

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

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Abstract

The most frequently observed biological impact of anthropogenic climate change over the past decades is major changes in phenology—the timing of recurring life history events. These shifts change when the growing season starts and when it ends, which modifies the growing season length. Earlier spring and delayed fall events support a long-lasting and intuitive assumption that these shifts extend seasons and thus increase growth. However, research from recent years has cast doubt on this hypothesis by demonstrating that, despite an earlier growth onset, longer seasons did not increase the growth rate nor overall annual increment in trees. To address this decoupling, we propose to use a full-factorial design of Cool/Warm, Spring/Fall treatments to test whether trees under experimental conditions can benefit from longer seasons during the first and the following year. More specifically, we want to demonstrate whether the treatment conditions during year one lead to a carry-over effect on the growth during year two. Using 15 replicates per treatment across 7 species, our modelling approach examines the relative effects of each treatment on the outcome of each year and for each species, potentially revealing how different species may respond to a longer growing season, which is expected to keep shifting with climate change.

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 & Medvigh, 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 and thus feedbacks to future climate (Richardson *et al.*, 2013b; Swidrak *et al.*, 2013). In addition, 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.

We propose the following conceptual framework to formulate our hypothesis. During a growing season, trees accumulate non-structural carbohydrate (NSC) to support growth and metabolism (Chapin *et al.*, 1990; Richardson *et al.*, 2013a). Given that a large portion of the tree's annual photosynthesis products are allocated to the NSC pool, understanding the relationship between the supply and demand for NSC is important. This pool is depleted when demand exceeds supply (e.g. in the spring when trees produce a new leaf cohort) and is refilled when supply exceeds demand (e.g. when leaves are at their full photosynthesis capacity) (Richardson *et al.*, 2013a). Although we did not directly measure NSC contents, we hypothesize that trees that can take advantage of extra days to photosynthesize will refill more their NSC pool and will reinvest it during the following season into structural growth.

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 caliper (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 *et al.*

