GENETIC IMPROVEMENT OF *PINUS VIRGINIANA* MILL. FOR CHRISTMAS TREE PRODUCTION

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ABSTRACT

Genetic variation in Virginia pine (*Pinus virginiana* Mill.) for growth and quality traits important for Christmas tree production was investigated using 120 first and second generation open-pollinated families. The species showed considerable genetic variation for quality traits from age 1 to age 4. Height, subjective quality scores and retail value (economic) were under strong genetic control at the family level. Retail value had the highest genetic correlations with quality score (0.44 to 0.94). Genetic gain for retail value of Virginia pine for Christmas tree production is unique, because the gains directly reflect the actual economic gains from selection. Selection of the top 15 families for seed production yielded 12.6%, or $US 1.60 gain over the checklots. Forward selection of the best 12 trees of the top 12 families yielded $US 2.70 (21.5%) gain over two checklot families. Growers using the five best families tested would increase their revenue by $US 2.40/tree or, $US 6,000.00/ha (at a 2 m × 2 m spacing), over currently used planting stock. There was a 51% difference between the first and second generation families for height at age 4. Gain per year from indirect selection at age 3 was almost as high as direct selection of retail value at age 4; 99% and 85% for family and within-family selections, respectively. If test maintenance and measurement costs were considered, indirect selection at age 3 would be more efficient than direct selection of retail value.

Key words: *Pinus virginiana*, tree improvement, genetic variation, genetic gain, genetic correlation, heritability, indirect selection, Christmas tree production

INTRODUCTION

Virginia pine (*Pinus virginiana* Mill.) is grown as a Christmas tree species throughout the Coastal Plain and Piedmont of the Southern United States. In this region, it is probably the most cultured Christmas tree species. A combination of attributes makes Virginia pine a worthy Christmas tree species. Due to its relatively rapid growth, Virginia pine Christmas trees of the most popular height class, ~2 m, can be harvested in 3 to 6 years. Virginia pine needles are relatively short (3.8–7.6 cm) reducing interference with hanging ornaments. This species' branches are relatively fine but strong enough to hold ornaments. It also responds readily to shearing producing a full dense crown and has a pleasant pine scent. Virginia pine grows well on a variety of sites and, at least for Christmas tree rotations can be readily grown in the Coastal Plain of the South, outside of its natural range.

Several negative characteristics of Virginia pine offset its beneficial ones for Christmas tree produc-tion. Naturally, Virginia pine stems are extremely crooked and the crown form is unkempt and scrubby. The species requires frequent (usually twice per growing season) shearings to produce the dense cone-shaped crown that the U.S. public demands for Christmas trees. Virginia pine is highly susceptible to Nantucket pine tip moth [(*Rhyacionia frustrana* (Comstock)] infestations. Controlling this pest is quite intensive and is best accomplished by trapping adult moths and tracking degree-days in order to time the required two to four pesticide applications each growing season (GARGUIULLO *et al.* 1983). While Virginia pine naturally has a dark green color, as is the general case with the southern pines, this color turns yellowish during the winter so that most Christmas tree growers apply colorant on their marketable trees. Due to the cumulative effects of these defects and the large amount of natural variation in the species, growers often only sell half or less of the Virginia pine trees that they grow as Christmas trees (FRAMPTON 2001).

Potentially, the use of genetically improved planting stock could ameliorate many of the problems associated with Virginia pine Christmas tree production. Past research has shown that traits which are related to Christmas tree quality and value such as height, stem straightness, density of foliage, crown symmetry, and branches per whorl are under genetic control (BAILEY et al. 1974; MEIER & GOGGANS 1977). Furthermore, the retail value of Virginia pine Christmas trees has been reported to be under strong genetic control (KNOTH et al., 2002). This study further investigates the inheritance of traits important for Christmas tree production in Virginia pine and estimates gains from the use of genetically improved planting stock. Efficiency of indirect selection of retail value of Christmas trees were explored for various correlated traits for family and within-family selection schemes.

MATERIALS AND METHODS

Plant Material
A total of 120 seedlots of Virginia pine were obtained from seed orchards or clone banks of six organizations (Bowater, Inc., Cokesbury Seed Orchard, Kimberly-Clark, N.C. Division of Forest Resources, Texas Forest Service and MeadWestvaco Corp.). Most seedlots were open-pollinated families collected from either first ($n = 56$) or second ($n = 60$) generation selections. These selections were from forestry tree improvement programs where rapid

stem growth and stem straightness were favored. Two checklots were bulked seed orchard collections from the N.C. Division of Forest Resources and had also been selected for growth and straightness. Five seedlots obtained from the Texas Forest Service were top families in a tree improvement program based upon Christmas tree quality. Two checklots were bulked from sets of five open-pollinated families from the privately owned Cokesbury Seed Orchard and had been selected for Christmas tree quality.

Seeds were placed into stratification in mid-March for two months, sown into Ray Leach Super Cells containing 164 cm^3 of medium (2 peat: 2 vermiculite: 1 perlite), and grown in a greenhouse in Raleigh, North Carolina. Seedlings were placed outdoors to harden-off in October of 1997.

Field Culture
Seedlings were hand planted into four field sites during November 1997 (Rocky Mount and Salisbury), December 1997 (Clinton) and January 1998 (Reidsville) (Fig. 1). Three sites, which were formerly farm fields, were tilled before planting while the fourth site (Salisbury) was largely pasture and was ripped prior to planting. Spacing was 1.8 × 3.0 m. All sites received pre-plant fertilization according to results from soil nutrient analyses. Subsequent fertilization at each site was based on nutrient analysis of foliar and soil samples and varied across sites and years.

