

A Bayesian Nonlinear Multilevel Model of Urban Tree Growth

November 24, 2018

1 Introduction

Modeling the growth of trees has been important to estimate timber production and other ecosystem services of forests for decades. Multilevel modeling is an attractive modeling approach because it provides a coherent framework to account for the many levels of observation or of groupings in data and to pool information across groups (Lappi and Bailey, 1988). This paper has two main contributions. First, we demonstrate the use of Stan via the `brms` package in R to fit bayesian nonlinear multilevel models to predict tree diameter growth from age (Carpenter et al., 2017; Bürkner, 2017). Second, we apply the method to the Urban Tree Database (McPherson et al., 2016a,b). This dataset is the result an over a decade long effort to collect age and size data on thousands of trees in 17 cities across the US. Multilevel modeling has the potential to extract more information from the data and improve predictions compared to the existing approach. Improving predictions of tree size from tree age will improve our ability to predict the important ecosystem services these trees provide urban dwellers.

The existing approach to modeling the diameter growth of trees in the urban tree database (UTD) was to fit a separate model for each tree species in each city and test several model forms (various polynomials and log transformations) with different weights and then select the model with the lowest Akaike Information Criterion (AIC). This approach has several limitations, many highlighted in the report. First, while the model form selected provided the lowest AIC, many of the estimates are not biologically realistic (for example, estimates of diameter may begin to increase or decrease sharply at old ages, cubic and quadratic fits, respectively). Therefore, the researchers cautioned against applying the models beyond the range of the data, or sometimes even within the range of data if the estimates were unrealistic. These unrealistic estimates and the inability to extrapolate severely limits managers' ability to predict growth over meaningful time scales (a century rather than a few decades). A second limitation is that some models predict negative diameters, an impossibility. Third, models are only provided for the cities and the species sampled. If a manager wants to predict the diameter growth of a tree species in an unsampled city, the researchers recommend using the model from the reference city in the same climate region. However, many of the reference cities are on the border of climate regions and as noted in the UTC report there is known large variability in growth within regions (see figure 5 in the UTD report originally from McPherson and Peper 2012, comparing Cheyenne to Ft. Collins. The figure is reproduced in supplementary figures). Furthermore, if a manager wants to predict growth for an unsampled species or a species that was sampled in a different city it is not obvious which equation to use and the additional uncertainty that this introduces is not quantified.

Our approach addresses the above limitations. First, we use a weibull curve, commonly used in forestry growth equations for its biological realism, which makes extrapolation to ages outside the data range less fraught. Second, using this sigmoidal curve and modeling diameter with a gamma distribution ensures our estimates of diameter are positive. Third, by modeling the weibull curve parameters as functions of species, city, and climate, we are able to borrow information across cities and across species to provide predictions and associated

uncertainty of diameter growth, even in cities or species with very little or no data.

Sigmoidal curves very similar to the weibull have been used before in modeling urban tree diameter growth as a function of age. Frelich (1992) use the Chapman-Richards growth curve of form $y = B_0(1 - \exp(B_1x))^{B_2}$ to predict DBH from age for healthy trees (12 species, 221 trees total) in Minneapolis and St. Paul, Minnesota. This equation form worked very well (8 out of 12 species had an R^2 over .9), but the trees used were only healthy open grown trees, which is not representative of urban trees generally. Following Frelich (1992), in an early version of the urban tree database, McPherson and Simpson (1999) fit the same curve to a small number of observations and adjusted parameters for different locations based on the number of frost free days. The amount the parameters were adjusted was based on expert opinion, not data. Peper et al. (2001a) and Peper et al. (2001b) compared the Chapman-Richards curve to logarithm regression and selected the logarithm regression based on a higher R^2 . Subsequent UTD growth equations did not use sigmoidal curves (McPherson et al., 2016b).

Multilevel modeling was first introduced to forestry by Lappi and Bailey (1988) and has since been widely used to account for multiple levels of variability (observations correlated within groups) in allometric and growth equations. Indeed, one of the test datasets in R to demonstrate nonlinear multilevel modeling are observations of orange tree growth (R Core Team, 2016). Hall and Bailey (2001) give a general overview of the frequentist multilevel approach and an example of loblolly pine height growth in the Southeastern US. Levels/groups in their model are plot and tree nested within plot, and they use tree density as a plot level covariate. Nothdurft et al. (2006) provide another example of modeling tree height growth using norway spruce in Germany. They use the Sloboda function and levels in the model are plot and trees nested in plot with elevation as a plot level covariate. Li et al. (2011) provide a bayesian example modeling balsam fir height growth in Maine using the Chapman-Richards equation, also with tree nested within plot. They found the bayesian approach has similar parameter point estimates to the frequentist approach. In an urban tree context, Peper et al.

(2014) model DBH growth with repeat measures data on individual trees and test a varying coefficients model because they have repeat measures on individual trees.

Compared to past work, our approach is more complex from a modeling standpoint in the use of a bayesian approach with both nested and non-nested groupings and group level predictors. The bayesian multilevel/hierarchical modeling framework has many strengths as discussed in Li et al. (2011) (and others) and includes the ability to sample parameter values from the entire posterior, rather than maximum likelihood estimates. Nonlinear multilevel models in the frequentist approach depend on linear approximations such as first-order taylor expansion, which is not required in the bayesian framework. Summary statistics of parameters (mean, median, quantiles) can be easily calculated from posterior samples and the common assumption in the frequentist paradigm that parameters are normally distributed can be relaxed. The ability to incorporate prior information from experts or past studies on parameters is another strength of the bayesian approach.

From the perspective of urban ecosystem services and disservices, the size of trees is directly related to their potential to reduce noise, air pollution, and storm water runoff. It is also related to their potential to interfere with infrastructure such as roads and powerlines. Thus models to predict urban tree growth are useful to managers and scientists interested in better quantifying urban tree impacts on human wellbeing.

2 Methods

2.1 Data

The urban tree database (UTD, McPherson et al. (2016a)) consists of measurements on 14487 trees of 170 species in 17 cities. However, largely because of the difficulty is measuring tree age, there are only 12687 trees with complete age and diameter data (161 species, 17 cities, 309 species by city combinations 1).

Some species were measured in multiple cities, but not most. The number of trees of

each city by species combination sampled ranged from 1 (both *Liquidambar styraciflua* and *Prunus serrulata* in Queens, NY) to 79 (*Quercus laurifolia* in Charleston, SC). The median number of trees in each species-city combination was 37.

Age is defined in this dataset as time since planting, since this is the record kept by cities. Actual age of the trees may be several years more. Diameter (cm) of the trees is measured at breast height (1.37m above ground).

In the UTD, trees are classified taxonomically down to cultivar for some individuals, but here we aggregate cultivars up to the species level. Species are then nested within Genera.

The 17 cities in the UTD cover much of the US geographically, 2, and much of the variation in climate, 3. However, New York City only has a few observations and the data for Indianapolis is missing too.

Rather than using the aggregated sunset zones as done in UTD, we used growing degree days (GDD) and precipitation data from climate NOAA’s climate normals to continuously vary equation parameters across climate. Figure 3 shows each census tract centroid in the conterminous US plotted in GDD and precipitation space. We approximated the GDD and precipitation for each tract by assigning the values of the weather station closest to the centroid. This allows us to vary our model continuously across geographic space in a way that better captures the natural gradients of climate.

