

Genetic variation in basal area increment phenology and its correlation with growth rate in loblolly and slash pine families and clones

Veronica I. Emhart, Timothy A. Martin, Timothy L. White, and Dudley A. Huber

Abstract: We quantified basal area increment phenology over a 2-year period in one loblolly pine (*Pinus taeda* L.) and four slash pine (*Pinus elliottii* Engelm. var. *elliottii*) full-sib families propagated as rooting cuttings. In 2002, basal area growth started in March and stopped in October for both species, while in 2003, initiation and cessation occurred 2 weeks earlier for all families. In both years, peaks in basal area increment occurred in short (2–3 week) periods in the early spring for all families, followed by linear basal area growth until cessation. While there were significant size differences among taxa (species and families) at age 6 and 7 years, genetic differences in basal area growth rate were only expressed during short, discrete time periods primarily in the spring and fall. Basal area growth rate increased during periods when water soil availability increased (up to 300 mm), but an excess in water availability in the soil had a negative impact on growth. Within-family individual-tree broad-sense heritabilities ranged from 0.01 to 0.37 for all traits. In general, heritabilities were higher for growth traits than for phenological traits for all families. Both the strength and direction of correlation estimates of phenological traits with growth rate varied across families and years.

Résumé : Les auteurs ont quantifié la phénologie de la croissance en surface terrière sur une période de 2 ans au sein d'une descendance biparentale de pin à encens (*Pinus elliottii* Engelm. var. *elliottii*) et de quatre descendance biparentales de pin de Floride établies à partir de boutures racinées. En 2002, la croissance en surface terrière a débuté en mars et s'est terminée en octobre chez les deux espèces. En 2003, le début et la fin de la croissance ont eu lieu 2 semaines plus tôt chez toutes les descendance. Pendant les deux années, le pic de croissance en surface terrière est survenu durant une courte période (2 à 3 semaines), tôt au printemps, pour l'ensemble des descendance, suivi par une croissance en surface terrière linéaire jusqu'à la fin de la période de croissance. Il y avait des différences significatives de taille entre les espèces et les descendance à l'âge de 6 et 7 ans, mais des différences génétiques dans le taux de croissance en surface terrière ont été observées uniquement pour de courtes périodes bien définies, principalement au printemps et à l'automne. Le taux de croissance en surface terrière augmentait pendant les périodes où la disponibilité en eau dans le sol augmentait (jusqu'à 300 mm). Cependant, un excès d'eau disponible dans le sol avait un impact négatif sur la croissance. Les héritabilités intrafamiliales au sens large estimées sur la base des arbres pris individuellement variaient de 0,01 à 0,37 pour tous les caractères. En général, les héritabilités étaient plus élevées pour les caractères de croissance que pour les caractères phénologiques pour l'ensemble des descendance. Le sens et l'amplitude des corrélations estimées entre les caractères phénologiques et le taux de croissance variaient d'une descendance à l'autre et d'une année à l'autre.

[Traduit par la Rédaction]

Introduction

Loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*) are widely planted as commercial timber species in the southeastern United States (Smith et al. 2004). From the early 1950s, large-scale tree breeding

programs in the southeastern United States have worked to improve forest productivity by selecting trees for superior growth rate, form, and disease resistance (McKeand et al. 2003). The improved material currently being established in commercial plantations is deployed from bulked orchard seed, half-sib families, and full-sib families, with growing interest in the deployment of outstanding clones.

The extensive natural range of loblolly and slash pines, spanning different environmental conditions, has resulted in accumulation of adaptive genetic variation across time and differences in growth potential among sources (Burns and Honkala 1990). To develop tree breeding programs it is necessary to understand the genetic variation of selected traits, their correlations, and the effect of the environment on genotypic expression (White 1987). In Florida, winter temperatures are rarely low enough to prohibit positive photosynthetic rates and considerable transpiration (McGarvey 2000; Martin

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2000). These mild winter conditions, plus an abundant rainfall through the summer, may have resulted in the evolution of longer growing seasons and (or) faster growth.

Most pines experience a cycle of bud set and growth cessation in the latter part of the growing season, followed by deepening dormancy, cold hardening, dormancy release in the winter, and bud break in the spring (Dougherty et al. 1994). In the case of loblolly pine, the wide natural distribution, spanning different ecotypes and environments, contains a diverse range of chilling requirements to promote dormancy release, length of the growing period, and rate of growth. For instance, while it has been established that chilling is required for loblolly pine northern ecotypes, it is unclear that there is a true dormancy and chilling requirement for southern-latitude sources (Carlson 1985).

Increase in the diameter of tree stems occurs primarily from meristematic activity in the vascular cambium, a cylindrical lateral meristem located between the xylem and phloem of the stem, branches, and woody roots. The time of 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). Fluctuations in environmental stresses affect cambial growth to a large extent by altering the supply of photosynthate to the branches and stem (Kozlowski 1971; Sevanto et al. 2003). For example, cambial growth is sensitive to available water, with several aspects being responsive to the amount and seasonal distribution of rainfall, including number of xylem cells produced and ring width, seasonal duration of cambial growth, proportion of xylem to phloem increment, time of latewood initiation, duration of latewood production, and wood density (Kozlowski 1971; Cregg et al. 1988; Downes et al. 1999; Mäkinen et al. 2000, 2001; Bouriaud et al. 2005).

The amount of growth in a particular season is determined by the date of growth initiation, the date of growth cessation (which together with growth initiation determines growth duration), and the average daily growth rate for the growth period. The cessation of shoot and cambial activity is one determining factor, and the more fully the plant can utilize the growing season, without suffering from spring and fall frost, the greater the potential annual growth, final harvest, and return on the investment in planting stock. Much of the interest in forest tree phenology is related to these practical questions (Lieth 1974).

The total growth period from initiation to cessation, both for height and cambial activity, has been studied on an individual-tree basis in many North American tree species, but little information on genetic variation is available. Seasonal periodicity of tree growth has been studied in evergreen and deciduous trees (Jackson 1952; Harkin 1962; Langdon 1963; Emminham 1977; Li and Adams 1994; McCrady and Jokela 1996; Zhang et al. 1997; Jayawickrama et al. 1998; Yu et al. 2001). Wide variation among species in duration of the period of growth was recorded by Jackson (1952). Cambial growth of some species lasted only about 80 days and others grew for up to 200 days. Several of the species that initiated growth early in the season had long periods of growth, while some of the late-starting species exhibited shorter periods.

