

**Stand dynamics, growth, and yield of genetically  
enhanced loblolly pine (*Pinus taeda* L.)**

by

Charles Obuya Sabatia

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Harold E. Burkhart, Chair

Thomas R. Fox

Philip J. Radtke

Marion R. Reynolds, Jr.

Shepard M. Zedaker

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diameter distribution, intraspecific competition, genetic uniformity

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### ABSTRACT

Genetic improvement has been an integral part of loblolly pine plantation forestry in southern United States for about 60 years with focus on improving timber yield, wood quality, and pest and disease resistance. Advances in techniques of genetic selection, breeding, and propagation of planting material have made it possible to achieve genetic gains that are likely to result in significant changes in loblolly pine stand dynamics. Height-age relationships, height and diameter relationships and distributions, and intraspecific competition were investigated in second generation open-pollinated, controlled-pollinated, and clonal loblolly pine with an objective of characterizing the nature and magnitude of changes in these characteristics due to genetic improvement and clonal forestry. Genetic improvement and/or clonal forestry had no practical effect on parameters of the height-age and height-diameter relationships beyond the effect on the asymptote parameter of the Chapman-Richards and Korf equations that were used to model these relationships. Genetic improvement resulted in an increase in the mean of height distribution without a corresponding increase in the mean of the diameter distribution, but had no effect the variance and skewness of the distributions. Thus, growth and yield models in which basal area is a function of height at a specific age (site index) are likely to over predict genetic gains in basal area growth and volume yield. Increase in stand density resulted in an increase in variance of the diameter distribution of non-clonal stands but had no effect on the variance of the diameter distribution of clonal stands. Thus, diameter distribution of clonal stands may differ from that of non-clonal stands after crown closure despite the distributions not being different before and during early stages of crown closure.

This study also evaluated methods that may be used to predict height growth of new genetic varieties and those that may be used to assess intraspecific competition in forest stands. Mixed-model approach of calibrating a height-age relationship to a new loblolly pine clone gave biased estimates for clones that were at the extremes of the distribution of the groups. The use of maximum likelihood with simulated annealing (MLSA) to evaluate competitive interactions among trees in loblolly pine stands gave non-unique estimates of optimum competitor selection radius. A simpler technique that uses Pearson correlations was proposed and was found to work better than MLSA.

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yield modeling studies. The help of Clara Anton-Fernandez with R programming language is invaluable. It would have been more difficult for me to do meaningful data analysis without her help. Her help with data collection together with the assistance of fellow graduate students Nabin Gyawali, Ram Thapa, and Juwon Shin contributed a great deal to the timely completion of the research work reported in this dissertation. The contribution of other past and present forest biometrics graduate students Kevin Packard, Mathew Russell, Micky Allen, and Gavin Corral to my overall professional experience while at Virginia Tech is acknowledged.

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## **Preface**

This dissertation is organized under what is referred to as the manuscript format. The individual manuscripts make up Chapters 3, 4, and 5. Dr. Burkhart and I plan to submit these manuscripts for publication to Forest Science, Canadian Journal of Forest Research, and/or Forest Ecology and Management journals. The manuscripts will be revised and “tightened” before submission.

# Chapter 1

## Introduction and objectives

### 1.1. Introduction

Loblolly pine (*Pinus taeda* L.) plantations form a significant proportion of forest land in the southern United States. In the early 2000's there were over 30 million acres of pine plantations in southern United States composed mainly of loblolly pine, with projections that the acreage would increase to 55 million acres by 2040. Southern forests produced 58% of United States and 15.8% of world's timber with the world's proportion projected to increase by about 30% by 2040 (Wear and Greis 2002). Loblolly pine makes up about 80% of the approximately 2 million acres of forest plantations planted annually in southern United States (McKeand et al. 2003)

Genetic improvement programs for loblolly pine are continuously changing the varieties of loblolly pine planted in southern United States hence changing the dynamics of loblolly pine stands. The improvement programs, started in the early 1950's, have mainly focused on improving growth, disease and pest resistance, wood quality, and tree form (Zobel and Talbert 1984). The programs have progressed through three cycles of breeding and selection. In the early 2000's, first generation seed orchards supplied 46% of seed for loblolly pine plantation establishment with the rest coming from second generation seed orchards and none from third generation orchards (McKeand et al. 2003). Currently, third generation orchards supply about 12% of the seed with about 77% coming from second generation orchards (Virginia Department of Forestry 2009). Plantations established with first generation seed orchard seeds produce 7 –

12% more volume and those established with seed from second generation orchards are expected to produce 13 – 21% more volume than those established with genetically unimproved seeds (Li et al. 1999). Fusiform rust (caused by *Cronartium quercuum* (Berk) Miyabe ex Shirai f. sp. *fusiforme*) incidence is expected to be 20 – 25% lower in second generation improved plantations than in the genetically unimproved plantations. Third, fourth, and so on breeding cycles are expected to bring about further improvements in volume growth and the other traits and possibly further changes in loblolly pine stand dynamics.

Most planting material has been propagated from seed as open-pollinated (OP) half-sibling (half-sib) varieties but in the last 10 years controlled pollination (CP) and clonal propagation techniques are gaining ground. About 100 million full-sibling (full-sib) CP seedlings and 10 million somatic embryogenesis clones have been planted in the last ten years (McKeand et al. 2007). According to genetic theory, full-sib CP seedlings have a much higher level of genetic uniformity than OP half-sib seedlings with clones representing the highest level of within stand genetic uniformity (White et al. 2007, p. 439 – 477). The recent developments in propagation methods are bound to bring about more within stand genetic uniformity that could significantly affect loblolly pine stand dynamics. In addition, advanced selection and breeding techniques such as marker-assisted selection, marker-assisted breeding, and genetic engineering are currently being used (White et al. 2007, p. 553 – 591). These are likely to result in greater genetic gains that may result in even more drastic changes in loblolly pine stand dynamics.