2024 FUELINEX EXPERIMENTAL DESIGN

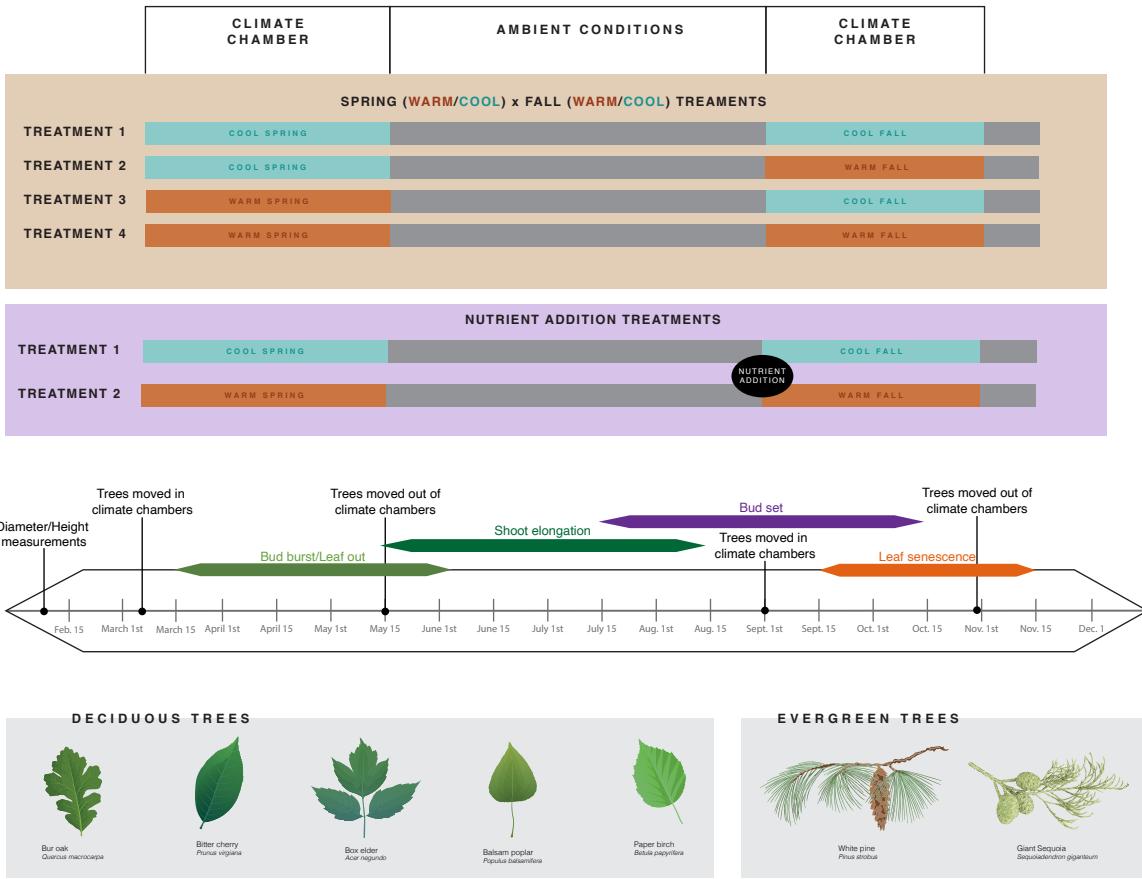


Figure 1: Experimental design during the 2024 growing season. Cooling treatments are represented in blue, and warming treatments are in orange. The grey zone in the middle represents an approximate period during the growing season where all treatments were together at ambient conditions. The colored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

(2016) using the rstan package version 2.32.7 (Carpenter *et al.*, 2017) in R. The bounding box volume is $RCD^2 \times H$, but we refer to it just as volume.

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

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 randomly generated initial conditions from the priors. Model fits were assessed with a $\hat{R} < 1.01$, high effective sample size and no divergent transitions. We extracted 4000 random draws from the posterior distribution for each allometric coefficients to estimate the biomass from the diameter and height measurements from 2023, 2024, and 2025. 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 ($\Delta B_1 = B_{2024} - B_{2023}$) and ($\Delta B_2 = B_{2025} - B_{2024}$).

Carry-over effect model

Using the estimated biomass increment for 2024 and 2025, we jointly fit ΔB_1 and ΔB_2 . We fit the model with randomly generated initial conditions from the priors, with the same number of iterations as the allometry model. Model fits were also assessed with a $\hat{R} < 1.01$, high effective sample size and no divergent transitions. We verified the model fit with posterior predictive checks where the posterior distribution of the treatment effects for each species is compared to the allometry output for year 1 (Figure 5) and year 2 (6).

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

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

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

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

$$(5)$$

We used a common σ_y across the two years because we measure biomass increments on the same individuals, thus these contributing errors (e.g. measurement error, individual tree variation[?]) should come from the same distribution. Because we have little information on the relative response of each species to the different treatments, we used weakly informative priors for each parameter:

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

$$\sigma_y \sim \text{logNormal}(0, 0.5) \quad (7)$$

Results

Allometry model

Our allometry model which we used to fit height, diameter and biomass data shows, as expected that biomass increases with volume accross all species. While our model appears to generally fit the data well ($\pm 50\%$ of the data within the 50% quantiles), it might overfit around the highest volumes values 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. We define a difference between treatments when their means are outside each other's IQR (thicker line), visually assessed with (Figure 3). The biomass of Acer, Betula, Pinus and Prunus remained relatively constant across treatments. For Quercus the warm spring treatments (WC, WW) had the lowest biomass, with little effect of the autumn treatments. For Populus, the warm spring, cool fall treatment (WC) is higher than cool spring, cool fall, but is not different from the other two treatments (CW, WW). Finally, the cool spring, cool fall (CC) treatment had much lower biomass increment than the other treatments for Sequoiadendron, with little difference across the other three treatments (WC, CW, WW).