Langdon (1963) studied growth patterns of slash pine (*Pinus elliottii* Engelm. var. *densa* Little & Dorman) in south

Florida (Fort Myers) for 4 years and found that diameter growth occurred for approximately 10 months per year (from March through December). Initiation of diameter growth was believed to be promoted by apically produced hormones (Savidge and Wareing 1984). Diameter growth has been reported to initiate before or almost simultaneously with height growth for loblolly pine (Zahner 1962) and for slash pine (Kaufmann 1977). Conifers usually continue diameter growth into the fall after height growth has stopped, as reported for Douglas-fir and loblolly pine (Emminham 1977; Jayawickrama et al. 1998).

Previous research in loblolly and slash pine diameter growth phenology has provided important knowledge about the duration of cambial activity (Jackson 1952; Harkin 1962; Langdon 1963; McCrady and Jokela 1996; Zhang et al. 1997; Jayawickrama et al. 1998). However, there is a lack of information about how the duration of cambial growth might influence the differences in growth rate between species planted in the same area and also the growth differences among families within species and clones within families.

This study examines the following hypotheses: there is significant genetic variation in basal area growth phenology among slash and loblolly pine genotypes (species, families, and clones), and where it exists, genetic variation in basal area growth phenology is correlated with variation in annual basal area increment. The specific objectives are to compare 2 years of basal area growth phenology among species, families, and clones and estimate genetic parameters for basal area growth phenology, its correlation with growth rates, and the genotype interaction with seasonal environmental changes.

Materials and methods

Study site and plant material

The study area was located on lands managed by Rayonier Inc. in Bradford County, Florida. The climate is humid and subtropical with a mean annual temperature of 21 °C and a mean annual rainfall of 1316 mm, with over 50% of the precipitation occurring from June through September. Periods of drought are normally present in the spring and fall. The mean annual rainfall during the period 1999–2001 was 967 mm, in contrast to 1405 and 1184 mm in 2002 and 2003, respectively (NOAA 2003). The soils are classified as Pomona and consist of very deep, somewhat poorly to poorly drained soils that are formed in sandy and loamy marine sediments (sandy, siliceous, hyperthermic Ultic Alaquods). Slopes are 0%–2%. In a typical profile, the spodic horizon occurs at 30–60 cm with an argillic horizon at 90–120 cm. The water table is typically at a depth of 15–45 cm for 1–3 months and a depth of 25–100 cm for 6 months or more during most years (Soil Survey Staff 1998).

The study took place in an experiment containing 16 full-sib and half-sib loblolly and slash pine families planted in 337 m² family plots in January 1997. The experiment was arranged in a randomized complete block design, with four replicates. For this study, we used one full-sib loblolly pine family (henceforth designated L4) and four full-sib slash pine families (henceforth designated S1, S2, S3, and S10). The parental material was selected in southeast Georgia and north Florida. Each plot contained 60 clones propagated as

rooted cuttings from a single family, planted at 1.7 m × 3.4 m spacing (1730 trees/ha). Cuttings were taken from donor hedges in the spring and were rooted and grown in a greenhouse for 6 months before planting. Each family plot contained the same 60 genotypes, but with the ramets planted into different randomly determined planting locations in the plot. In total, we studied approximately 1200 trees: 60 trees per family plot × 5 families × 4 replications. Fertilization and weed control were applied periodically to reduce interspecific competition and prevent nutrient deficiency (Emhart 2005).

Basal area increment measurements

Phenology was evaluated as periodic basal area growth increment, as determined from repeated DBH measurements throughout growing seasons in 2002 and 2003. Families S1, S2, S3, S10, and L4 were monitored for diameter increment once a month in the summertime and every 10–15 days during the period of growth initiation and cessation in the spring and fall, respectively. Diameter increment was measured with a digital caliper (model 18 ES, Mahr, Germany, resolution 0.01 mm) over four plexiglass plates permanently attached to the tree stem in north–south and east–west orientations. Diameter measurements were done such that two replications were measured on day 1 and two replications on day 2 for each time period.

Phenological traits

From the periodic diameter measurements, a cumulative basal area growth curve for two growing seasons was plotted for each tree, and dates of basal area growth initiation and cessation were estimated by graphic interpolation as the dates when 5% and 95% of annual growth were completed, respectively (Hanover 1963). Duration of basal area growth (in days) was calculated as the difference between dates of cessation and initiation. Basal area increment per year (in mm²) was calculated as the difference in individual tree basal area between the 5% and the 95% dates of initiation and cessation, respectively. Basal area growth rate (in mm²/day) was calculated as the ratio of annual basal area increment and duration of basal area growth.

Meteorological data and water balance

Climatic data were collected at the Gainesville Regional Airport (about 20 km from the study site; NOAA 2003) and a research weather station 8 km from the study site. Meteorological variables included hourly radiation, mean air temperature, and daily rainfall. A simple water balance model was computed to estimate soil water reserves at daily time steps and to quantify soil water deficit. The model is given by

$$[1] \quad R_n = R_{n-1} + P_n - T_n$$

where R_n is soil water reserve on day n , R_{n-1} is soil water reserve of the day before, P_n is precipitation on day n , and T_n is transpiration on day n . The water-holding capacity between 0 and 1 m depth for this site was estimated at 260 mm according to soil texture and flatwoods Spodosols moisture release curves (H.L. Gholz, personal communication, 1998). Plot-level transpiration (T_n) was estimated as follows. Maximum hourly potential evapotranspiration (PET, mm) was

calculated by dividing measured hourly radiation by the latent heat of vaporization of water; maximum plot-level transpiration was then calculated as 60% of PET and was assumed to occur when all-sided leaf area index (LAI) > 6.0. At LAI < 6.0, transpiration was estimated to decline linearly with declining LAI (Martin and Jokela 2004). Plot-level leaf area index was calculated from litterfall data as in Martin and Jokela (2004). Because understory vegetation was sparse, only pine LAI was considered. The resulting model (eq. 1) incorporated variation in environmental conditions (daily precipitation, hourly radiation) as well as plot-level leaf area index to produce a plot-level index of soil water availability. We chose to use this index instead of modeling soil water balance explicitly, because the hydrology of flatwoods spodosols in this region is quite complex (Abrahamson and Hartnett 1990).

