

Carry-over effect of a longer season on the following year's tree growth

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Introduction

Human-induced greenhouse gas emissions have affected Earth's climate and are projected to keep changing it for many centuries (Intergovernmental Panel On Climate Change, 2023). The most frequently observed biological impact of climate change over the past decades is major changes in phenology—the timing of recurring life history events (Parmesan & Yohe, 2003; Cleland *et al.*, 2007; Lieth *et al.*, 1974; Woolway *et al.*, 2021; Menzel *et al.*, 2006). Shifts in spring and autumn phenology modify when the growing season starts and when it ends. These shifts in growing season length could have impacts on ecosystems, but anticipating these consequences requires understanding how much, and why it has changed (Duputié *et al.*, 2015).

Spring phenological events (e.g. budburst and leafout) have been advancing from 0.5 (Wolfe *et al.*, 2005) to 4.2 days/decade (Chmielewski & Rötzer, 2001; Fu *et al.*, 2014) and are mainly driven by temperature (Chuine, 2010; Cleland *et al.*, 2007; Peñuelas & Filella, 2001), especially for trees. In contrast, autumn phenology (e.g. budset and leaf senescence) has delayed with climate change—though shifts in the autumn have been much smaller than those in the spring (Gallinat *et al.*, 2015; Jeong & Medvigy, 2014)—and its drivers are also far less understood (Piao *et al.*, 2019).

Shifts in spring and autumn phenology in trees support a long-lasting and intuitive assumption that earlier spring and delayed autumn events extend seasons and thus increase growth (Keenan *et al.*, 2014; Stridbeck *et al.*, 2022). However, research from recent years has cast doubt on this hypothesis (Dow *et al.*, 2022; Green & Keenan, 2022; Silvestro *et al.*, 2023). For instance, Dow *et al.* (2022) showed that despite an earlier growth onset, longer seasons did not increase the growth rate nor overall annual increment in trees. This could substantially affect forest carbon-cycle model projections on and thus feedbacks to future climate (Richardson *et al.*, 2013; Swidrak *et al.*, 2013). These projections could be impacted by the different effects that an earlier start and a later end of season have on trees, which we propose to study under experimental conditions.

Experiments are extremely useful in teasing apart co-occurring realities in natural environments. For example, warm springs and severe droughts later in the summer often happen together within a single year, making it difficult to tease these effects apart from observational data. Manipulative experiments, in contrast, have the capacity to separate the relative effect of each phenomenon (Morin *et al.*, 2010; Primack *et al.*, 2015), but also have major limitations, especially when working on trees. Logistical constraints of working with adult trees mean that experiments are most often performed on juvenile trees. While saplings are critical for their role in forest regeneration projections, their responses often do not directly translate to mature trees, which hold the overwhelming carbon biomass proportion of forests (Augspurger & Bartlett, 2003; Silvestro *et al.*, 2023; Vitasse, 2013). However, even if young trees are often more plastic than adult forms, their responses can still provide valuable insights into differences across species and populations (Wolkovich *et al.*, 2025).

We aim to understand how different tree species, vary in their growth responses to different season lengths. To achieve this, we deployed a large-scale experiment, during which we artificially controlled the growing season length for seven species of tree saplings (2-3 years old). With this experiment our objectives are to

assess tree species' potential to prolong or stretch their activity schedule and analyze how this translates (or not) into growth, during the current year (2024) and in the following year (2025).

Methods

Species selection and growing conditions

We used seven species of tree saplings for our experiment (Fuelinex). We arranged the trees in three blocks, each containing all 6 treatments and 7 species, with two of these blocks placed under an open-walled and well-ventilated polytunnel greenhouse. All saplings were connected to a drip irrigation system (40 PVC frame from Netafilm 54 with a Toro controller) to maintain constant irrigation across the season.

Tree measurements and biomass

: Using red paint, we marked the trees on their trunk at 3 cm from the soil in February 2024 (2023 growing season). Then we measured the diameter at the top of that mark using a digital calliper (accuracy $\pm 0.01\text{cm}$) and height from that mark to the bottom of the highest apical bud with a metal ruler (accuracy $\pm 0.1\text{cm}$). We measured those two same points in the winter (2024 growing season) and in the fall (2025 growing season) of 2025. In the fall of 2025, we destructively collected above ground biomass after measuring diameter and height.

