E. and Bailey, R. L.: A test of six methods for estimating true heights from stem analysis data. For. Sci. 33: 3—13 (1987). —— Finns, L., Friedman, S. T. and Brotschol, J. V.: Handbook of Quantitative Forest Genetics. Kluwer Academic Publishers, Dordrecht, The Netherlands (1992). —— Foster, G. S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. For. Sci. 32: 944—959 (1986). —— Fowler, D. P.: Strategies for the genetic improvement of important tree species in the Maritimes. For. Can. Inf. Rep. M-X-156 (1986). —— Fowler, D. P. and Park, Y. S.: Population studies of white spruce. I. Effects of self pollination. Can. J. For. Res. 13: 1133—1138 (1983). —— Franklin, E. C.: Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genet. 28: 207—212 (1979). —— Gallant, R. A.: Nonlinear statistical models. John Wiley and Sons, New York, NY (1987). —— Gordon, I. L., Blyth, D. E. and Balaam, L. N.: Variance of heritability ratios estimated from phenotypic variance components. Biometrics 28: 401—415 (1972). —— Hazel, L. N.: The genetic basis for constructing selection indices. Genetics 28: 476—490 (1943). —— Holst, M. J. and Teich, A. H.: Heritability estimates in Ontario white spruce. Silvae Genet. 18: 23—27 (1969). —— Khalil, M. A. K.: Heritability of juvenile characters of white spruce (Picea glauca (Moench) Voss) in central Newfoundland, Canada. Theor. Appl. Genet. 69: 247—251 (1985). —— King, J. N., Dancik, D. P. and Dhir, N. K.: Genetic structure and mating system of white spruce (Picea glauca) in a seed production area. Can. J. For. Res. 14: 639—643 (1984). —— King, J. P. and Rudolf, P. O.: Development of white spruce and Norway spruce trees from several seed sources 29 years after planting. USDA For. Serv. Res. Note NC-70 (1969). —— Kuhnke, P. H.: Silviculture statistics for Canada. Forestry Canada Inf. Rep. NOR-X-301 (1989). —— Lin, C. Y.: A simple stepwise procedure for deriving selection index with restrictions. Theor. Appl. Genet. 70: 147—150 (1985). —— Magnussen, S.: Selection index: economic weights for maximum simultaneous genetic gain. Theor. Appl. Genet. 79: 289—293 (1990). —— Magnussen, S.: Index selection with nonlinear profit function as a tool to achieve simultaneous genetic gain. Theor. Appl. Genet. 82: 305—312 (1991). —— Magnussen, S., and Kremer, A.: Selection for an optimum tree growth curve. Silvae Genetica, in press (1993). —— Magnussen, S. and Park, Y. S.: Growth-curve differentiation among Japanese larch provenances. Can. J. For. Res. 21: 504—513 (1991). —— Matheson, A. C. and

Raymond, C. A.: Effects of thinning in progeny tests on estimates of genetic parameters in Pinus radiata. Silvae Genet. 33: 125—128 (1984). —— Merrill, R. E. and Mohn, C. A.: Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. Can. J. For. Res. 15: 494—497 (1985). —— Miller, R. G., Jr.: Simultaneous statistical inference. Springer-Verlag, New York (1981). —— Morrison, D. F.: Multivariate statistical methods. McGraw-Hill, New York (1976). —— Murray, G.: Variation in height of white spruce provenances after 10 and 20 years in five field tests. Pages 82—89. In: Proc. 29th Northeastern Forest Tree Improv. Conf., Morgantown, WV (1984). —— Namkoong, G., Usanis, R. A. and Silen, R. R.: Age-related variation in genetic control of height growth in Douglas-fir. Theor. App. Genet. 42: 151—159 (1972). —— Nienstaedt, H.: Inheritance and correlation of frost injury, growth, flowering, and cone characteristics in white spruce, Picea glauca (Moench) Voss. Can. J. For. Res. 15: 498—504 (1984). —— Nienstaedt, H. and Kang, H.: Establishing a Picea glauca (Moench) Voss base breeding population for the Lake States region of the United States. Silvae Genet. 36: 21—30 (1987). —— Nienstaedt, H. and Riemenschneider, D. E.: Changes in heritability estimates with age and site in white spruce, Picea glauca (Moench) Voss. Silvae Genet. 34: 34—44 (1985). —— Nienstaedt, H. and Teich, A. H.: Genetics of white spruce. USDA For. Serv. Res. Paper WO-15 (1972). —— Rauscher, H. M.: White spruce plantations in the upper Great Lakes region: Status and problem solving needs. North. J. Appl. For. 4: 146—149 (1987). —— Rauter, R. M. and Ying, C. C.: Genetic Improvement of white spruce. In: Tree Impr. Symposia. Ont. Min. Nat. Resources and The Great Lakes Forest Research Centre. Toronto, Ont. 19—21 Sept. 1978. (1979). —— Shapiro, S. S. and Wilk, M. B.: An analysis of variance test for normality (complete samples). Biometrika 52: 591—611 (1965). —— Snedecor, G. W. and Cochran, W. G.: Statistical Methods. 6th Edition. Iowa State University Press, Ames, Iowa (1971). —— Tallis, G. M.: Selection for optimum growth curve. Biometrics 24: 169—177 (1968). —— Teich, A. H.: White spruce provenances in Canada. Env. Canada, Forestry Serv. Inf. Rep. PS-X-40 (1973). —— Teich, A. H., Skeates, D. A. and Morgenstern, E. K.: Performance of white spruce provenances in Ontario. Can. For. Serv. Petawawa Forest Exp. Station and Ont. Min. of Nat. Res., For. Res. Branch Special Joint Report no 1 (1975). —— Ying, C. C. and Morgenstern, E. K.: Correlations of height growth and heritabilities at different ages in white spruce. Silvae Genet. 28: 181—185 (1979).

Genetic Variation in Second-Year Slash Pine Shoot Traits and Their Relationship to 5- and 15-Year Volume in the Field

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Summary

Seedlings of 64 open-pollinated slash pine (Pinus elliottii Engelm. var. elliottii) families were grown from seed to 18 months of age in raised outdoor boxes under 2 nitrogen (N) treatments (5 ppm and 50 ppm). Twenty-one shoot characteristics were measured and analyzed, of which the most promising twelve were evaluated for use in multitrait selection indices to predict parental breeding values of 5- and 15-year field volume. Genetic parameters were estimated for each seedling trait and individual-tree heritabilities ranged from 0.15 to 0.70. There was a moderate to high degree of genetic commonality for all traits across both N treatments (type B genetic correlations = 0.56 to 0.97). Caliper, green weight, and total height at 18 months were genetically correlated within each treatment (type A genetic correlations = 0.72 to 0.97) and bud burst was not correlated with any trait in either treatment. Family means for height at 13 months (low N treatment),

the difference in heights between 9 months and 13 months (low N), bud burst (high N), and total numbers of branches (high N) were the traits most positively correlated with 15-year breeding values for field volume growth ($r_{j\text{-}m}$ = 0.24 to 0.37). All possible 2- and 3-trait indices were formed and correlations between predicted genetic values and true breeding values (Corr(g,ĝ)) were calculated to assess indices with the best predictive ability. Total numbers of branches (high N), total numbers of cycles (high N), and the difference in height from 9 to 13 months (low N) formed the most precise index for predicting 15-year volume (Corr(g,ĝ) = 0.51). This 3-trait index was not effective at identifying the best 10% of the families used in the experiment.