2.2 Modelling

2.2.1 Model requirements

We sought a model of tree growth that would adequately represent the known biological dynamics of tree growth, namely that diameter growth rate starts slow, reaches a maximum at a young age, and then gradually declines to nearly zero. Unlike tree height, which often reaches a true asymptote, diameter of trees must always increase, however slightly, because the growth of new wood is essential for proper function. While there is no true asymptote for tree diameter, they often reach a practical one. An additional feature to the data is that

age is time since transplanting. This means trees can have substantial diameter at age 0.

The type of curve that meets these criteria would be an asymmetric sigmoidal curve with an intercept. A modified weibull is such a curve that has worked well in forestry and is the one we use here (Weiskittel et al., 2011). However, there are many other curves such as the Chapman-Richards that meet these criteria and could also be used.

Another characteristic of tree growth curves is heteroskedasticity, namely that as the age of trees increases, so does the variability around the mean. Often past modelers controlled this using log - log transformations (Troxel et al., 2013), but we wanted to keep units in their original scale. We tested fitting models where the variance was a linear function or a smoothed spline function of age. However, this still could yield negative predictions at low ages. Instead we adopted the approach of modeling DBH from a gamma distribution, which yielded more realistic posterior predictions.

We fit models of generally increasing complexity starting a single weibull curve for all trees and then varying the curve parameters by city, by genus and species, and by climate. Using approximate leave-one-out cross validation we selected the model with the highest estimated log posterior density (Vehtari et al., 2017). The following section details this model. The source code for this paper and details for all other models tested is available on github.

2.2.2 Likelihood

$$y_{igsc} \sim \text{Gamma}(\mu_{igsc}, \alpha_y)$$

$$\mu_{igsc} = \beta_{igsc}^{(0)} + \beta_{igsc}^{(1)}(1 - \exp(-\beta_{igsc}^{(2)} x_{igsc}^{\beta_{igsc}^{(3)}}))$$

where:

y_{igsc} is the diameter at breast height of tree i of genus, g , species, s , and city, c . y_{igsc} has a gamma distribution with mean, μ_{igsc} , and shape, α_y .

$i = 1, \dots, n_{sc}$; where n_{sc} is the number of trees sampled for species, s , and city, c .

$g = 1, \dots, G$; where G is the number of genera (G)

$s = 1, \dots, S_g$; where S_g is the number of species in genus g .

x_{igsc} is the transplant age in years of tree $igsc$ (i.e. years since transplanting).

$\beta_{igsc}^{(0)}$ is the intercept, or the diameter of a tree at time of transplanting.

$\beta_{igsc}^{(1)}$ (plus $\beta_{igsc}^{(0)}$) is the asymptote of the sigmoidal weibull curve.

$\beta_{igsc}^{(2)}$ and $\beta_{igsc}^{(3)}$ affect the rate of growth. $\beta_{igsc}^{(2)}$ provides flexibility to have slow or fast growth at young ages.

For each $\beta_{igsc}^{(j)}$, $j = 0,1,2$:

$$\beta_{igsc}^{(j)} = \beta_0^{(j)} + \gamma_{gs}^{(j)} + \delta_c^{(j)}$$

for $\beta_{igsc}^{(3)}$:

$$\beta_{igsc}^{(3)} = \beta_0^{(3)} + \tau_1 * \text{precip}_c + \tau_2 * \text{gdd}_c + \tau_3 * (\text{precip}_c * \text{gdd}_c) + \gamma_{gs}^{(3)} + \delta_c^{(3)}$$

where $\beta_0^{(j)}$ is the mean for $\beta_{igsc}^{(j)}$. $\gamma_{gs}^{(j)}$ is genetic (genus and species) effect on $\beta^{(j)}$. $\delta_c^{(j)}$ is the city effect on $\beta^{(j)}$

The species effect is nested within the genus effect. Both are normally distributed, such that:

$$\gamma_{gs}^{(j)} \sim N(\gamma_g^{(j)}, \sigma_{\text{genus:species}}^{(j)})$$

$$\gamma_g^{(j)} \sim N(0, \sigma_{\text{genus}}^{(j)})$$

The effect of city is normally distributed:

$$\delta_c^{(j)} \sim N(0, \sigma_{\text{city}}^{(j)})$$

2.2.3 Priors

The priors were selected to make biologically unrealistic parameters highly improbable, but they have a small effect on the posterior estimates. The β 's and α_y are gamma distributed, while the variance parameters are half-normal. More details on the selection of priors are available in supplementary materials and code. Many priors that might appear to be narrow (e.g Half-Normal(0,.1)) are actually fairly wide given the scale of the predictors and the reasonable range of some parameters.

3 Statistical Inference

3.1 Model fitting in Stan

Stan is a probabilistic programming language for bayesian inference (Carpenter et al., 2017). It uses No-U-Turn sampler, an adaptive form of Hamiltonian Monte Carlo sampling, to effectively draw samples from the specified log posterior density. Here, we access Stan via the R package `brms` (Bürkner, 2017). `brms` allows the user to specify the likelihood and priors in syntax similar to the R package `lme4` commonly used for frequentist multilevel (mixed effects) models. This makes using Stan much simpler and concise because it frees the user from the need to optimize Stan code (`brms` is already very efficient) and can convert a few lines of R code into many lines of Stan. `brms` is not as flexible as Stan, but still can be used to fit many types of models including nonlinear multilevel regression models, such as ours here. Some of the key advantages of fitting a model in Stan via `brms` include relatively simple syntax and efficient posterior sampling for multilevel non-linear models. The bayesian approach gives better estimates of parameter uncertainty and provides a formal way to include prior information.

Posterior distributions with 80% interval and median for parameters are shown in figures 4, 5, 6, 7, 8, 9, 10.

3.2 Model Comparisons

Our approach increased model complexity at each step, first fitting a single weibull curve to all trees, and then allowing all parameters to vary by city, genus, and climate. Table 1 provides short descriptions of the models tested and the brms syntax used. Note, in the code used parameters were rescaled so that all parameters would be on roughly the same order of magnitude. This scaling was omitted from table 1 for clarity. After fitting a complex model where all of the β 's could vary by city, genus, and species, we sought a slightly simpler model and dropped the variation of the asymptote by city (model 6).

Table 2 shows the models ranked by the approximate leave-one-out expected log pointwise predictive density (Vehtari et al., 2017). Lower values indicate better model predictive performance. The standard error for the elpd difference of 131 between model 6 and model 7 is 21.4, giving strong evidence that model 6 is superior to the other models.

4 Results

4.1 Climate Effects on Growth Rate

There is a positive effect of growing degree days (gdd) and annual precipitation (precip) on tree diameter (dbh), and a positive interaction between the two. Marginal effects of climate on posterior mean of DBH for a tree 25 years after planting are shown in figure 11, standard error of this mean is in figure 12. There is an estimated 40cm difference in dbh between an average tree in Orlando, FL and one in Boise, ID.