Forest growth and yield simulators are used to support decision making in the management of loblolly pine plantations in southern United States. Some of the commonly available ones include the individual tree distance-dependent simulator PTAEDA4.0 (Burkhart et al. 2008) and the whole stand diameter distribution simulator FASTLOB (Amateis et al. 2001)

developed by the Forest Modeling Research Cooperative at Virginia Tech. The Plantation Management Research Cooperative at The University of Georgia has also developed a number of loblolly pine growth and yield simulators. These simulators are made up of systems of growth and yield equations that were developed using data from genetically unimproved and first generation OP genetically improved stands. Over time, the simulators have been enhanced with adjustment mechanisms that enable them to accurately predict growth and yield under different intensities and combinations of silvicultural treatments including site preparation, fertilization, thinning, pruning, and control of competing vegetation. Differences in genetic potential among different loblolly pine genetic varieties are accounted for through site index adjustment (Li et al. 1999; McKeand et al. 2006; Newton 2003; Talbert et al. 1985). This has probably worked well for stands from provenance and first generation OP planting material where genetic improvement has been assumed to affect height growth and diameter growth in similar proportions with no significant effect on other aspects of stand development (Buford and Burkhart 1985, 1987). However, there is need to review this approach given the higher genetic gains associated with CP and clonal planting material, and the potential for reduced of genetic variability among trees in monoclonal stands. There is also a possibility of genetic improvement gains in diameter growth not being proportional to the gains in height growth as has been observed in radiata pine (*Pinus radiata* D. Don) (Carson et al. 1999).

## **1.2. Objectives**

The goal of this dissertation was to improve the accuracy of currently available loblolly pine growth and yield models in predicting growth and yield in loblolly pine stands of enhanced

genetic material. Specifically, the dissertation investigated the effect of genetic improvement, through tree breeding and cloning, on aspects of stand dynamics that are commonly used to model growth and yield in loblolly pine stands. The specific aspects of stand dynamics investigated were:

- 1) Height-age relationships (Chapter 3)
- 2) Height-dbh relationships (Chapter 4)
- 3) Height and dbh distributions (Chapter 4)
- 4) Competition among trees in a stand (Chapter 5)

The objectives of the investigations were to characterize the nature and magnitude of the changes in these stand relationships hence providing information to be used in adapting currently available loblolly pine growth and yield models to genetically enhanced loblolly pine planting stock.

### 1.3. Literature cited

Amateis, R.L., H.E. Burkhart, H.L. Allen, and C. Montes. 2001. FASTLOB (A stand-level growth and yield model for fertilized and thinned loblolly pine plantations). Department of Forestry, Virginia Tech, Blacksburg, VA.

Buford, M.A., and H.E. Burkhart. 1985. Dynamics of improved loblolly pine plantations and the implications for modeling growth of improved stands. P. 170 - 177 *in* Proceedings of the 18th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Long Beach, MS.

Buford, M.A., and H.E. Burkhart. 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci.* 33:707 - 724.

Burkhart, H.E., R.L. Amateis, J.A. Westfall, and R.F. Daniels. 2008. PTAEDA4.0: Simulation of Individual Tree Growth, Stand Development, and Economic Evaluation in Loblolly Pine Plantations. Department of Forestry, Virginia Tech, Blacksburg, VA.

Carson, S.D., O. Garcia, and J.D. Hayes. 1999. Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *For. Sci.* 45:186 - 200.

Li, B., S.E. McKeand, and R.J. Weir. 1999. Tree Improvement and sustainable forestry-Impact of two cycles of loblolly pine breeding in the USA. *For. Genet.* 6:229 - 234.

McKeand, S.E., R.C. Abt, H.L. Allen, B. Li, and G.P. Catts. 2006. What are the best loblolly pine genotypes worth to land owners? *J. For.* 104:352 - 358.

McKeand, S.E., T.J. Mullin, T.D. Byram, and T.L. White. 2003. Deployment of genetically improved loblolly and slash pines in the south. *J. For.* 101:32 - 37.

McKeand, S.E., B.J. Zobel, T.D. Byram, and D.A. Huber. 2007. Southern pine tree improvement-A living success story. P. 3 - 5 *in* Proceedings of the 29th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Galveston, TX.

Newton, P.F. 2003. Systematic review of yield responses of four North American conifers to forest tree improvement practices. *For. Ecol. Manage.* 172:29-51.

Talbert, J.T., R.J. Weir, and R.D. Arnold. 1985. Costs and benefits of a mature first-generation loblolly pine tree improvement program. *J. For.* 83:162 - 166.

Virginia Department of Forestry. 2009. Forest Research Review April 2009. Virginia Department of Forestry. 12 p.

Wear, D.N., and J.G. Greis. 2002. Southern forest resource assessment. USDA For. Serv. Gen. Tech. Rep. SRS-53. 635 p.

White, T.L., W.T. Adams, and D.B. Neale. 2007. Forest Genetics. CAB International, London. 682 p.

Zobel, B.J., and J.T. Talbert. 1984. Applied Forest Tree Improvement. Bruce Zobel and John Talbert, Raleigh, NC. 505 p.