Genetic parameters and statistical analyses

Analysis of variance (ANOVA) was used to test the significance of the effects for phenological and growth data. The year effect was considered initially in the model, but because a nonsignificant clone × year interaction was found for all traits, we dropped it from the model and analysis was done separately for each year. The significance of the clone × year variance component was tested using the likelihood ratio test (Wald 1943; Wolfinger 1996). Family was considered a fixed effect because the inference was only regarding these families. Clone was considered a random effect because the inference was regarding a population from which the different within-family clones were drawn. PROC GLM in the SAS[®] was used to test for the significance of random effects (clone), while PROC MIXED was used to test the fixed effects (species and families) (SAS Institute Inc. 1990; Littell et al. 1996). The linear model considered for the analyses was

$$[2] \quad Y_{ijkl} = \mu + b_i + S_j + F_{k(j)} + c_{l(jk)} + bS_{ij} + bF_{ik(j)} + \epsilon_{ijkl}$$

where

Y_{ijkl} is the performance of the ramet of the l th clone within the k th family nested in the j th species in the i th replication; $i = 1, 2, 3, 4$ for replications; j is slash or loblolly pine; $k = 1, 2, 3, 4, 10$ for families; $l = 60$ identification numbers for 60 clones within each of the five families; μ is the population mean; b_i is the random variable of replication ~ NID (0, σ_b^2) (NID, normally and independently distributed); S_j is the fixed effect of species (slash or loblolly); $F_{k(j)}$ is the fixed effect of family nested within species; $c_{l(jk)}$ is the random variable of clone nested within family and species ~ NID (0, σ_c^2); bS_{ij} is the random variable for replication × species interaction ~ NID (0, σ_{bS}^2); $bF_{ik(j)}$ is the random variable for replication × family(species) interaction ~ NID (0, σ_{bF}^2); and ϵ_{ijkl} is the error term ~ NID (0, σ_ϵ^2).

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

Table 1. Results from ANOVA showing significance levels and species and family least square means for individual-tree stem growth and phenological traits for two growing seasons for loblolly and slash pine (S1, S2, S3, S10) families in north-central Florida.

Trait	Significance by effect (<i>P</i> value)			Species mean		Slash pine family mean			
	Species	Family	Clone	Slash	Loblolly	Family S1	Family S2	Family S3	Family S10
Year 2002									
Initiation ^a	0.8160	0.1120	0.0534	68.43	69.00	70.31	63.57	70.83	68.99
Cessation ^a	0.3542	0.1870	0.2141	302.16	304.82	306.43	301.66	301.44	299.12
Duration (days)	0.5456	0.2966	0.0131	233.71	235.82	236.13	238.03	230.59	230.10
Volume at 6 years (dm ³)	0.0797	0.1062	<0.0001	25.37	31.58	26.32	26.10	23.55	27.52
BA increment (cm ²)	0.0784	0.0586	<0.0001	23.81	26.98	24.94	25.04	22.12	23.14
BA growth rate (mm ² /day)	0.0945	0.2783	<0.0001	10.18	11.47	10.57	10.50	9.59	10.05
Year 2003									
Initiation ^a	0.0815	0.3384	0.0062	55.85	53.86	56.21	54.94	56.79	55.45
Cessation ^a	0.0459	0.0853	0.0007	291.01	276.51	297.03	291.00	280.87	295.12
Duration (days)	0.0711	0.0774	0.0050	235.18	222.64	240.82	236.12	224.09	239.69
Volume at 7 years (dm ³)	0.0835	0.0687	<0.0001	38.31	44.30	38.67	38.87	34.67	41.03
BA increment (cm ²)	0.1312	0.0894	<0.0001	21.98	24.26	22.80	22.83	19.69	22.60
BA growth rate (mm ² /day)	0.0385	0.4796	<0.0001	9.35	10.81	9.45	9.63	8.87	9.45

Note: BA, basal area.

^aInitiation and cessation are days after 1 January to complete 5% and 95% of seasonal diameter growth.

and one loblolly pine family. For each family two types of genetic parameters were estimated: within-family broad-sense heritability for each trait and within-family genetic correlations among traits. Within-family variance and covariance components were obtained using ASREML, a statistical package that fits linear mixed models using restricted maximum likelihood (Gilmour et al. 1997).

Within-family individual-tree broad-sense heritability was calculated as

$$[3] \quad H_{WF}^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$$

where σ_c^2 is the variance among clones within family and σ_e^2 is the residual variance as defined in eq. 2. Theoretically, the broad-sense within-family heritability contains half the additive genetic variance, three-quarters of the dominance genetic variance, and most of the epistatic genetic variance (Falconer and Mackay 1996). The standard error for heritability estimates was calculated from Dickerson (1962). The residual likelihood ratio test (Wald 1943; Wolfinger 1996) was used to test heterogeneity of variances among slash pine families, and heritabilities were estimated separately or pooled, as appropriate.

Within-family genetic correlations among basal area phenological traits and growth rate were calculated following Falconer and Mackay (1996) as

$$[4] \quad r_{g_{xy}} = \frac{\sigma_{c_{xy}}}{\sigma_{c_x} \sigma_{c_y}}$$

Standard errors for genetic correlations were estimated using ASREML (Gilmour et al. 1997). Within-family genetic correlations between years were estimated considering the 2 years as two different traits using eq. 4.