4.2 Comparing to Existing Equations

Figure 13 compares our model to existing UTD equations for *Acer platanoides* (Comparisons for all species and cities are in supplementary figures). In the case of Fort Collins, UTD and our equations have high agreement. Similarly in Minneapolis, however we are able to provide

more reasonable extrapolation. In the case of Boise, UTD predicts declining DBH at large ages, and in Longview it predicts rapidly increasing DBH at large ages. Our model does not fit the sample of data from those individual cities as well, but it shares information across all cities so that it will likely make a better out of sample prediction and extrapolates more reasonably. In the case of Queens, there were only two observations and so the UTD growth equation was a straight line (there may be a missing point used to fit the line which is not in the data and would explain why the line doesn't connect the two observations). By borrowing information across all cities, we are able to make a more reasonable prediction even with only two observations in that city.

4.3 Uncertainty increases when predicting out of sample cities, genera, and species

It is also possible to make predictions to unsampled cities and species while accounting for the increased uncertainty. Figure 14 shows how the predictive interval for DBH increases for an unknown species of *Acer* (second column) and increases even more for an unknown genus and unknown species (third column). For an unsampled city, such as St. Louis, MO (second row), uncertainty is higher than for a sampled city, Sacramento, CA (first row). The large 95% predictive intervals for a tree of unknown genus and species shows how great the genetic variability is across trees.

5 Discussion

Our selected model provides biologically realistic estimates of tree diameter growth for all species and cities observed, and also a way to make predictions for species with little or no data while appropriately reporting uncertainty. Our model will make better out of sample predictions than the existing UTC equations which are overfit to single species by cities combinations. We found the growth curve parameters, β_0 , β_2 , β_3 , vary more across cities,

than they do across genera, and there is much less variation due to species within genera. This suggests that management practices and other factors that vary across cities can have a stronger impact on growth than the genetic potential of trees. This result is not surprising for β_0 , the diameter of trees when they are transplanted, since it is almost completely determined by management decisions about when a tree is large enough to withstand the urban environment. Differences in other growth parameters across cities have been found before. As noted by Peper et al. (2001a), differences in the dimensions of sweetgum and camphor in Modesto and in Santa Monica were due to different pruning regimes and cultural practices. While including more information at the genus level such as leaf foliar traits or wood characteristics (e.g. Dietze et al. 2008) could certainly help explain variation in growth, our results show that an information on city-level management practices would do more to improve predictive performance, especially in unsampled cities.

There is evidence that growth rate (β_3) varies with climatic differences across cities, but there is still considerable uncertainty in these effects due largely to the relatively small sample size of cities and their uneven distribution in climate space. 25 years after planting, the model predicts that trees in warm and wet climates (e.g. central florida) will be about 60 cm greater in DBH than trees grown in cool dry climates (e.g. Fort Collins). While this is physically possible, the high uncertainty qualifies this estimate. Orlando is the only city sampled from a very warm and wet climate, its large influence in the model and the high uncertainty suggests more cities need to be sampled in places like Louisiana and eastern Texas.

The mean asymptote for diameter growth of common urban species (β_1) is about 150 cm (95% CI: 131 - 171). This varies considerably by genus and at times in unrealistic ways due to data limitations. For example, the estimated mean asymptotic DBH for *Prunus* (cherry), a small tree is 194 cm, while for *Robinia pseudoacacia*, a larger tree, it is 107 cm. *Prunus* has such a large estimated asymptote because there are several trees younger than 30 with a DBH greater than 80 cm, but the oldest tree sampled was just 30 years old. Extrapolation

and the interpretation of β_1 as the asymptotic DBH should be used with caution depending on the presence of observations at large ages. Half of the species observed have an oldest tree of less than 55 years. While our method improves upon existing methods, extrapolation to ages great than those sampled should be done with caution. To make better predictions of diameter at large ages, older and larger trees are needed. Since finding large old trees in urban environments would require more challenging work, one alternative could be to create constraints on maximum DBH based on the largest individuals (called champion trees) of the species found anywhere (not just in urban areas).

Estimates of uncertainty reveal where new observations are most needed. Sampling older trees would improve extrapolation to century scales, new cities in warm and wet climates will improve extrapolation to more regions across the country, sampling less common species will improve estimates of how all (not just common) urban trees grow, and repeated measures on individual tree would improve predictions for trees that are already planted (not just those at age 0).

There are also a number of modeling extensions that could improve either predictive performance or quantification of uncertainty. Additional covariates at the level of individuals (e.g. location relative to street, sidewalk, and utilities) and at the level of a city or species could improve prediction. The age of trees in the dataset is actually highly uncertain. The bayesian approach allows the modeling of age as a random variable and including age as a part of the posterior could give a more honest quantification of the uncertainty in tree diameter growth. Other dimensions of trees, such as height and crown width could also be included in a multivariate model.

6 Conclusion

We have demonstrated the usefulness of the bayesian multilevel approach for urban tree diameter growth modeling. We make more biologically realistic estimates of growth than

the existing approach and we have improved predictions of older trees, and trees in cities or species with little or no data. Our model can be applied to trees in cities across the US by adjusting growth parameters based on the number of growing degree days and annual precipitation and uncertainty is accounted for. The use of `brms` as an interface to Stan makes fitting the model relatively easy, however selecting appropriate priors required considerable thinking to select biologically appropriate values. The model along with the data and relevant code are published online and are available for scientists and managers to use as an input into ecosystem services modeling.

References

- Bürkner, P.-C. (2017). Brms: An r package for bayesian multilevel models using stan. *Journal of Statistical Software*, 80(1):nil.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., and Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, 76(1):nil.
- Dietze, M. C., Wolosin, M. S., and Clark, J. S. (2008). Capturing diversity and interspecific variability in allometries: A hierarchical approach. *Forest Ecology and Management*, 256(11):1939–1948.
- Frelich, L. E. (1992). Predicting dimensional relationships for twin cities shade trees.
- Hall, D. B. and Bailey, R. L. (2001). Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models. *Forest science*, 47(3):311–321.
- Lappi, J. and Bailey, R. L. (1988). A height prediction model with random stand and tree parameters: An alternative to traditional site index methods. *Forest Science*, 34(4):907–927.

- Li, R., Stewart, B., and Weiskittel, A. (2011). A bayesian approach for modelling non-linear longitudinal/hierarchical data with random effects in forestry. *Forestry*, 85(1):17–25.
- McPherson, E. G. and Simpson, J. R. (1999). Carbon dioxide reduction through urban forestry. *Gen. Tech. Rep. PSW-171, USDA For. Serv., Pacific Southwest Research Station, Albany, CA.*
- McPherson, E. G., van Doorn, N. S., and Peper, P. J. (2016a). Urban tree database.
- McPherson, E. G., van Doorn, N. S., and Peper, P. J. (2016b). Urban tree database and allometric equations.
- Nothdurft, A., Kublin, E., and Lappi, J. (2006). A non-linear hierarchical mixed model to describe tree height growth. *European Journal of Forest Research*, 125(3):281–289.
- Peper, P. J., Alzate, C. P., McNeil, J. W., and Hashemi, J. (2014). Allometric equations for urban ash trees (*fraxinus* spp.) in oakville, southern ontario, canada. *Urban Forestry & Urban Greening*, 13(1):175–183.
- Peper, P. J., McPherson, E. G., and Mori, S. M. (2001a). Equations for predicting diameter, height, crown width, and leaf area of san joaquin valley street trees. *Journal of Arboriculture*, 27(6):306–317.
- Peper, P. J., McPherson, E. G., and Mori, S. M. (2001b). Predictive equations for dimensions and leaf area of coastal southern california street trees. *Journal of Arboriculture*, 27(4):169.
- R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Troxel, B., Piana, M., Ashton, M. S., and Murphy-Dunning, C. (2013). Relationships between bole and crown size for young urban trees in the northeastern usa. *Urban forestry & urban greening*, 12(2):144–153.