## **Chapter 2**

### **Literature review**

#### **2.1. Effects of genetic improvement on forest stand dynamics**

Genetic improvement in forestry may affect growth and yield related characteristics such as height and diameter or basal area growth, diameter and height distributions, survival, taper, and stand carrying capacity. It may also affect quality characteristics such as forking, stem straightness, branch angle, internode length, fusiform rust incidence, wood specific gravity, wood microfibril angle etc. Among the growth and yield related characteristics, height growth is probably the most studied and the most utilized measure of the effect of genetic improvement on stand growth. Growth gains from genetic improvement programs have been commonly reported as height or site index gains with reported volume gains having been estimated from the gains observed in height growth (Dhakal et al. 1996; Li et al. 1999; Matziris 2005; Newton 2003; Talbert et al. 1985). This may be attributed to the fact that most progeny testing has been done using single tree plots or row plots given their higher statistical power and convenience (White et al. 2007, p. 376 – 387) and also due to short testing period of approximately 6 to 8 years (Zobel and Talbert 1984, p. 425 – 428). Under these conditions, height growth is probably the most reliable measure of genetic gain among the genetic varieties under investigation.

### 2.1.1. Height growth

Height growth is important as an indicator of site quality and consequently is a key component of growth and yield models. Studies in ponderosa pine (*Pinus ponderosa* Laws.) (Namkoong and Conkle 1976), loblolly pine (Buford and Burkhart 1987; Knowe and Foster 1989; Nance and Wells 1981; Sprinz et al. 1989), maritime pine (*Pinus pinaster* Ait.) (Magnussen and Kremer 1993), Chinese fir (*Cunninghamia lanceolata* Lamb.) (Tang et al. 2001), and Scots pine (*Pinus sylvestris* L.) (Andersson et al. 2007) have shown that stands of different genetic varieties grow along different height trajectories. Genetic improvement through selection for faster height growth would therefore result in a change in the height growth trajectory of the population being modeled or managed, under plantation forest management.

Studies on the effect of genetic variety on height growth trajectory have been reported for Chinese fir and loblolly pine. In Chinese fir, Tang et al. (2001) used the model

$$\ln(H_{iA}) = \ln(S_i) + \beta \left( \frac{1}{A} - \frac{1}{\text{Index Age}} \right) + \varepsilon_{iA} \quad (2.1)$$

where  $H_{iA}$  is the dominant height for the  $i^{\text{th}}$  genetic variety at the age  $A$ ,  $S_i$  is the site index exhibited by the  $i^{\text{th}}$  genetic variety, *Index Age* is 15 years,  $\beta$  is the slope parameter, and  $\varepsilon_{iA}$  is the random error due to the observed dominant height of the  $i^{\text{th}}$  genetic variety at age  $A$  ( $\varepsilon_{iA} \sim N(0, \sigma_{\varepsilon A}^2)$ ); to investigate the effect of genetic variety on the height-age relationship of the trees. The authors observed that the height growth trajectories of stands of the different Chinese fir provenances, growing in the same location, differed in  $S_i$  values but not in the  $\beta$  parameter values of equation 2.1. That is, height growth trajectories of stands of the different provenances differed only in asymptote. In loblolly pine, the effect of genetic variety on parameters of height

growth models has been studied by different researchers. However, there has not been agreement among their findings on the nature of the differences in height growth trajectories among loblolly pine genetic varieties. The researchers in loblolly pine mainly used the Korf height-age function (Zeide 1993)

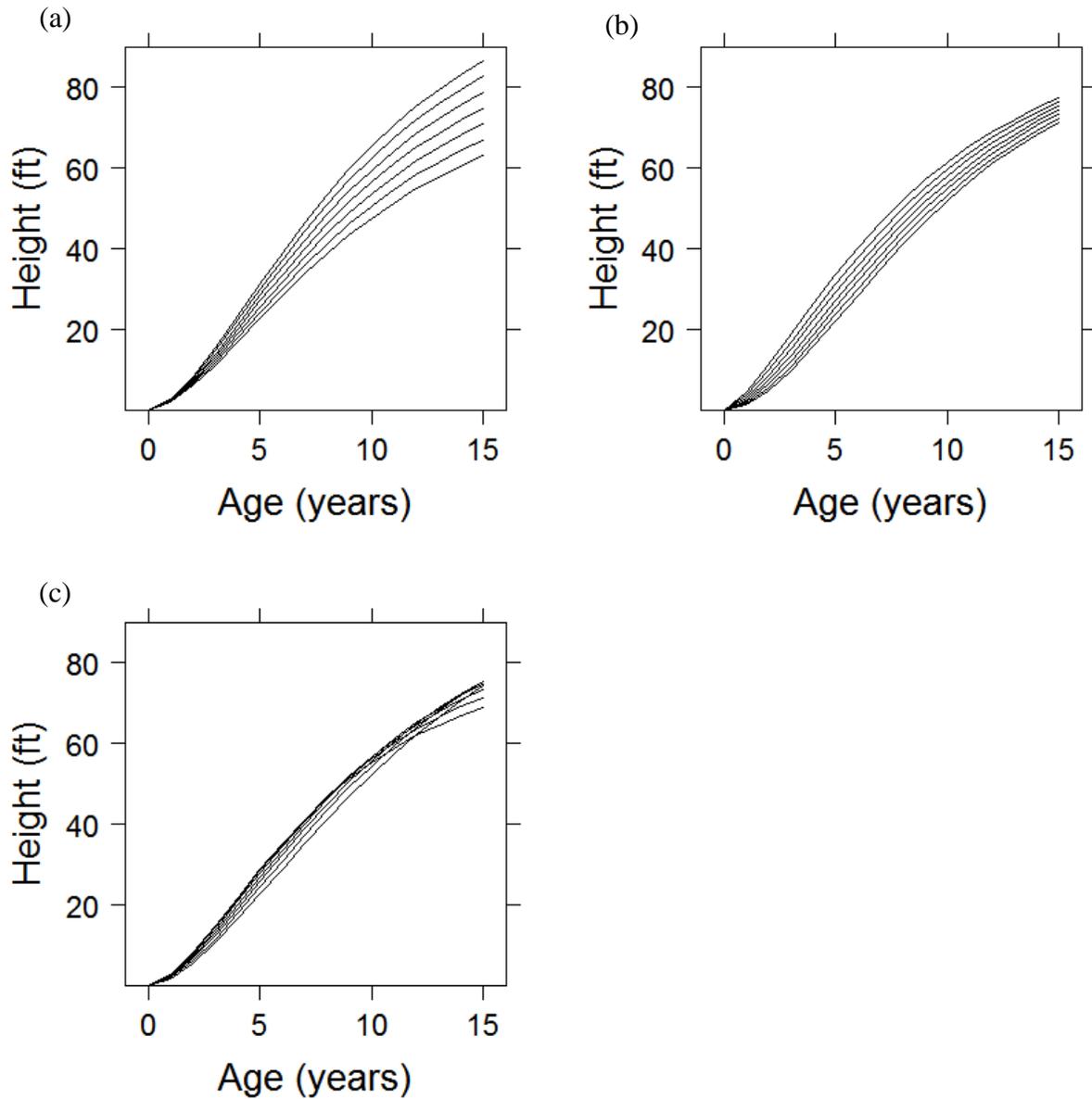
$$\ln(H_{iA}) = \beta_1 + \beta_2 A^{-1} + \varepsilon_{iA} \quad (2.2)$$