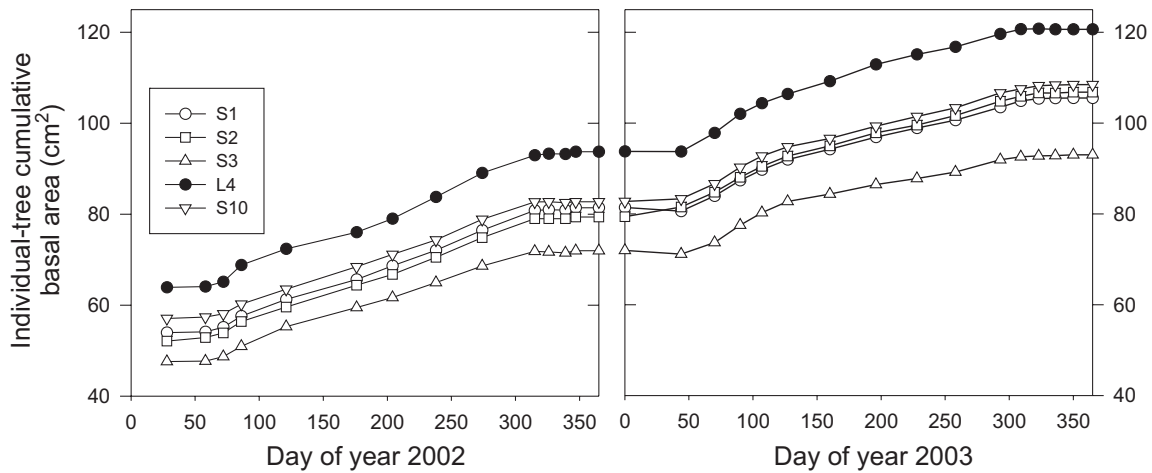
Results

Genetic variation among species and families

In 2002, species and families within species were not significantly different at an $\alpha = 0.05$ for any phenological or growth trait, while in year 2003, date of growth cessation and daily basal area growth rate were significant at the species level, with loblolly pine ceasing growth earlier and growing more than slash pine (Table 1 and Fig. 1). In 2002, the mean date of basal area growth initiation was 10 March (69 days after 1 January) for the single loblolly pine family and 1 day earlier for the slash pine families. Basal area growth cessation for the loblolly pine family on average occurred on 1 November, resulting in a mean duration of basal area growth of 236 days. In the case of slash pine families, mean cessation was on 28 October, and the duration of basal area growth was 234 days (Table 1).

In 2003, basal area growth started and finished 1–2 weeks sooner than in 2002 for both loblolly and slash pine families (Table 1). For loblolly pine, basal area growth began on 23 February and finished by 4 October, resulting in a mean duration of basal area growth of 223 days (13 days fewer than in 2002). For slash pine, basal area growth began, on average, on 25 February and ended on 17 October, for a duration of 235 days (only 1 day shorter than in 2002, Table 1). In 2003, more growing days for slash pine than for loblolly pine might explain why the difference between species in total basal area growth was less than in the previous year ($26.98 \text{ cm}^2 - 23.81 \text{ cm}^2 = 3.17 \text{ cm}^2$ in 2002 versus $24.26 \text{ cm}^2 - 21.98 \text{ cm}^2 = 2.28 \text{ cm}^2$ in 2003). This is supported by the fact that the slash pine families with longest (S1) and shortest (S3) duration had greater differences in basal area growth in 2003 than in 2002 ($24.94 \text{ cm}^2 - 22.12 \text{ cm}^2 = 2.82 \text{ cm}^2$ in 2002 versus $22.8 \text{ cm}^2 - 19.69 \text{ cm}^2 = 3.11 \text{ cm}^2$ in 2003). 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. Early cessation in year 2003 than in 2002

Fig. 1. Family mean cumulative basal area growth curves for years 2002 and 2003 in loblolly and slash pine families in north-central Florida.



and the difference in total annual increment between years could possibly be due to the differences in amount and seasonal distribution of rainfall between 2002 and 2003 (1405 mm and wet soil conditions by the end of the year in 2002 and 1184 mm and dry conditions by the end of the year in 2003; Fig. 2).

In general, loblolly pine tended to accumulate more stem volume through age 6 and 7 years than did slash pine. This was manifested by larger yearly and daily basal area increments, but these differences among species were only significant for daily basal area growth in 2003 ($P < 0.05$, Table 1).

All families showed similar patterns of basal area increment across the growing season in years 2002 and 2003, that is, shapes of the cumulative basal area curves were quite similar (Fig. 1). In general, basal area growth peaked in early spring and then remained relatively constant throughout the remainder of the growing season (Fig. 1, 2). The differences at the species level and among families within slash pine accumulated across time. Daily average basal area growth rate was only significantly different at the species level in 2003 (Table 1).

Despite the apparent lack of variation in basal area growth rate indicated by the cumulative growth data (Fig. 1), peaks in basal area increment occurred in the early spring in both years (Fig. 2). Significant species and family differences were found for critical spring periods when growth rates were highest: in year 2002 measurement period 3 (March) and in 2003 measurement periods 1 and 2 (end of February and mid-March, respectively).

In 2002 (the wetter year), daily basal area growth in our study was weakly negatively correlated with soil water balance (Fig. 3A). In contrast, in 2003 (the drier year), daily basal area growth was positively associated with calculated soil water balance (Fig. 3B). The total amount of rainfall in 2002 was 1405 mm, 177 mm above average. Wet conditions were present, especially between June and December, and presumably had a negative effect on growth (Fig. 2). On the other hand, in a year with average rainfall, as in 2003, where rainfall totaled 1184 mm (44 mm less than in a normal year), a strong correlation was observed with more growth associated with higher levels of soil water availability. In year 2003, we found that daily basal area growth followed a

similar pattern as that of soil water balance (Fig. 2B). For both years and both species, the highest growth rates in basal area were reached in conditions where the soil water balance was around 300 mm.