Experimental design

Individuals from each species were randomly selected for a full factorial design of Warm/Cool, Spring/Fall treatments with two additional treatments to test nutrient effects in the fall (Figure 3), for a total of 15 replicates/treatment/species. On 6 March 2024, we placed the Cool Spring individuals in climate chambers to delay the start of their growing season, while the Warm Spring replicates remained at ambient conditions. Once all Warm Spring individuals had fully leafed out, we removed the Cool Spring replicates from the chambers and placed them back at ambient conditions for the whole summer. On 4 September 2024, we placed the trees for the Warm Fall treatments in the climate chambers. The temperature was set to fit the mean 30-year weekly maximum temperature of the previous month (e.g. 1st week of September set to the average of the 1st week of August). The Cool Fall treatment trees remained at ambient conditions. In 2025, all the trees were kept at ambient conditions together at Totem field during which we recorded the same phenophases.

Statistical analyses

Using diameter (RCD), height (H) and above-ground biomass (B) for 2025, we fitted two allometric coefficients (β_1) and (β_2) for each species, using the following equation for tree saplings from [Annighöfer*].

$$\begin{aligned} B &\sim \text{logNormal}(\mu, \sigma_{allo}) \\ \mu &= \beta_1 \times (RCD^2 \times H)^{\beta_2} \\ \beta_1 &\sim \text{logNormal}(\log(0.5), 0.3) \\ \beta_2 &\sim \text{Normal}(0.7, 0.2) \\ \sigma_{allo} &\sim \text{Normal}(0, 2) \end{aligned}$$

We used 2000 warmup and 1000 sampling iterations, 4 chains using initial conditions for [β_1, β_2 and σ_y]. We used 4000 random draws from the marginal posterior distribution with the error for the two allometric coefficients to estimate the corresponding biomass of the first (2023), second (2024) and the third (2025) diameter and height measurements. Then using a mean biomass point estimate for each tree at each year, we calculated the growing season increment of 2024 (ΔB_1) and 2025 (ΔB_2). Where ($\Delta B_1 = AGB2024 - AGB2023$) and ($\Delta B_2 = AGB2025 - AGB2024$).

Carry-over effect model

Using the estimated biomass increment for 2024 and 2025, we jointly fit ΔB_1 and ΔB_2 using Stan with the rstan package version 2.32.7 (Carpenter *et al.*, 2017) to run the Stan code in R. [add priors, chains, rhat, etc.]

$$\Delta B_1 \sim \mathcal{N}(\mu_1, \sigma_y) \quad (1)$$

$$\mu_1 = \begin{cases} \alpha_{cc1} & \text{if trt = CC} \\ \alpha_{wc1} & \text{if trt = WC} \\ \alpha_{cw1} & \text{if trt = CW} \\ \alpha_{ww1} & \text{if trt = WW} \end{cases} \quad (2)$$

$$\Delta B_2 \sim \mathcal{N}(\mu_2, \sigma_y) \quad (3)$$

$$\mu_2 = \begin{cases} \alpha_{cc2} & \text{if trt = CC} \\ \alpha_{wc2} & \text{if trt = WC} \\ \alpha_{cw2} & \text{if trt = CW} \\ \alpha_{ww2} & \text{if trt = WW} \end{cases} \quad (4)$$

$$\sigma_y \sim \text{logNormal}(0, 0.5) \quad (5)$$

Because we have little information as the relative response to each species to the different treatments, we used weakly logNormal priors for each treatment parameter:

$$\alpha_{cc,wc,cw,ww} \sim \text{logNormal}(1, 1) \quad (6)$$

Derived treatment contrasts (Year 1):

$$\alpha_1 = \alpha_{cc1} \quad (7)$$

$$\alpha_{S1} = \alpha_{wc1} - \alpha_{cc1} \quad (8)$$

$$\alpha_{F1} = \alpha_{cw1} - \alpha_{cc1} \quad (9)$$

$$\alpha_{SF1} = \alpha_{ww1} - \alpha_{cc1} - \alpha_{S1} - \alpha_{F1} \quad (10)$$

