**Title:** Effect of spring temperatures on tree growth phenology in a temperate deciduous forest

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### Abstract

**Keywords**:

### Introduction

As global atmospheric greenhouse gas levels are rising, and little meaningful policy is being implemented in response, our planet is expected to surpass the 2.5 degree C warming mark that the Paris accord pledged to avoid. The absence of human intervention increases our reliance on natural systems to soften the blow of climate change. Plant life, especially forests, make up a large portion of these natural systems, offering many valuable ecosystem services. For one, they house an astonishing 80% of terrestrial species and are capable of removing the greenhouse gas CO2 from the atmosphere and storing it in the trees or soil. Forests sequester about one-third of all anthropogenic CO2 and store ~45% of all terrestrial carbon (Bonan, 2008). However, their future under the current era of rapid change is uncertain (Friedlingstein et al, 2006).

Reducing this uncertainty requires better understanding of the drivers of tree growth (Bugmann et al, 2019). Tree growth is sensitive to climatic factors like precipitation, temperature, and cloudiness in early growing season (Helcoski et al, 2019; Ciais, 2003; Goulden, 1996), as well as other physical factors including nitrogen content of soil, increasing atmospheric CO2, deposition of atmospheric pollutants in acid rain (Mathias & Thomas, 2018), and invasion by pests or pathogens. Understanding how growth is influenced by these factors is essential for developing accurate models to inform forest managers and policy makers about the role of future forests in climate change mitigation efforts.

#relavant? reworded first line above# (Understanding how growth is influenced by multiple factors at once is essential for developing accurate models to inform forest managers and policy makers about the role of future forests in climate change mitigation. CO2 concentrations in the atmosphere are increasing, and in a perfect scenario, trees and other plants would simply speed up growth in response to this, increasing photosynthetic efficiency in a process called CO2 fertilization (Strain and Cure, 1986; Huang et al., 2007). However, factors other than CO2 also limit tree growth, and seasonal temperature averages and precipitation patterns are changing concurrently. It is anticipated that, throughout much of the United States, future heat and drought may limit tree growth more strongly than it can be enhanced by elevated CO2 (Charney et al, 2016).) #

In recent decades, an increase in average Spring temperatures has been attributed to climate change. This relatively small increase has already been impacting many natural systems including forests (Parmesan & Yohe, 2003; Zhihong, 2006). The effects of this Spring warming on leaf phenology have been extensively studied (Way, 2011; Klosterman & Hufkins & Richardson, 2018) leading to many interesting observations. As temperatures are increasing, some regions have seen earlier leaf out in deciduous trees, sometimes matched or exceeded by earlier leaf senescence, meaning a potential shift in growing season timing or length (Ibáñez et al, 2010; Jeong et al., 2011). The timing of Spring warming also has a significant effect on leaf phenology response. Warming events later in Spring were shown to impact leaf emergence timing more than earlier Spring warming (Freidl et al, 2014) and earlier leaf emergence has been shown to cause complex lagged effects on subsequent seasonal growth in European broad leaf deciduous and mixed forests (Crabbe et al, 2016). Another study found that the velocity of leaf development is correlated to bud burst timing, such that the later in the Spring bud burst occurred, the faster leaves developed and vice versa (Klosterman & Hufkins & Richardson, 2018).

However, the fine-scale responses of temperate deciduous species to a warming Spring are not commonly researched due to the increased effort required. Shifts in leaf phenology timing could be accompanied by a change in stem-growth phenology, which would likely affect woody productivity, carbon and nutrient cycling, and water use patterns in temperate forests (Keeling et al, 1996;). Many observations of climate induced phenological shifts are based on GIS, eddy-covarience measurements, or other broad scale measurements of phenological timing, and do little to discern differences between individual species, where leaf and stem-growth phenology can be decoupled (D’Orangeville et al, in review). To date, very little research, has been done on the phenology of stem-growth.

In fact, we know little about the stem-growth phenology of temperate deciduous species — let alone how these are affected by changes in Spring temperature patterns. Timing of intraannual stem-growth is extremely important as it could have profound impacts on ecosystem interactions, as well as dictate periods of highest drought sensitivity of NPP in temperate forests (Foster, 2014; ). For example, if a drought were to occur when trees were at their peak growth rates, it could decrease that year’s NPP substantially, and subsequently, reduce the total amount of carbon sequestered contributing to a negative climate feedback loop (source?). Recent results from a paper by D’Orangeville et al. (in review) have shown that wood-type plays a significant role in the timing of leaf and wood phenology. They showed that ring-porous trees begin growth earlier in the season compared to diffuse-porous trees, but both reached 75% total annual growth around the same time. This implies evolutionary differences in the mechanisms controlling growth of these species, which have the potential to expose each group to different climate stresses (source for RP vs DP?).

