SEED SOURCE INFLUENCES ON HEIGHT-DIAMETER RELATIONSHIPS IN LOBLOLLY PINE PLANTATIONS

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Height-diameter relationships describe the mean tree height across the range of diameter at breast height and are influenced by the environmental and genetic factors involved in stand development. Tree breeders are interested in the genetic influences on the height-diameter relationship because variation in height-diameter curves reflects differences in stem allometry and resource allocation. Timberland managers routinely use regional height-diameter models in growth and yield systems that account for stand age, density, and site productivity but do not explicitly include genetic information (Burkhart and Tome 2012, p. 281), which has created the need to assess the amount of variation that exists among families. Previous work with loblolly pine data has indicated that for a given site, family and seed source affect the level of the height-diameter curve without altering the basic shape of the curve (i.e. an anamorphic effect) (Buford and Burkhart 1987, Lynch et al. 2010). Furthermore, the level of the curve was found to be strongly related to the dominant height, suggesting that family and seed source can be adequately accounted for by adjusting site index inputs in regional height-diameter models. However, more recent research has found differences in curve shape (i.e. polymorphic effects) among loblolly pine clones (Sabatia and Burkhart 2013, Egbäck et al. 2015). The objectives of this study were to test for a genotype by environment interaction on the height-diameter relationship and determine if family effects could be effectively explained by seed source and dominant height.

Materials and Methods

This analysis utilized age eight measurements from the Plantation Selection Seed Source Study, which is comprised of more than 140 pollen-mix families of first generation loblolly pine from seven seed sources (Chamblee 2011). Data were available for 18 locations that were planted across the southeastern US using single-tree plots and 24 blocks per site. The height-diameter relationship was investigated using an allometric equation of the form

$$\ln(H) = \alpha + \beta D^{-1} \qquad (1)$$

where H is the total tree height for diameter at breast height D and $\ln()$ is the natural logarithm. The intercept, α, is the asymptote parameter and dictates the level of the curve. The slope, β, isthe shape parameter and describes how rapidly the asymptote is approached. A mixed-effects form of Equation 1 was used to assess the effects of family, location, and their interaction as

$$\ln(H_{ijk}) = (\alpha_0 + a_{1i} + a_{2j} + a_{3ij}) + (\beta_0 + b_{1i} + b_{2j} + b_{3ij}) D_{ijk}{}^{-1} + \varepsilon_{ijk} \qquad (2)$$

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where a_{1i}, a_{2j}, and a_{3ij} are random effects for location i, family j, and their interaction, respectively, corresponding to the asymptote parameter and similarly for b_{1i}, b_{2j}, and b_{3ij} for the shape parameter. The formulation of Equation 2 is such that the fixed effects parameters α_0 and β_0 represent the population average values analogous to α and β from Equation 1. The ε_{ijk} is the random stochastic error due to tree k with $\varepsilon_{ijk} \sim N(0, {\sigma_\varepsilon}^2)$. Random effects were assumed to follow a normal distribution with mean zero with independence among subjects. The variance-covariance matrix of the random effects allowed correlations between the level and shape parameters for a given factor. Models were fit with restricted maximum likelihood. Likelihood ratio tests (LRT) were used to compare reduced forms of Equation 2 to assess the significance of family and interaction effects. Seed source was added as a fixed effect into the asymptote and shape parameters using dummy variables. A forward selection procedure was used to identify the combination of seed source regions that were most important. The adequacy of utilizing site index to account for genetic variation was assessed by adding dominant height as a fixed effect into the asymptote and shape parameters of Equation 2 and using likelihood ratio tests to determine if the random effects for family and family by location interaction could be removed without significantly weakening model fit.

Results and Discussion

The LRTs indicated significant family and location effects were present in both the level and shape of the height-diameter curve. These results suggest that pollen-mix families vary in curve shape, whereas previous studies have found that open-pollinated half-sibs did not (Buford and Burkhart 1987) and clones did (Sabatia and Burkhart 2013, Egbäck et al. 2015). The model was ill-conditioned when including the family by location interaction in both the asymptote and shape parameters, indicating that the interaction effect can be explained by either the level or shape of the curve (Pinheiro and Bates 2000, p. 156). Including dominant height in the model eliminated the need for the interaction effect, suggesting that the phenomena that influence genotype by environment interaction for height are the same as detected by the height-diameter model. The reader is referred to Chamblee (2011) for a thorough discussion on the family by location interaction effect on height observed in this data set.