Attempts were made to control Nantucket pine tip moth infestations at each site. During the first
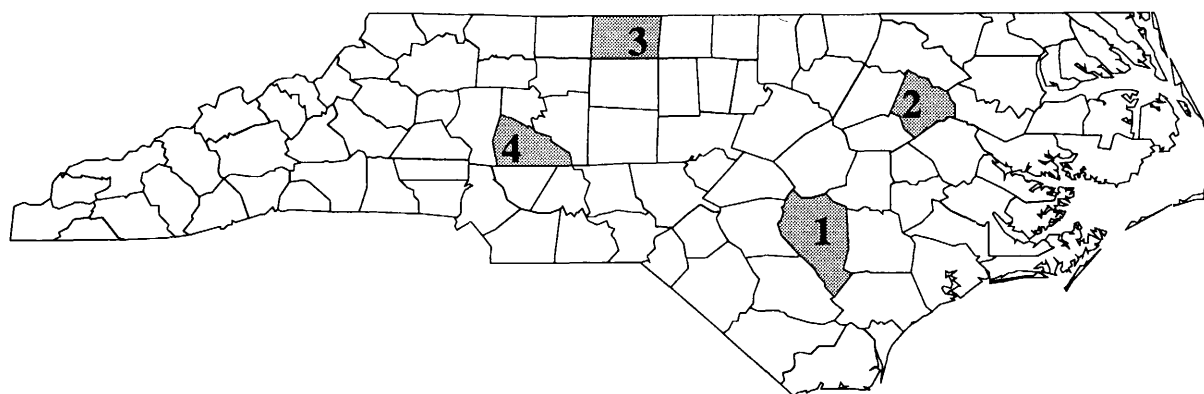
Site number	Physiographic region	Field Station	Town	County
1	Coastal Plain	Horticultural Crops Research Station	Clinton	Sampson County
2	Coastal Plain	Upper Coastal Plain Research Station	Rocky Mount	Edgecombe County
3	Piedmont	Upper Piedmont Research Station	Reidsville	Rockingham County
4	Piedmont	Piedmont Reseaerch Station	Salisbury	Rowna County

Figure 1. Location of Virginia pine progeny test established in North Carolina during the 1997–1998 planting season.

three growing seasons, timing of pesticide (mostly dimethoate) applications was mostly based on trapping adult moths and a heat sum model (GARGIULLO et al. 1983) except for year two at the Clinton site when biweekly applications were made during the spring and summer months. During the final growing season, pesticide applications followed optimal spray periods for the nearest location provided by FETTIG et al. (2000). The effectiveness of control efforts varied across sites and years.

Chemical sprays, mowing or a combination were employed to manage weeds. Weed management methods and effectiveness also varied across sites and years. A single contracted crew sheared the studies, in June, during the third growing season and during June and September during the fourth growing season.

Experimental Design

The experimental design at each site was a randomized block with single-tree plots. Seedlots were replicated at 35 blocks (except 32 at Reidsville). An additional "demonstration block" was planted at each site (except Reidsville) that contained five-tree row-plots of 84 selected seedlots. In seedlots with insufficient seedlings, seedlings were randomly assigned to sites and blocks/site. A total of 16,440 seedlings were planted across all four sites. However, 14,883 seedlings were used in the analyses with the number of seedlings/seedlot ranging from 7 to 69 (31 average).

Measurements

Total height to the nearest 0.5 cm was measured on the greenhouse tubelings prior to planting and to the nearest cm at the end of each growing season in the field. Growth cycles were counted and other traits were assessed on subjective scales as follows. Tip moth damage was assessed on the following infestation scale: 1 = all buds infested, 2 = high (over 2/3 of buds infested), 3= medium (1/3 to 2/3 of buds infested), 4 = low (less than 1/3 of buds infested) and 5 = no buds infested. Straightness was assessed on a 1 to 5 scale with 1 being excessively crooked and 5 being straight. Foliage color was assessed on the following scale: 1 = pale green or yellow, 2 = acceptable green and 3 = excellent green. Quality was assessed on the following scale: 1 = cull, 2 = average and 3 = excellent. All traits were measured annually, except that the effects of shearing made assessing the number of growth cycles and tip moth damage unfeasible for the fourth growing season. Retail value after the fourth growing season was determined as follows. First, three Christmas tree growers independently surveyed each test site and assigned a

retail value to each tree (U.S. Dollar). Unmarketable trees were given a value of $0.00. Then, the average of three retail values was taken as tree's retail value.

Statistical Analyses

Analyses of variance (ANOVA) for all traits were conducted based on individual-tree observations using the Mixed procedure of SAS (SAS Institute 1996) and the following linear mixed model:

$$Y_{ijkl} = \mu + S_i + R_{j(i)} + F_k + FS_{ik} + E_{ijkl} \qquad [1]$$

where, Y_{ijkl} is the lth observation of the jth replication within the ith site for the kth family; μ is the overall mean; S_i is the ith site ($i =1,...,4$); $R_{j(i)}$ is the jth block within the ith site ($j =1,...,36$); F_k is the general combining ability of the kth family, assuming normally and independently distributed (NID) (0, σ_F^2), ($f = 1,...,120$); FS_{ik} is kth family by ith site interaction ~NID (0, σ_{FS}^2) and E_{ijkl} is the error term ~NID (0, σ_E^2). The mixed model can be written in a matrix notation:

$$y = X\beta + Z\gamma + e \qquad [2]$$

where, y is the $n \times 1$ vector of observations, β is the $p \times 1$ vector of fixed effects that includes the intercept, sites and replications within sites, γ is the $q \times 1$ vector of random effects family and family by site interaction, e is $nx1$ the vector of random residuals. X and Z are design matrices that relate elements of β, γ and e to y. It was assumed that the expected values of fixed effects are $E(y) = X\beta$, and the expected values of random effects are $E(\gamma) = E(e) = 0$. The covariance matrix of observations is $Var(y) = ZGZ^T +R$ (LITTLE et al. 1996). The first term accounts for the additive genetic effects, while the second term accounts for random residual effects. Since the residual errors have a constant variance and are uncorrelated, the error variance matrix is a diagonal matrix ($R=I\sigma_e^2$) with the residual errors variances (σ_E^2) in the diagonal and 0 values in the off diagonals.