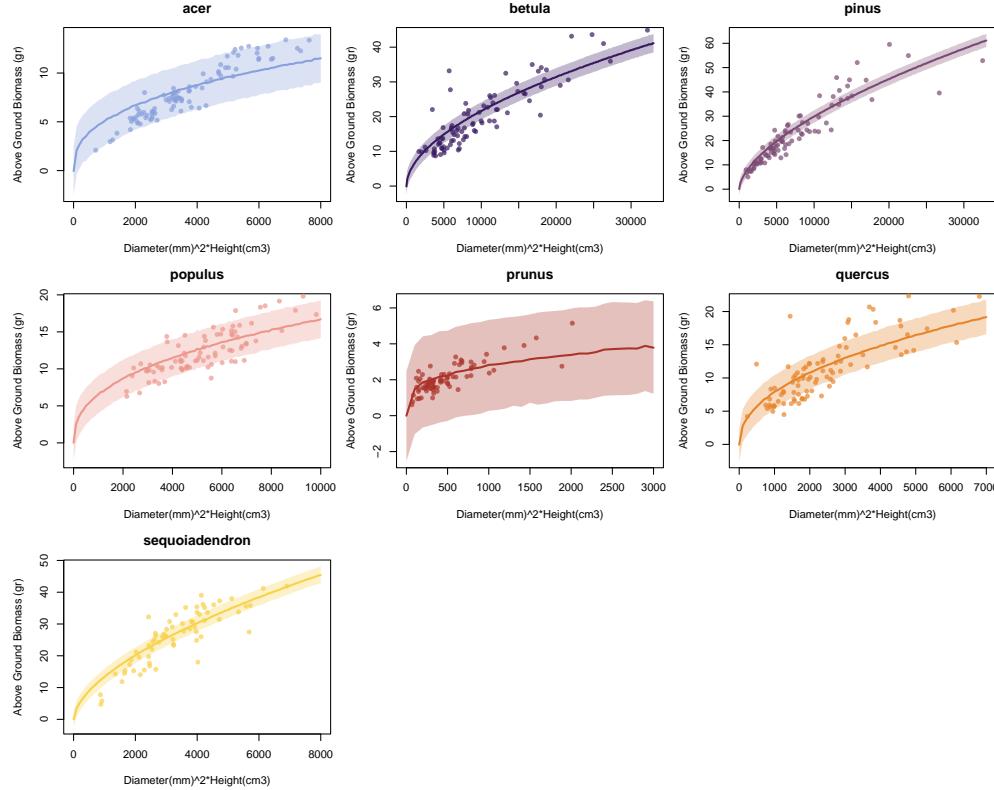


Figure 2: Posterior predictive check for the allometry model across the seven species for the final biomass measurements. The y-axis represents the above-ground biomass estimated for the simulated volume values, on the x-axis. The line represents the mean, and the shaded area, the 50% confidence intervals.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

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, Pinus and Prunus remained stable across all four treatments. For Betula, the warm spring, cool fall had a larger biomass increment compared to cool spring, cool fall and cool spring, warm fall. Unlike 2024, we found no difference across treatment for Populus, Quercus, nor Sequoiadendron.

Discussion

Species responses to treatments

Our results show how the growth response to different season length changed across different species. 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 (Chapin *et al.*, 1990; Hessl *et al.*, 2026). Populus reacting during the treatment year, but did not display a carry-over effect in 2025, in accordance with its non-determinate growth strategy (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 *et al.* (2025)—utilizing all carbon sources for growth seasonally, thus removing the capability of carry-over strategies. In contrast with Betula, sharing similar growth strategies, this species did not react to the treatments in 2024, but carried over a treatment effect in 2025. Moreover, the positive effect in 2025 of the warm spring treatments indicates that Betula may utilize the earlier start of season to increase its overall photosynthesis, allocating some of this excess of carbon supply to increase its growth in 2025. However, we