or the Chapman-Richard's height-age function

$$H_{iA} = \beta_1 (1 - \exp(-\beta_2 A))^{\beta_3} + \varepsilon_{iA} \quad (2.3)$$

(Richards 1959). In equations 2.2 and 2.3,  $H_{iA}$  is the total height of the  $i^{\text{th}}$  genetic variety at age  $A$ ,  $\beta_1$  is the asymptote parameter,  $\beta_2$  is the rate parameter,  $\beta_3$  is the shape parameter, and  $\varepsilon_{iA}$  is a random error due to the observed total height at age  $A$  ( $\varepsilon_{iA} \sim N(0, \sigma_{\varepsilon A}^2)$ ). Nance and Wells (1981) using equation 2.2 with data from first generation half-sib loblolly pine genetic varieties concluded that, for stands growing in the same location, genetic variety only affected the asymptote parameter. Buford and Burkhart (1985, 1987) reached similar conclusions with the same equation using data from loblolly pine provenance and first generation half-sib genetic varieties. By these conclusions, height growth trajectories of different loblolly pine genetic varieties growing in the same location were adequately represented by a series of anamorphic height-age curves (Figure 2.1(a)). Sprinz (1989), using data from first generation half-sib loblolly pine, concluded that genetic variety affected the shape but not the asymptote parameter of equation 2.3. According to this conclusion, different loblolly pine genetic varieties growing in the same location would grow towards the same asymptote with different shapes (Figure 2.1 (b)). Knowe and Foster (1989), using equation 2.3 with loblolly pine half-sib growing stock data, concluded that genetic variety affected the asymptote and the rate parameters. According to their

conclusion, different loblolly pine genetic varieties growing in the same location would grow to different asymptotes at different rates as shown in Figure 2.1(c). Sabatia et al. (2009) using equation 2.3 on loblolly pine clonal genetic varieties data with mixed-effects model analysis concluded that genetic variety affected both the asymptote and the shape parameters of the height-age equation. A plot of the height-age trajectories using the genetic variety-specific parameter estimates with equation 2.3 (Figure 1 of Sabatia et al. 2009), however, resulted in a trend similar to that in Figure 2.1(a) putting in doubt the practical significance of the variation of the shape parameter with genetic variety.



**Figure 2.1:** Hypothetical height growth trajectories in loblolly pine under the assumption of (a) genetic variety affecting only the asymptote parameter (b) genetic variety affecting only the shape parameter and (c) genetic variety affecting the asymptote and the rate parameters of the Chapman-Richards height-age equation.

The height growth trajectories in Figure 2.1(a) appear to be more appropriate in explaining observed height growth in loblolly pine varieties of varying genetic potentials (see Buford and Burkhart (1987) Figure 1 and Figure 2; Sprinz et al. (1989) Figure 3; and Figure 4). Thus the effects of genetic variety on the other parameters, as observed by the researchers whose conclusions led to height-age trajectories as those in Figure 2.1 (b) and (c), could be more due to the assumptions made or conditions imposed during the analysis or due to due to the type of analysis done than due to differences caused by genetic differences among the varieties. Sprinz et al. (1989) imposed a common asymptote to all genetic varieties that they studied. Knowe and Foster (1989) did not compare the fit of the asymptote and rate equation to that of an asymptote and shape equation as they did not fit an equation with asymptote and shape parameters in the model. In addition the different authors did not evaluate the biological significance of the additional significant parameters. It is known that, under the p-value approach of statistical inference, the power of statistical tests is extraordinarily high when sample size is very large. The mentioned studies were associated with sample sizes of hundreds to thousands. In such cases, very small differences that may not be meaningful in practice may get detected as statistically significant. Prediction is the main interest in most forest growth and yield applications; hence statistical significance that does not result in a significant practical change in model predictions may not be important. Further analysis that compares prediction biases and standard errors of estimate, due to the different parameter combinations in the model, can provide insight into the biological significance of the differences among the models with different parameter combinations.