Key words: Heritability, genetic correlation, type B genetic correlation, juvenile-mature correlations, selection indices, genetic gain efficiency.

Introduction

Currently, only 1 tree improvement program in North America utilizes an operational technique to select genetically superior families at an early age without field testing (Lowe and van Buijtenen, 1989). A variety of juvenile traits (before age 5) have been identified as possible early selection criteria in conifers (e.g., numbers of stem units, cyclic growth, annual height increment), but results have not been conclusive enough for tree improvement programs to adopt early testing techniques operationally. Future evaluations of early selection traits should be based not only on juvenile — mature correlations but also on other estimates of genetic parameters and genetic gain to clearly identify which traits can be used in operational early testing (Li et al., 1992).

Early selection researchers have based their choice of potentially useful juvenile traits on genotypic and phenotypic age-age correlations. These efforts to correlate juvenile traits with mature field performance have produced inconsistent results due to 1) low heritabilities for the juvenile or mature-target traits (Franklin, 1979; Gill, 1987), 2) maternal seed effects on juvenile performance (Barnes and Schweppenhauser, 1978; Cannell et al., 1978), 3) small or imprecise phenotypic or family mean correlations between juvenile and target traits (Cotterill and Dean, 1988), and 4) imprecise genetic parameter estimates due to inadequate numbers of families and individuals within-families (Lambeth, 1983; Burdon, 1989).

Previous early selection studies with conifers have reported results for juvenile shoot traits (e.g., total height, lengths and numbers of cycles) that were correlated with later field performance (e.g., height or volume) (Williams, 1987; Riemenschneider, 1988; Li et al., 1991). Attempts to correlate mature performance with length of juvenile growing season (bud burst to bud set) have been widely tested with some conifer species such as Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), but not with the southern pines of the United States. Cannell et al. (1978) found that the date of first-year bud set was poorly correlated with eight-year volume of loblolly pine (Pinus taeda L.). For Douglas-fir, Campbell (1986) reported that height growth was genetically correlated across seed sources with the duration of growing season for second-year seedlings. Ritters and Perry (1987) determined that the date of second-year bud burst was significantly correlated (p < 0.10) with 15-year field height. White et al. (1981) corroborated other studies that found genetic differences between Douglas-fir provenances in bud burst date.

Conifers exposed to different test environments have displayed significant differences between populations and families for juvenile shoot components (Wheeler, 1979; White et al., 1981; Chase, 1988; Bridgwater, 1990; Carter et al., 1990). For southern pines, different fertilizer treatments have promoted differential genetic expression of juvenile shoot traits and revealed potentially useful early selection traits (Li, 1989; DeWald et al., 1992; Li et al., 1992). For slash pine (Pinus elliottii Engelm. var. elliottii), which has evolved on nitrogen (N) deficient soils (Pritchett and Comerford, 1983), significant family x N treatment interactions for height growth have been reported (Pritchett and Goddard, 1967; Holaday, 1973; Jahromi et al., 1976).

Although individual juvenile traits have been identified as useful for predicting mature performance, rarely have combinations of juvenile traits measured in controlled environments (i.e., greenhouse, growth chamber, nursery bed) been used to predict the genetic value of a target trait (indirect testing). Correlated response (Falconer, 1981), which uses one indirect trait to predict a single target trait, has been used to assess early selection efficiency with loblolly pine (Lambeth, 1980, 1983; Foster, 1986; Li et al., 1992). With slash pine, combinations of juvenile traits have been shown to more precisely predict target genetic values than individual juvenile traits (White and Hodge, 1991; Smith, 1992). Different combinations of juvenile traits can be used to predict the same target genetic value (e.g., 15-year breeding value for volume growth), and they can be compared for selection efficiency using the correlation (Corr(g,ĝ)) between the true and predicted genetic values (White and Hodge, 1991). Corr(g,ĝ) is also the gain per unit of selection intensity and can be used as a basis for identifying useful combinations of juvenile traits.

In this paper, we report results on 12 shoot traits from 2-year-old slash pine that may have value as early selection criteria. This study was part of a larger investigation which tested the usefulness of other slash pine juvenile traits in early selection (Surles et al., in review; Smith, 1992). The objectives of this experiment were to 1) estimate genetic parameters for seedling traits grown in 2 N treatments, 2) determine which traits are related to 5- and 15-year field performance, 3) predict a target genetic value (field volume) with all possible combinations of juvenile traits in 2- and 3-trait indices, and 4) identify trait combinations that are potentially useful in multi-trait selection indices.

Materials and Methods

Plant Material

The 64 open-pollinated slash pine families used in this study were a random sample of 2300 first-generation selections made by members of the Cooperative Forest Genetics Research Program (CFGRP) from natural stands in northeast Florida and southeast Georgia, U.S.A. All the families have been field tested at a minimum of 4 progeny test locations and measured for height, diameter at breast height, and volume at ages 5-, 10-, and 15-years (White and Hodge, 1988; Hodge and White, 1992). Most of the families were in more than 4 tests (range = 4 to 16), and the median family was tested in 8 locations. All selections currently exist as clones in 2 seed orchards owned by ITT-Rayonier and Container Corporation of America in northeast Florida. Seeds were harvested in 1987 and 1989.

Seedling Culture

The seeds were soaked for 24 hours in room temperature tap water and stratified in a refrigerator at 3° C for 2 weeks. The seeds were sown during the week of April 9, 1990 in 8 seedling boxes (20m long x 2m wide x 1m deep) containing coarse sand as a growing medium. The boxes were located outdoors, approximately 17 km north of Gainesville, Florida (29° N, 82° W) in the University of Florida's Austin-Cary Memorial Forest. Each box was underlain with 12 cm of coarse gravel and horticultural landscape cloth to promote drainage and to keep roots inside the boxes. Fertilization began 3 weeks after germination to avoid damping-off, and the seedlings were fertilized and watered twice weekly with a low (5 ppm) or high (50 ppm) N-fertilizer solution. Other nutrients besides N were supplied in non-limiting proportions according to Ingestad's (1979) recommendations for pine

species, and the boxes were flushed monthly to prevent nutrient accumulation. In late September 1990, fertilizer and watering regimes were changed to 1 per week to slow growth and promote bud set. Biweekly fertilization was started again in March 1991. The pH of the nutrient solution was adjusted to 5.0 to 5.4 with concentrated sulfuric acid. The nutrient solutions and growing medium were sampled periodically for nutrient analysis.