Sites were significantly different for height growth, so that to remove scale effects, height was standardized by dividing observations with the respective site's standard deviation before conducting ANOVA. Except retail value, all other categorical traits were transformed by adding 0.5 to the assessed value and taking the square root of the resulting sum prior to ANOVA.

Since breeding values have more desired properties over heritability based gain estimations when data are unbalanced (XIANG & LI 2001, HUBER 1993), the family and individual-tree breeding values

were used to calculate genetic gains for various selection scenarios. Absolute breeding values of families were calculated using the Best Linear Unbiased Predictors ($Z\gamma$) of families, population standard deviation (σ_p) and the standardized overall mean of the trait (μ) across sites:

$$BVf = \sigma_p 2(Z_p \hat{\gamma} Z_p^T) + X\mu \qquad [3]$$

where, *BVf* is the vector of absolute breeding values of half-sib families, Z_p is the design matrix of half-sib families.

Individual-tree breeding values were predicted by solving the mixed-model equations obtained from the SAS Mixed procedure. Individual-tree breeding values are BLUPs and calculated as the difference between observed values (**y**) and predicted values ($X\beta$-$Z\gamma$) of individual observations as shown in the following formula (XIANG & LI 2003).

$$\hat{A} = C^T V^{-1} (y - X\hat{\beta} - Z\hat{\gamma})$$

$$= \left(\frac{\sigma_{GCA}^2}{\sigma_E^2} Z_p Z_P^T + 3 \frac{\sigma_{GCA}^2}{\sigma_E^2} I \right) (y - X\hat{\beta} - Z\hat{\gamma}) \qquad [4]$$

Where $\hat{A}$ is the vector of predicted individual-tree breeding values, C^T is the transposed covariance matrix of the **y** vector and the genetic effects, V^{-1} is the inverse variance matrix of **y** vector, Z_p is the design matrix of half-sib families, **I** is the identity matrix of individual-trees. In estimation of individual-tree breeding values, relationship in the data were taken into account using pedigree information and performing analyses with the ASReml software (GILMOUR *et al.* 2002).

The seedlots (half-sib families) in the experiment were not truly half-sibs but there was a loose relationship between genotypes, e.g., some second generation parents had common ancestors from the first generation parents and common grandparents with the first generation parents. In order to accommodate complex relationships in the data, a relationship matrix **A** was created using pedigree information and implementing analysis using the ASReml software (GILMOUR *et al.* 2002). We did not find significant differences in variance component estimates using the **A** matrix or not using it. Thus, the covariance between half-sibs was assumed 1/4 of additive genetic variance σ_A^2. Similarly, assuming zero dominance variance, within half-sib family genetic variance is $\sigma_{Aw}^2 = \sigma_A^2 - \sigma_F^2 = 3\sigma_{GCA}^2$ (FALCONER & MACKAY 1996). Using causal variances from the mixed model, narrow-sense heritabilities were estimated for mass selection (individual-tree), and

for indirect index selection (combined family and within-family) between different ages and traits.

$$h_i^2 = \frac{\sigma_A^2}{\sigma_F^2 + \sigma_{FS}^2 + \sigma_E^2} \qquad [5]$$

$$h_f^2 = \frac{\frac{1}{4}\sigma_A^2}{\sigma_F^2 + \frac{\sigma_{FS}^2}{s} + \frac{\sigma_E^2}{sb}} \qquad [6]$$

$$h_w^2 = \frac{\frac{3}{4}\sigma_A^2}{\frac{s-1}{s}\sigma_{FS}^2 + \frac{sb-1}{sb}\sigma_E^2} \qquad [7]$$

where, h_i^2 is individual-tree heritability, h_f^2 is half-sib family mean heritability, h_w^2 is within-family heritability, σ_A^2 is additive genetic variance ($\sigma_A^2 = 4\sigma_F^2$), σ_F^2 is half-sib family variance, σ_{FS}^2 is genotype-environment interaction variance, σ_E^2 is within-family (residual) variance, *s* is number of sites ($s = 4$), *b* is number of blocks within each site ($b = 36$). Standard errors of heritabilities were estimated using the Delta method (LYNCH & WALSH 1998).

Additive genetic (r_A) and product-moment phenotypic (r_P) correlations were estimated between pairs of traits. Additive genetic correlations between pair of traits were estimated by fitting a multivariate model using the ASReml software (GILMOUR *et al.* 2002). To explore indirect selection efficiencies between age 4 retail value and younger height and quality assessments, age-age genetic correlations were estimated between height and retail value, and between quality and retail value. Interclass correlations (type B genetic correlation) among the pair sites were estimated for retail value (LYNCH & WALSH 1998).

$$r_B = \frac{\sigma_F^2 + [(2 - N_E)/N_E]\sigma_F^2}{\sigma_F^2 + \sigma_{FS}^2} \qquad [8]$$

where N_E is number of environments. When there are two environments, the equation reduces to $r_B = \sigma_F^2/(\sigma_F^2 + \sigma_{FS}^2)$. The r_B is interpreted as an interclass correlation of genotypic value in different environments and indicates the significance of genotype-environment interaction.