### 2.1.2. Height-dbh relationships

Height-dbh relationships are useful in forest management for recovering heights of trees where only the dbh is given. This is useful in whole stand diameter distribution growth and yield models where the stand diameter distribution is predicted and heights have to be assigned to the trees in the various diameter classes before volume yield can be computed. While there are numerous published studies on genetic improvement in forest trees, very few report changes in height-dbh relationship due to genetic improvement. This may be attributed to the absence of stand-like conditions in most genetic improvement studies where single trees or single rows of trees form experimental plots.

The effect of genetic improvement on height-diameter relationships in forest trees has mainly been studied by investigating the effect of genetic variety potential on parameters of height-dbh equations. Using the log transformed Korf height-dbh equation

$$\ln(H_{ij}) = \beta_1 + \beta_2 D_{ij}^{-1} + \varepsilon_{ij} \quad (2.4)$$

$H_{ij}$  is the total height and  $D_{ij}$  the dbh of the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety,  $\beta_1$  is the natural log transformation of the asymptote parameter,  $\beta_2$  is the rate parameter, and  $\varepsilon_{ij}$  is a random error due to the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$ ), Buford (1986) concluded that height-dbh relationships among loblolly pine seed source varieties of different genetic potentials differed only in the asymptote parameter with taller growing seed sources having larger asymptote parameters. Buford and Burkhart (1987) reached a similar conclusion with data from loblolly pine first generation half-sib genetic varieties. Similar conclusions were also arrived at

by Weng et al. (2008) in jack pine (*Pinus banksiana* Lamb.). Using the Chapman-Richards height-dbh model

$$H_{ij} = \beta_1(1 - \exp(-\beta_2 D_{ij}))^{\beta_3} + \varepsilon_{ij} \quad (2.5)$$

where  $H_{ij}$  is the total height and  $D_{ij}$  the dbh of the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety,  $\beta_1$  is the asymptote parameter,  $\beta_2$  is the rate parameter,  $\beta_3$  is the shape parameter, and  $\varepsilon_{ij}$  is a random error due to the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$ ), the authors observed that height-dbh relationships among jack pine progenies from seed orchards of different rouging levels differed only in the asymptote parameter. Similar to the findings in loblolly pine, the progenies with a higher level of genetic improvement had larger asymptote parameters. The results of these studies imply that at a given diameter, trees of the genetically better varieties were taller.

It is however not clear from the studies cited previously whether the taller trees in the genetically better varieties were also larger in dbh. The mentioned studies did not report analyses on dbh distributions, height distributions, and basal areas hence it is not possible to assess the relationship between the increases in height, with genetic improvement, to dbh development with genetic improvement. However, there is evidence that genetic improvement can result in a gain in height growth without a corresponding gain in dbh growth. In the study by Weng et al. (2008), age 15 mean dbh values that do not appear to be significantly different are reported together with mean height values that show that the trees in the genetically superior progenies could be slightly taller (Table 1 of Weng et al. 2008). Martin and Shiver (2002) detected no significant differences in average dbh at age 12 (p-value = 0.0601) due to different levels of genetic improvement (unimproved, first generation mixed variety open pollinated, and first generation single variety open pollinated) in loblolly pine in the Coastal Plain of Georgia

and northern Florida. Significant differences ( $p\text{-value} < 0.0001$ ) were however detected in average dominant height for the different levels of genetic improvement with the improved varieties having taller dominant heights. In a different study, Adams et al. (2008) reported no significant differences ( $p\text{-value} > 0.05$ ) in mean dbh at age 17 for loblolly pine varieties, including a commercial check, grown at a spacing of 5ft by 5ft in the Mississippi North Central Plateau. The mean dbh for the commercial check ranked 4 out of 9 in an 8 ft by 8ft spacing and 2 out of 9 at a 10ft by 10ft spacing, with the differences showing overlaps across genetic varieties. However, reported mean height at age 17 for the commercial check (ranked last) was significantly smaller ( $p\text{-value} < 0.05$ ) than the mean heights of the other varieties at all the spacings. These observations suggest that genetic selection for faster growth may result in stands that have taller trees but whose diameters are not larger than the diameters of those in stands of lower genetic potentials. This result may be attributed to the fact that genetic selection of forest trees for faster growth is mostly based on height growth. According to Kroon et al. (2008), such selection would result in trees that allocate more resources to height growth than diameter growth, which the authors described as slender and taller.

Genetic improvement can result in a gain in height growth that is accompanied by a gain in dbh growth. In radiata pine in New Zealand, Carson and Hayes (1998) reported significant differences among the mean diameters ( $p\text{-value} = 0.0019$ ) and mean heights ( $p\text{-value} = 0.0403$ ) in unthinned stands of different levels of genetic improvement— unimproved, plus tree collections, seed orchard open pollinated, and seed orchard control pollinated. In the study by Martin and Shiver (2002), significant differences were observed in mean dbh ( $p\text{-value} = 0.0102$ ) and mean dominant height ( $p\text{-value} < 0.0001$ ) among the different levels of genetic improvement in loblolly pine in the Piedmont of South Carolina, Georgia and Alabama. For Douglas-fir

(*Pseudotsuga menziesii* [Mirb.] Franco) in the Oregon cascades, St. Clair et al. (2004) reported significant differences in mean dbh and mean height (p-value = 0.05), at age 5, among the different levels of genetic improvement studied – unimproved, intermediate first generation control pollinated, and elite first generation control pollinated.

