

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 1), 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*].

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

Posterior predictive behavior of the model shows that our model recovered the data well (Figure 4). We ran the model with a warm-up of 1000 iterations and a sampling phase of 1000 sampling iterations, for a total of 4000 sampling iterations across the 4 chains. We used initial conditions for $[\beta_1, \beta_2]$ and σ_y . We extracted 4000 random draws from the posterior distribution for each allometric coefficients to estimate the 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 ($\Delta B_2 = AGB2025 - AGB2024$).

2024 FUELINEX EXPERIMENTAL DESIGN

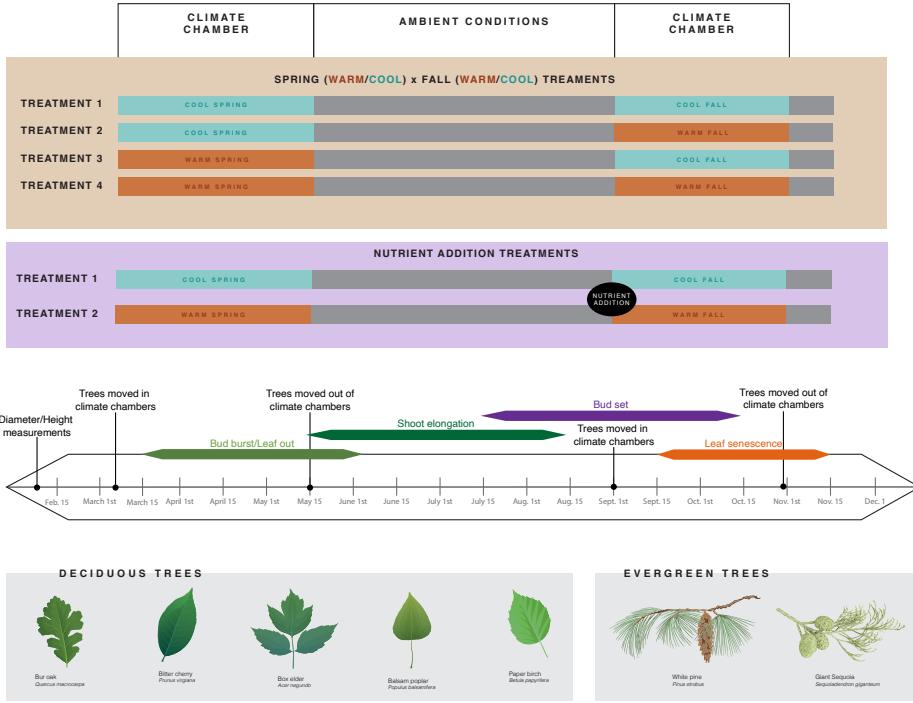


Figure 1: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions. The colored arrows represent the approximated periods during which we recorded the phenostages.

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.]

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

$$\mu_1 = \begin{cases} \alpha_{cc1} & \text{if trt} = \text{CoolSpring and CoolFall} \\ \alpha_{wc1} & \text{if trt} = \text{WarmSpring and CoolFall} \\ \alpha_{cw1} & \text{if trt} = \text{CoolSpring and WarmFall} \\ \alpha_{ww1} & \text{if trt} = \text{WarmSpring and WarmFall} \end{cases} \quad (2)$$

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

$$\mu_2 = \begin{cases} \alpha_{cc2} & \text{if trt} = \text{CoolSpring and CoolFall} \\ \alpha_{wc2} & \text{if trt} = \text{WarmSpring and CoolFall} \\ \alpha_{cw2} & \text{if trt} = \text{CoolSpring and WarmFall} \\ \alpha_{ww2} & \text{if trt} = \text{WarmSpring and WarmFall} \end{cases} \quad (4)$$

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

We used a common σ_y across the two years because we measure biomass increments on the same individuals, thus capturing residual error not captured by the parameters. Because we have little information as

the relative response to each species to the different treatments, we used weakly informative 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 model

Biomass increased with volume accross all species and while our model appears to generally fit the data well, it might be underfit for *Prunus* (Figure 2).