Clonal variation and within-family inheritance of phenological traits and stem growth

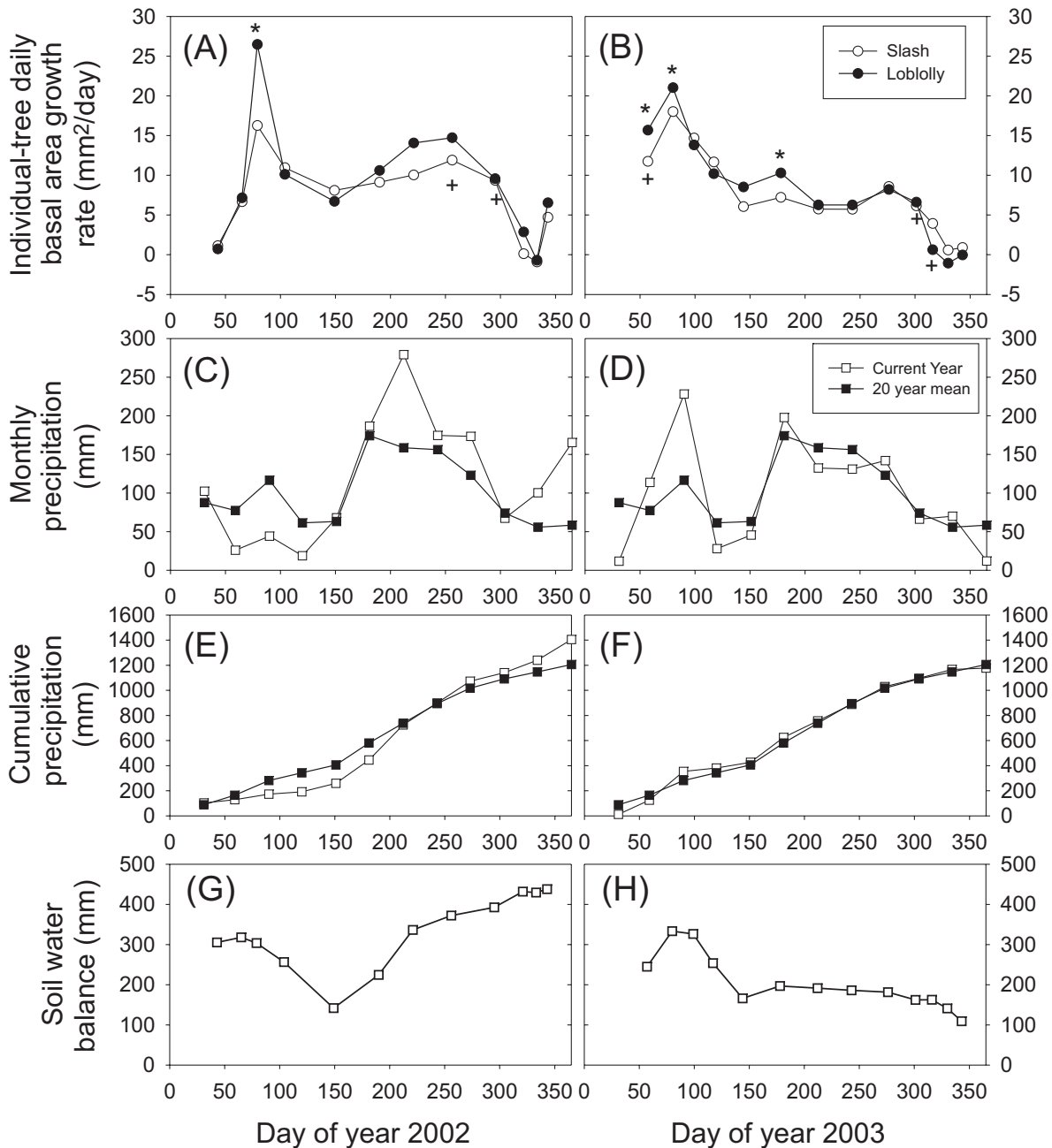
At the clonal within-family level (pooled across families), differences in initiation, cessation, and duration of basal area increment in the growing season were more apparent than were family- and species-level differences in both 2002 and 2003 (Table 1). Traits related to individual-tree stem growth, such as volume, and yearly and daily basal area increment were also different among clones within families in both years (Table 1). Analyses of the data separately by family showed that phenological traits differed among clones for some families and did not differ for other families in both years. Only family S2 showed significant clonal variation in all phenological traits in 2003. Volume, yearly basal area increment, and daily basal area growth had significant within-family clonal variation in 2002 and 2003 for all families (Table 2).

For phenological traits, individual-tree broad-sense heritabilities were low to moderate, ranging from 0.01 to 0.24 (Table 3). In contrast, within-family heritabilities for stem growth traits were moderate to high in both years, ranging from 0.10 to 0.37 (Table 3). Family S2 tended to have higher within-family broad-sense heritabilities than did the other slash pine families, in most cases due to higher clonal variation within that family as opposed to lower residual environmental variance.

Genetic correlations among phenological traits and stem growth

When phenological traits did not differ significantly among clones within a family, genetic correlations were not estimated. Among the estimates, many genetic correlations relating phenological traits to growth were not significantly different from zero (Table 4). In 2002, genetic correlations between initiation and duration were strong and negative in families L4, S1, and S2, which indicated that clones with early growth initiation also had a tendency to grow longer

Fig. 2. Species mean daily basal area growth increment in 2002 (A) and 2003 (B) for loblolly and slash pines in north-central Florida, where an asterisk indicates significant differences between species ($P < 0.05$) and a plus indicates significant differences among slash pine families ($P < 0.05$); current-year and 20-year mean monthly precipitation in 2002 (C) and 2003 (D); cumulative precipitation in 2002 (E) and 2003 (F); and mean plot-level soil water balance (error bars indicating standard error) in 2002 (G) and 2003 (H). Precipitation data from Gainesville Regional Airport, NOAA (2003).



and that clones that initiated later also tended to have a shorter growing season. Also, genetic correlations between cessation and duration were positive and strong in families S2 and S3, meaning that clones that had a tendency to cease growth late in the year also grew for a longer period of time.

In 2003, genetic correlations between initiation and cessation were significant and moderately positive only for family S2 (Table 4). The genetic correlations were positive and strong between cessation and duration for all families, meaning that clones that stopped growth later also grew for a lon-

ger period of time. In general, these results suggest that variation in duration of the growing season among individuals in these families was more a function of cessation date than initiation date, but all these traits were weakly inherited (Table 4).