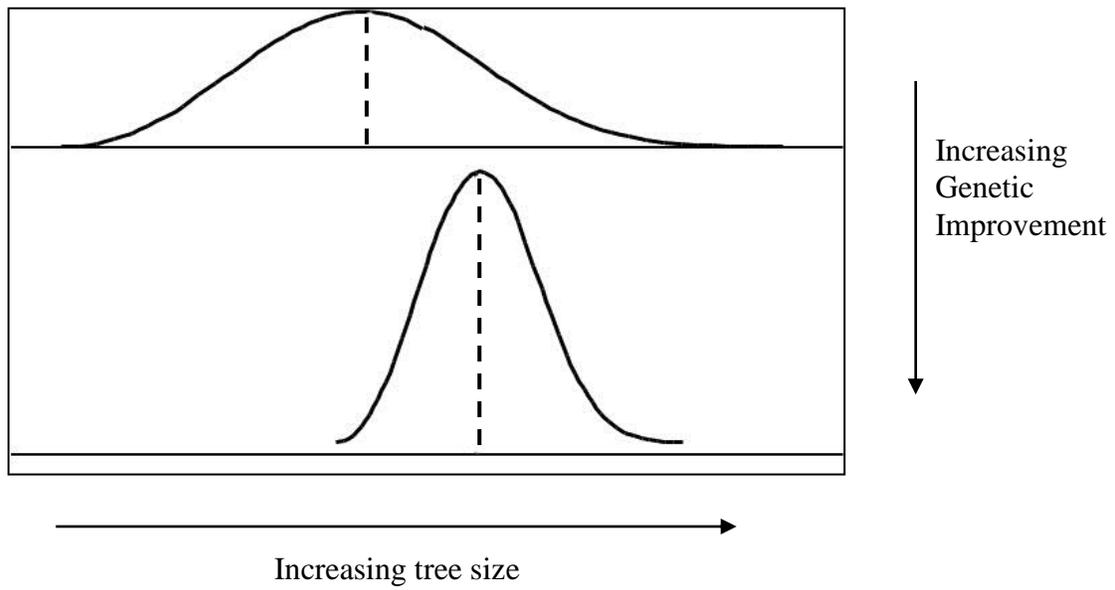
It is clear that genetic improvement of forest trees through selection for faster growth would result in taller trees. But the effect on dbh may vary. In some cases the trees may be larger in dbh and in some cases the dbh may not be different from that of the genetically unimproved varieties.

### ***2.1.3. Height and dbh distributions***

The distribution of heights and dbh in a forest stand determines the product class distribution of that stand and hence its economic value. The effect of genetic improvement on these distributions affects the stand's economic value. Quantifying this effect is an important part of quantifying the effect of genetic improvement on stand economic value. It has however not been easy to quantify this effect as very little research has been reported on effect of genetic improvement on stand dbh and height distributions. Genetic theory dictates that genetic improvement should result in an increase in mean tree size and a decrease in the variability (Figure 2.2) as selection for larger tree size is expected to result in larger average tree size and the planting of progeny from the selected tree(s) is expected to result in a stand with lower genetic variability than a stand in the unselected population. The decreased genetic variability would result in decreased phenotypic, in this case tree size, variability given the relationship

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 \quad (2.6)$$

where  $\sigma_P^2$  is the phenotypic variance,  $\sigma_G^2$  is variance due to genetics, and  $\sigma_E^2$  is variance due to effect of microsite. The implications of this decrease on stand productivity were investigated, through simulation, by Mitchell (1975) and also by Nance and Bey (1979) who concluded that a decrease in tree dbh variability due to genetic selection would lower stand volume productivity and/or value as a result of fewer trees in the larger dbh classes. The authors argued that the decreased size variability would result in decreased expression of dominance and hence delayed mortality of the smaller trees, curtailing the progression of the trees into the larger dbh classes. Studies that have been carried out to investigate this hypothesis are few and have not detected decreased tree size variability with genetic improvement.