While not entirely impossible, it is difficult to record intraannual growth or compare interspecific responses to Spring warming using leaf-phenology or other indirect observations. A solution to this is the use of dendrometer bands. Dendrometer bands allow a look at individual trees’ intraannual growth at a fine temporal scale (source?). Using many measurements taken within a year, we can model the growth of individual trees and extract growth milestones and variables for interspecific, intraspecific, and temporal comparison (McMahon & Parker, 2014). This allows the determination of variable responses of all tree species within a single forest, meaning a better understanding of future growth under projected climate conditions. Here, we use 9 years of biweekly dendrometer band measurements for 4 species to characterize intraannual stem-growth phenology within the ForestGEO plot at SCBI, calculating for each tree in each year where data was available: the day of year (DOY) where 25, 50, and 75% annual growth was achieved; the maximum growth rate; the DOY where maximum growth rate was achieved; and the total growth. Correlation between these variables and Spring temperatures over the 9 year study period (2011-2019) were assessed using a linear mixed model in a heriarchal bayesian framework.

We hypothesized that (1) stem-growth phenology variables would occur earlier in warmer years as compared to cooler years and (2) both wood types would increase total growth and max growth rate in response to warmer Spring temperatures.

### Materials and Methods

*Study sites and data*

Study sites included **2/3** temperate forests in the Eastern United states, **both/all** part of the Forest Global Earth Observatory [ForestGEO; Anderson-Teixeira et al. 2015] (**Table 1?**). **Both/all** sites are dominated by broadleaf deciduous trees. *(insert site descriptions, including lat/long, elevation, plot size, climate info, dominant species. If we include SERC and if space permits, we may put this in a table, otherwise just text)*

Our first study site was the forest dynamics plot located at the Smithsonian COnservation Biology Institute 5 KM South of Front Royal, Virginia within the Blue Ridge Mountains (38 °53036.6″ N, 78°08043.4″W; elevation 273–338 m). The forest here was established in the mid-19th century after conversion from agricultural fields. Dominate canopy species within the 25.6 HA forest plot include tulip poplar (Liriodendron tulipifera), hickories (Carya spp.), and oaks (Quercus spp.). The climate is humid temperate, with a mean annual precipitation of 998 mm, January temperatures averaging 1 degrees C and July temperatures averaging 24 degrees C (Helcoski et al, 2019).  
The second study site was Harvard Forest in the central Massachusetts town of Petersham (42°53′ N, 72°17′ W, elevation?). Harvard forest was established in 1907 as a study site for university students and researchers. (Previous use?) Dominate species within the approximately 13 HA plot are hemlock (Tsuga spp.), oak (Quercus spp.) and maple (Acer spp.). The climate is temperate continental with a mean annual precipitation of 1120 mm, January temperatures averaging -12 degrees C and July temperatures averaging 19 degrees C (D’Orangeville et al, ).

The third study site was the forest dynamics plot located at the Smithsonian Ecological Research Center in Edgewater, Maryland near a sub estuary of the Chesapeake Bay (38°88′ N, 76°55′ W, elevation?). The forest here established roughly 120 years ago, while the plot was established in 2007. The 16 HA plot is dominated by tulip poplar (Liriodendron tulipifera), oak (Quercus spp.), beech (Fagus spp.), hickory (Carya spp.), and maple (Acer spp.). (Climate summary)

Within the plot, metal dendrometer bands were installed on *>#* trees and measured approximately every 1-2 weeks within the growing season for *9* years (*list ranges, for each site if different*). *(don’t bother to mention biannual bands, unless you end up using the data–which you could, for annual growth, if you’d like to increase the sample size. You can put exact numbers of bands per year in an SI file.*) The number of bands measured at each site fluctuated somewhat as trees were added or dropped (e.g., because of tree mortality) from the census *(Table S1)*. Across years, the number of bands sampled averaged *~150* at SCBI, # at Harvard Forest*, and # at SERC*. *(summary of how bands were distributed across species, focusing on ring/ diffuse porous distinction. details in an SI table)*

(After cleaning: 2011- 105 trees; 2012 - 102 trees; 2013 - 102 trees; 2014 - 149 trees; 2015 - 149 trees; 2016 - 149 trees; 2017 - 148 trees; 2018 - 146 trees; 2019 - 145 trees *–put this in Table S1*).