- Vehtari, A., Gelman, A., and Gabry, J. (2017). Practical bayesian model evaluation using leave-one-out cross-validation and waic. *Statistics and Computing*, 27(5):1413–1432.
- Weiskittel, A. R., Hann, D. W., Kershaw, J. A., and Vanclay, J. K. (2011). *Forest Growth and Yield Modeling*. []. John Wiley & Sons, Ltd.

7 Figures and Tables



Figure 1: Number of trees sampled of each species and city combination in the urban tree database.

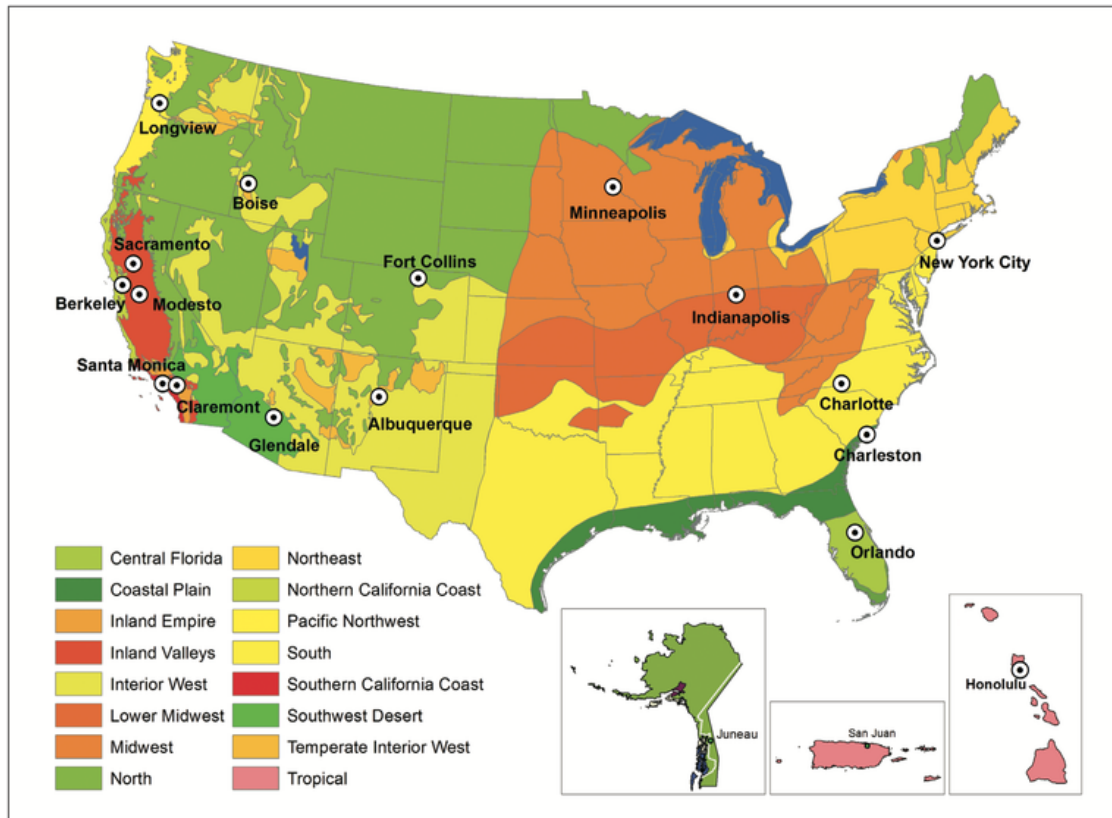


Figure 9—Climate zones were aggregated from 45 Sunset climate zones into 16 zones. Each zone has a reference city where tree growth data were collected. Sacramento, California, was added as a second reference city (with Modesto) to the Inland Valleys zone.

Figure 2: 16 climate regions and 17 representative cities in the UTD (McPherson et al., 2016b).

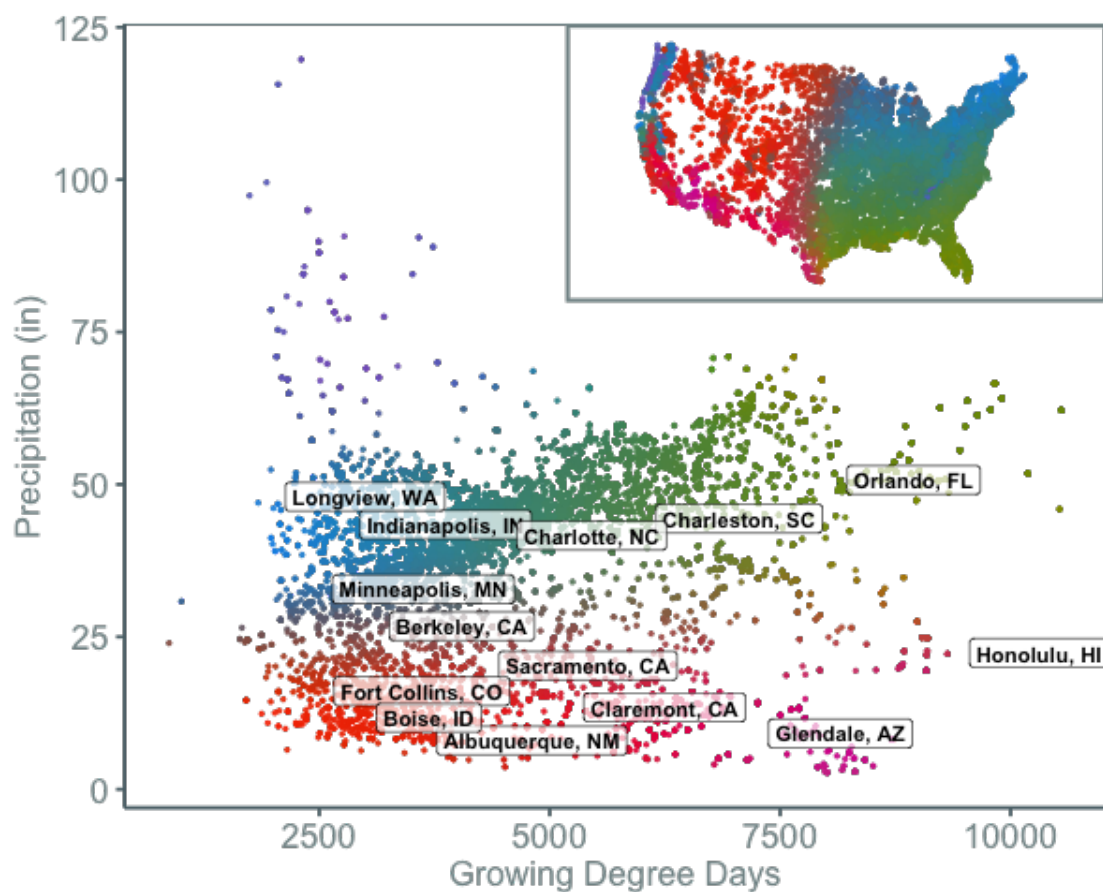


Figure 3: US census tract centroids with UTD reference cities overlaid in growing degree day (GDD) and precipitation climate space and matching color gradient in geographic space. The reference cities cover climate space well, and variation in precipitation and growing degree days is continuous.