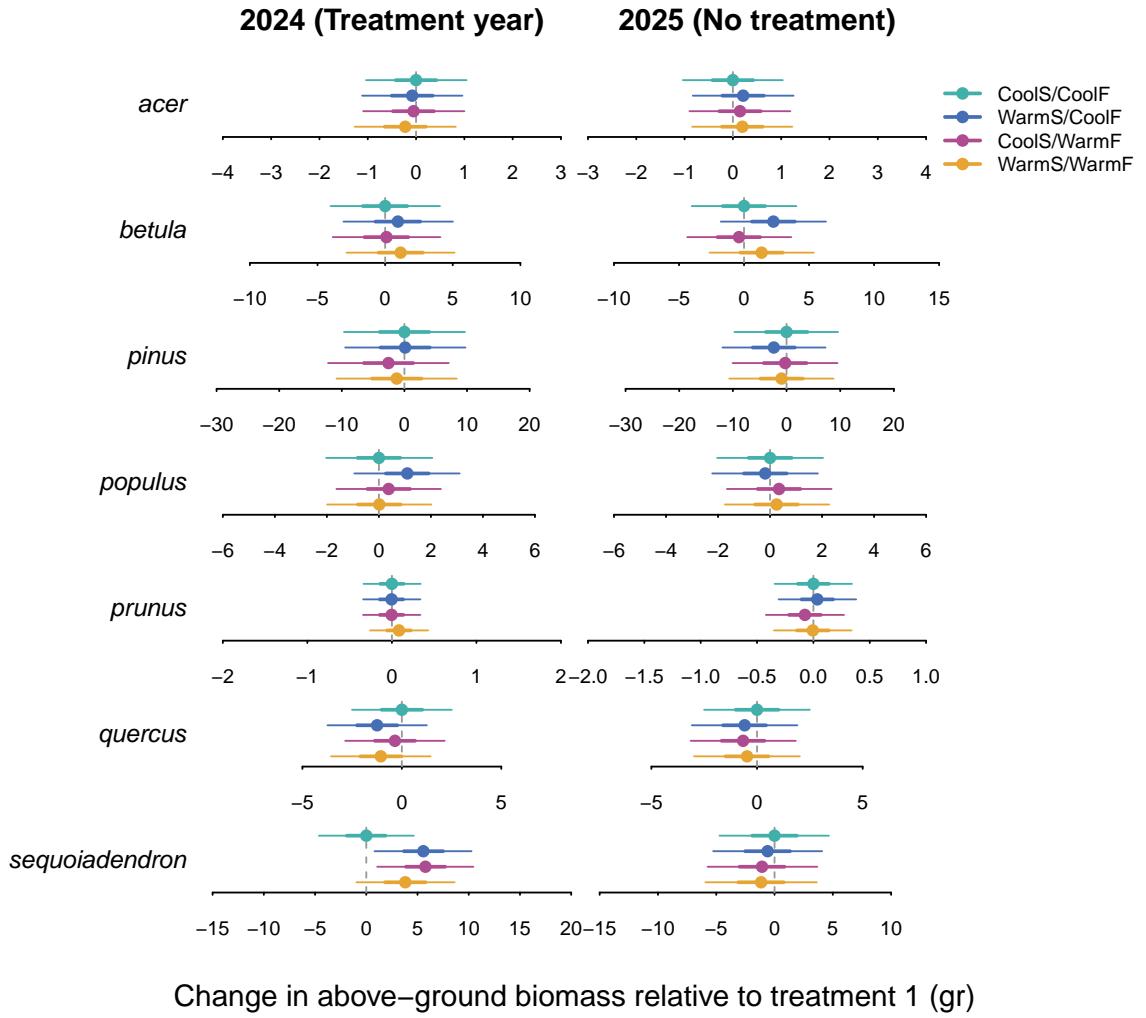


Figure 3: Estimated treatment effects across species for the treatment year (2024) and the following year (2025). The dots represent the posterior mean, and the lines represent the 50% and 90% quantiles of the posterior predictive distribution for each treatment.

may miss a mechanistic response of Betula to the treatments in 2024 that may underlie this unexpected behavior.

Quercus also reacted counterintuitively, exhibiting a treatment effect on the current year growth, but not carried-over in the next year. Quercus being a determinate species, we did not expect it to react in the current year, instead exhibiting treatment effects in the subsequent year.

With Acer, Pinus and Prunus showing the same growth response across treatments indicates these species may be little flexible, both in the short and long-term responses to growing season length.