Experimental Design

Seedlings were grown at a 15 cm x 15 cm spacing in a randomized complete block, split-plot design with 2 main-plot treatments (high and low N) and 4 blocks (2 N treatments x 4 blocks = 8 boxes). Each box was divided into 5 sections, each section representing a different harvest date. This study was part of a larger investigation of nitrogen-use efficiency and early selection, thus only one-fifth of the total number of seedlings in each box (i.e., a single harvest date) was used for this study. Six seedlings from each of the 64 families were randomized within each main-plot of each block for a total of 3072 seedlings (2 N treatments x 4 blocks x 64 families x 6 seedlings).

Traits Measured

Twenty-one traits were measured and analyzed of which the most promising 12 are reported here (*Table 1*). Date of second-year bud burst (BB1 and BB2) was recorded by attaching flat wooden sticks (with marks at 2 cm and 6 cm above the dormant shoot tip) to the terminal shoot of each seedling during the first week of January 1991. Observations were made every 2 or 3 days and the Julian date was recorded when each seedling's bud passed each mark on the stick.

Total heights were recorded at four time intervals during the second growing season at 9, 13, 16, and 18 months after germination. Heights were measured from 1 cm above the epicotyl scar to the terminal tip of the stem. Total numbers of branches (TOTBRCH), caliper (CAL), total number of cycles or flushes (TOTFL), and total green weight (WEIGHT) were all measured during a final destructive harvest 18 months after germination.

Statistical Analysis

An analysis of variance (ANOVA) based on plot means (averages of the 6 seedlings from a given family in each whole-plot) and combined over N treatments was conducted to test for N treatment, family, and family x treatment interaction for the 12 shoot traits (SAS Institute Inc., 1988). Family (σ_f^2) and plot (σ_p^2) variance components were then estimated in separate ANOVA's for the high and low N treatments because the error variances in the 2 treatments were quite different. Sequentially adjusted mean squares (Type 1) were equated to their expectations to solve for the variance components. Harmonic means (n) of the number of observations per plot were calculated for each trait in both treatments to estimate within-plot (σ_w^2) variance components, and individual-tree (h^2) and family heritability (h_f^2) estimates were obtained as (FALCONER, 1981):

$$h^2 = \sigma_A^2/\sigma_p^2 = 4\sigma_f^2/(\sigma_f^2 + \sigma_p^2 + \sigma_w^2) \qquad \textbf{Eq. 1}$$

$$h_f^2 = \sigma_f^2/(\sigma_f^2 + \sigma_p^2/4 + \sigma_w^2/4n) \qquad \textbf{Eq. 2}$$

Standard errors of heritability estimates were calculated as in NAMKOONG (1979, p. 233).

Type A genetic correlations, which measure the additive genetic correlation between pairs of traits in the same treatment, were estimated as given by MODE and ROBINSON (1959):

$$r_{Ag(ij)} = \sigma_{(ij)}/(\sigma_{fi}^2 \, \sigma_{fj}^2)^{0.5} \qquad \textbf{Eq. 3}$$

where $r_{Ag(ij)}$ is the estimated genetic correlation for traits i and j in one N treatment, $\sigma_{(ij)}$ is the estimated family covariance between traits i and j from an analysis of covariance, and σ_{fi}^2 and σ_{fj}^2 are the estimated family variances for traits i and j, respectively, with all parameters estimated from the ANOVA for one N treatment. Standard errors were estimated using MODE and ROBINSON's (1959) methods.

Type B genetic correlations (BURDON, 1977), which in this study quantify family x N treatment interaction, were estimated for each trait as:

$$r_{Bg} = \sigma_f^2/(\sigma_f^2 + \sigma_{ft}^2) \qquad \textbf{Eq. 4}$$

where r_{Bg} is the estimated Type B genetic correlation for a given trait expressed in the 2 N treatments, σ_f^2 is the estimated family variance from the combined ANOVA, and σ_{ft}^2 is the estimated family x N treatment variance from the combined ANOVA. A correction term (K) was used to adjust the type B genetic correlation for the heterogeneity of variances among treatments (DICKERSON, 1962; YAMADA, 1962):

$$K = (\sigma_{f1} - \sigma_{f2})^2/2 \qquad \textbf{Eq. 5}$$

where σ_{f1} and σ_{f2} are estimated family standard deviations from the separate ANOVA for the 2 N treatments. K was subtracted from σ_{ft}^2 and resulted in σ_{ft*}^2, and the adjusted type B genetic correlation was estimated as:

$$r_{Bg}* = \sigma_f^2/(\sigma_f^2 + \sigma_{ft*}^2) \qquad \textbf{Eq. 6}$$

Standard errors for the unadjusted type B genetic correlations were estimated using MODE and ROBINSON's (1959) methods and were taken as the standard errors for the adjusted correlations.

Genophenotypic correlations (WHITE and HODGE, 1991) were estimated between the family means of seedling traits with the predicted breeding values of 5- and 15-year volumes from the CFGRP field trials by direct correlation of the 64 pairs of numbers for each trait combination. Best linear prediction (HENDERSON, 1984) was used to predict parental breeding values for field volume at age 15 for each of the 64 parents (WHITE and HODGE, 1988). Similar procedures were used to predict breeding values at age 5. The predicted breeding values for 5- and 15-year volume were taken as true breeding values because they were derived from progeny test data collected across many sites and tests.

The indirect index selection procedures developed by WHITE and HODGE (1991) were used to identify shoot components that were valuable in 2- and 3-trait indices for predicting parental 5- and 15-year breeding values. The correlation (Corr(g,ĝ)) between predicted genetic values (using combinations of juvenile traits) and true genetic values (15-year breeding values) was used to assess the

Table 1. — Shoot trait definitions, means, heritability estimates (with standard errors[a]), and type B genetic correlations (with standard errors) for slash pine seedling traits grown under low and high N treatments[b].

Trait	Definition	Means		h^2		h^2_L		$r_{Bg}*$
		Low N	High N	Low N	High N	Low N	High N	
BB1	2cm bud growth (days)[c]	59.21	49.77	0.39 (0.09)	0.47 (0.10)	0.68 (0.06)	0.75 (0.04)	0.69 (0.13)
BB2	6cm bud growth (days)[c]	70.80	60.73	0.28 (0.07)	0.46 (0.09)	0.64 (0.07)	0.77 (0.04)	0.74 (0.13)
TOTBRCH	Total branches (#)	10.94	17.25	0.50 (0.09)	0.45 (0.12)	0.79 (0.04)	0.63 (0.12)	0.63 (0.13)
CAL	Caliper (cm)	1.41	2.26	0.47 (0.09)	0.50 (0.12)	0.77 (0.04)	0.66 (0.06)	0.80 (0.12)
TOTFL	Total flushes (#)	6.22	6.73	0.50 (0.10)	0.59 (0.13)	0.78 (0.04)	0.68 (0.06)	0.82 (0.10)
WEIGHT	Total green weight (g)	221.54	796.56	0.42 (0.09)	0.25 (0.09)	0.75 (0.04)	0.49 (0.10)	0.89 (0.33)
HT1	Total height 9 months (cm)	19.17	45.07	0.33 (0.08)	0.70 (0.12)	0.68 (0.06)	0.84 (0.03)	0.82 (0.18)
HT2	Total height 13 months (cm)	68.93	113.55	0.28 (0.07)	0.50 (0.10)	0.65 (0.07)	0.75 (0.05)	0.71 (0.17)
HT3	Total height 16 months (cm)	107.95	152.09	0.33 (0.09)	0.30 (0.10)	0.60 (0.07)	0.52 (0.09)	0.65 (1.06)
HT4	Total height 18 months (cm)	121.90	164.74	0.37 (0.08)	0.40 (0.13)	0.72 (0.05)	0.52 (0.09)	0.97 (0.14)
HT2-1	HT2 - HT1 (cm)	49.58	68.34	0.16 (0.05)	0.15 (0.04)	0.58 (0.08)	0.60 (0.08)	0.56 (0.19)
HT4-1	HT4 - HT1 (cm)	102.72	117.90	0.33 (0.08)	0.26 (0.11)	0.69 (0.06)	0.40 (0.10)	0.80 (0.19)