Measurements were timed to begin before beginning of spring growth and to continue through the cessation of growth in the fall. *(Give specifics, which may vary by site. Note that we adjusted timing at SCBI when we observed early leaf-out of understory shrubs/herbs)*

The dendroband data were manually cleaned by visual inspection. Three classes of mistakes: 1. Error in measurement - weekly measurement was drastically different from previous week and following week. Mistakes were removed from the raw data before modeling. (## cases) 2. Band slip or stuck - measurements freeze and remain unchanged until sudden jump followed by normal growth pattern. Band slips were sometimes followed by measurements indicating the band became stuck; in these cases, the tree was thrown out for the corresponding year. In cases where the slip was followed by normal growth, the initial slip-point was removed, and the following points were shifted down to the pre-slip level. (## cases) 3. Other - cases where data was clearly wrong but with unknown causes. This seemed to happen mostly in 2011, when the program was just beginning. In cases where several measurements were an issue, they were simply removed. If there were no clear solutions to ‘fix’ the data, the entire year was removed from the analysis.

Daily maximum temperatures (TMAX) were obtained from a meteorological tower adjacent to the SCBI ForestGEO plot (data can be found on the ForestGEO climate portal, DOI on github). The R package climpact was used to plot TMAX for visual inspection (# points removed?). Climpact also identifies readings that were greater than 3 standard deviations away from yearly means. These points were labeled as outliers and removed from the dataset. Gaps in the SCBI meteorological tower data were subsequently filled using TMAX readings obtained from a National Center for Environmental Information (NCEI) weather station located in Front Royal, Virginia (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00443229/detail>).

leaf phenology data?

• leaf phenology data from NEON and/or satellite-based (leaf phenology network: <https://www.usanpn.org/news/spring>) ?

• NDVI or PRI? <https://onlinelibrary.wiley.com/doi/10.1111/gcb.15112> (from Ian)

• From Ian: I noticed how the growth patterns observed by remote sensing pretty much mirror what Sean was finding with his dendro R package (btw is that functional on CRAN yet?) for both SERC and SCBI dendroband data.

perhaps bring in cores?

• Sean’s model

• Climwin

The period where the phenology milestone(s) were most affected by changes in early Spring temperature was determined using the R package Climwin. This package tests the correlation between climate variables (TMAX) and biological variables (DOY, max rate DOY, total growth) within a specified time-frame, reporting correlation and delta AIC’s of each ‘window’. as the best-model. We instructed Climwin to search for the best window beginning at February 1st and ending at the mean DOY for each phenology variable (chart in SI?). This was done to find corresponding (median of 95% CI window open and close) start and end dates for the analysis of ring-porous and diffuse-porous trees, as well as all trees pooled together.

*Analysis*

Here, I’ll insert a reference to Sean’s paper (McMahon & Parker, 2015). This is pulled from references.bib.

-Mixed effect model

A mixed effect model was used to test the response of wood phenology variables (25% DOY, 50% DOY, 75% DOY, max-rate, max-rate DOY, total growth) to fixed effects of wood-type and Spring temperature, along with random effects of species and tag. We ran two separate models of each wood phenology variable for each of our major wood-types, and one combined model to use for comparison. Models were run using the LME4 package in R (Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed‐effects models using lme4. J. Stat. Softw., 67, 1–48.)

• Bayesian heirarchal model This mixed-effect model was run within a heirarchal bayesian framework.

### Results

• variable averages

Pooled across all species and all years the average DOY where max growth rate was achieved is DOY: 158, the DOY where 25% was achieved is DOY: 129, 50% - DOY: 157, 75% - DOY:184.

Ring-porous (1395 obs) max growth rate – DOY: 147, max growth rate = .048 (find units in Sean’s function), 25% - DOY: 113, 50% DOY: 147, 75% - DOY: 181…68 days

Diffuse-porous (993 obs) max growth rate – DOY: 172, max growth rate = .068 (find units in Sean’s function), 25% - DOY: 153, 50% - DOY: 171, 75% - DOY: 190… 37 days

• Climwin results

• Accounting for random effects of species and tag, pre-season temperatures had a greater effect on ring-porous species than diffuse-porous.