Carryover model and treatment effects

For the growing season during which the treatments occurred (2024), the treatment effect of each species differed considerably (Figure 3). The biomass of *Acer* and *Prunus* remained relatively constant across treatments, except for a slight positive effect in *Prunus* with Warm spring/Warm fall (WW). As for *Betula*, the warm spring treatments seem to slightly increase growth, with little effect of the autumn treatments. In contrast, *Quercus* shows the opposite trend where the cool spring treatments had the largest biomass, but again with little effect of the autumn treatments. For *Pinus* the cool fall treatments (CC, WC) had the largest effect dragging, both warm fall treatments (CW, WW) to lower biomass values and to higher values for the cool fall treatments. For *Populus*, a warm spring and a cool fall (WC) had the largest positive effect, with little difference across the other treatments. Finally, the cool spring, cool fall (CC) treatment was much lower than the other treatments for *Sequoiaadendron*.

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 (Figure 3). Similarly to 2024, *Acer* remained stable across all four treatments. However, the direction of the treatment effects for *Betula* persisted, but its magnitude increased. For *Pinus*, the effect of each treatment shifted direction, though in small magnitude. We observed a similar response for *Populus*, but only for the warm spring, cool fall (WC) treatment where it went from the highest biomass to the lowest. *Prunus* shifted slightly where the cool and warm spring, cool fall (CC, WC) had the largest biomass. For *Quercus*, cool spring, cool fall (CC) remained with the highest biomass, but, with little difference across all treatments. Finally, the cool spring, cool fall (CC) treatment for *Sequoiaadendron* shifted from the lowest biomass, to a similar response across all treatments.

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,

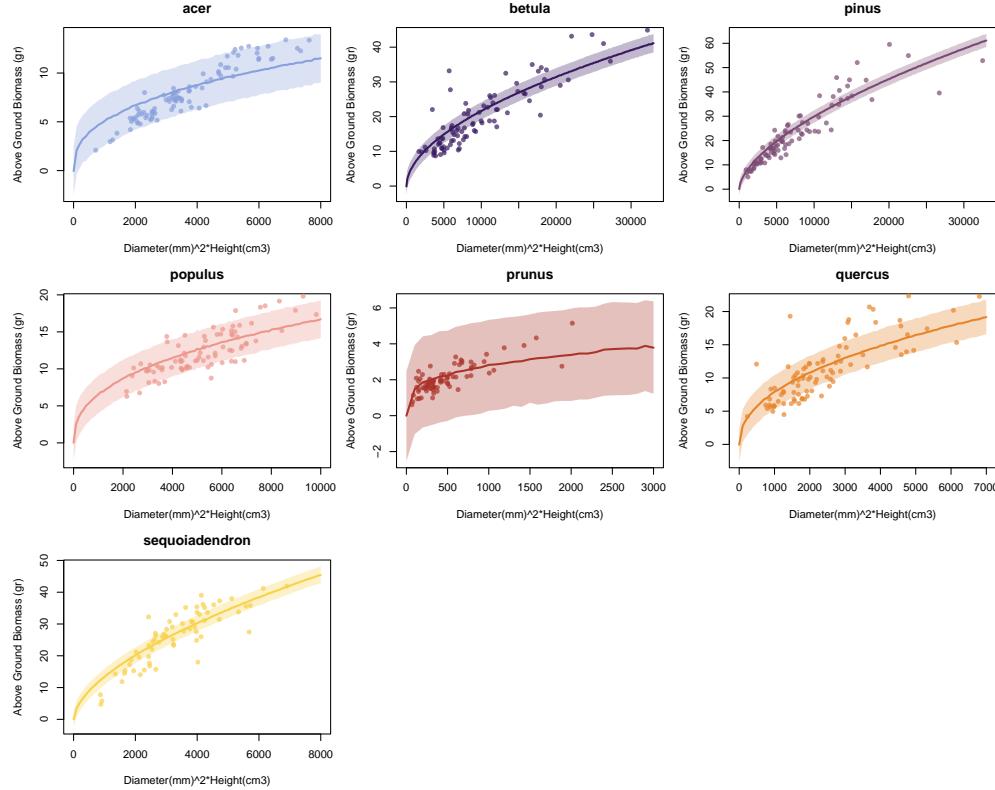


Figure 2: Posterior predictive check for the allometry model across the seven species for the final biomass measurements. The y-axis represents the above-ground biomass estimated for the simulated volume values, on the x-axis. The line represents the mean, and the shaded area, the 50% confidence intervals. The dots represent the empirical data used to fit the model.

both in the short and long-term responses 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 (NSC), which they can use in a subsequent season [Hessl2026Carbon, Chapin1990]. Thus, the positive effect in 2025 of the warm spring treatments indicates that this species may utilize the earlier start of season 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 determinate counterpart [Baumgarten unpublished]. This may explain the short-term growth response (2024), but this flexibility may have led this species to opportunistically increase its photosynthetic rate.