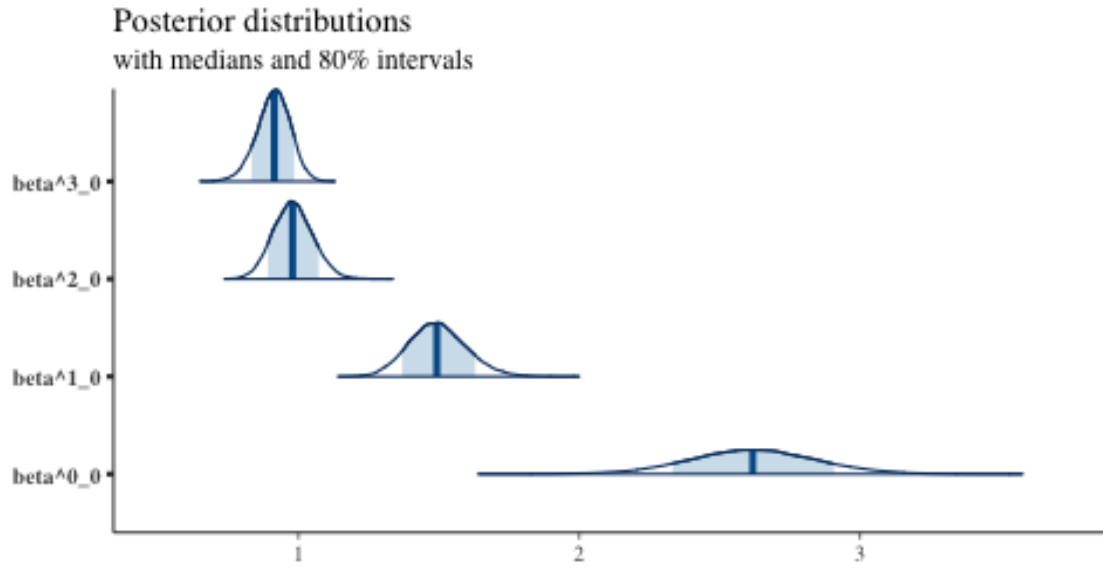


Figure 4: Marginal posterior distributions of $\beta_0^{(j)}$

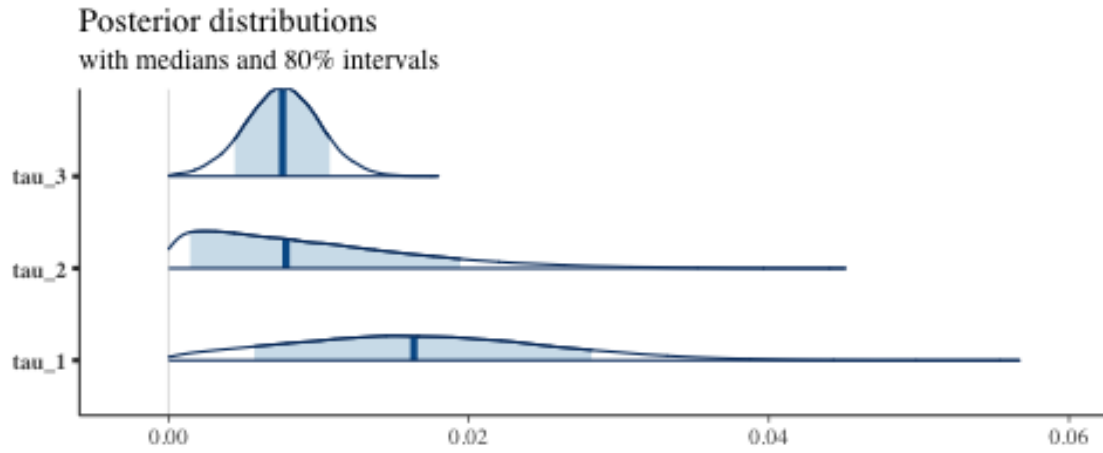


Figure 5: Marginal posterior distributions of τ 's

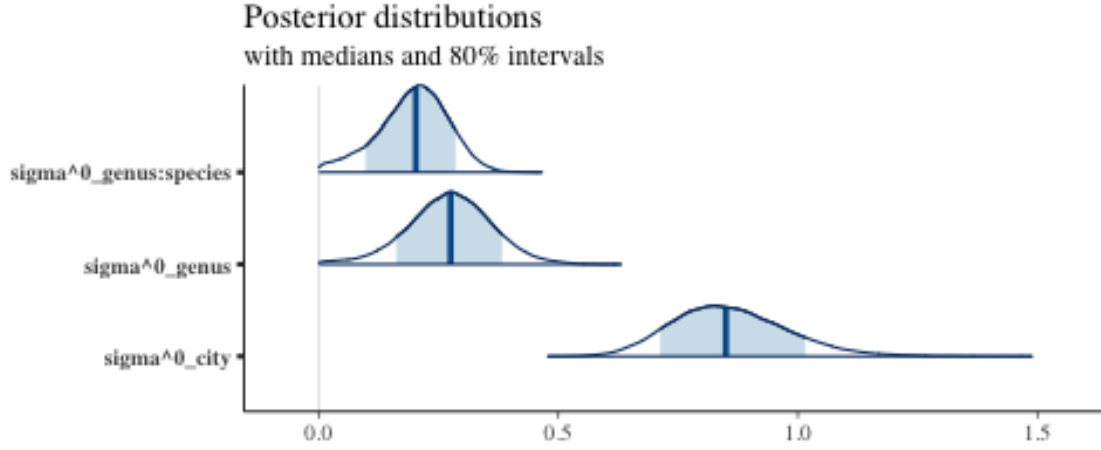


Figure 6: Marginal posterior distributions of $\sigma^{(0)}$'s