Selection efficiencies (gain per year) were estimated by comparing indirect selections of height and the quality traits at earlier ages with direct selection on retail value at age 4. Genetic gain per year (SE$_{GPY}$) from the correlated response (CR) was calculated as the ratio of genetic gain over *j*+*t* years, where *j* is early age measurements ($j \le l$, j=1,...4), *t* is

number of years required to produce seed after selection (t = 6) (XIANG et al. 2003). Similarly, genetic gain per year from direct selection of retail value was calculated as the ratio of the direct response (R) over the $l+t$ years, where l is the selection age (l = 4). The CR/R ratio gives the efficiency of indirect selection over the direct selection:

$$ SE_{GPY} = \frac{\frac{1}{j+t}CR}{\frac{1}{j+t}R} = \frac{i_j h_j h_l r_{A(jl)} \sigma_{Pl}/(j+t)}{i_l h^2 \sigma_{Pl}/(1+t)} \quad [9] $$

Assuming the same selection intensities for direct and indirect selections ($i_j = i_l$), the efficiency of indirect selection becomes,

$$ SE_{GPY} = \frac{(l+t)r_{jl}h_j}{(j+t)h_l} \quad [10] $$

In equation [9], $h_j h_l r_{A(il)}$ is called coheritability between two correlated traits (Falconer and Mackay 1996). This genetic parameter is a good indicator in predicting efficiency of indirect selection of a desired trait. The higher the coheritability, the higher genetic gain in late-trait l from selection on early-age trait j. Coheritabilities (h_{jl}^2) between height-retail value and quality-retail values were estimated using the following equation.

$$ h_{jl}^2 = r_{A(ij)}h_j h_l = \frac{Cov_{A(ij)}}{\sqrt{\sigma_j^2}\sqrt{\sigma_i^2}}\sqrt{\frac{\sigma_j^2}{\sigma_{pj}^2}}\sqrt{\frac{\sigma_l^2}{\sigma_{pl}^2}} = \frac{Cov_{A(ij)}}{\sqrt{\sigma_{pj}^2}\sqrt{\sigma_{pl}^2}} \quad [11] $$

where $Cov_{jA(il)}$ is genetic covariance between traits j and l, σ_{pj}^2 and σ_{pl}^2 are phenotypic variances of two traits.

RESULTS AND DISCUSSION

ANOVA Results

Effects tested in the ANOVAs were statistically significant ($P \leq 0.05$) for almost all traits and ages. Exceptions were 'family' effects for quality at age 1 (P =0.0673), and 'site × family' interaction effects for tip moth infestation at ages 2 (P =0.0953) and 3 (P =0.2147), color at age 3 (P =0.9465), and straightness at age 4 (P =0.3738).

Age and Site Trends

Height increased from a pre-plant mean of 0.22 m to 1.78 m after four growing seasons in the field (Fig. 2a). The Reidsville site had the shortest growing season as well as a heavy clay soil and so, showed

considerably slower growth than the other three sites.. Annual tip moth infestation ratings averaged 3.80 to 4.34 on the five-point scale although no age or site trends were apparent. Annual color ratings averaged 1.89–1.98 on the three-point scale. Ages 3 and 4 were slightly higher (greener) than ages 1 and 2 as was the Reidsville site relative to the other three sites. Straightness appeared to decrease with age of the study from 4.14 (age 1) to 2.91 (age 4) on the five-point scale. The number of growth cycles increased from 1.9 during year 1 to 3.41 during year 2 then decreased to 2.78 in year 3. This decrease was at least partially due to shearing. The quality rating for years 1 and 2 was slightly less than for years 3 and 4 and Reidsville tended to have slightly better quality trees than the other three sites. Overall retail value was $11.33 at age 4. This average value includes cull trees ($0/tree) and so, is less than the average that growers realize for marketable trees. Mean retail value at the Clinton site was $16.60, over three times that at the Reidsville site, $5.62 (Fig. 2b). The Rocky Mount and Salisbury sites were intermediate in retail value.

Although 'site × family' interactions were significant for most traits, type B genetic correlations between pairs of sites were relatively high for retail value, ranging from 0.64 to 0.93. SHELBOURNE (1972) suggested that separate selection and breeding programs are not justified when type B correlations exceed 0.67. Only two of the six possible correlations between pairs of sites were less than this value, but not by much; Clinton-Reidsville (0.64) and Clinton-Salisbury (0.65). Additionally, from a practical perspective, development of separate Virginia pine Christmas tree genetic improvement programs for various sites is not economically or logistically feasible. Thus, the following discussion focuses on selection and breeding for performance across the four test sites which represent the general Christmas tree production area at least in North Carolina, if not across the entire Southeast.