Derived treatment contrasts (Year 2):

$$\alpha_2 = \alpha_{cc2} \quad (11)$$

$$\alpha_{S2} = \alpha_{wc2} - \alpha_{cc2} \quad (12)$$

$$\alpha_{F2} = \alpha_{cw2} - \alpha_{cc2} \quad (13)$$

$$\alpha_{SF2} = \alpha_{ww2} - \alpha_{cc2} - \alpha_{S2} - \alpha_{F2} \quad (14)$$

Results

Allometry

Biomass increased with volume accross all species and while our model appears to generally fit the data well, it might be underfit for *P. virgiana* (Figure 1). Retrodictive check histogram across the whole data is presented in (Figure 4).

Main model

For the growing season during which the treatments occurred (2024), the treatment effect on each species is different. Indeed, for Acer and Prunus, biomass was constant across treatments, except for a slight positive effect for Prunus with WW. As for Betula, the differences were not high, but the warm spring treatments

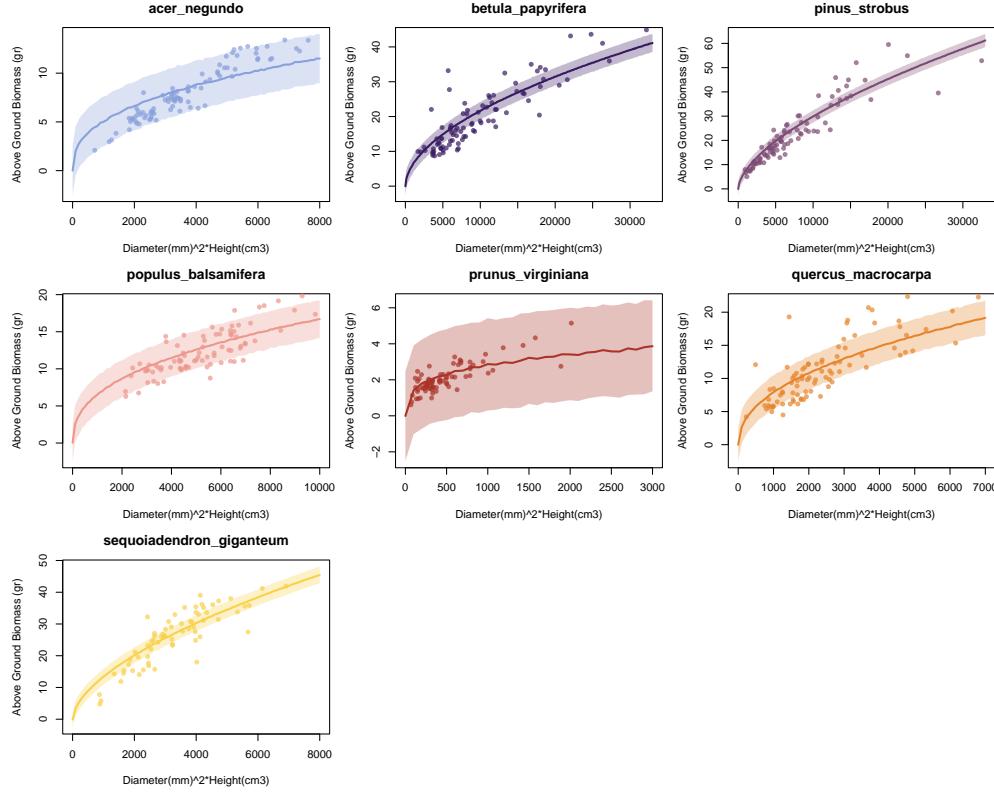


Figure 1: Posterior predictive check for the allometry model across the seven species for the final biomass measurements. The y-axis represents the above-ground biomass estimated for the simulated volume values, on the x-axis. The line represents the mean, and the shaded area, the 50% confidence intervals. The dots represent the empirical data used to fit the model.

seem to slightly increase growth, with little effect of the autumn treatment. Quercus shows a contrasting trend where the cool spring treatments had the largest biomass. For Pinus it seems that the fall treatments had the largest effect dragging, both warm fall treatments to lower biomass values and to higher values for the cool fall treatments. Any warming treatment for Populus increased biomass, with cool spring and cool fall having the lowest value and warm spring, cool fall at the highest. Finally, the cool spring, cool fall treatment was much lower than the other treatments for Sequoiadendron, with warm spring, cool fall and cool spring, warm fall being equally higher than the other two treatments.