### Discussion

-Growth timing We have shown that intraannual growth patterns in North American temperate trees change in response to increasing Spring temperatures. The magnitude of these changes depends largely on the evolutionary differences inherent in the two wood types analyzed here. Ring-porous trees must repair winter embolism of their large xylem vessels before leaf expansion, achieving roughly 25% total yearly growth simultaneously with bud burst, and 50% yearly growth around the time of 75% leaf emergence (D’Orangeville et al,). On the other hand, diffuse-porous trees are less prone to cavitation and so do not need to repair winter embolism before bud burst, allowing up to 75% leaf out before reaching their 25% yearly growth totals (D’Orangeville et al). These differences are likely evolutionary hydraulic adaptations to climate(). The presence of wide-xylem cells in ring-porous trees allows for greater water conductivity in the Spring at the cost of increased cavitation risk during Spring drought, and high likeliehood of damage during frost events (Cochard & Tyree, 1990). The pre-leaf stem growth occurring in these species is fueled by carbon stores, often used for other cell maintenance activities within the plant (). The dependence on these carbon stores for cambial activation could prove to be a detriment to the tree, as exhaustion of reserves leads to carbon starvation (). Diffuse-porous trees have narrower xylem cells lowering the risk of cavitation, but leading to a decreased water conductivity in the Spring, revealing a growth strategy more focused on a relatively faster, shorter growing season in the Summer. This allows the diffuse-porous trees to conserve their carbon stores, making them potentially more resistant to pest/pathogen invasions?, but exposing them to higher temperatures and drought risk during their Summer-centered growth period.

The mechanisms controlling activation of cambium reactivation is still a mystery, as some speculate Auxin, the chemical believed to kick-start the reactivation process, originates in the leaves(). However, the fact that ring-porous species complete 25% growth before the presence of leaf buds indicates there may be another source of Auxin production.

Ring-porous trees reach 25% and 50% growth milestones earlier (insert actual # days?) in the year, while 75% remains statistically unchanged, in response to warmer temperatures during early Spring. This implies that the growing season of ring-porous trees expanded due to Spring temperatures, which are projected to continue to increase as anthropogenic global warming intensifies. The reactivation of cambial cells is likely beginning earlier potentially exposing these trees to higher risk of cavitation or damage during frost events (Cochard & Tyree, 1990). Damage of this nature would then need to be repaired using carbon reserves which may be in short demand as they are already being used for initial growth. Hypothetically, this could lead to carbon starvation in some trees. Alternatively, the extension of growth season and higher yearly growth totals like we see here, could give ring-porous trees a competitive advantage over their non-responsive diffuse-porous counterparts. In the long term, this could lead to changes in species dominance within temperate forests (talk more aobut this?).

Meanwhile, diffuse-porous growth timing seems relatively unaffected by early Spring temperatures, instead showing a higher correlation with late Spring or Summer temps. This disconnect means that diffuse-porous trees will continue to focus their growing season in the Summer, which is projected to become less conducive to tree growth as temperatures and drought intensity increase. However, diffuse-porous trees are adapted to survive in drought conditions, and may continue to be successful even in future climate scenarios (RIght? seeing conflicting reports. Sources.). Studies have found that these diffuse-porous trees in the Eastern USA show the largest reduction in ring-width increment during, and following, Summer droughts (Kannenberg et al, 2018) as well as being generally more sensitive to Summer precipitation patterns (Elliot et al, 2015). The potential for more frequent reduction in growth coupled with the increased growing season length of ring-porous species may lead to an alteration in forest species composition. –the range of some of these species may migrate North to cooler summer conditions becoming potentially extant in the Southern / mid Atlantic of the USA.– (Is mortality of ring-porous species higher in recent decades? Hard to pinpoint, but would likely be caused by warmer early-spring followed by late frost events exhausting NSC reserves?)

This analysis is one of a first generation of intraannual dendroband tree growth studies, and as such, is the metaphorical tip of the ice berg. Here, we focused our analysis purely on early Spring warming. This falls short of the reality of our changing climate, where each season is being affected in some way, leading to a combination of stressors on plant growth. For example, diffuse porous trees seemed to show little, if any, relationship with the climate window defined here, but if we shift that window forward 20 days, the effect increases dramatically, signalling a greater importance of May/June TMAX on trees of that wood type (figure or table?). This revelation agrees with the results from Helcoski et al (2019), which found differences in interspecific growth responses to several climate variables throughout the year using tree cores. Additionally, Other studies have found that Autumn leaf senescence is being delayed potentially in response to warmer temperatures in the previous year’s Winter or Autumn (), changes in chilling requirements due to current year Autumn and winter temperatures (), and stunted total productivity induced by drought and high TMAX in the current year’s Summer (), diffuse porous trees increased growth during the following growing season when winter temperatures (TMIN) were lower (Benito & Pederson, 2015; Elliot et al, 2015). How these relationships may impact intraannual growth patterns or variables like those described here is uncertain, but identifying such relationships will help us further understand how climate change is impacting forests.