Heritabilities

Annual estimates of individual-tree heritabilities are presented in Fig. 3 while annual family and within-family heritability estimates for height quality and retail value are presented in Fig. 4a. Generally, individual-tree heritabilities were low to moderate while family mean heritabilities (not all shown) were moderate to high. For height, individual-tree heritability dropped from 0.44 after the first year in the field but then remained relatively constant (0.28–0.30) while the height family mean heritability remained constant throughout the rotation (0.84 –0.87). Tip moth code, straightness and number of
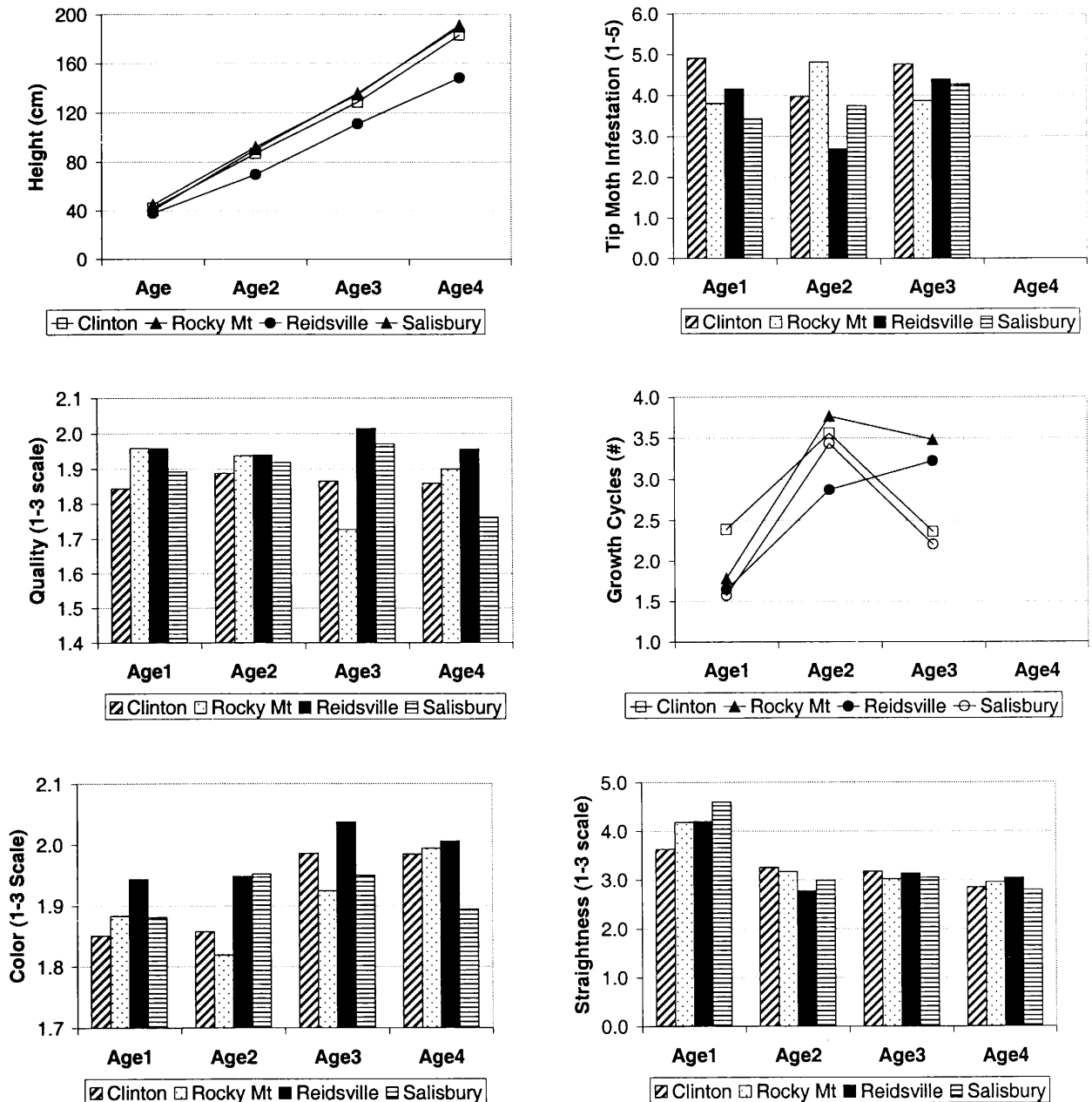
Figure 2a. Site means of variaous Cristmas tree characteristics for a Virginia pine progeny test series established in North Carolina during the 1997–1998 planting season.

growth cycles did not display pronounced chrono-logical changes in heritabilities. However, herita-bilities for color increased from age one to three then decreased at age four. The decrease in heritability at age four was likely a result of assessing traits about three months earlier than in previous years before true winter-dormant color had had a chance to develop. Individual-tree heritabilities for quality steadily increased over the rotation (from 0.01 to 0.13) as did quality family mean heritabilities (0.20

to 0.71). Retail value at age four had both the highest individual-tree (0.17) and family mean heritability (0.77) of all traits assessed except height. These retail value heritability estimates are congru-ent with those reported earlier from a three-site test series of 20 open-pollinated families in South Caroli na; 0.21 and 0.68 for individual-tree and family heritability, respectively (KNOTH *et al.* 2002).

Standard errors of heritability estimates were generally low and ranged from 0.02 to 0.15 for
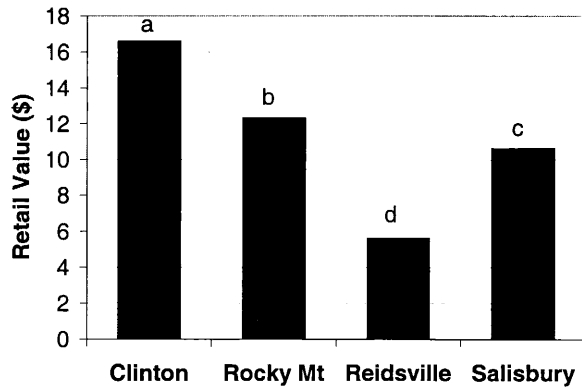
Figure 2b. Site means for retail value 9USD0 of Virginia pine Christmas trees at age č. Test sites with a different letter on bar are significantly different from each other.

individual-tree and within-family estimates and from 0.01 to 0.06 for family mean estimates. Low standard errors of heritabilities from this study suggest that these estimates are reliable. This was expected since 120 families, each with an average of 31 seedlings, were tested per site. Additionally, replication of families over four sites, and the use of a single-tree plot field design contributed to the small standard error estimates.