With respect to genetic correlations between stem growth variables and phenological variables, significant correlations were found primarily in family S2, varying from moderately to strongly positive ($r_g = 0.31-0.85$, Table 5). In 2002, duration had a positive strong genetic correlation with basal area

Fig. 3. Relationship between individual-tree daily basal area (BA) increment and simulated daily plot-level soil water balance in loblolly and slash pines in 2002 (A) and 2003 (B). The line shows a linear regression through data. (A) Daily BA growth = $13.7929 - 0.0187 \times (\text{soil water balance})$; $R^2 = 0.11$, $P < 0.0001$. (B) Daily BA growth = $-1.9424 + 0.0478 \times (\text{soil water balance})$; $R^2 = 0.49$, $P < 0.0001$.

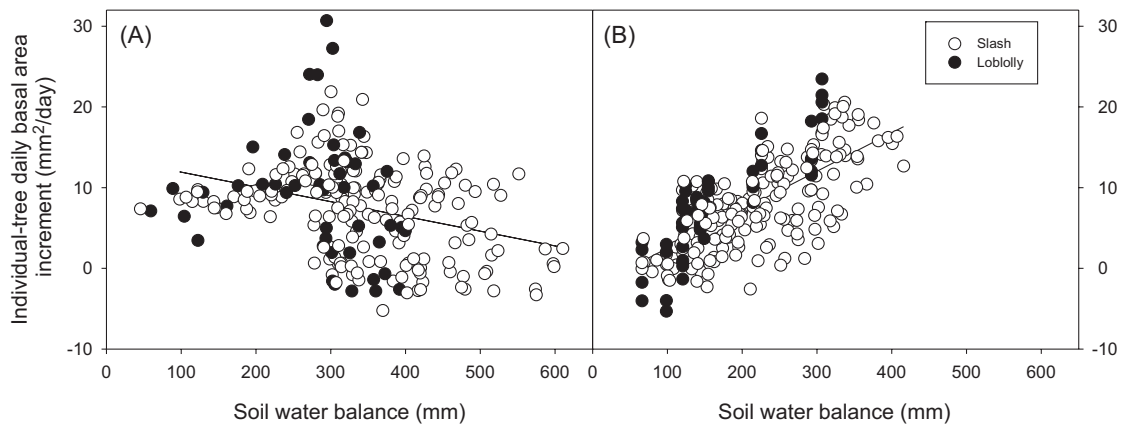


Table 2. Results from ANOVA showing significance levels (P values) for clonal within-family variance component for tree stem growth and phenological traits for two growing seasons in loblolly (L4) and slash pine (S1, S2, S3, S10) families in north-central Florida.

Trait	Within-family clonal variation				
	Family L4	Family S1	Family S2	Family S3	Family S10
Year 2002					
Initiation	0.0003	0.0311	0.1964	0.1577	0.1880
Cessation	0.3200	0.3489	0.1145	0.1541	0.3753
Duration	0.0695	0.1608	0.0498	0.2409	0.1593
Volume at 6 years	0.0015	<0.0001	<0.0001	0.0720	0.0390
BA increment	<0.0001	0.0042	<0.0001	0.0191	0.0277
BA growth rate	<0.0001	0.0028	<0.0001	0.0279	0.0286
Year 2003					
Initiation	0.0253	0.4211	0.0011	0.0706	0.4932
Cessation	0.2165	0.3028	0.0028	0.1302	0.1550
Duration	0.3215	0.3770	0.0068	0.1146	0.3893
Volume at 7 years	0.0001	0.0003	<0.0001	0.0206	0.0318
BA increment	<0.0001	0.0043	<0.0001	0.0524	0.0004
BA growth rate	<0.0001	0.0016	<0.0001	0.0536	<0.0001

Note: BA, basal area.

increment in family S2. In 2003, initiation, cessation, and duration had moderately positive genetic correlations with basal area increment in family S2 ($r_g = 0.86$). At the same time, initiation in 2003 for family L4 showed a strong positive genetic correlation with basal area increment. Correlations of phenological variables with total volume after the 2002 and 2003 growing seasons were similar to the patterns of correlation with basal area increment, reflecting consistency between phenology and increment during the year and phenology and cumulative stem growth.

Analysis across years 2002–2003

There was no significant clone \times year interaction for any basal area phenological trait and basal area growth trait. Within-family estimates of genetic correlations between years were high (from 0.91 to 1; data not shown), indicating that the interactions were not biologically important.

Discussion

After 2 years of basal area growth phenology measurements, we found that initiation, cessation, and duration of basal area growth did not present significant variation among species and families, and this is partially explained by the limited geographic range from which the selections were made. Since phenology is closely related to latitude and altitude (Campbell 1986; Jayawickrama et al. 1998; Nielsen and Jørgensen 2003), growth initiation, cessation, and duration should depend on the study location and geographic origin of the sampled seed or vegetative propagule. Our results are in agreement with what Langdon (1963) reported on growth patterns of slash pine in south Florida (Fort Myers). He found that diameter growth occurred for approximately 10 months of the year (from March through December), and the total amount of diameter growth and its seasonal distribution responded to climatic variation. With

Table 3. Estimates of within-family individual-tree broad-sense heritabilities (H_{WF}^2) for growth and phenological traits by year in loblolly (L4) and slash pine (S1, S2, S3, S10) families growing in north-central Florida.

Trait	H_{WF}^2				
	Family L4	Family S1	Family S2	Family S3	Family S10
Year 2002					
Initiation	0.20 (0.07)	0.10 (0.06)	0.07 (0.07)	0.09 (0.08)	0
Cessation	0	0	0.08 (0.07)	0.07 (0.08)	0
Duration	0.08 (0.06)	0.07 (0.06)	0.11 (0.07)	0.05 (0.08)	0
Volume at 6 years	0.18 (0.07)	0.25 (0.07)	0.26 (0.08)	0.10 (0.08)	0.10 (0.07)
BA increment	0.24 (0.07)	0.15 (0.07)	0.37 (0.08)	0.15 (0.09)	0.13 (0.07)
BA growth rate	0.23 (0.07)		0.19 (0.04) ^a		
Year 2003					
Initiation	0.12 (0.07)	0.03 (0.06)	0.24 (0.08)	0.10 (0.09)	0.03 (0.06)
Cessation	0.05 (0.06)	0.05 (0.06)	0.19 (0.08)	0.08 (0.08)	0.09 (0.07)
Duration	0.04 (0.06)	0.05 (0.06)	0.16 (0.08)	0.09 (0.08)	0.03 (0.06)
Volume at 7 years	0.20 (0.07)	0.20 (0.07)	0.29 (0.08)	0.14 (0.09)	0.11 (0.07)
BA increment	0.34 (0.07)		0.21 (0.05) ^a		
BA growth rate	0.32 (0.07)		0.23 (0.05) ^a		

Note: Values in parentheses are standard errors. BA, basal area.