We present a stepping stone for future studies to build upon.

Content to incorporate: N. American strategies have conservative strategies when it comes to phenology, as historically they’ve been subject to more spring frosts. Thus, climate change is having less impact (Zohner et al., 2020)

### Acknowledgements

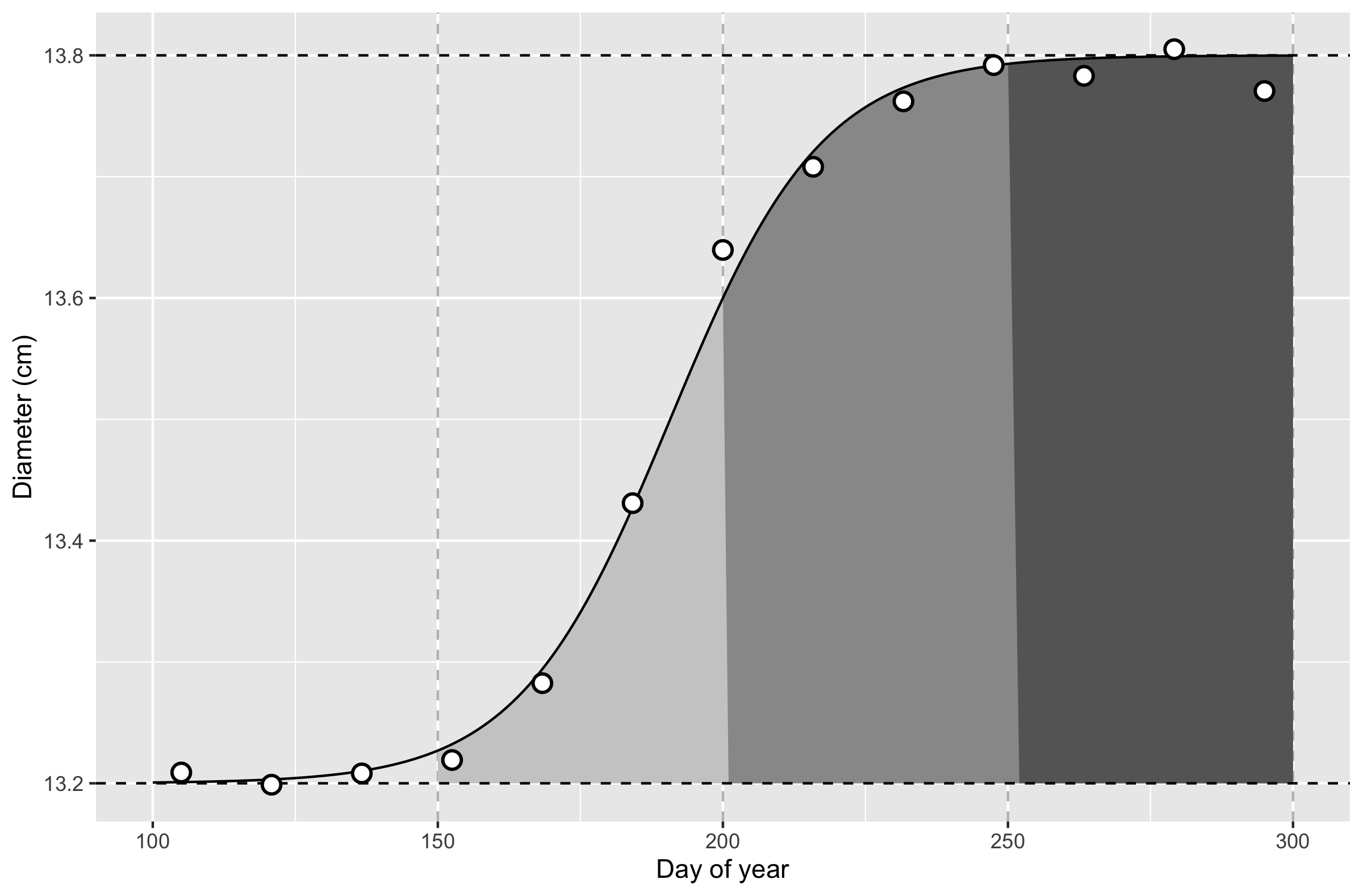
ForestGEO

### Authors’ contributions

### Figures

**Figure 1**