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 (Hessl *et al.*, 2026; Richardson *et al.*, 2013b). Therefore, we explain the muted treatment effects of 2025 vs 2024 for Sequoiadendron by their seasonal strategy to primarily allocating their photosynthates directly to growth and defense and to a lesser extent, for long-term storage.

Model

Our modelling approach has limitations. First, negative growth increments (ΔB) in tree should be rare, but our normal likelihood allows for more of these values than it is realistically possible. Fitting the data using a log-normal likelihood would make these negative increments impossible, which is biologically more realistic. Second, using a point estimate from the allometry model to fit the carry-over model, we used a "short-cut" that lacks statistical rigor. However, the posterior estimates for the allometry model, when fitting both models jointly, resulted in biomass independence from bounding box volumes (i.e. β_2 values approximating 0). In contrast, fitting the allometry model separately led to good posterior predictive checks showing the expected behavior of increasing biomass, with bounding box volume[refer to figure]. This biomass independence of the full model, may be caused by issues with combining the posteriors of the allometry and carryover models, signified by the treatment effects and their corresponding likelihood error approximating zero. We deem these results from the full model to be improbable.

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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

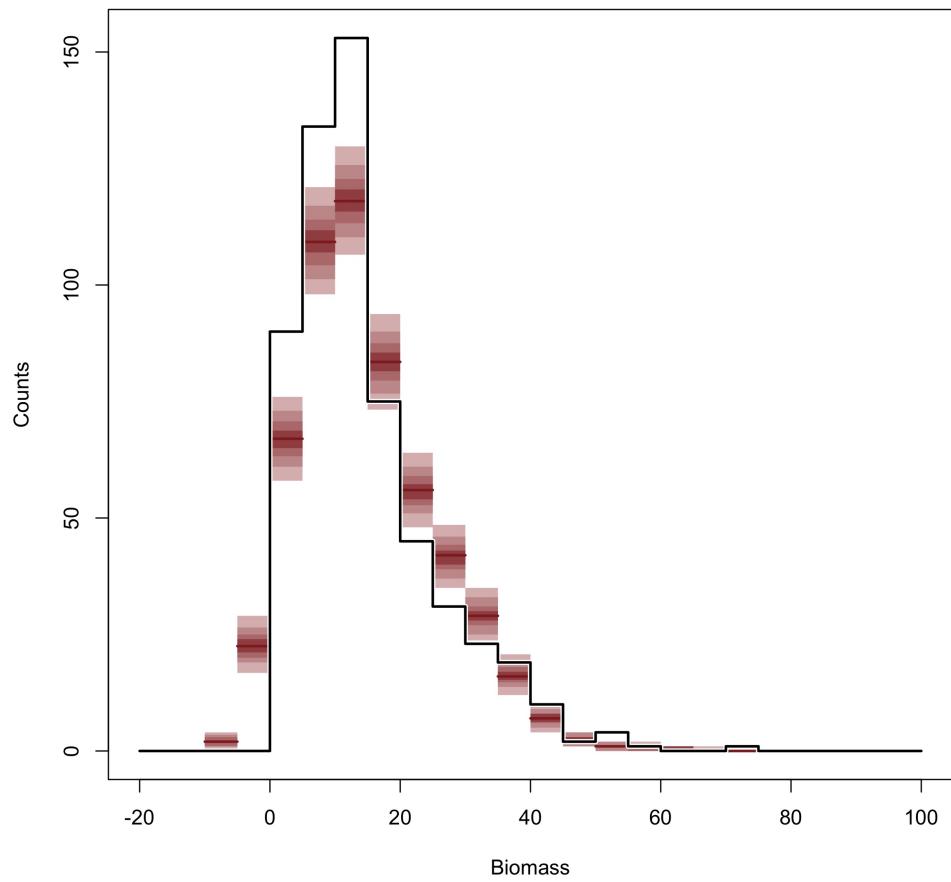


Figure 4: Posterior predictive behavior of the allometry model. The black solid line represents the data used to fit the model. The red solid line represents the average quantiles across each markov chain [?]