^aValues of H_{WF}^2 in slash pine were pooled by family because variance components were homogeneous.

Table 4. Estimates of within-family genetic correlations between growth phenological traits in 2002 (above the diagonal) and in 2003 (below the diagonal) in loblolly (L4) and slash pine (S1, S2, S3, S10) families growing in north-central Florida.

	Family L4			Family S1			Family S2			Family S3			Family S10		
	I	C	D	I	C	D	I	C	D	I	C	D	I	C	D
I	—	na	-0.98 (0.33)	—	na	-0.85 (0.41)	—	-0.47 (0.91)	-0.82 (0.35)	—	0.46 (0.72)	0.02 (0.86)	—	na	na
C	0.96 (0.61)	—	na	0.60 (2.06)	—	na	0.67 (0.28)	—	0.91 (0.21)	-0.25 (0.72)	—	0.89 (0.17)	1.00 (2.6)	—	na
D	0.93 (1.04)	0.99 (0.06)	—	0.49 (2.59)	1.00 (0.09)	—	0.56 (0.34)	0.99 (0.01)	—	-0.42 (0.67)	0.98 (0.02)	—	1.00 (2.6)	1.00 (0.31)	—

Note: Values in parentheses are standard errors. I, initiation of basal area growth; C, cessation of basal area growth; D, duration of basal area growth. na, not estimated because within-family clonal variance was zero.

respect to diameter growth cessation date, similar results were found by Jayawickrama et al. (1998), that is, a loblolly pine provenance from Gulf Hammock (Florida) grew until day 299 and 313 in two different years.

Comparing studies done in northern regions with slash and loblolly pine, our results showed earlier initiation date, later cessation date, and longer season length. For example, in a site close to Athens, Georgia, Jackson (1952) found that loblolly and slash pines started diameter growth between the end of March and the beginning of April, with a duration of 5–6 months. In South Carolina, McCrady and Jokela (1996) found that in loblolly pine diameter growth initiated by the end of March and finished by August–September, giving a mean diameter growth duration of 5 months. No significant differences were found among families in initiation or cessation of diameter growth.

One of the interesting results we found in this study was related to the finding that cumulative basal area growth curves across years were similar between species and among slash pine families and that genetic variation in total basal area growth was restricted to short time periods during the

growing seasons. From this study we can conclude that the differences between loblolly and slash pine accumulated slowly over time through age 6 and 7 years. Also, these results suggest that at least some of the genetic differences in cumulative growth (as shown in Fig. 1) are manifested not through constant expression of consistent growth rate differences, but rather through elevated growth rate during very discrete periods of time (as shown in Fig. 2). In other words, the basal area growth rates of taxa are remarkably similar for most of the year, but in the spring some environmental variables or genetic differences in phenology trigger more rapid growth in some taxa, which essentially raises the intercept of the linear cumulative basal area functions for the rest of the year (Fig. 1).

Similar trends in diameter growth were found by others authors. Linear radial growth was observed over the entire growing season in slash and loblolly pine trees by Jackson (1952), except for a period of slow growth in the late summer, which was probably associated with soil moisture depletion. Similar linear trends were reported by McCrady and Jokela (1996) in loblolly pine families. Cregg et al. (1988)

Table 5. Estimates of within-family genetic correlations between growth and phenological traits by year in loblolly (L4) and slash pine (S1, S2, S3, S10) families growing in north-central Florida.

Trait	L4	S1	S2	S3	S10
Basal area increment 2002					
Initiation	-0.05 (0.26)	-0.12 (0.45)	na	na	na
Cessation	na	na	na	na	na
Duration	0.32 (0.35)	na	0.85 (0.28)	na	na
Basal area increment 2003					
Initiation	0.86 (0.27)	na	0.59 (0.22)	0.22 (0.84)	na
Cessation	na	na	0.59 (0.23)	na	na
Duration	na	na	0.53 (0.25)	na	na
Volume age 6					
Initiation	0.03 (0.29)	0.06 (0.37)	na	na	na
Cessation	na	na	na	na	na
Duration	0.29 (0.40)	na	0.83 (0.36)	na	na
Volume age 7					
Initiation	0.94 (0.32)	na	0.31 (0.25)	0.76 (0.50)	na
Cessation	na	na	0.66 (0.23)	na	na
Duration	na	na	0.65 (0.25)	na	na

Note: Values in parentheses are standard errors. na, not estimated because within-family clonal variance was zero.

reported that unlike height growth, rapid diameter growth can be maintained over the entire growing season and the rate of diameter growth of loblolly pine, observed during a year when moisture deficits did not develop, was almost constant over the period from day 50 to 290. In agreement with other studies in loblolly and slash pines, peaks in basal area increment in early spring were also reported by Zhang et al. (1997) and Langdon (1963); accelerating growth in spring was also reported for Norway spruce (Bouriaud et al. 2005). But these studies in conifers did not identify genetic differences in tree growth rate at this temporal scale. In the case of hardwoods, growth and phenology studies in hybrid aspen clones (*Populus tremula* × *Populus tremuloides*) compared growth patterns in temperate climates throughout the year (Yu et al. 2001). Peaks in diameter growth occurred at the end of spring and beginning of summer. Hybrid clones had higher growth rates than did the pure *P. tremula* and also accumulated larger annual diameter increment.

While we found an almost linear trend in basal area growth through the season, it is important to consider that on a biomass basis that may not be the case, because of higher specific gravity in latewood formation in the last half of the year. Unfortunately, at the time of the study, we did not have appropriate equations to estimate stem biomass by family or by species or specific gravity measurements to address this issue. Positive contributions to future research in southern pine basal growth phenology can be attained with the incorporation of biomass components.