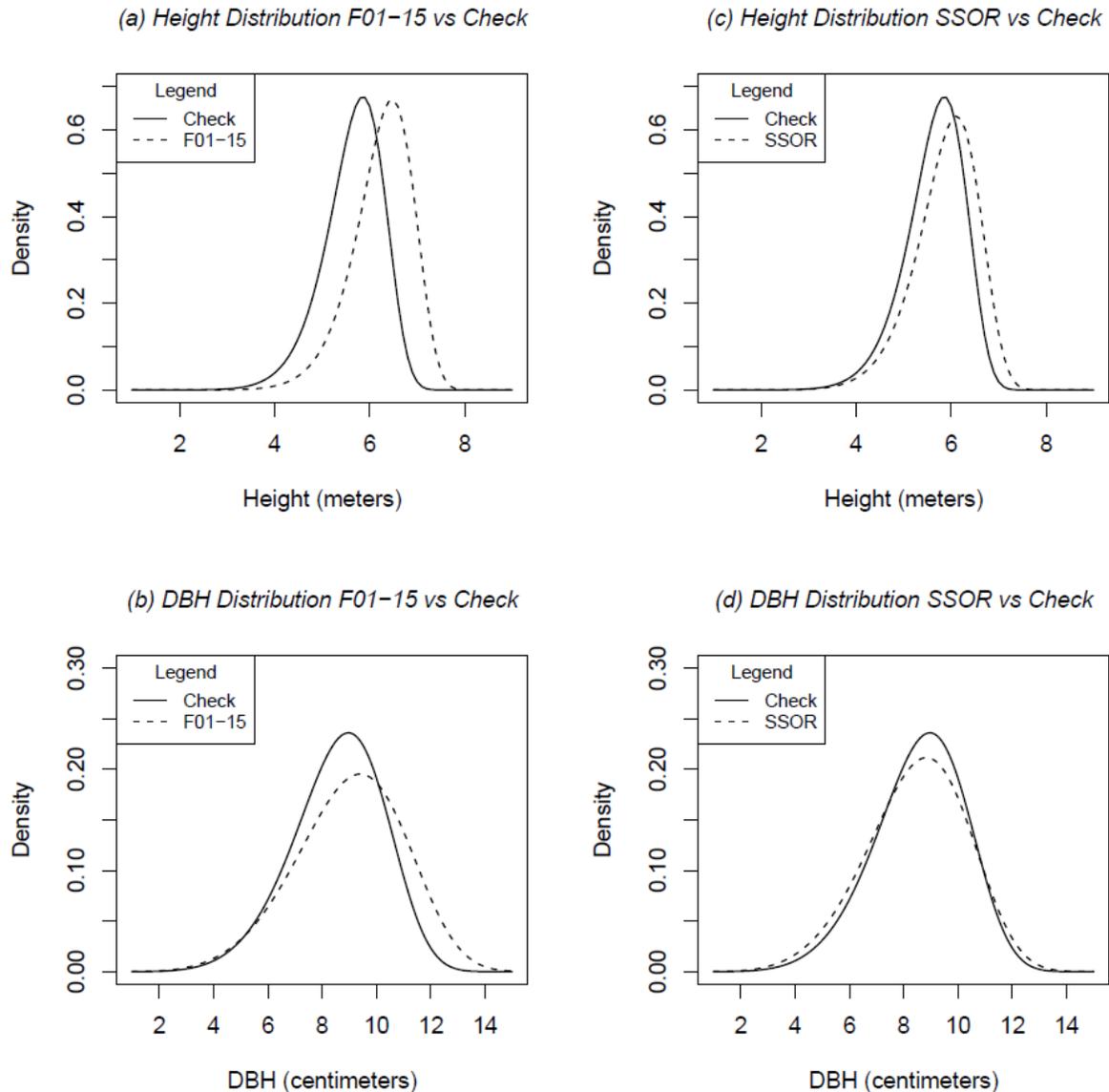


**Figure 2.2:** Theoretical change in tree size distribution with genetic improvement

Buford and Burkhart (1985), using Bartlett's test of homogeneity of variance, concluded that dbh and height variance was homogenous among different loblolly pine seed source and first generation OP genetic varieties including a check variety that was established with unimproved seed. Carson and Hayes (1998), using analysis of variance (ANOVA) tests on standard deviations of the distributions, reached a similar conclusion on dbh and height distributions in unthinned radiata pine stands of different genetic improvement levels - unimproved, plus tree collections, seed orchard OP, and seed orchard CP. The authors in the two studies argued that with the absence of a significant difference in the variability of dbh and height distributions among stands of different levels of genetic improvement, specification of stand characteristics for the improved stands should enable one to recover the dbh and height distributions correctly without any further amendments. Thus height and dbh distributions, hence stand volume and value of a genetically variety, can be recovered from adjustment of a stand characteristic such as site index. This principle has been widely applied in predicting the benefits from genetic improvement of forest trees (Dhakal et al. 1996; Li et al. 1999; Matziris 2005; Newton 2003; Talbert et al. 1985). An adjustment of one variable may, however, not hold in all the cases as there is a possibility of genetic improvement affecting height distribution in a way that is different from the effect on dbh distribution.

In the study by Carson and Hayes (1998), despite there being no statistically significant differences in variance and skewness of the dbh and height distributions, the skewness of the dbh distribution appeared to become more negative with increasing level of genetic improvement, changing from -0.07 in the unimproved to -0.42 in the control pollinated in unthinned stands. This trend suggests that tree improvement may result in stands with more trees in the larger diameter classes. The skewness of the height distribution did not trend with level of genetic

improvement suggesting that effect of genetic improvement on stand height distribution may be different from the effect on stand diameter distribution. In a study on black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* Moench.), Weng et al. (2010) concluded that genetic improvement level – wild collections, plus tree selections, first generation seed orchards, rouged seed orchards, and elite provenance selections would affect the scale parameter but not the shape parameter of a 2-parameter Weibull distribution for heights and diameters at age 15. Improved stands generally had larger scale parameters than stands of wild collections resulting in an apparent upward shift in mean tree size with genetic improvement (Figure 1 of Weng et al. 2010). This was however not consistent for diameter distributions. For black spruce, there was a significant difference in the scale parameter for both dbh and height distribution between the plus tree selection stands and the wild check stands. However, for stands of plus tree provenance material and those of rouged seedling seed orchard material, the scale parameter was significantly different for height distribution but not for dbh distribution (Figure 2.3). This provides further evidence that the effect of genetic improvement on height distribution may be different from the effect on dbh distribution.



**Figure 2.3:** Height and diameter distributions at age 15 for black spruce stands of different genetic improvement levels, in New Brunswick, Canada. The distributions were generated using parameters estimated by Weng et al. (2010)<sup>1</sup>. The genetically improved stands are F01-15 from plus tree selection and SSOR from rouged seedling seed orchard. The genetically unimproved stands are represented by ‘Check’.