[a] h^2 and h^2_f calculated with equations 1 and 2, $r_{Bg}*$ calculated with equation 6.
[b] significant family effects from combined and separate analysis of variance at $p \leq 0.01$ level
[c] Julian day of bud burst.

precision of the prediction. Corr(g,ĝ) approaches 1 as the predicted genetic value approaches the true genetic value. All possible combinations of traits were tried in 2- and 3-trait indices, and those with the highest Corr(g,ĝ) were considered potentially useful.

Results

Cultural and Seed Effects

Mean date of bud burst occurred ten days earlier in the high N treatment (Table 1). Total heights from all time intervals were consistently larger in the high N treatment, although the magnitude of the difference between treat-

ments decreased considerably from HT1 to HT4. Caliper, green weight, and total branch number were all significantly larger in the high N treatment. TOTFL was similar in both treatments.

Crown closure occurred at approximately 12 months after germination in the high N treatment compared to 16 months in the low N treatment. As a result of the increased above and below-ground competition for light and nutrients, mortality increased dramatically from 2% at 13 months to 47% at 18 months in the high N treatment but stayed relatively constant throughout the experiment (3% at 9 months to 5% at 18 months) in the low N treatment.

Seed characteristics (total seed weight, seed coat weight, embryo weight, and megagametophyte weight) were measured as part of the larger study (SURLES et al., in review) and were more positively correlated with the height measurements in the low N treatment than in the high N treatment (Figure 1). Seed embryo weight was the most highly correlated with HT2 in the low N treatment (r = 0.49). Total seed weight was less correlated with all the height measurements in both N treatments compared to the other three seed components.

Genetic Parameter Estimates

Family effects were significant (p≤0.01) for all traits in both the separate ANOVA's and also those combined across
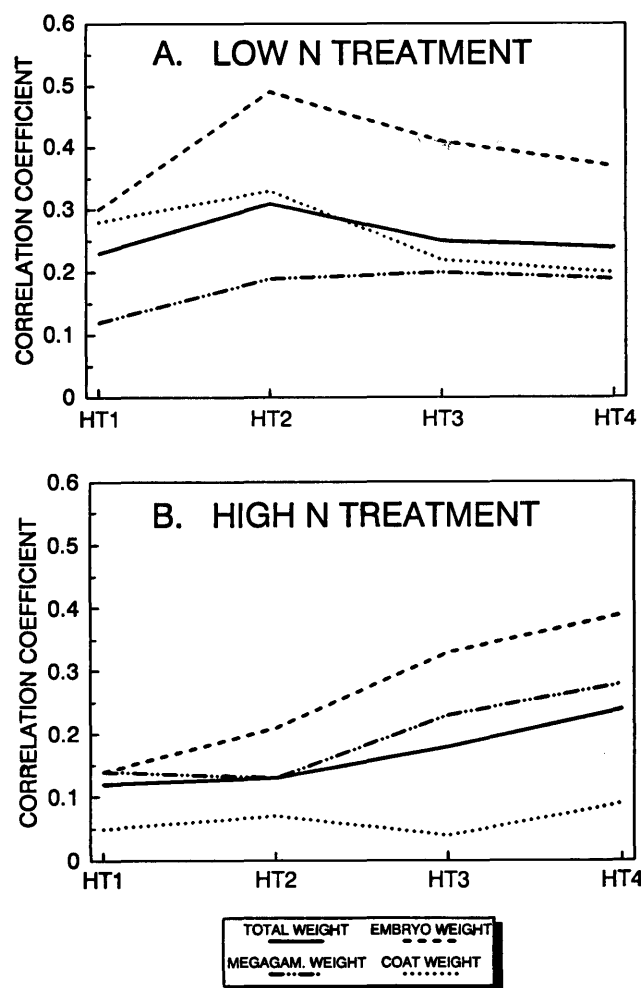

Figure 1. — Family mean correlations between second-year total height increments and seed weight components for 64 slash pine families grown in: A) low N treatment and B) high N treatment.

N treatments. In the combined ANOVA, family x N treatment interactions were significant (p≤0.01) for all traits except WEIGHT (p≤0.02) and HT3, HT4, and HT4-1 (non-significant). Across all 12 traits, there was no clear trend of higher estimates of individual-tree heritability (h^2) or family heritability (h_f^2) in either treatment (Table 1). HT1 in high N had a high estimate of h^2 (0.70 ± 0.12) compared to the low N estimate (0.33 ± 0.08). Throughout the second-year, heritability estimates for height remained consistent in the low N treatment ($h^2 \approx 0.30$), while they fluctuated greatly in the high N treatment ($h^2 \approx 0.30$ to 0.70). Lower estimates of h_f^2 for HT3 and HT4 in the high N treatment were attributable to the loss of a large number of trees due to mortality from inter-tree competition.

BB1 and BB2 both had higher heritability estimates in the high N treatment. Both measures of bud burst had small or negative type A genetic correlations (r_{Ag}) with most other traits in both N treatments (Table 2). For example, negative correlations of BB1 with caliper (r_{Ag} = —0.26 and r_{Ag} =—0.31) indicate that later bud burst was genetically associated with smaller caliper across the 64 families in the low N and high N treatments, respectively. Of special note, BB1 and BB2 were not highly correlated with any of the height measurements or TOTFL. CAL was strongly correlated with WEIGHT in both treatments and all the height measurements in the low N treatment. WEIGHT was positively correlated with all heights in both treatments. TOTBRCH was strongly correlated with all other traits except BB1 and BB2 in both treatments and HT2-1 and HT2 in the high N treatment.

HT4 and WEIGHT were the most stable traits across treatments with type B genetic correlations (r_{Bg*}) of 0.97 and 0.89, respectively (Table 1). TOTBRCH, HT2-1, and HT3 were the least stable traits (r_{Bg*} = 0.56 to 0.65). Correlations for height measurements changed considerably throughout the second-year (r_{Bg*} = 0.65 to 0.97).