Water soil availability was found to be associated with daily basal area growth rate. Basal area growth rate increased as water soil availability increased, when water was limiting, but excess water availability in the soil had a negative effect on growth, perhaps caused by plant stress due to prolonged root inundation. Studies in flatwoods soils in

north-central Florida have shown reduced radiation use efficiency when soil water balance was high (i.e., wet conditions), and this effect can have a direct impact on tree growth rates (Martin and Jokela 2004). Langdon (1963) also reported that excess soil water appeared to depress growth in slash pine in south Florida. Bouriaud et al. (2005) studied the influence of climatic variables on annual radial growth and wood density on Norway spruce. They found that numerous decreases in radial growth rate were closely related to the calculated soil water deficit. Also, wood density increased with decreasing radial growth rate in the second half of the growing season affected by drought. Similar results were reported by Cregg et al. (1988), where early-season diameter growth rate for loblolly pine was a function of available soil moisture and temperature. While soil moisture availability is the most often cited environmental driver of diameter growth phenology, it is possible that other factors such as accumulation of chilling hours and photoperiod also impact the timing of growth. However, few studies have decoupled these environmental effects from one another (Dougherty et al. 1994), and additional manipulative studies would likely be informative.

Among the five families we studied, the phenotypic expressions of phenological traits associated with basal area growth were under weak genetic control. It should be noted, however, that these heritabilities are expected to be smaller than broad-sense heritabilities values usually reported in the literature, because in this study they are estimated within full-sib families and half the additive genetic variation and three-fourths of the dominance variation as well as most of the epistatic variance occurs within full-sib families (Falconer and Mackay 1996). With respect to diameter growth, Li and Adams (1994) estimated individual heritabilities for diameter growth initiation ($h^2 = 0.23$), and cessation ($h^2 =$

0.11) in 15-year-old Douglas-fir, values that are comparable with those in our study. At the same time, Li and Adams (1994) did not detect significant family differences in duration of diameter increment, suggesting that the small variation in date of diameter growth cessation among families may have been related to summer dry conditions. Other studies have shown that summer drought has little effect on variation in cambial growth initiation, but reduces variation in cambial growth cessation among coastal Douglas-fir provenances (Emmingham 1977). In our study, we did not detect an association between clonal variation within-family for initiation or cessation and soil water balance and the presence of relatively dry spring or late summer.

In all families, we found high genetic correlation between years for all traits and no significant clone \times year interaction component for all traits. From this analysis we can conclude that each of the basal area growth phenological traits and each of the basal area growth rate traits were genetically controlled by a similar set of genes in 2002 and 2003. The fact that genetic rankings were consistent despite contrasting weather conditions in the two measurement years suggests that these results are robust. Nevertheless, it would be desirable to test the stability of phenological traits for even longer time periods. In another study with loblolly pine, Jayawickrama et al. (1998) found no significant provenance \times year interaction, and significant year \times family within-provenance interactions were found for height growth and height growth cessation.

Conclusions about the relationship between duration and basal area growth rate can be drawn only for family S2, where within-family clonal variation was significant. For this family, genotypes that extended the period of basal area growth also showed larger basal area increment in a year. The duration of basal area growth was mainly a function of cessation date. For all families, it was difficult to conclude with our data whether the genetic variation that was present in basal area growth was due to longer duration of season growth or to faster growth per unit of time, or both. Genetic correlations among clonal values for basal area growth and phenological traits are scarce in the literature; most of the reported results are phenotypic correlations at the family level. One of the few studies on genetic control of cambial phenology found that Douglas-fir genotypes with early growth initiation also tended to cease growth early ($r_g = 0.60$, Li and Adams 1994). They also suggested that variation in growth duration among individuals is primarily a function of variation in date of growth cessation ($r_g = 0.77$). Height phenology studies in *Picea abies* in northern Europe showed that there was a consistently low or lack of correlation between the shoot elongation period and either total height or leader length (Ekberg et al. 1994).

Reported phenotypic correlations in southern pines for both diameter and height growth are more closely related to growth rate than to phenological traits such as cessation (McCrary and Jokela 1996; Jayawickrama et al. 1998). Jackson (1952) found that there was no consistent relationship between the starting date and rapidity of growth in slash and loblolly pine trees. For Douglas-fir saplings, most of the differences among populations in one season's growth were related to growth rate rather than to growth duration (Emmingham 1977). On the other hand, studies in aspen hy-

brids in temperate regions suggested that the fast overall growth is largely explained by longer vegetative period (r_p between growth period and diameter was 0.67–0.91 and highly significant; Yu et al. 2001).

Because cambial phenological traits appear to be weakly inherited and have small and inconsistent genetic correlations with growth, indirect responses in cambial phenology from selection of bole basal area or volume are expected to be small. The practical implications of these findings are that selection programs aimed at increasing growth rate are very unlikely to impact dates of initiation or cessation; thus, there are few concerns about increasing the likelihood of frost damage. Another important point to consider in indirect responses, as suggested by Langdon (1963), is the effect of length of growing season on wood properties. Trees that are capable of growing longer into the season may produce a higher proportion of summer wood to spring wood and have higher wood density than genotypes that cease growth early. Future research could help to determine whether families or clones that cease growth earlier do, in fact, have lower wood density. If so, this could then be incorporated into selection programs.

We conclude that the significant within-family clonal genetic variation in basal area growth and the stability of ranks across years found in this study contribute to our understanding of the potential impact that clonal selection can have on future forest plantation productivity. Poor consistency in direction and strength of genetic correlations between basal area increment and phenological traits indicated that in these slash and loblolly pine families initiation, cessation, or duration of growth were traits that did not have biological importance in determining how much a genotype will grow during the season. Basal area growth in loblolly and slash pine families and clones was sensitive to soil water availability, with stem growth declining both above and below an "optimum" soil water balance level. Finally, while there were significant size differences among taxa (species and families) at age 6 and 7 years, genetic differences in basal area growth rate were only expressed during short, discrete time periods in the spring and fall. This finding may have important implications for the timing of investigations attempting to determine the mechanisms underlying genetic growth differences, since growth rate, and possibly the physiological or gene expression traits controlling growth rate, may be similar throughout most of the growing season among taxa with contrasting long-term cumulative growth.

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