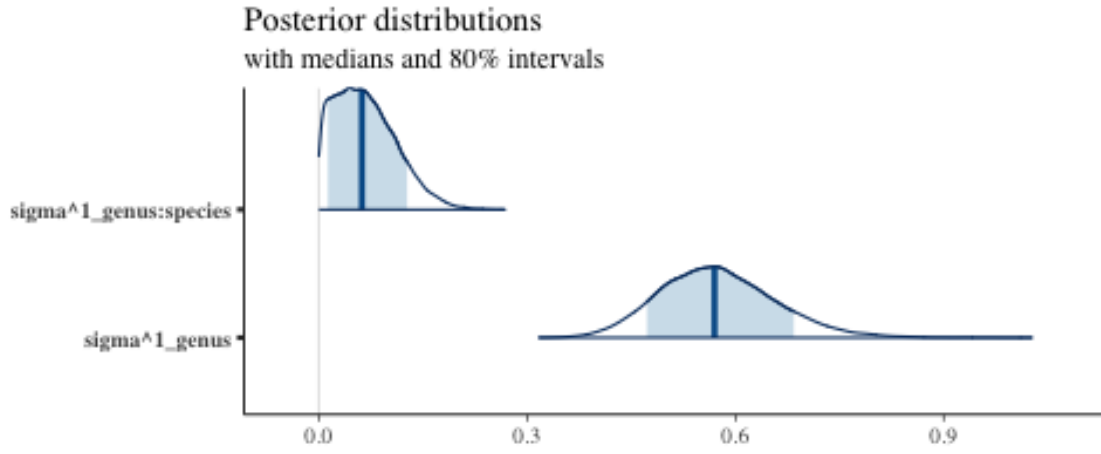


Figure 7: Marginal posterior distributions of $\sigma^{(1)}$'s

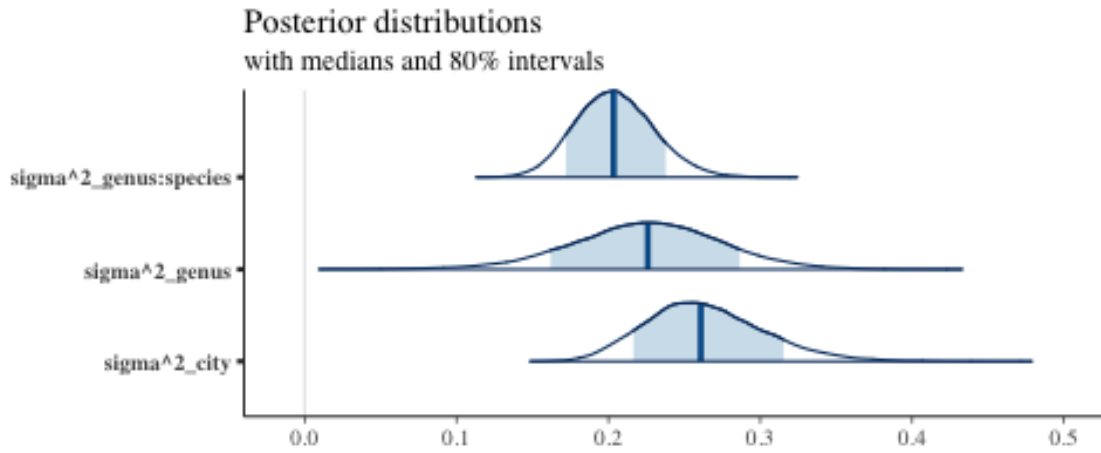


Figure 8: Marginal posterior distributions of $\sigma^{(2)}$'s

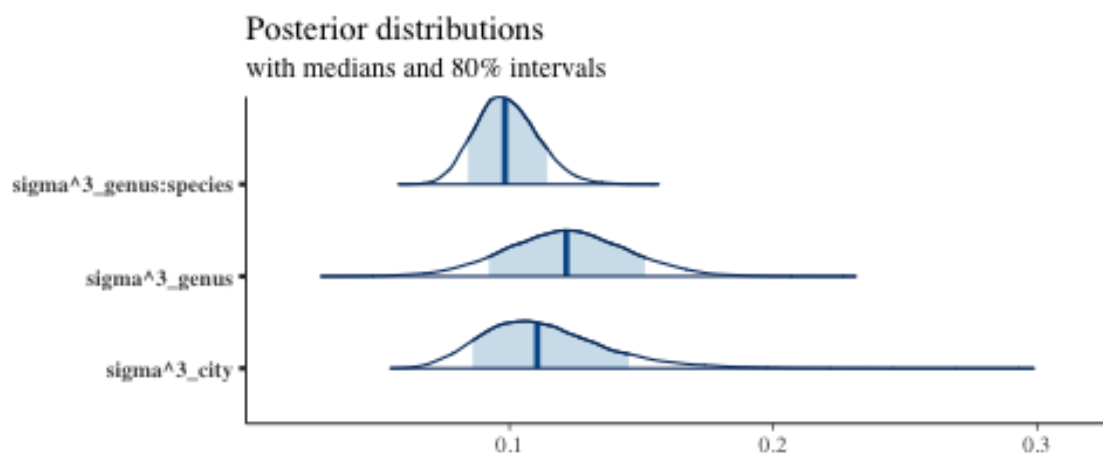


Figure 9: Marginal posterior distributions of $\sigma^{(3)}$'s