Evergreen trees usually store less NSC because unlike deciduous trees—which require growing a new leaf cohort every spring—they keep most of their leaves and need fewer leaf growth investment [Hessl2026Carbon; Richardson2013Se]. Therefore, we explain the muted treatment effects of 2025 vs 2024 for Sequoiadendron and Pinus by their strategy of seasonally primarily allocating their photosynthates directly to growth and defense and to a lesser extent, for long-term storage.

Model

Our study has limitations. First, negative growth increments (δ_B) in tree should be rare, but our normal likelihood allows for more of these values than it is realistically possible. We intended to address this by fitting a log-normal likelihood, that would have made negative increments very unlikely, but it always result in poor posterior geometry with hundreds of divergent transitions per chain, Neff going to zero and with

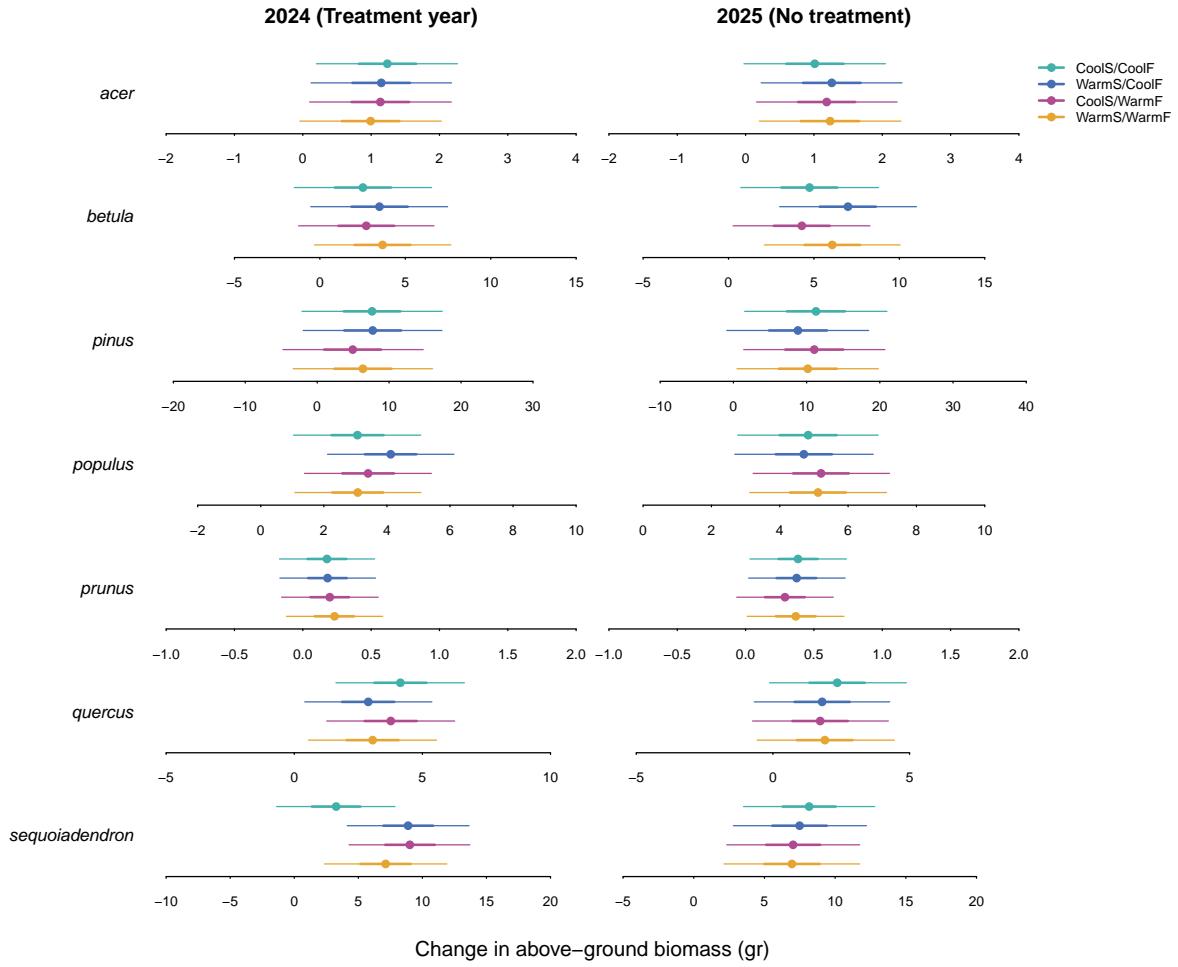


Figure 3: Estimated treatment effects across species for the treatment year (2024) and the following year (2025). The dots represent the posterior mean, and the lines represent the 50% and 90% quantiles of the posterior predictive distribution for each treatment.