As for the carry-over effect of the treatments on the second growing season (2025), some species shifted their trends in response to the treatments, while others muted the treatment effects. Acer remained stable across all four treatments. The direction of the treatment effect for Betula stayed constant, but its magnitude actually increased. For Pinus, the effect of each treatment shifted direction, though in very small magnitude. We observed a similar response for Populus, but only for the warm spring, cool fall treatment where it went from the highest biomass to the lowest. Prunus shifted slightly where the warm spring and cool spring, warm fall had the highest biomass. For quercus, cool spring, cool fall remained with the highest biomass, but, with little difference across all treatments. Finally, the cool spring, cool fall treatment for Sequoiadendron shifted from the lowest biomass, to a similar response across all treatments.

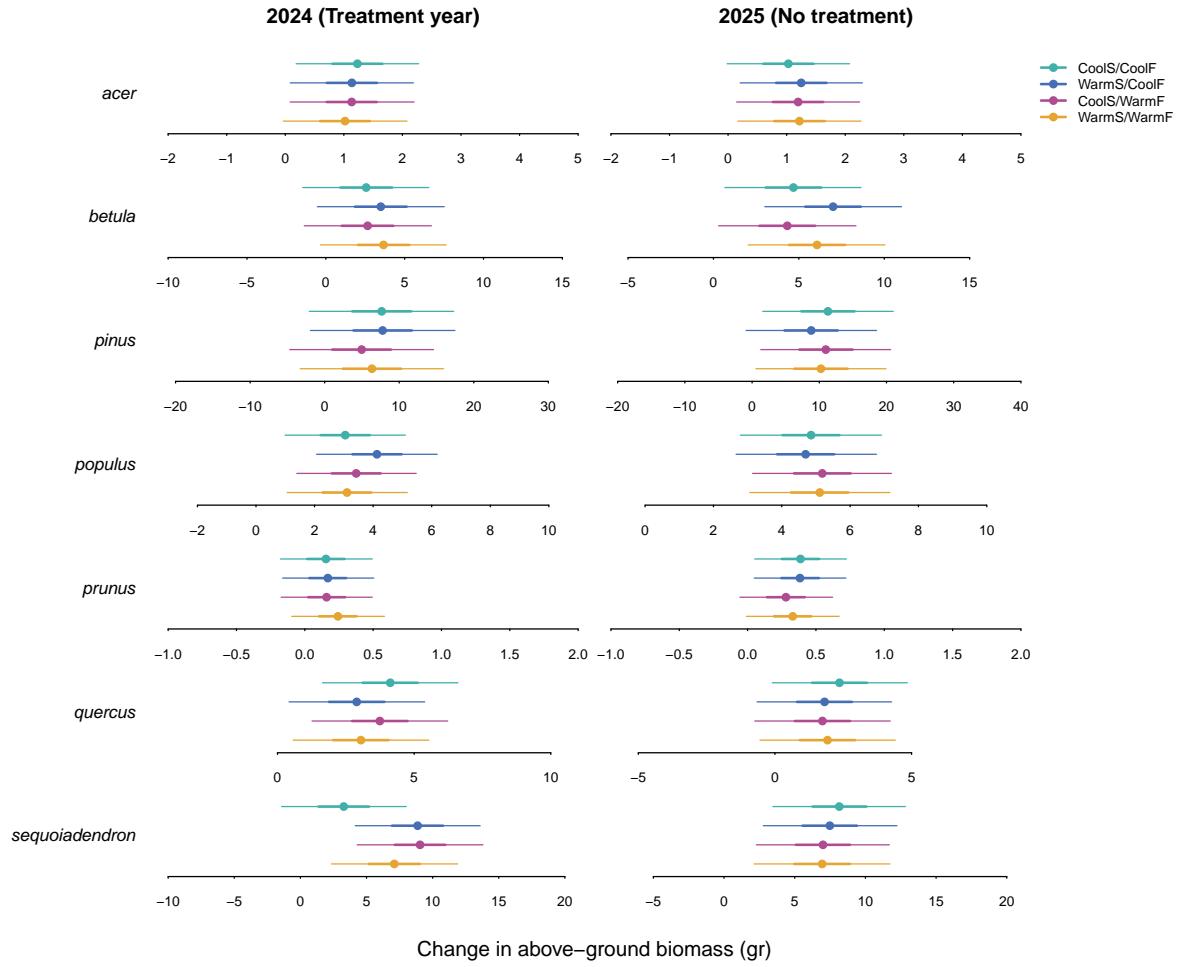


Figure 2

Discussion

Species responses to treatments

Our results show how the growth response to different season length changed across different species. With *Acer* showing the same growth response across treatments indicates that this species may be little flexible, both in the short and long-term response to growing season length. Photosynthates (products of photosynthesis) can be allocated to growth (biomass production), defense or storage. If the supply exceeds demand in a given season, trees store these compounds as non-structural carbohydrate, which they can use in a subsequent season. The treatment effects that increased for *Betula* in 2025 indicates that this species may utilize the earlier season (Warm spring) to increase its overall photosynthesis. It appears that *Betula* allocates some of this excess of carbon supply to increase