Family and within-family coheritabilities of height-retail value and quality-retail value are presented in Fig. 4b. Coheritability is an important genetic parameter for correlated response of a desired trait or indirect selection to make sound decisions in early selections (FALCONER & MACKAY 1996). Coheritabilities for height and quality with retail value were similar at ages 1 and 2. However, family coheritability of quality-retail value was almost two times greater than the height-retail value coheritability at age 3. There were no marked differences between within-family coheritabilities involving these two traits at any age. In general, coheritability estimates increased with age. These results suggest that, indirect selection for retail value from quality assessments at age 3 can be as efficient as direct selection of retail value at age 4.

Relationships Among Traits

The phenotypic correlation between nursery height and retail value at age 4 was 0.21. The relationship between height and retail value increased to 0.62 by age 4 (Fig. 5). Additive genetic correlations between height and retail value at age 4 were slightly lower than phenotypic correlations. However, the genetic and phenotypic time trends were similar. The genetic correlation between height and retail value at age four began at 0.06 in the nursery and increased to 0.56 at age 4.
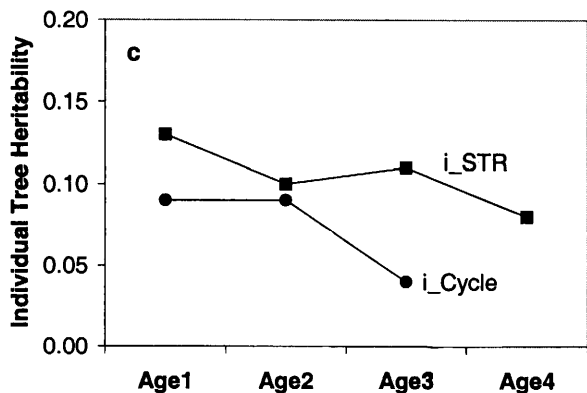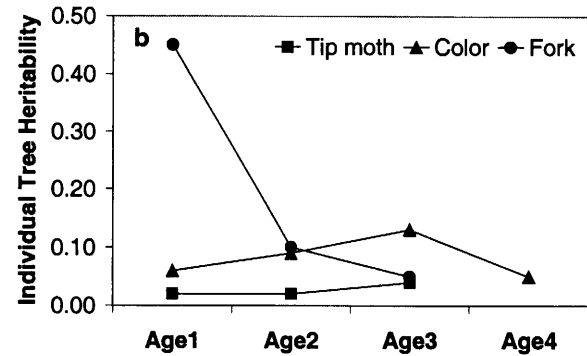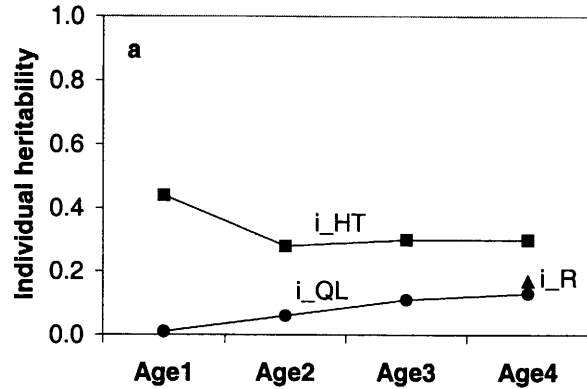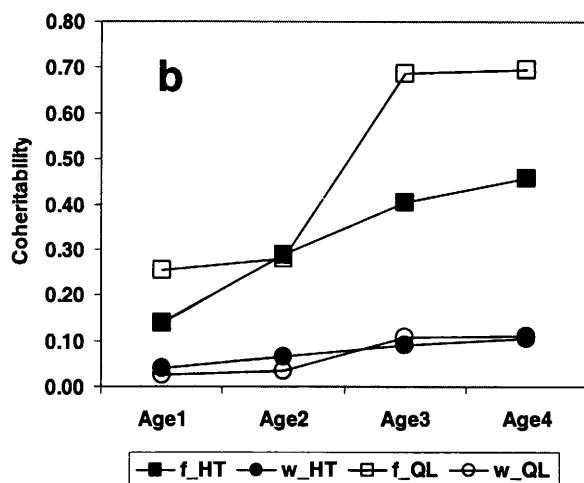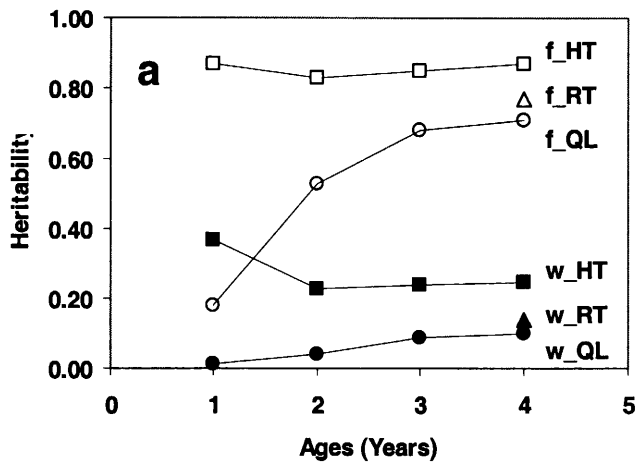

Figure 3. Time trends in narrow/sense individual-tree heritabilities for Christmas tree traits of Virginia pine. I_HT is height, i_QL is quality scores, i_R is retail value, i_STR is stem straightness and i_Cycle is growth cysles.