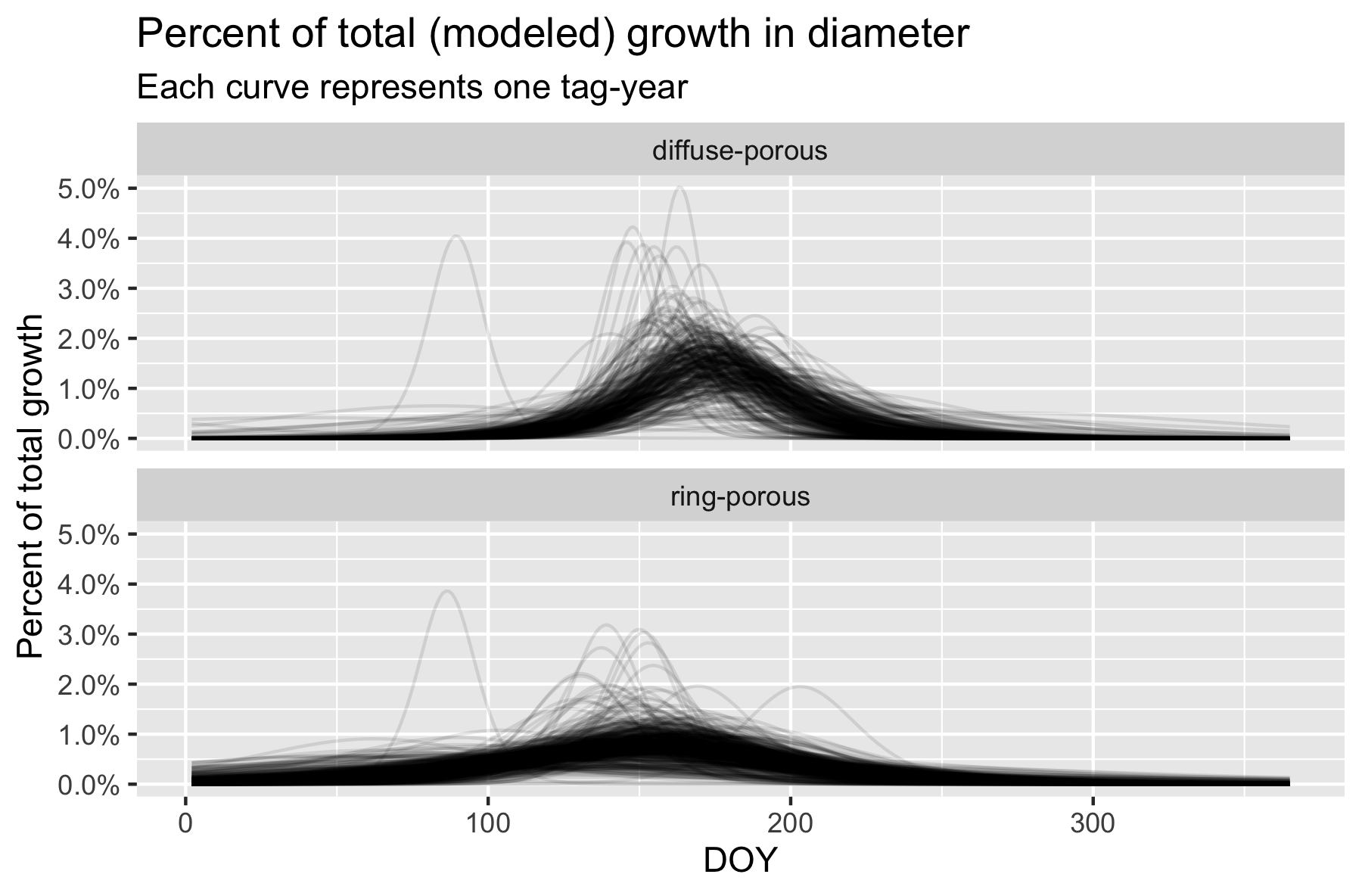
Based on D’Orangeville Figure 1



Logistic growth model

**Figure 2**

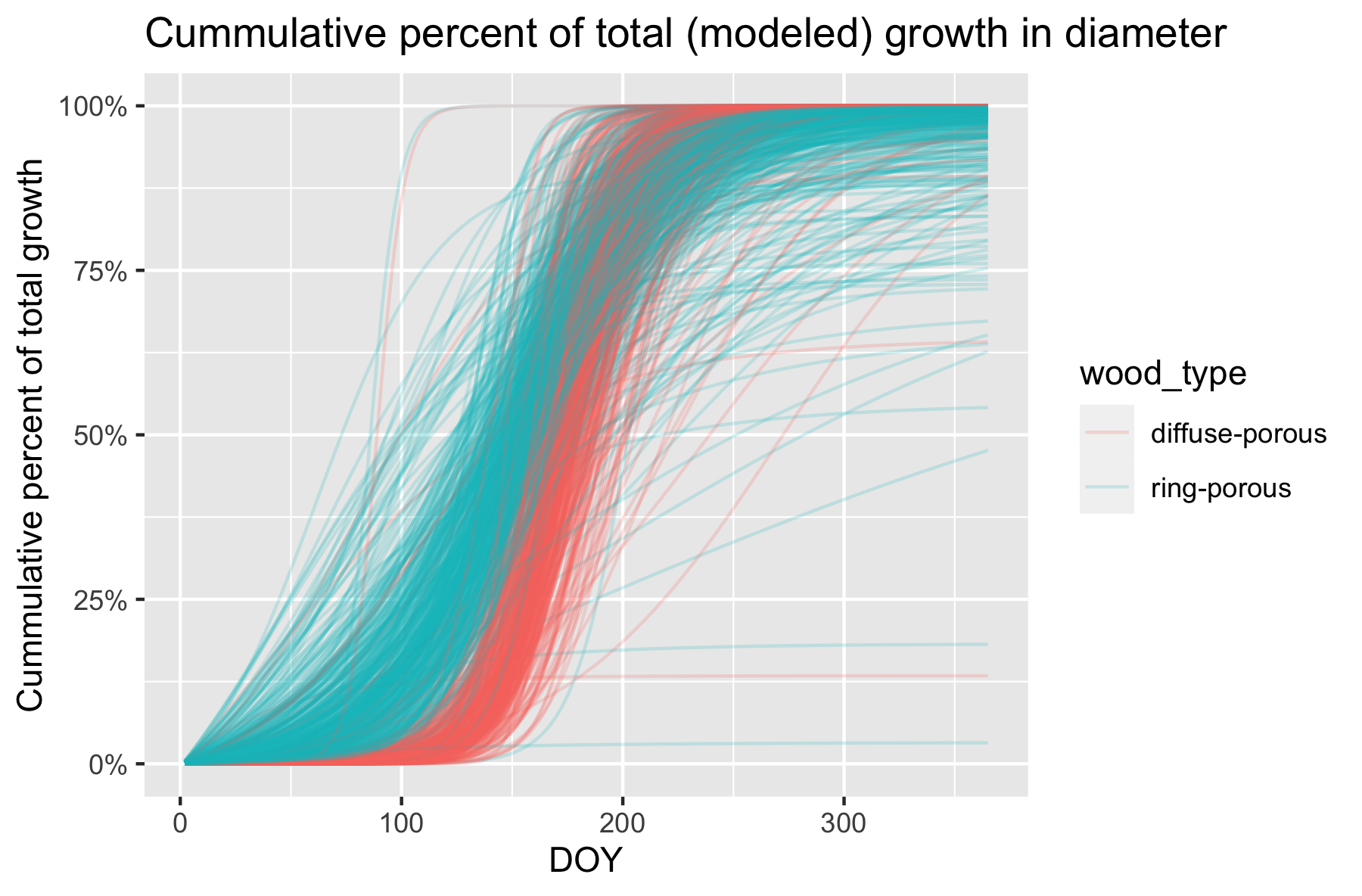
Based on D’Orangeville Figure 3.a), but with relative growth