its growth during the current year, but moreover, store some of these NSC to allocate an even greater growth portion in 2025. In addition, *Betula* is a non-determinate growth species (i.e. number of leaves is non pre-determined during the previous season). This strategy usually allows these species to be more flexible than their counterpart [Baumgarten unpublished]. This may explain the short-term growth response (2024), but this flexibility may also have led this species to opportunistically increase its photosynthetic rate—leading to increase NSC storage.

Evergreen trees usually store less NSC because unlike deciduous trees—which require to grow a new leaf cohort every spring—they keep most of their leaves and need fewer leaf growth investment [Hessl2026Carbon; Richardson2013Sesoo]. Therefore, we explain the muted treatment effects of 2025 vs 2024 for *Sequoiadendron* and *Pinus* by their

strategy of seasonally allocating their photosynthates directly to growth and defense and little for long-term storage.

Model

Our study has limitations. First, negative growth increments (δ_B), should be rare, but our normal likelihood allows for more of these than realistically possible. Future modelling of this dataset should account for this. We did not succeed in fitting a log-normal likelihood, that would have accounted for this because our model with this likelihood led to poor posterior geometry with hundreds of divergent transitions per chain, with Neff going to zero and with very high rhat values. In addition, future modelling approach should fit both models jointly instead of using a point estimate from the allometry model to fit the carry-over model. This would allow for [?]. When fitting both models jointly, the treatment effects always went to zero, with the only shared parameter, σ_y also being very close to zero.