Genetic correlations between quality scores at various ages and retail value at age 4 were generally high (>0.68), except for quality at age 2 (Figure 5). The genetic relationship between two traits increased to over 0.93 at ages 3 and 4. The sharp drop in the genetic correlation coefficient between quality scores and retail value at age 2 was likely due to Hurricane Floyd which severely impacted the Coastal Plain
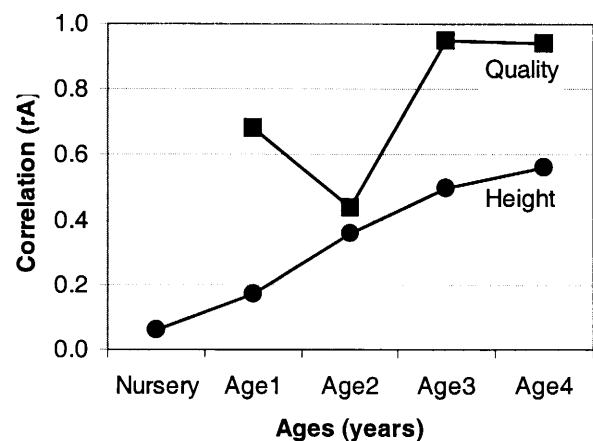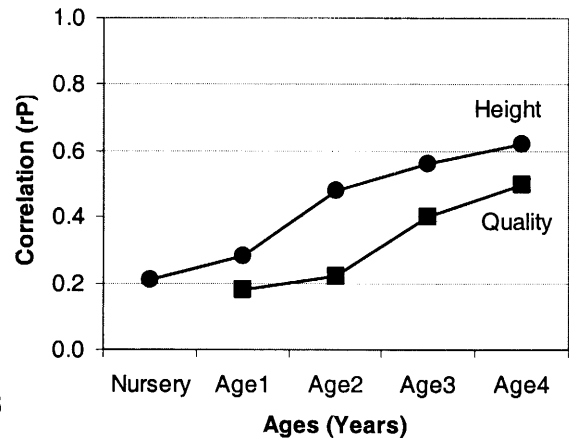
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Figure 5. Phenotypic (r_p) and additive genetic (r_A) correlations for height (circles) and subjective quality scores (squares) with Christmas tree retail value in Virginia pine.

Figure 4. Time trends of family/mean heritability, within /family heritability and coheritability of three economically most important traits of Virginia pine for Christmas tree production. (a) Half/sib family mean (f_) and within family (w_) heritabilities for height (HT), quality (QL) and retial value (RT) at different ages. (b) Coheritabilities between height and retail value (filled squares and circles) and quality-retial value (empty squares and circles) at different ages. F_ is family coheritability, w_ is within family heritability.

sites during mid-September 1999. Sustained heavy rains and steady strong winds bent the trees considerably damaging their crowns. In contrast to high genetic correlations, quality scores had weak to moderate phenotypic correlations with retail value. Phenotypic correlations with retail value at age 4 were 0.18 for quality at age 1 and increased to 0.50 for quality at age 4

Genetic Gains

Genetic gains for various backward family selection options for retail value and height, and a forward

selection option for retail value are presented in Table 1. On average, the best five parents had 20 % (35 cm) greater height than the two checklots at age 4. As the selection intensity decreased, gain for height decreased accordingly. For example, selection of the top 15 families yielded 16 % (29 cm) greater gain over the checklots. The checklots had an average height breeding value (176 cm), close to the overall mean breeding value (178 cm) so that genetic gains relative to the overall mean and checklots were similar. The performance of the bulked seedlots from the Cokesbury Seed Orchard was also evaluated. These seedlots averaged 185 cm in height at age 4. Selection of the Cokesbury seedlots gave 5 % (9 cm), and 4 % (7cm) gains, over the checklots and overall mean, respectively.

Genetic gain for retail value of Virginia pine for Christmas tree production is unique, because the gains directly reflect the actual economic gains from selection. Selection of the top 15 families for seed

production yielded 12.6 %, or $US 1.60 gain over the checklots (Table 1). When the top 5 families were selected, gain over the checklots increased to 18.7 %, or $US 2.40. Economic gains from selection of top families over the overall mean were even greater. The top 5 and 15 families had 34.8 % ($US 3.94) and 28.0 % ($US 3.20), respectively, greater economic values relative to the overall mean.

Success of past selection efforts are evident in these data. There was a 51% difference between the first and second generation families for best linear unbiased predicted height; 118 and 179 cm, respectively. The parents of these families had previously been selected for height growth and stem form in forest tree improvement programs. However, the difference between the first ($US 11.13) and second generation average predicted retail values ($US 11.20) were negligible (about 1%). Many trees of the fastest growing families had large gaps in their crowns reducing their desirability as Christmas trees. These results reflect 1) the lack of selection for Christmas tree quality traits such as crown density and uniformity, 2) the influence of shearing and, 3) the modest genetic correlation between height and retail value (r_A=0.56).

Two bulked seedlots from the Cokesbury seed orchard had specifically been selected for Christmas tree quality and these seedlots were among the best for retail value. These seedlots were ranked third and eighth among the 120 seedlots tested and, on average, $US 1.79 (13.9 %) and $US 3.32 (29.4 %) greater value than the checklots and overall mean, respectively.

Five families tested were chosen from a Texas Forest Service program to improve Christmas tree quality. The overall best family for retail value ($14.73) of the 120 families, TX 1-4, belonged to this group. The retail value ranking of the other four families from this group was variable and less impressive: 12th, 20th, 57th and 114th. The poorer performance of some of these families is unclear, but may be due to differences between regions, specific sites, cultural practices, grower preferences, etc.