very high \hat{R} values. Second, using a point estimate from the allometry model to fit the carry-over model, we used a "short-cut" that lacks statistical rigor. 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.

Future modelling of this dataset should account for rare negative growth increments, fit a joint allometry and carryover model.

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Data availability

- Allometry model Stan code
- Carry-over model Stan code:
- Allometry model R code
- Carry -over model R code.
- Data diameter and height measurements
- Biomass measurements
- Posterior predictive check marginal posterior histogram, year 1
- Posterior predictive check marginal posterior histogram, year 2
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Supplemental results

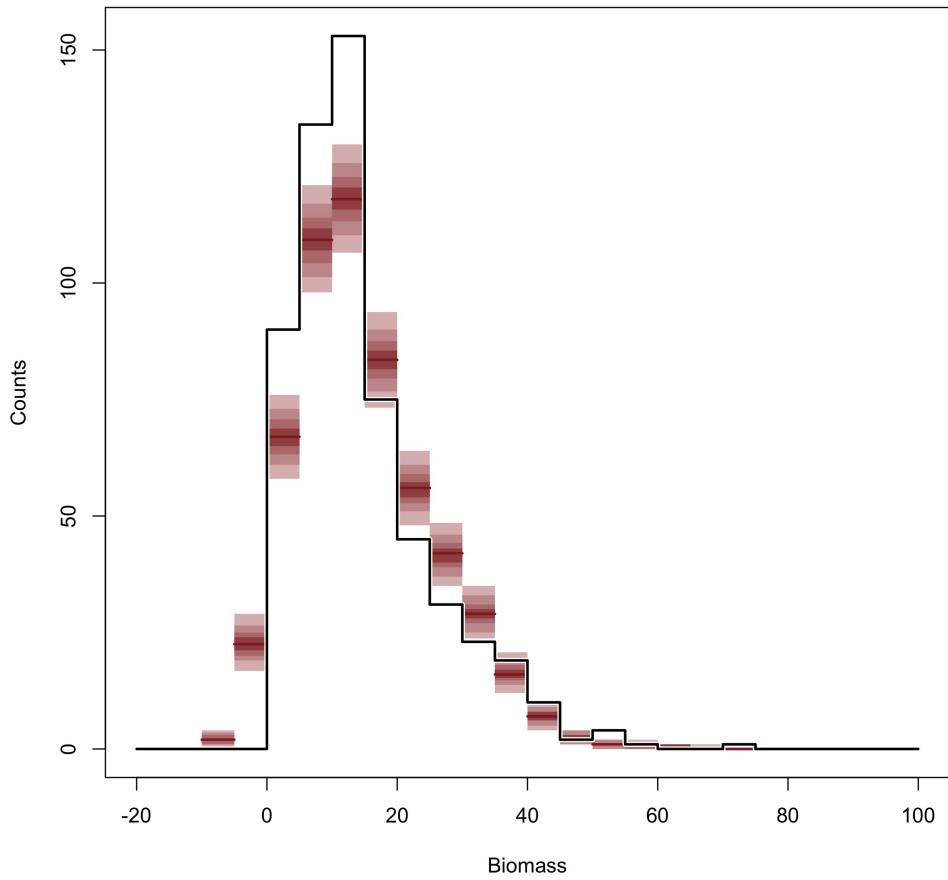


Figure 4: Posterior predictive behavior of the allometry model. The black solid line represents the data used to fit the model. The red solid line represents the average quantiles across each markov chain [?]