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Supplemental results

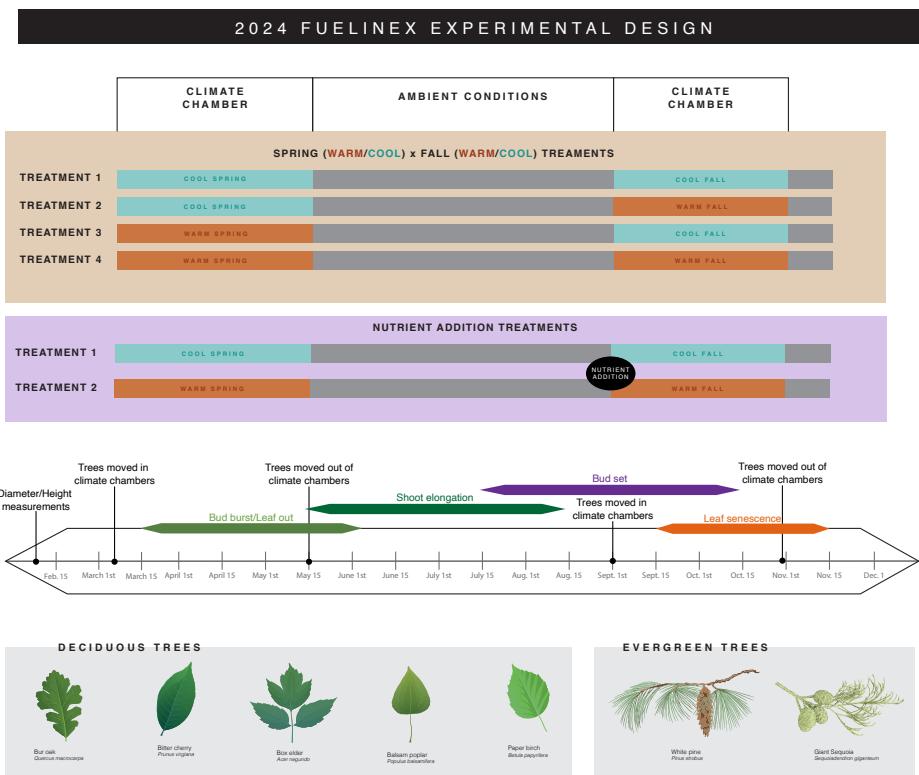


Figure 3

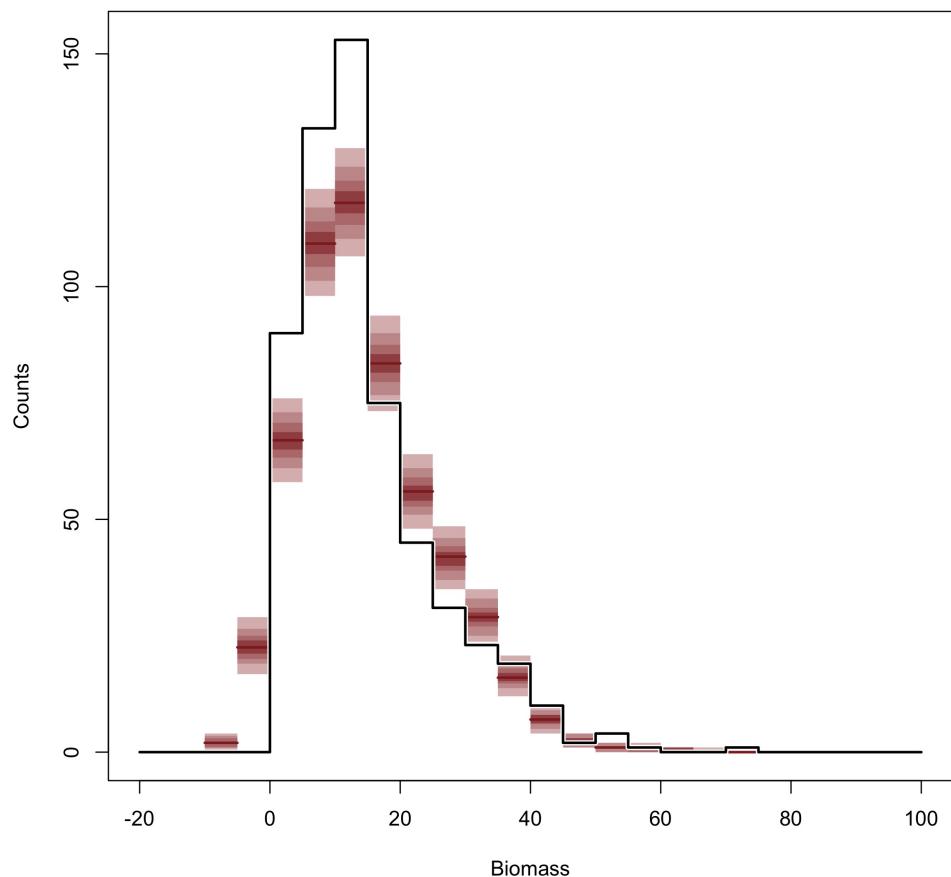


Figure 4