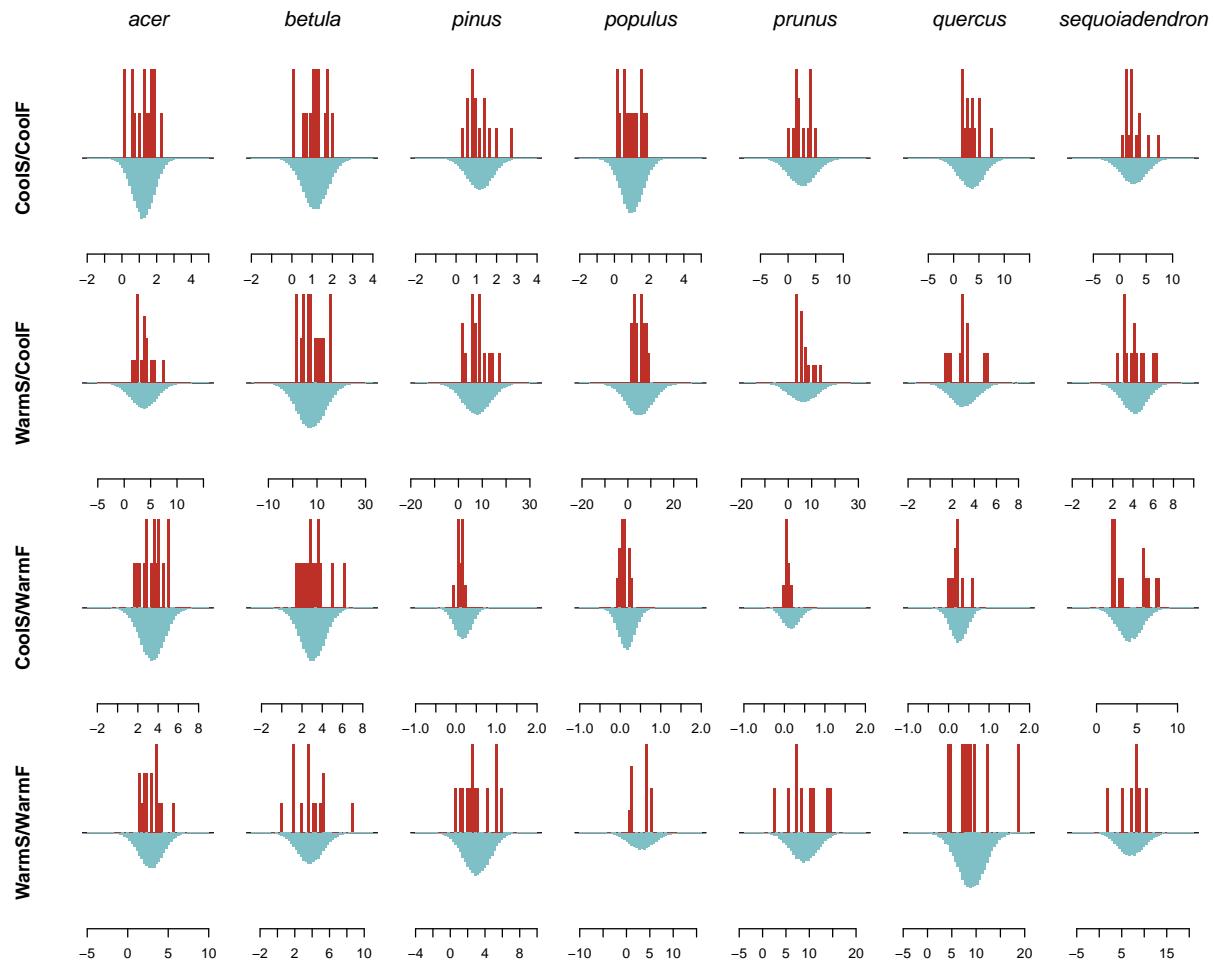


Figure 5: Histograms representing the estimated biomass increments and the effect for each treatment for 2024. The red histograms represent the fitted biomass increment, from the allometry model for each 15 replicates per species/treatment. The histogram in blue represent the model posterior distribution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

