Genetic Variation in Basal Area Increment Phenology and its Correlation with Growth Rate in Loblolly and Slash Pine Families and Clones

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Stand development is the result of complex interactions between genotypes and the environment in which they grow. Research into loblolly and slash pine plantations has shown that diameter growth rates differ between species, and among families within species when planted under common plantation conditions (Jackson 1952, Harkin 1962, Langdon 1963, McCrady and Jokela 1996, Jayawickrama et al. 1998). The time of the year during which the cambium is active varies with climate, species, crown class, seasonal development of leaf area in trees, and different parts of stems and branches (Kozlowski and Pallardy 1997). Throughout the entire life span of a tree, cambial growth is sensitive to available water in the soil (Bouriaud et al. 2005). This study contains the results of 2-years basal area increment phenology study conducted on lands managed by Rayonier located in Bradford County, Florida. The objectives of the study were to assess genetic variation between species, families and clones in basal area growth increment, phenology traits and to estimate genetic parameters.

MATERIAL AND METHODS

The genetic material consisted of half-sib and full-sib families of genetically-improved loblolly and slash pine produced by seedlings and rooted cuttings and planted in 337 m² family plots in January 1997. The research was concentrated in slash pine families 1, 2, 3, and 10 (S1, S2, S3, and S10 respectively), and loblolly pine family 4 (L4). Understory vegetation competition was controlled chemically and mechanically and fertilization was applied to prevent nutrient deficiency. Phenology was evaluated as growth periodicity increment of the cambial meristem as measured by repeated DBH measurements throughout growing seasons in 2002 and 2003. Diameter increment was assessed once a month in the summer time and every ten to fifteen days during the period of growth initiation and cessation in the spring and fall, respectively. Date of basal area growth initiation, cessation and duration of growth, as well as growth increment, and basal area growth rates were estimated from cumulative basal area growth curves of individual trees. A simple water balance model was computed to estimate soil water reserves at daily time steps, and quantify soil water deficit. The model allowed us to integrate environmental variables as for example, radiation, temperature and rainfall, as well as plot-level variable as transpiration in a common index to determine correlation between basal area growth and soil water availability. Analysis of variance (ANOVA) was used for phenological and growth data separately for each year. PROC GLM in the SAS® System was used to test for significance of random effects (clone), while PROC MIXED was utilized to test the fixed effects (species and families). With so few families, estimates of genetic parameters were restricted to within-family estimates obtained from clonal variation expressed within each of the four slash families and one loblolly pine family. Within family variance and covariance components were obtained using ASREML. Within-family individual tree broad sense heritability and genetic correlations among traits were calculated using standard methods.
RESULTS AND DISCUSSION

Significant differences at 5% were more apparent among clones within family, than among families or species level in phenological and growth traits both years. In 2002, basal area growth started in second week of March and finished by the end of October (5 and 95% criterion, respectively) for both species. In 2003, basal area growth initiated and finished two weeks earlier than in 2002 for slash pine and loblolly pine families. Annual basal area increment and daily basal area growth rate were larger for all families in 2002 than in year 2003, despite a shorter growing season for some families in 2002. These effects could possibly be due to the differences in amount of rainfall between these two years; year 2002 registered a rainfall of 1405 mm, while 2003 corresponded to 1184 mm (NOAA 2003). In general, loblolly pine tended to accumulate more volume through ages 6 and 7 than slash pine. This was manifested by larger yearly and daily basis basal area increments, but these differences among species were only significant at 5% level for daily basal area growth in 2003. From this study we can conclude that the differences between loblolly and slash pine accumulated slowly over time until ages 6 and 7.

All families showed similar patterns of basal area increment across the growing season in years 2002 and 2003, and shape of the curve were quite similar. In general, basal area increment had a nearly linear trend throughout the growing season, and the differences at the species level and among families within slash pine accumulated across time. Peaks in periodic basal area increment occurred for short (2-3 week) periods in the early spring both years in all families, followed by linear increase in basal area until growth cessation. Significant taxa differences were found in basal area growth rate at certain critical periods, setting a different intercept for the growth line for the better performing taxa (Figure 1).

Figure 1: Species mean daily basal area growth increment per time across years 2002 and 2003 for loblolly and slash pine in north central Florida. * Significant differences between species at 5%; + significant differences among slash pine families at 5%.

In 2003, a year with normal rainfall, basal area growth rate was associated with soil water balance (P<0.0001, R²=0.49). In 2002 (a wetter year), there was no correlation between soil water balance and basal area growth rate. Basal area growth rate increases as water soil availability increases, but an excess in water availability in the soil had a negative effect over growth.
At the clone within family level (pooled across families), differences in initiation, cessation and duration of basal area increment in the growing season were more apparent in 2003 than 2002. Traits related to individual tree stem growth such as volume, and yearly and daily basal area increment were different among clones within families in both years. Due to low variation among clones within-family for phenological traits, especially in 2002, within-family individual tree-broad-sense heritabilities were low to moderate, ranging from 0.01 to 0.24. In contrast, within-family heritabilities for stem growth traits were moderate in both years ranging from 0.10 to 0.37. These heritabilities are expected to be smaller than broad sense heritabilities values usually reported, because they are estimated within full-sib families and half the additive genetic variation and one fourth of the non-additive variation occurs among full-sib families (Falconer 1996). In general, phenotypic expression of phenological traits and basal area growth were under weak genetic control.

Both the strength and direction of correlation estimates among phenological traits varied across families and years. At the same time, phenological traits did not differ significantly among clones within family, especially in 2002, so genetic correlations should not be estimated, and just correlations significantly different from 0 were explained. In 2002, genetic correlations between initiation and duration were strong and negative in family L4, S1 and S2 (r_g=-0.82 to -0.98), which indicates that genotypes with early growth initiation also had a tendency to grow longer, and the opposite can be true too, that genotypes that initiated later also tended to have a shorter growing season. In 2003, between cessation and duration, the genetic correlation was positive and strong for all families (r_g=0.89-1), meaning that clones that stopped growth later also grew longer period of time. With respect to genetic correlations between stem growth variables and phenological variables, there was variation between years in the direction and strength of the correlations. Among the variables we investigated, daily basal area growth rate in both years showed the strongest genetic correlation with basal area increment across all families both years (r_g=0.96-1). Correlation of phenology variables with total volume after 2002 and 2003 growing seasons were similar to the patterns of correlation with basal area increment, reflecting consistency between phenology with increment in the year and phenology with cumulative stem growth. These results suggest that in year 2002 and 2003, genotypes that grew faster during the growing season also were the ones with more basal area increment and total volume. Finally, because cambial phenology traits appear to be weakly inherited and to have variation from year to year in the genetic correlations with growth, indirect responses in cambial phenology from selection of bole basal area or volume are expected to be small. None of the basal area growth phenological traits had a significant clone-by-year variance component; in most of traits the clone-by-year variance component was not significantly different from 0. From this analysis we can conclude that for basal area growth phenology and basal area growth rate traits, each trait was genetically controlled by a similar set of genes in year 2002 and 2003. From the selection point of view, high genetic correlation in phenology traits, means that clones within-family are stable across years, genotypes with a large basal area increment one year tend to have a large basal area increment the next year.

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