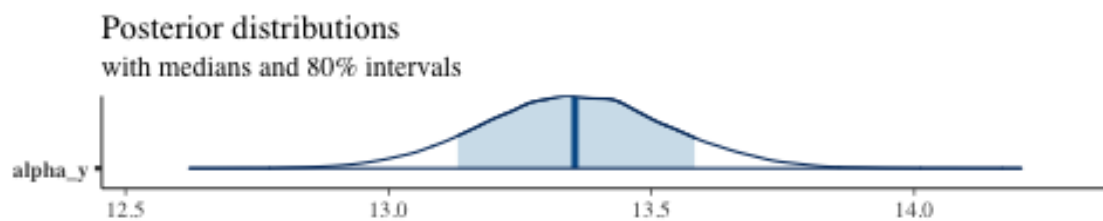


Figure 10: Marginal posterior distributions of α_y

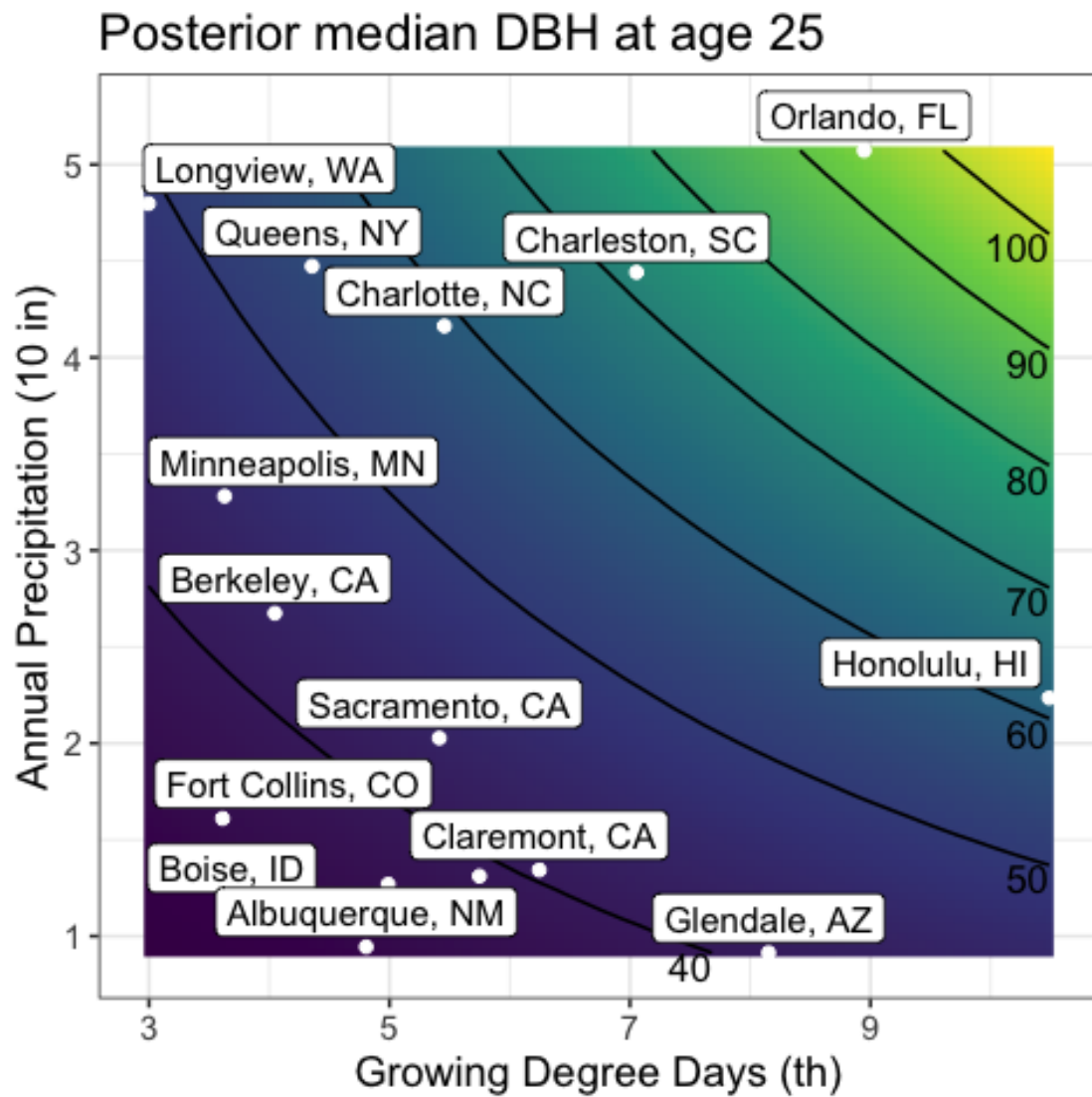


Figure 11: Posterior median DBH at 25 years after planting.

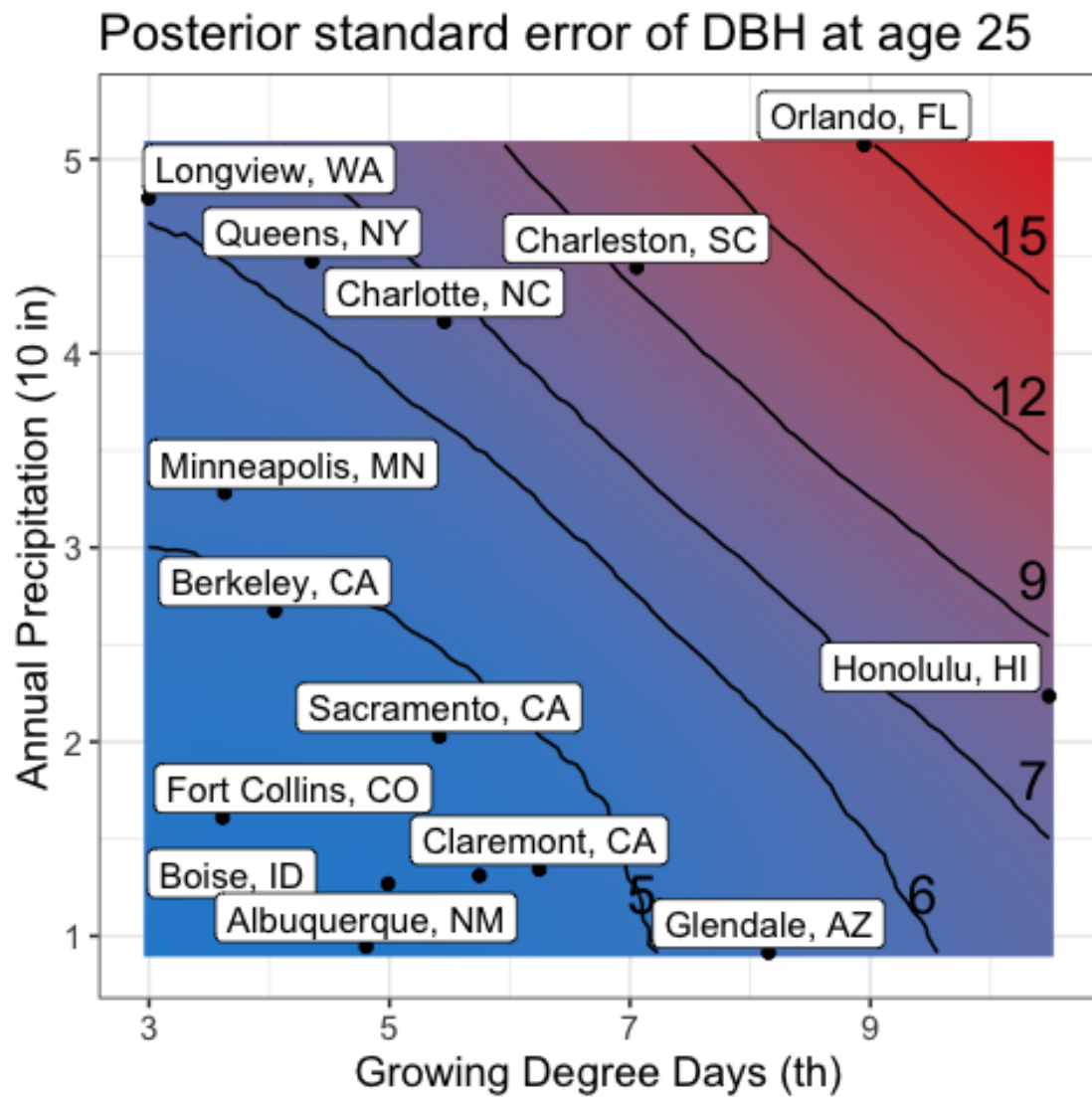


Figure 12: Posterior standard error of DBH at 25 years after planting.