Percent total (modeled) growth

**Figure 3**

Similar to D’Orangeville Figure 4.a), but with cummalative relative growth



Cummulative percent total (modeled) growth

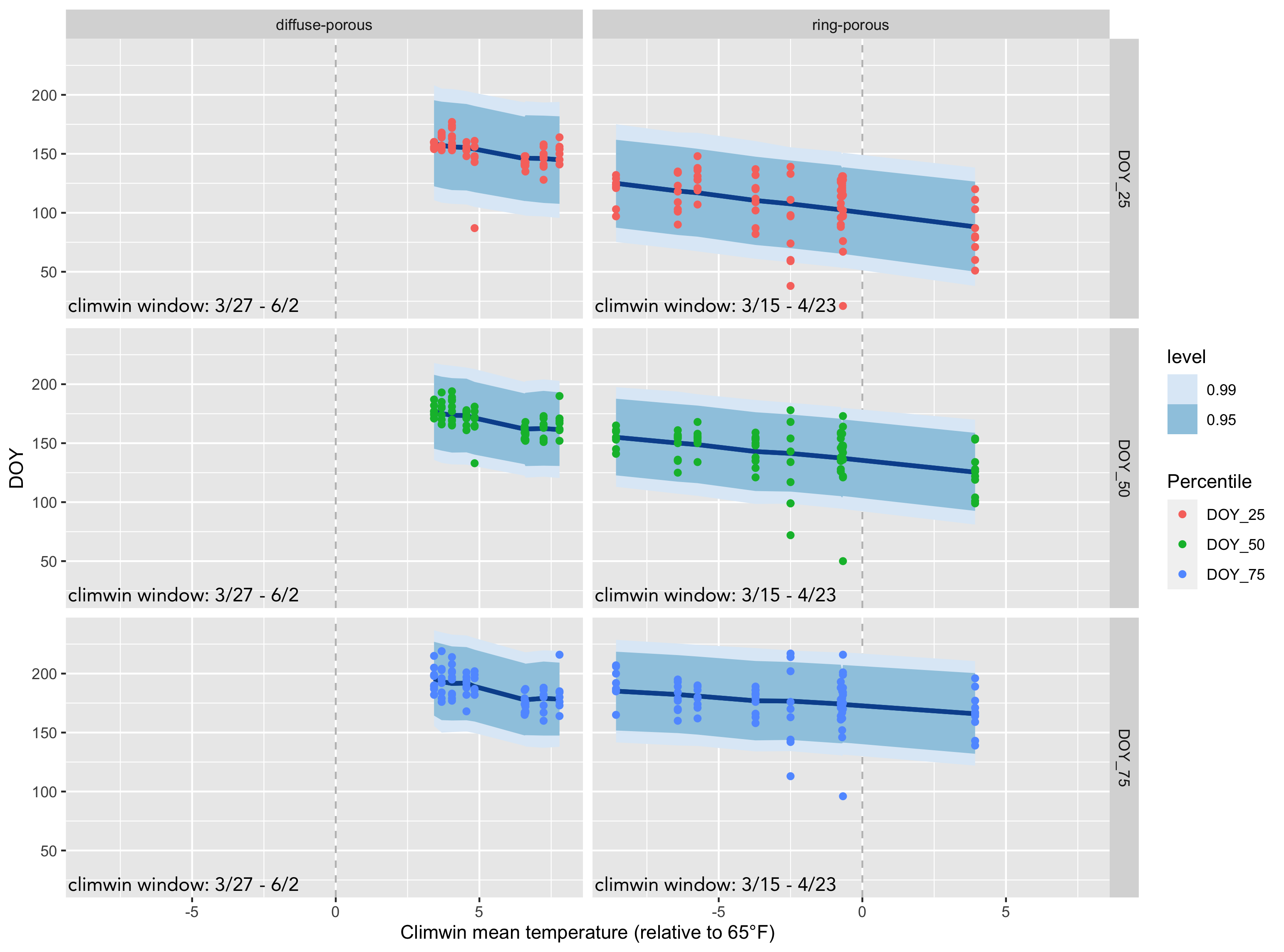
**Figure 4**

**Figure 5**

**Figure 6**

Notes for now:

1. Model was fit to a random sample of 20 out of 106 tags to speed up computation.
2. Climwin mean temperatures are recentered at 65F to help sanity check intercepts and slopes. 65F was chosen because it is a “typical” climwinmean value
3. The multivariate model for has:
   1. Fixed effects: The interaction between wood type (diffuse vs ring porous) and climwin mean
   2. Random effects: tag number (no species just yet)



Relationship between DOY and climwin mean tempeatures. For each observed climwin mean temperature value, the posterior mean of the fitted day of year is represented by the solid blue line and credible intervals are represented by bands.

### References

McMahon, S. M., & Parker, G. G. (2015). A general model of intra-annual tree growth using dendrometer bands. *Ecology and Evolution*, *5*(2), 243–254. <https://doi.org/10.1002/ece3.1117>