Juvenile — Mature Correlations

The strongest genophenotypic correlations (r_{j-m}) between second-year (2-year) traits and fifth-year (5-year) breeding values were with HT2 and HT2-1 in the low N treatment and HT4 in the high N treatment (Table 3). Second-year TOTFL displayed the lowest correlation with 5-year breeding values in both low and high N treatments (r_{j-m} = 0.00 and 0.08, respectively).

Genophenotypic correlations of 2-year traits with 15-year breeding values were lower than with 5-year breeding values for all traits except BB1 and BB2 in the high N treatment and HT2-1 in the low N treatment. As with the 5-year data, HT2-1 and HT2 had the highest correlation with 15-year breeding values (r_{j-m} = 0.37 and 0.30) in the low N treatment. BB1 and TOTBRCH had the highest 2-year with 15-year correlations in the high N treatment (r_{j-m} = 0.25 and 0.24, respectively). Again, TOTFL had the lowest correlations in both treatments.

Multi-Trait Indices

Combinations of traits from the 2 treatments had higher correlations between the true and predicted breeding values (Corr(g,ĝ)) than indices using traits from the same treatment (Table 4). The most precise 3-trait indices had estimates of Corr(g,ĝ) ≈ 0.50 meaning that about 25% of the variation in the 64 field breeding values could be accounted for by the selection index prediction. The 2-trait indices using one trait from each treatment had

Table 2. — Type A genetic correlations with standard errors for second-year slash pine seedling traits grown in low N (top half above diagonal) and high N (bottom half below diagonal) treatments [a].

Trait	BB1	BB2	TOTBRCH	CAL	TOTFL	WEIGHT	HT1	HT2	HT3	HT4	HT2-1	HT4-1
BB1		0.94±.31	-0.16±.17	-0.26±.18	-0.02±.17	-0.17±.18	-0.25±.19	0.14±.18	0.00±.19	-0.04±.18	0.16±.20	0.00±.18
BB2	0.94±.27		0.00±.17	-0.19±.18	0.04±.17	-0.10±.18	-0.22±.19	0.00±.19	-0.01±.20	-0.02±.18	0.13±.21	0.02±.18
TOTBRCH	-0.12±.18	0.04±.18		0.72±.21	0.60±.19	0.76±.22	0.58±.20	0.62±.22	0.67±.24	0.72±.22	0.54±.22	0.72±.23
CAL	-0.31±.19	-0.23±.18	0.73±.27		0.48±.18	0.96±.27	0.84±.26	0.86±.27	0.89±.29	0.83±.24	0.69±.25	0.80±.24
TOTFL	-0.37±.20	-0.07±.17	0.68±.25	0.52±.22		0.57±.19	0.55±.20	0.38±.19	0.56±.22	0.69±.21	0.18±.18	0.70±.22
WEIGHT	-0.36±.22	-0.24±.21	0.77±.33	0.97±.38	0.61±.28		0.84±.26	0.90±.28	0.92±.30	0.91±.27	0.74±.26	0.89±.27
HT1	-0.33±.17	-0.07±.15	0.46±.20	0.51±.20	0.62±.21	0.50±.23		0.78±.27	0.85±.30	0.85±.27	0.51±.23	0.78±.26
HT2	-0.24±.17	-0.05±.16	0.30±.19	0.58±.22	0.45±.20	0.57±.26	0.89±.25		0.99±.34	0.91±.29	0.93±.33	0.91±.29
HT3	0.08±.20	0.19±.21	0.65±.29	0.73±.30	0.74±.30	0.92±.40	0.61±.25	0.63±.26		1.01±.33	0.87±.32	1.00±.34
HT4	-0.07±.20	0.08±.20	0.58±.27	0.72±.29	0.66±.28	0.81±.36	0.55±.23	0.62±.25	1.00±.42		0.76±.27	0.99±.30
HT2-1	-0.09±.19	-0.02±.19	0.00±.21	0.50±.24	0.15±.20	0.50±.27	0.61±.23	0.90±.31	0.47±.26	0.47±.26		0.79±.28
HT4-1	0.04±.21	0.08±.21	0.39±.25	0.50±.26	0.43±.25	0.63±.32	0.10±.19	0.25±.21	0.86±.39	0.88±.39	0.25±.24	

[a] Type A genetic correlations calculated with equation 3.

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Table 3. — Genophenotypic correlations of second-year shoot trait family means with 5- and 15-year predicted breeding values for 64 families grown in low and high N treatments [a][b].

| | 2yr with 5yr correlation | | 2yr with 15yr correlation | |
Trait	Low N	High N	Low N	High N
BB1	0.24*	0.19	0.11	0.25**
BB2	0.18	0.20*	0.03	0.20*
TOTBRCH	0.20	0.26**	0.14	0.24**
CAL	0.27**	0.23*	0.21*	0.12
TOTFL	0.00	0.08	-0.07	-0.07
WEIGHT	0.28**	0.25**	0.20*	0.14
HT1	0.24*	0.19	0.09	0.08
HT2	0.36***	0.23*	0.30***	0.13
HT3	0.29**	0.26**	0.22**	0.16
HT4	0.28**	0.32***	0.19	0.17
HT2-1	0.36***	0.23*	0.37***	0.16
HT4-1	0.27**	0.28**	0.20*	0.16

[a]), [*]), [**]), [***]) significant at $0.05 \leq p \leq 0.10$, $0.01 \leq p \leq 0.05$, and $p \leq 0.01$, respectively.

[b]) Correlations are identical to $Corr(g,\hat{g})$ of a single-trait predictive index (WHITE and HODGE, 1991). The values in this table may be interpreted as the precision of a single-trait index and compared with those of table 4 for multitrait indices.

Table 4. — Correlations between true and predicted parental breeding values ($Corr((g,\hat{g})$) for selection indices predicting 15-year volume using combinations of second-year slash pine traits from seedlings grown in low and high N treatments (L and H, respectively).

| | | Low N | | High N | | Both Treatments | |
		Corr(g,ĝ)	Traits	Corr(g,ĝ)	Traits	Corr(g,ĝ)	Traits
Two Trait Indices		0.40	TOTFL HT2-1	0.38	TOTFL TOTBRCH	0.42	HT2-1 (L) BB1 (H)
		0.39	HT2-1 HT4-1	0.36	TOTBRCH BB1	0.41	HT2-1 (L) TOTBRCH (H)
		0.39	HT4 HT2-1	0.34	TOTBRCH WEIGHT	0.39	HT2-1 (L) BB2 (H)
Three Trait Indices		0.44	HT1 HT2 HT2-1	0.43	TOTBRCH TOTFL BB1	0.51	HT2-1 (L) TOTBRCH(H) TOTFL(H)
		0.41	TOTFL BB1 HT2-1	0.42	TOTBRCH TOTFL BB2	0.49	TOTFL (L) HT2-1 (L) TOTBRCH(H)
		0.40	TOTFL HT2 HT2-1	0.41	TOTBRCH TOTFL HT3	0.48	HT2-1 (L) HT4-1 (L) TOTBRCH (H)

Corr(g,ĝ) estimates of 0.42 which were similar to three-trait indices formed of traits from a single treatment. TOTBRCH (high N), TOTFL (both treatments), and HT2-1 (low N) appeared frequently in the highest ranking indices of all combinations of traits.