Including seed source in the asymptote parameter produced a significantly better model based on the AIC. Including seed source in the shape parameter did not produce a better fit than the model with seed source in the asymptote alone. The model from the forward selection procedure that produced the best AIC had dummy variables in the asymptote for Coastal North and South Carolina combined and for Virginia. The Coastal North and South Carolina families corresponded to height-diameter curves with higher asymptotes, whereas the Virginia families had a lower asymptote (Figure 1a). Based on the AIC, it was not necessary to differentiate between Lower Gulf, Upper Gulf, Coastal Georgia-Florida, and Piedmont regions.

When including dominant height in the model, the LRT indicated the family random effect for the asymptote could be removed without reducing model fit; however, removing the family effects for shape significantly impaired model fit. The estimated shape effects remaining after including dominant height are presented in Figure 1b, which illustrates the variation that cannot be explained by simply adjusting site index inputs to account for genetics. Although, a practical observation from Figure 1b is the unexplained variation among families decreases with increasing diameter (and thus individual tree value). Estimates of the potential bias in stand volume estimates when excluding genetic effects from height-diameter models are presented in Egbäck et al. (2015).

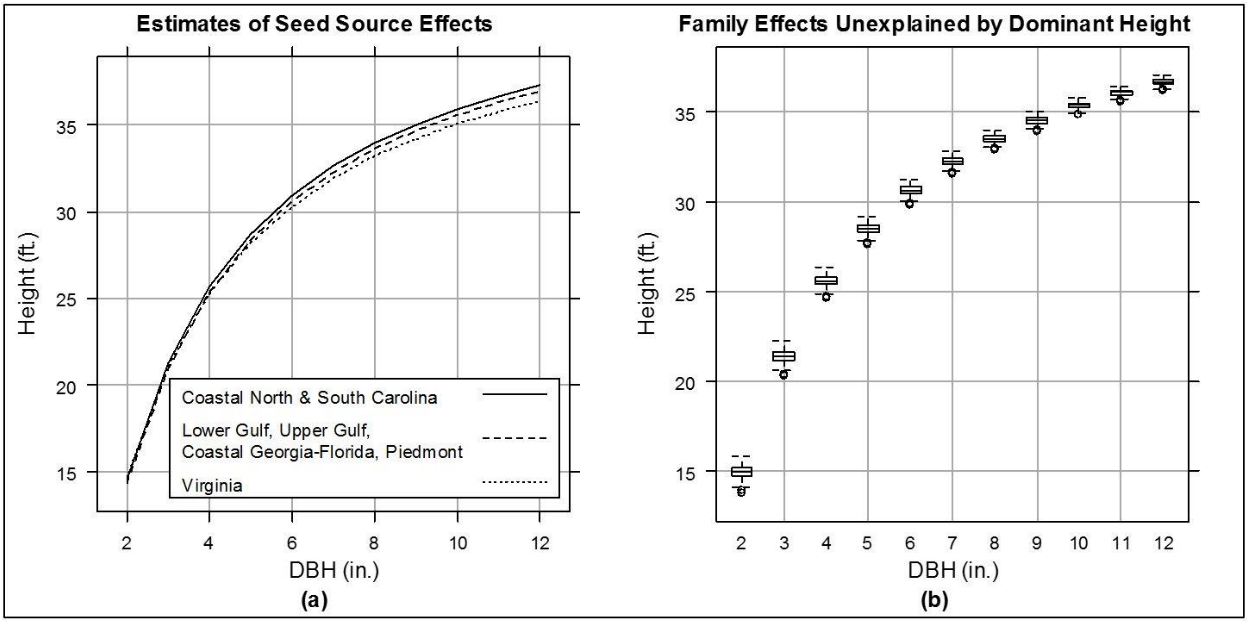

Figure 1. Height-diameter models with (a) estimated fixed effects for important seed sources and (b) boxplots of the spread of estimated random effects for family after accounting for dominant height.

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