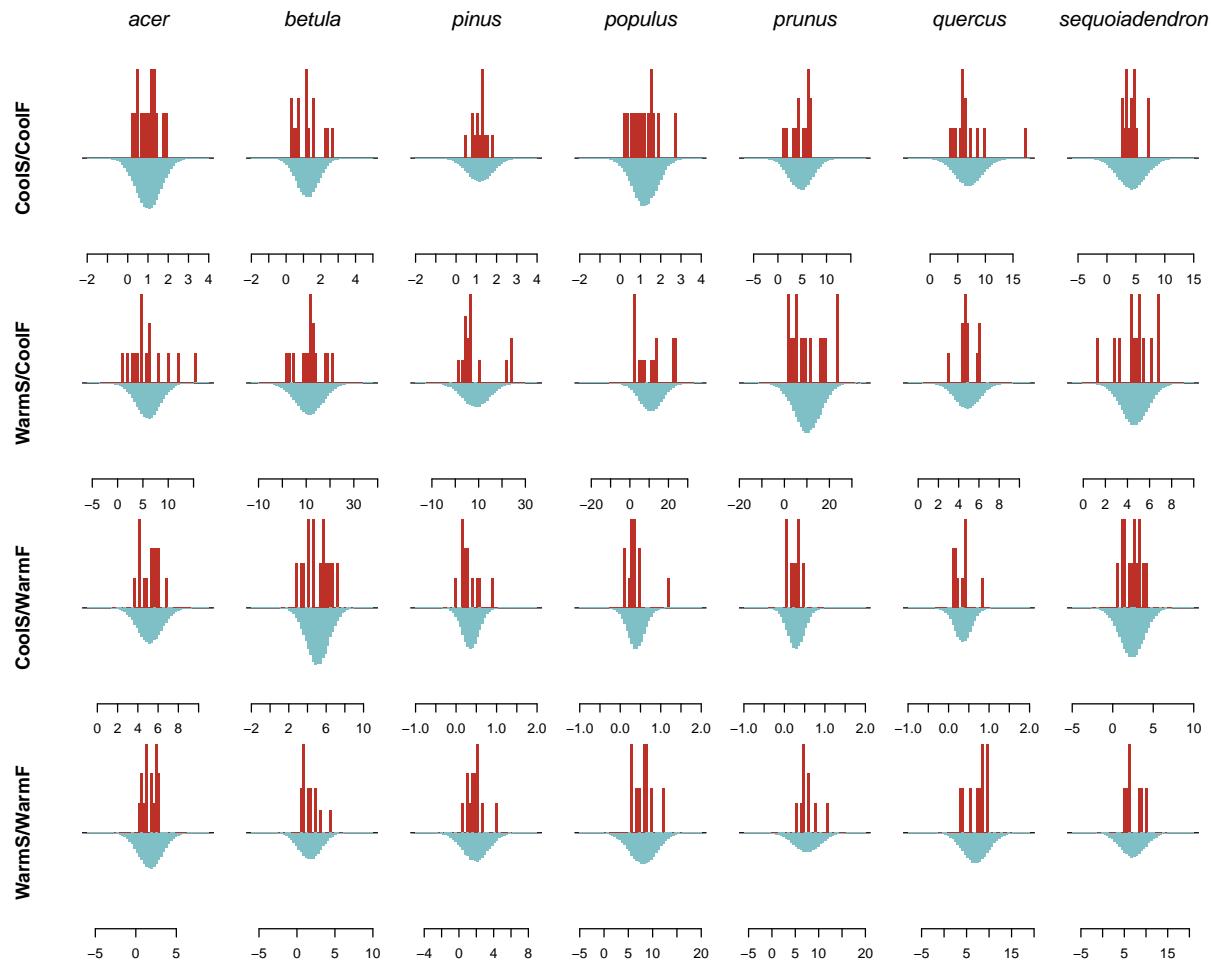


Figure 6: Histograms representing the estimated biomass increments and the effect for each treatment for 2025. The red histograms represent the fitted biomass increment, from the allometry model for each 15 replicates per species/treatment. The histogram in blue represent the model posterior distribution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