Discussion

Cultural Effects

Differential responses to fertilizer treatments have been previously found with juvenile slash pine families (PRIT-

CHETT and GODDARD, 1967; JAHROMI, 1971; HOLADAY, 1973; GODDARD et al., 1976; DEWALD et al., 1992). Our high N treatment accelerated growth and resulted in seedlings that were more physiologically mature (i.e., earlier formation of secondary needles and branch shedding) than seedlings in the low N treatment. The rapid juvenile growth in the high N treatment greatly accelerated the time at which competition effects (crown closure) occurred between individuals.

Bud burst took place earlier in the high N treatment and although late bud burst was considered a favorable mature trait with northern conifers (BONGARTEN and HANOVER, 1985), this may not hold true for slash pine which grows in an environment where early bud burst may be an advantage. Bud burst was not correlated with any other juvenile trait in either treatment which corroborated results from KAYA et al. (1989) who determined that the timing of Douglas-fir second-year bud burst was poorly correlated with second-year height components. Although we imposed the end of the growing season by harvesting seedlings in late October 1991 (end of second growing season), our results were not in agreement with BRIDGWATER et al. (1985) who implied that longer growing seasons for loblolly pine might lead to more cycles and more growth being produced annually. Our seedlings that began growing earlier in the year (February) did not have a significantly greater number of cycles (flushes) or taller height increment. Neither measure of bud burst (BB1 or BB2) was genetically correlated with TOTFL or HT4 in either N treatment. Our results also differ from work with lodgepole pine (*Pinus contorta* DOUGL.) that has shown the duration of the juvenile growing season was correlated with early height growth (CANNELL et al., 1981). Our findings do corroborate WILLIAM's (1987) observation that the fastest growing loblolly pine families were those that produced more growth per unit time rather than those with longer growing seasons.

Seed Effects

Seed effects, particularly embryo weights, may be confounding estimates of early seedling growth. Twenty-five percent of family mean variation in total height at 13 months was attributable to seed embryo weight in the low N environment (*Figure 1*). Several authors have indicated that seed effects diminish after first-year free growth (BARNES and SCHWEPPENHAUSER, 1978; CANNELL et al., 1978; WAXLER and van BUIJTENEN, 1981; WILLIAMS, 1987), but seed characteristics appear to affect additive genetic variance in slash pine past year one. SURLES et al. (in review) have demonstrated that some slash pine seed weight components are moderately correlated with 15-year breeding values (genophenotypic correlation of r = 0.50 between embryo weight and 15-year breeding value).

Changes in Heritabilities During Second-Year Growth

The decrease of individual-tree heritability (h^2) in the high N treatment from 9 months (HT1) to 16 months (HT3) after germination may be attributable to declining additive variance caused by intense inter-tree competition. COTTERILL and DEAN (1988) found that additive variance declined with stand closure and increased competition between individuals in a study with radiata pine (*Pinus radiata* D. DON). Our results agree with their observation that seedlings were able to express genetic potential for height growth before crown closure occurred. Our estimate for HT1 (h^2 = 0.70 ± 0.12) reflected this stage of

development. As crown closure was reached in the high N treatment (approximately 12 months after germination), estimates of h^2 decreased. As in FRANKLIN (1979), the decrease in heritability was due to the phenotypic variance increasing much more than additive variance during this time interval. The rise of h^2 estimates from HT3 to HT4 may be due to the increased expression of additive genetic potential following the self-thinning of seedlings due to competition in the boxes. In the low N treatment, estimates of h^2 remained constant throughout the second-year, possibly because of a lack of competition and canopy closure.

Genotype x Treatment Interactions

HT4 and WEIGHT displayed a high degree of commonality of gene effects across the 2 N treatments with type B genetic correlations (r_{Bg}) of 0.97 and 0.89, respectively. LI et al. (1992) obtained a slightly lower estimate (r_{Bg}=0.78) for second-year height with loblolly pine families grown under several irrigation and fertilization treatments. When $r_{Bg} \approx 0.67$, genotype x environment (g x e) interaction variance is half the size of additive variance, and this was the approximate level of g x e interaction observed for 5-, 10-, and 15-year slash pine volume growth across field sites (HODGE and WHITE, 1992).

Juvenile — Mature Correlations

Our genophenotypic correlations of second-year shoot traits with 5- and 15-year breeding values were higher than SQUILLACE and GANSEL's (1974) family mean correlation of 0.10 between 3-year and 25-year height with slash pine families. With data interpolated from WAKELEY (1971), these same authors derived a family mean correlation of 0.59 between 3-year and 30-year heights with open-pollinated families. FRANKLIN and SQUILLACE (1973) found family mean correlations between 3-year and 25-year height of 0.56, and 0.43 between 3-year with 25-year volume. For total height, our most precise correlation was between HT2 (13 months) with 15-year breeding values (r_{j-m} = 0.30 in low N) and HT2 with 5-year breeding value (r_{j-m} = 0.36 in low N).

For loblolly pine, LI et al. (1992) found a family mean correlation of 0.68 between second-year height from a well-watered and fertilized treatment with eight-year field height. This estimate was much higher than any of our correlations from the high N treatment. WILLIAMS (1987) determined that cyclic growth length was the best predictor of 8-year height and volume from 18-month-old seedlings and calculated a family mean correlation of 0.62 between cyclic growth length and 8-year height. FOSTER (1986) obtained genetic correlations between second-year height and 15-year volume of 0.41 and a correlation of 0.57 between 2-year height and 10-year volume. These estimates are higher than our correlations between 2-year height with 5- and 15-year breeding values (*Table 3*).

In work with other conifers, RITTERS and PERRY (1987) found a family mean correlation of 0.57 and 0.49 for Douglas-fir bud burst (with 15-year height growth) at 117 and 285 days after germination, respectively. In our high N treatment, bud burst was significantly correlated with 15-year volume (r_{j-m} = 0.25, p = 0.05). GILL (1987) determined that phenotypic correlations between juvenile height and 27-year height of Sitka spruce improved from the first year to third year (r_{j-m} = —0.15 to 0.39). We found that in the low N treatment, juvenile — mature correlations be-

tween total height and 15-year breeding values increased from 6 months ($r_{j-m} = 0.16$) to 13 months ($r_{j-m} = 0.30$), but then decreased at 18 months ($r_{j-m} = 0.19$). In the high N treatment, first-year correlations between total height with 15-year breeding values were higher than between 2-year with 15-year correlations ($r_{j-m} = 0.24$ vs. 0.16) (SMITH, 1992). In work with jack pine (*Pinus banksiana* LAMB.), CARTER et al. (1990) obtained a phenotypic correlation of 0.49 between 2-year and 7-year height with seedlings grown under accelerated conditions. RIEMENSCHNEIDER (1988) obtained a genetic correlation of 0.84 between 2-year and 7-year heights. Again, these estimates are higher than our genophenotypic correlation of 0.32 (significant at p = 0.01 level) between 2-year height and 5-year breeding values.