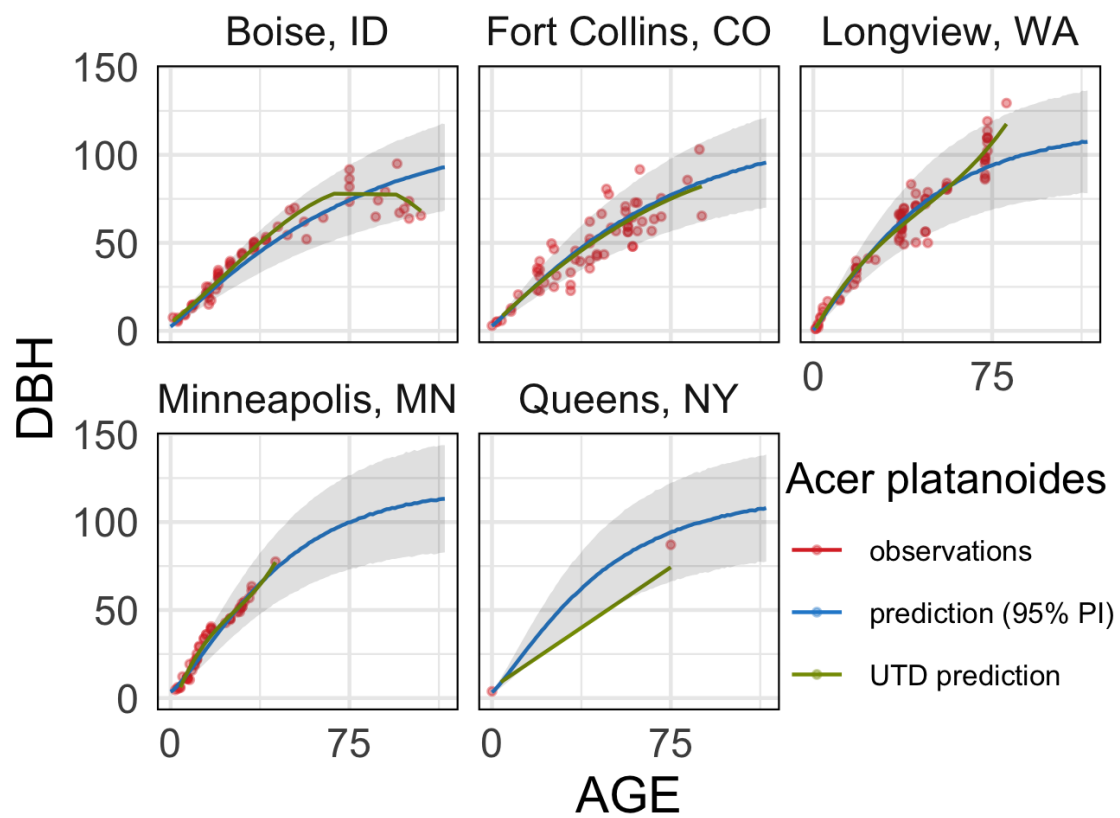


Figure 13: red points are observations, blue lines are predictions of the model and shading indicates 95% prediction interval, green lines show UTD equations

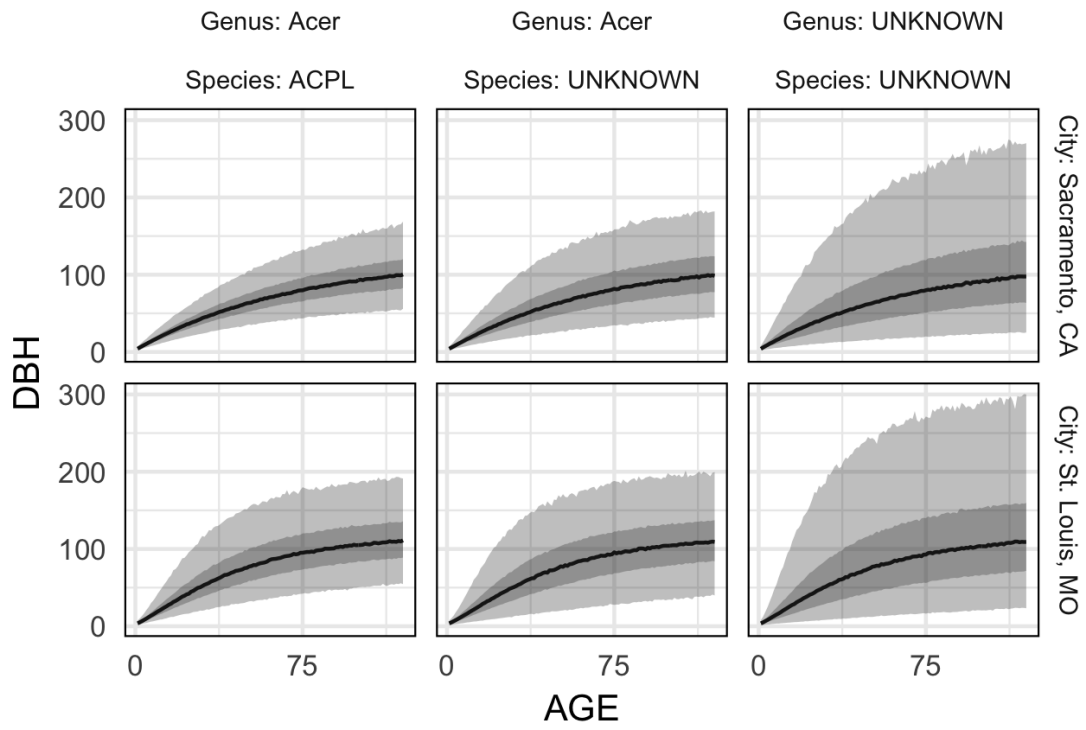


Figure 14: Uncertainty in mean diameter growth increases for unsampled genera, species, and cities. DBH estimate shown in black, 50% predictive interval in dark gray and 95% predictive interval in gray.

Table 1: Model numbers, short descriptions, and brms formula syntax. $\beta^{(i)}$'s are recoded as b_j for conciseness.

Model	Description	brms formula syntax
1	No varying parameters	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim 1$ $b1 \sim 1$ $b2 \sim 1$ $b3 \sim 1$
2	Parameters vary by city	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim (1 \mid \text{City})$ $b1 \sim (1 \mid \text{City})$ $b2 \sim (1 \mid \text{City})$ $b3 \sim (1 \mid \text{City})$
3	Parameters vary by genus and species Species is nested in genus	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim (1 \mid \text{Genus} / \text{Species})$ $b1 \sim (1 \mid \text{Genus} / \text{Species})$ $b2 \sim (1 \mid \text{Genus} / \text{Species})$ $b3 \sim (1 \mid \text{Genus} / \text{Species})$
4	Asymptote (β_1) varies by climate	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim 1$ $b1 \sim \text{gdd} * \text{precip}$ $b2 \sim 1$ $b3 \sim 1$
5	Growth rate (β_3) varies by climate	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim 1$ $b1 \sim 1$ $b2 \sim 1$ $b3 \sim \text{gdd} * \text{precip}$
6	Parameters vary by city, genus, and species (but asymptote does not vary by city). Growth rate varies by climate.	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$ $b1 \sim (1 \mid \text{Genus}/\text{Species})$ $b2 \sim (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$ $b3 \sim \text{precip} * \text{gdd} + (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$
7	Parameters vary by city, genus, and species. Growth rate varies by climate.	$DBH \sim b0 + b1 * (1 - \exp(-b2 * AGE^{b3}))$ $b0 \sim (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$ $b1 \sim (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$ $b2 \sim (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$ $b3 \sim \text{precip} * \text{gdd} + (1 \mid \text{City}) + (1 \mid \text{Genus}/\text{Species})$

Table 2: $\widehat{elpd}_{\text{loo}}$ is the estimated expected log pointwise predictive density. $\text{elpd}_{\text{diff}}$ is the difference from the $\widehat{elpd}_{\text{loo}}$ of the top model. See Vehtari et al. (2017) for details of elpd_{loo} .

	Model	$\widehat{elpd}_{\text{loo}}$	$\text{elpd}_{\text{diff}}$
Best	6	-18845.41	0.00
	7	-18976.38	-130.97
	3	-18989.24	-143.83
	2	-19764.48	-919.06
	5	-20180.41	-1334.99
	4	-20195.21	-1349.80
Worst	1	-20513.12	-1667.70