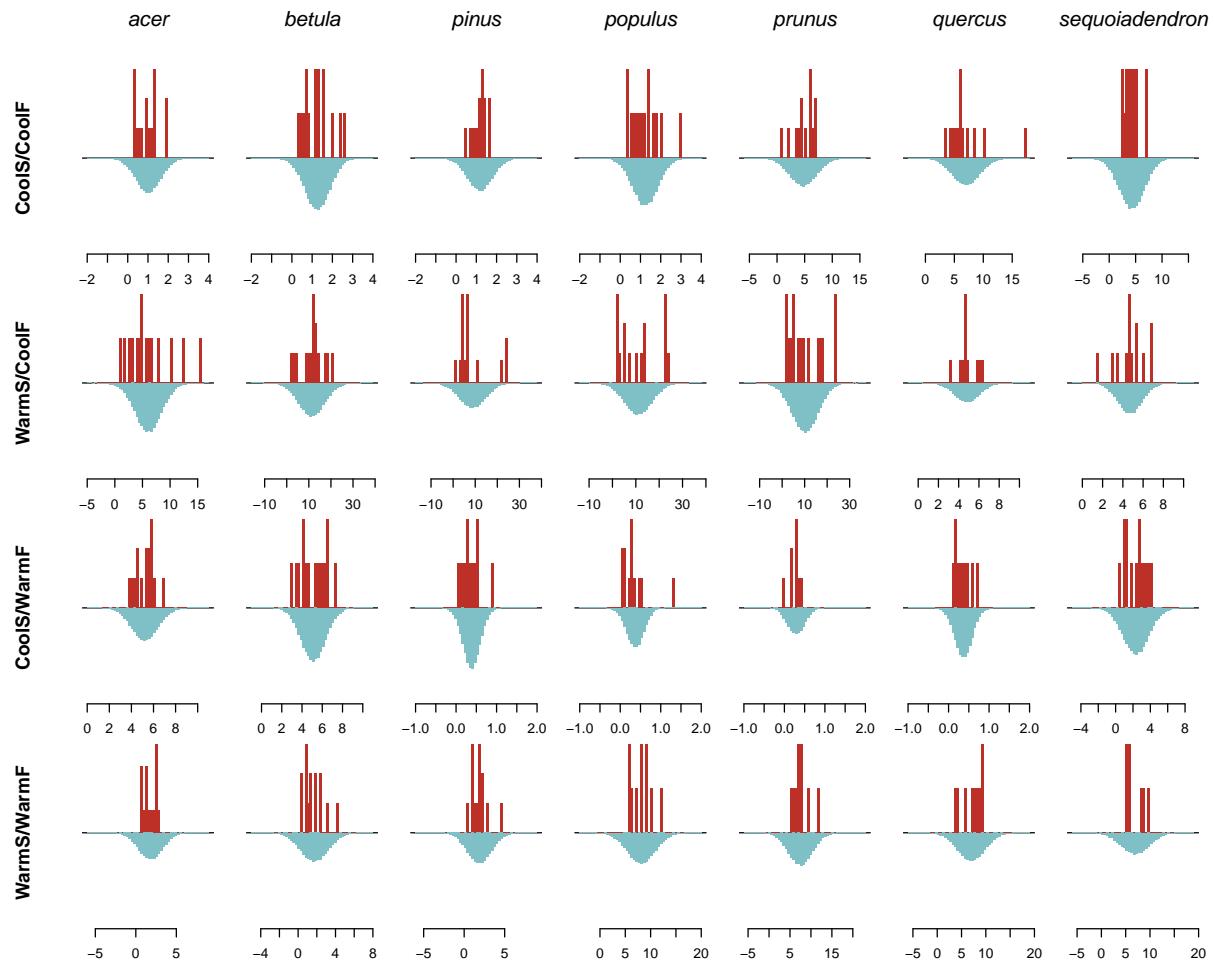


Figure 5: Histograms representing the estimated biomass increments and the effect for each treatment for 2024. The red histograms represent the fitted biomass increment, from the allometry model for each 15 replicates per species/treatment. The histogram in blue represent the model posterior distribution for each treatment parameter.