The best 12 progeny from the top 12 families had an average $US 15.00 individual-tree breeding value (Table 1). Selection of the top 12 families and the best trees within-families for a forward selection of a seed orchard yielded $US 2.70 gain or 21.5 % over the two checklot families. Selected trees had $US 3.80 (34.1%) gain over the overall mean.

Correlated Response

While direct selection for retail value at age 4 ap-

Table 1 Genetic gain estimates for height and retail value of Virginia pine Christmas trees resulting from various selection schemes.

| Seedlots	Breeding value	Genetic gain			
		Versus checks		Versus overall mean	
		%	value	%	value
		Height (cm)			
Best 5	211	20	35	19	33
Best 10	208	18	31	17	30
Best 15	205	16	29	15	27
Cokesbury Seed Orchard	185	5	9	4	7
Checklots	*176*	–	*0.0*	*–1.0*	*–1.8*
Overall mean	**178**	**1.0**	**1.8**	–	**0**
		Retail value ($)			
Best 5	15.3	18.7	2.4	34.8	3.9
Best 10	14.8	15.2	2.0	30.8	3.5
Best 15	14.5	12.6	1.6	27.8	3.2
Cokesbury Seed Orchard	14.7	13.9	1.8	29.4	3.3
Checklots	*12.9*	–	–	*13.5*	*1.5*
Forward selection (12 best trees)	15.0	21.5	2.7	34.1	3.8
Overall mean	**11.3**	**–11.9**	**–1.5**	–	–
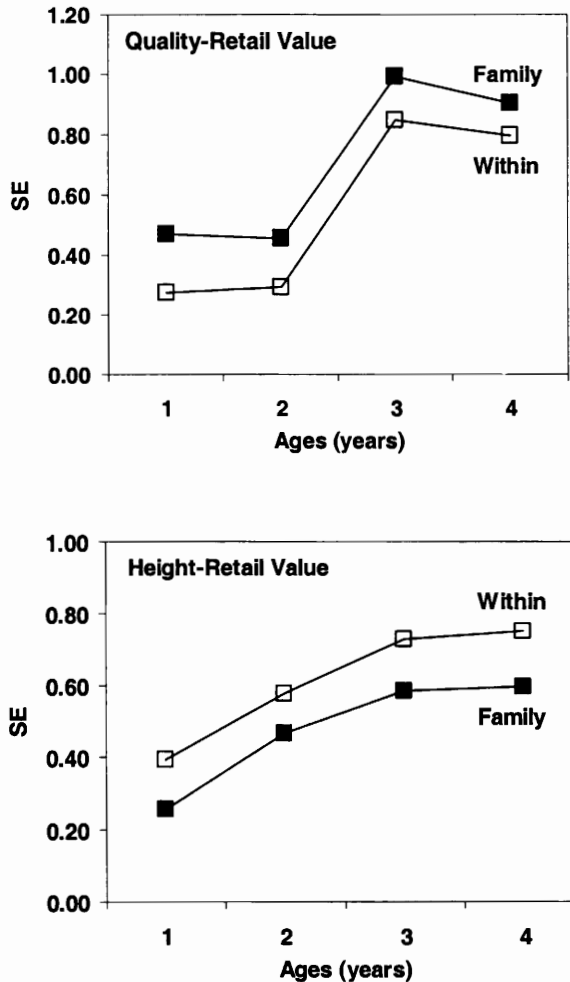
Figure 6. Selection efficiency for retail value when selection applied on quality or height at different ages for family and within family selections.

pears very effective, the efficiency of indirect selection of retail value based on height and quality at earlier ages was calculated to appraise further improvement of gain per year (Figure 6). When quality was used as the secondary trait, the optimal selection age for retail value was age 3. Gain per year from indirect selection at age 3 was as high as direct selection of retail value at age 4; 99 % and 85 % for family and within-family selections, respectively. If test maintenance and measurement costs were considered, indirect selection at age 3 would be more efficient than direct selection of retail value. Indirect selections for retail value at ages 1 and 2 were not as efficient as at age 3; less than 50 and 30% for family and within-family selection, respectively. Low selection efficiency at age 2 was mainly due to a weak genetic correlation between quality scores and retail value (Figure 5).

Indirect selection efficiencies of retail value from height measurements increased with age, both for family and within-family selection (Figure 6). At age 3, the indirect selection efficiency of family and within-family were 0.60 and 0.75, respectively. In contrast to indirect selection from quality, within-family indirect selection from height was more efficient than family selection. This was mainly due to greater within-family heritabilities for height (0.23 = 0.37) compared to retail value within-family heritability (0.14). The results suggested that subjective quality scores at age 3 could be used for family selection coupled with age 3 height measurements for within family selection. The unexpected drop in genetic correlation between quality and retail value argues against further reduction of the selection age for Virginia pine. However, since the age 2 genetic correlations between quality and retail values were adversely affected by a hurricane, future investigations may demonstrate acceptable efficiency with indirect selection at age 2.

CONCLUSION

Results from this study as well as a similar, but smaller, South Carolina study (KNOTH *et al.* 2002) indicate that the retail value of Virginia pine for Christmas tree usage is under strong genetic control. Growers using the five best families tested would increase their revenue by $US 2.40/tree or, $US 6,000.00/ha (at a 2 m × 2 m spacing), over currently used planting stock. Retail value should continue to increase with further tree improvement efforts. While direct selection on retail value at age 4 is productive, faster gains can be made by indirect selection of quality and height growth at age 3. Plans are underway to assortively mate the elite selections from these tests. Virginia pine's early and precocious coning ability will accelerate such efforts. Results from this study indicated that these efforts should further enhance the economic return from Virginia pine Christmas tree production in the southern United States.

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