Genetic Gain

Our 2- and 3-trait indices formed with combinations of traits from both treatments yielded the most precise estimates of the true breeding values. This was the same result obtained with 1-year slash pine shoot traits grown under the same N conditions (SMITH, 1992). The precision of these indices was enhanced by using one trait (i.e., TOTFL, high N) that was weakly correlated with the target genetic value (15-year breeding value) and two traits (i.e., TOTBRCH, high N and HT2-1, low N) that were not correlated with each other but significantly correlated with 15-year breeding value. HT2-1 (low N), TOTBRCH (high N), or TOTFL (both treatments) appeared in all of the most precise predictions of parental breeding values (Corr(g,ĝ) > 0.47). BB1 (high N), BB2 (high N), HT2 (low N), and HT4-1 (low N) were also in a high percentage of the most precise indices.

Corr(g,ĝ) expressess the correlation between the predicted breeding values (ĝ) from finite, indirect tests that have error, and true breeding values (g) that are assumed to have no error because they were derived from many tests in many field locations. In this experiment, Corr(g,ĝ) also expressess the selection efficiency (undiscounted) of finite, indirect early testing compared to direct testing across infinite number of sites at age 15. Thus, for a given selection intensity, Corr (g,ĝ) equals the genetic gain in 15-year volume achievable from indirect selection at year-2 relative to the maximum possible gain achievable from direct selection at 15-years (WHITE and HODGE. 1991). This means that use of the best 3-trait juvenile index to select the best families for volume at age 15 is expected to achieve 51% (Corr(g,ĝ) = 0.51) of the genetic gain compared to perfect selection based on true breeding values that are known without error.

In some instances, a selection index may be better at identifying poor performers than superior families, or vice versa. To determine if our best three-trait index more precisely predicted the 15-year breeding values of the best or worst growing families used in this experiment, a comparison was made between selection gain efficiencies of the highest ranking families (according to the true breeding value) versus the lowest ranking families. For example, to calculate the selection efficiency of selecting the top 10% (6 out of 64 families), the top 6 families were selected according to the selection index or the known true breeding values. The known true breeding values of the index selected group were averaged and divided by the average of the group selected based on the true breeding values. If the index is equally effective at identifying family performance throughout the range of

true breeding values, then the selection efficiency should approximate 0.51 (Corr(g,ĝ) of the three-trait index). In fact, when the top 10%, 25% and 50% of the 64 families used in this study were selected based on the best 3-trait index, a selection efficiency of 38%, 53% and 58% was achieved, respectively. For the bottom 10%, 25% and 50% of the families used in this experiment, a selection efficiency of 46%, 49% and 48% was attained, respectively. These differences may be due to sampling (i.e., experimental error), but there is some indication that the index was least effective at identifying the very best families. Across the rest of the range, the selection efficiencies approximated the 51% indicated by Corr(g,ĝ).

Conclusions

Of the 12 second-year slash pine shoot components we examined in the 2 N treatments, we recommend using the change in height from 9 to 13 months (HT2-1, low N), total number of branches (TOTBRCH, high N), total number of cycles or flushes (TOTFL, both treatments), 2 cm bud growth (BB1, high N), 6 cm bud growth (BB2, high N), height at 13 months (HT2, low N), and the change in height from 9 to 18 months (HT4-1, low N) as early selection criteria based on their performance in multi-trait indices. Caliper (CAL, low N) and WEIGHT (low N) should also be considered because they were stable across both treatments, had high h^2 estimates, and had significant juvenile — mature correlations. In future work, these traits should be analyzed with other potentially useful juvenile shoot and root traits (i.e., shoot biomass and root lengths) in multi-trait selection indices to identify combinations of characteristics that precisely predict parental breeding values.

References

BARNES, R. D. and SCHWEPPENHAUSER, M. A.: *Pinus patula* SCHIFDE and DEPPE progeny test in Rhodesia: genetic control of nursery traits. Silvae Genet. **27**, 200—216 (1978). —— BONGARTEN, B. C. and HANOVER, J. W.: Accelerating seedling growth through photoperiod extension for genetic testing: a case study with blue spruce (*Picea pungens*). Forest Sci. **31**, 631—643 (1985). —— BRIDGWATER, F. E., WILLIAMS, C. G. and CAMPBELL, R. G.: Patterns of leader elongation in loblolly pine families. For. Sci. **31**, 933—944 (1985). —— BURDON, R. D.: Genetic correlations as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet. **26**, 168—175 (1977). —— BURDON, R. D.: Early selection in tree breeding: principles for applying index selection and inferring input parameters. Can. J. For. Res. **19**, 499—504 (1989). —— CAMPBELL, R. K.: Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. Silvae Genet. **35**, 85—96 (1986). —— CANNELL, M. G. R., BRIDGWATER, F. E. and GREENWOOD, M. S.: Seedling growth rates, water stress responses and root-shoot relationships related to eight-year volumes among families of *Pinus taeda* L. Silvae Genet. **27**, 237—249 (1978). —— CANNELL, M. G. R., THOMPSON, S., and LINES, R.: Heights of provenances of *Pinus contorta* in Britain correlated with seedlings phenology and the duration of bud development. Silvae Genetica **30**, 166—173 (1981). —— CARTER, K. K., ADAMS, G. W., GREENWOOD, M. S. and NITSCHKE, P.: Early family selection in jack pine. Can. J. For. Res. **20**, 285—291 (1990). —— CHASE, C. D.: Early genetic evaluation of slash pine. M. S. thesis. Univ. of Florida, Gainesville, FL. 113 pp., (1988). ——

