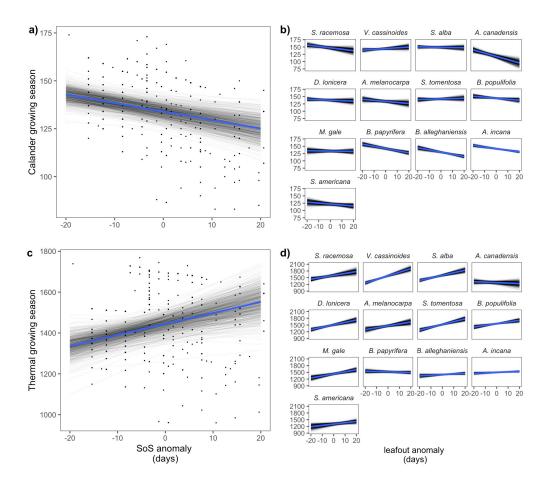


Figure 2: The relationship between Start of Spring (SoS; calendar day of leafout) and growing season length differs between the calendar growing season and the thermal growing season. An increasing later SoS resulted in a shorter calendar growing season (a) and this pattern was consistent across species in our study (b). In contrast, an increasing later SoS 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) 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.

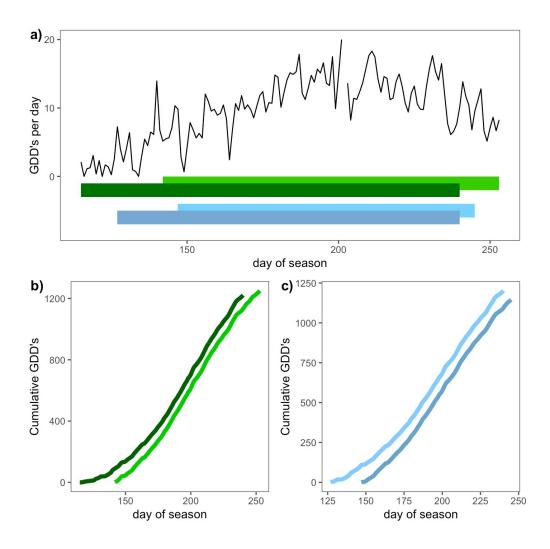


Figure 3: Thermal conditions vary across the calendar growing season, which can generate a complex relationship between the calendar and thermal growing seasons. Panel a) depicts the daily heat sums at the Weld Hill Research Building in 2019 and the calendar growth season of early and late leafing individuals 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	n
Acer pensylvanicum	tree	2
Acer spicatum	tree	NA
$Alnus\ incana$	shrub	31
$A melanchier\ canadensis$	shrub	6
$Aronia\ melanocarpa$	shrub	12
$Betula\ alleghaniens is$	tree	24
Betula papyrifera	tree	13
Betula populifolia	tree	24
Diervilla lonicera	shrub	16
Myrica gale	shrub	15
Quercus alba	tree	NA
Quercus rubra	tree	NA
$Sambucus\ racemosa$	shrub	11
$Sorbus\ americana$	shrub	5
Spiraea alba	shrub	19
$Spiraea\ tomentosa$	shrub	21
Vaccinium myrtilloides	shrub	NA
$Viburnum\ cassinoides$	shrub	25

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