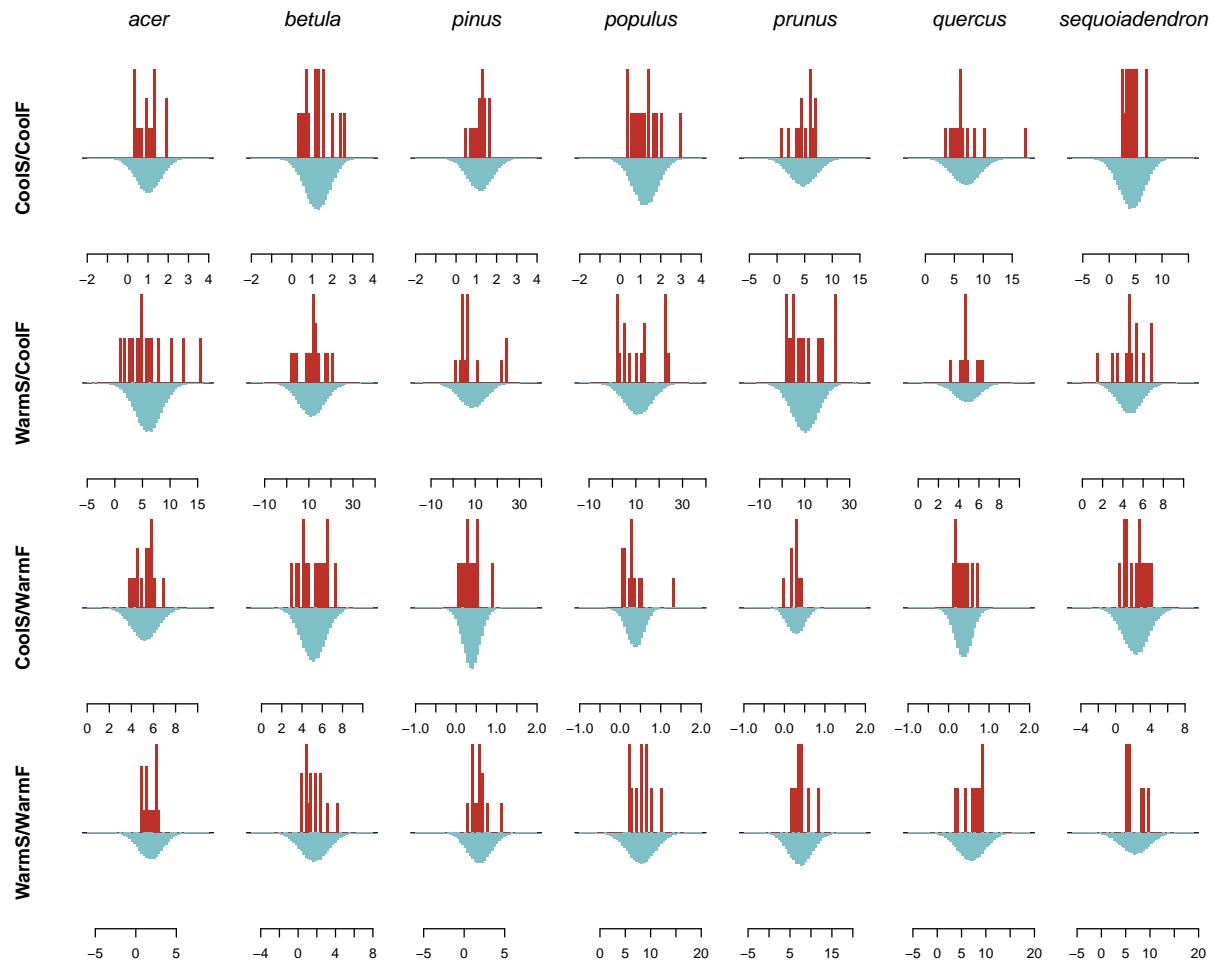


Figure 6: Histograms representing the estimated biomass increments and the effect for each treatment for 2025. The red histograms represent the fitted biomass increment, from the allometry model for each 15 replicates per species/treatment. The histogram in blue represent the model posterior distribution for each treatment parameter.