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COTTERILL, P. P. and DEAN, C. A.: Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. Silvae Genet. 37, 138—146 (1988). —— DEWALD, L., WHITE, T. L. and DURYEA, M. L.: Growth, phenology and nutrition of four slash pine families grown at 10 different N levels. Tree Physiol., in press (1992). —— DICKERSON, G. E.: Implications of genetic-environmental interaction in animal breeding. Anim. Prod. 4, 47—64 (1962). —— FALCONER, D. S.: Introduction to Quantitative Genetics. Longman and Co., New York, NY. 340 pp., (1981). —— FOSTER, G. S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. For. Sci. 32, 944—959 (1986). —— FRANKLIN, E. C.: Model relating levels of genetic variance to stand development in four North American conifers. Silvae Genet. 28, 207—212 (1979). —— FRANKLIN, E. C. and SQUILLACE, A. E.: Short-term progeny tests and second generation breeding in slash pine. Can. J. For. Res. 3, 165—169 (1973). —— GILL, J. G. S.: Juvenile-mature correlations and trends in genetic variances in sitka spruce in Britain. Silvae Genet. 36, 189—194 (1987). —— GODDARD, R. E., ZOBEL, B. J. and HOLLIS, C. A.: Responses of Pinus taeda and Pinus elliottii to varied nutrition. In: Tree Physiology and Yield Improvement. Eds. M. G. R. CANNELL and F. T. LAST. Academic Press, New York, NY. pp. 449—462 (1976). —— HENDERSON, C. R.: Applications of Linear Models in Animal Breeding. University of Guelph, Guelph, Ontario, Canada. 462 pp. (1984). —— HODGE, G. R. and WHITE, T. L.: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. Silvae Genet. 41, 252—262 (1992). —— HOLADAY, A. S.: Genetic and fertilizer effects on apical growth of slash pine. M. S. thesis. Univ. of Florida, Gainesville, FL. 45 pp., (1973). —— INGESTAD, T.: Mineral nutrient requirements of Pinus silvestris and Picea abies seedlings. Physiol. Plant. 45, 373—380 (1979). —— JAHROMI, S. T., GODDARD, R. E. and SMITH, W. H.: Genotype X fertilizer interactions in slash pine: growth and nutrient relations. Forest Sci. 22, 211—219 (1976). —— KAYA, Z., CAMPBELL, R. K. and ADAMS, W. T.: Correlated response of height increment and components of increment in 2-year-old Douglas-fir. Can. J. For. Res. 19, 1124—1130 (1989). —— LAMBETH, C. C.: Juvenile-mature correlations in Pinaceae and implications for early selection. Forest Sci. 26, 571—580 (1980). —— LAMBETH, C. C.: Early testing: an overview with emphasis on loblolly pine. In: Proc. 17th South. For. Tree Improve. Conf. June 7—9, Athens, GA. pp. 297—311 (1983). —— LAMBETH, C. C., VAN BUIJTENEN, J. P., DUKE, S. D. and McCULLOUGH, R. B.: Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genet. 32, 210—215 (1983). —— LI, B.: Genetic variation among loblolly pine families in seedling growth, root and shoot morphology and nitrogen use efficiency, and use of these traits for potential early genetic selection. Ph. D. dissertation. North Carolina State Univ., Raleigh, NC. 131 pp., (1989). —— LI, B., McKEAND, S. E. and ALLEN, H. L.: Seedling shoot growth of loblolly pine families under two nitrogen levels as related to 12-year height. Can. J. For. Res. 21, 842—847 (1991). —— LI, B.,

WILLIAMS, C. G., CARLSON, W. C., HARRINGTON, C. A. and LAMBETH, C. C.: Gain efficiency in short-term testing: experimental results. Can. J. For. Res. 22, 290—297 (1992). —— LOWE, W. J. and VAN BUIJTENEN, J. P.: The incorporation of early testing procedures into an operational tree improvement program. Silvae Genet. 38, 243—250 (1989). —— MODE, C. J. and ROBINSON, H. F.: Pleiotropism and the genetic variance and covariance. Biometrics 15, 518—537 (1959). —— NAMKOONG, G.: Introduction to quantitative genetics in forestry. U. S. Dep. Agric., Tech. Bull. No. 1588, 342. pp., (1979). —— PRITCHETT, W. L. and COMERFORD, N. B.: Nutrition and fertilization of slash pine. In: The Managed Slash Pine Ecosystem. Ed: E. L. STONE. Univ. of Florida, Gainesville, FL. pp. 69—90 (1983). —— PRITCHETT, W. L. and GODDARD, R. E.: Differential responses of slash pine progeny lines to some cultural practices. Soil Sci. Soc. Amer. Proc. 31, 280—284 (1967). —— RIEMENSCHNEIDFR, D. E.: Heritability age-age correlations and inferences regarding juvenile selection in Jack pine. For. Sci. 34, 1076—1082 (1988). —— RITTERS, K. H. and PERRY, D. A.: Early genetic evaluation of open-pollinated Douglas-fir families. For. Sci. 33, 577—582 (1987). —— SAS Institute: SAS/STAT guide for personal computers. SAS Institute, Inc. Cary, NC. 378 pp. (1988). —— SMITH, C. K.: Genetic variation in juvenile slash pine shoot components and their relationship to mature field performance. M. S. thesis Univ. of Florida, Gainesville, FL. 66 pp. (1992). —— SQUILLACE, A. E. and GANSEL, C. R.: Juvenile — mature correlations in slash pine. Forest Sci. 20, 225—229 (1974). —— SURLES, S. E., WHITE, T. L., HODGE, G. R. and DURYEA, M. L.: Relationships among seed weight components, seedling growth traits and predicted field breeding values in slash pine. In review (1992). —— WAKELEY, P. C.: Relation of thirtieth-year to earlier dimensions of southern pines. For. Sci. 17, 200—209 (1971). —— WAXLER, M. S. and VAN BUIJTENEN, J. P.: Early genetic evaluation of loblolly pine. Can. J. For. Res. 11, 351—355 (1981). —— WHEELER, N.: Effect of continuous photoperiod on growth and development of lodgepole pine seedlings and grafts. Can. J. For. Res. 9, 276—283 (1979). —— WHITE, T. L., CHING, K. K. and WALTERS, J.: Effects of provenance, years and planting location on bud burst of Douglas-fir. Forest Sci. 25, 161—167 (1979). —— WHITE, T. L. and HODGE, G. R.: Best linear prediction of breeding values in a forest tree improvement program. Theor. Appl. Genet. 76, 719—727 (1988). —— WHITE, T. L. and HODGE, G. R.: Indirect prediction of genetic values. Silvae Genet. 40, 20—28 (1991). —— WHITE, T. L. and HODGE, G. R.: Test designs and selection ages for advanced-generation progeny tests of slash pine. Silvae Genet. 41, 293—302 (1992). —— WHITE, T. L., LAVENDER, D. P., CHING, K. K. and HINZ, P.: First-year height growth of southwestern Oregon Douglas-fir in three test environments. Silvae Genet. 30, 173—178 (1981). —— WILLIAMS, C. G.: The influence of shoot ontogeny on juvenile-mature correlations in loblolly pine. Forest Sci. 33, 411—422 (1987). —— YAMADA, Y.: Genotype by environment interaction and genetic correlation of the same trait under different environments. Jap. Jour. Genet. 37, 498—509 (1962).

Variation and Inheritance of Manoyl Oxid Acid in Pinus sylvestris (L.)

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Summary

The occurrence of manoyl oxid acid in clones and controlled crosses of Pinus sylvestris was investigated. The occurrence of manoyl oxid acid is under genetic control but there is not a simple Mendelian monogenic mechanism. It is suggested that manool is a precursor for manoyl oxid acid.

Key words: Pinaceae, Scots pine, genetics, biosynthesis.

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Introduction

In Scots pine needles pinifolic acid and its monomethyl ester are the dominating diterpenoids together with minor amounts of abietic, pimaric and 4-epiimbricatolic acids (ENZELL and THEANDER, 1962; TOBOLSKI and ZINKEL, 1982; ANDERSSON et al,. 1990). In some individual pine trees the diterpene alcohol isoabienol is the dominating compound while it is totally lacking in others (GREF, 1981). Manoyl oxid acid, the major resin acid of Pinus resinosa needles, has been found to be the principal resin acid of Pinus nigra and of Pinus sylvestris in central Europe (TOBOLSKI and ZINKEL, 1982; ZINKEL et al., 1985) but very seldom in Scots pine native to Scandinavia (ANDERSSON et al., 1990).