<sup>1</sup> Weng, Y. H., Y. Park, D. Simpson, K. Tosh, and M. Fullarton. 2010. Tree improvement effects on tree size distributions for *Picea glauca* and *Picea mariana* in New Brunswick, Canada. *Scand. J. For. Res.* 25: 10 – 20.

Reported studies that have investigated the effect of genetic improvement on stand level tree size distribution have not provided sufficient information to enable a complete assessment of the effect of genetic improvement on tree size distributions. Buford and Burkhart (1985) only reported the effect of genetic improvement on variability of dbh and height distributions. Information on the mean and the skewness of the distributions, and whether the effect of genetic improvement on height distribution was similar to the effect on dbh distribution was not reported. Weng et al. (2010) only reported the effect on Weibull distribution parameters. The effect on other distributional aspects such as the mean, variance, and skewness was not reported. While the authors showed that changes in the height distribution Weibull scale parameter with genetic improvement could be predicted from the observed gain in site index, they did not show how this could be done for dbh distribution. A knowledge gap therefore exists in the relationship between change in height distribution and change in dbh distribution, with genetic improvement.

## **2.2. Effect of clonal forestry on forest stand dynamics**

According to Libby and Ahuja (1993) clonal forestry involves the use of superior well tested clones for plantation establishment. Cloning or vegetative propagation of forest trees without knowledge of the genetic worth of the clones does not qualify to be clonal forestry. Clonal forestry has been carried out in angiosperms for over 50 years (Lindgren 2002). In conifers, clonal forestry is recent, having become more feasible with the development of somatic embryogenesis, a technology that has made it possible to mass-produce conifer clones (Allen et al. 2005; McKeand et al. 2007; Park et al. 1998; Sutton 2002). Clones may be established in plantations as single clones or clonal mixtures. According to genetic theory, single clone stands

should be more productive (due to higher genetic gain with clonal propagation) and phenotypically more uniform than same variety seedling stands. The stands are expected to be phenotypically more uniform given that

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2$$

$$\text{but } \sigma_G^2 = 0 \text{ in single clone stands, hence } \sigma_P^2 = \sigma_E^2 \quad (2.7)$$

where  $\sigma_P^2$  is the phenotypic variance,  $\sigma_G^2$  is variance due to genetics, and  $\sigma_E^2$  is variance due to effect of microsite. The phenotypic variability in a single clone stand is due to the variance component due to microsite only. For growth traits, single clone stands are therefore expected to have less variability in dbh distribution, height distribution, heights within a dbh class, taper, and crown size. If better adapted to the site, they are likely to exhibit a higher site index and produce more volume given the higher genetic gains.

Low heritabilities among growth traits and somatic mutations within individuals being cloned may cause single clone stands to have phenotypic variability that is not different from that of same variety seedling stands. Traits with low heritabilities have a large proportion of phenotypic variance made up of microsite variance component hence within stand variability may not be significantly lower in the single clone stands for such stands. Somatic mutations introduce genetic heterogeneity within individuals being cloned hence clones from different parts of the individual will be genetically variable (Libby and Ahuja 1993). Single clone stands from such individuals are genetically heterogenous and may not have phenotypic variability different from that of same variety seedling stands. It is also possible that single clone stands may not produce more volume than similar seedling stands. The genetic uniformity in clonal stands may

result in increased competition among the trees in the stand, a condition that may lower overall productivity due to poor ecological resource partitioning in such stands.

Average tree level differences between the growth of seedlings and clones have been widely studied in different species (Fielding 1970; Foster et al. 1987; Frampton et al. 2000; Gaspar et al. 2005; Karlsson and Russell 1990; Klomp and Hong 1985; Niskanen et al. 2008; Stelzer et al. 1998; Struve and McKeand 1990; Struve et al. 1984). Findings from these studies have shown that growth of clones is generally not different from that of seedlings. Differences in the growth during the ages just after planting have been attributed to differences in morphological and physiological conditions of seedlings and clones at planting time (Foster et al. 1987; Foster et al. 2000; Karlsson and Russell 1990; Klomp and Hong 1985). However, conclusions from these studies may not reflect the performance of seedlings and clones under stand level conditions as single-tree or row plots were used in the design of the studies. Studies comparing stand level performance of seedlings to clones are few with most of them having been carried out in Eucalyptus (Binkley et al. 2002; Boyden et al. 2008; Gemmel et al. 1991; Sale 2005). Some of the results from these studies have been conflicting. In 10-year old Norway spruce (*Picea abies* (L.) H.Karst.) in Sweden, clonal stands had larger mean height and mean diameter at 0.6ft above ground level than seedling stands from the same seed orchard (Gemmel et al. 1991). Among several 6 to 8 year old Eucalyptus stands in Brazil, clonal stands of *Eucalyptus grandis*, *E. saligna*, *E. urophylla*, and *E. grandis* x *E. urophylla* cross, had faster volume growth and lower coefficient of variation (CV) in tree volume than seedling stands of *E. saligna* (Binkley et al. 2002), but the converse was true in 5½-year old seedlings of *E. grandis* and clones from a *E. grandis* x *E. urophylla* cross in South Africa (Sale 2005) and also in 4½-year old seedlings of *E. grandis* and clones from a *E. grandis* x *E. urophylla* cross in Brazil

(Boyden et al. 2008). Species differences among the clones and seedlings used in the Eucalyptus studies may be the cause of the conflicting results.

Results on within stand competition from the studies on Eucalyptus suggest that there could be differences between clonal stands and seedling stands on this aspect of stand dynamics but the effects may not be well known. Sale (2005) observed that the rate of self thinning was slower in clonal stands of *E. grandis* x *E. urophylla* than in seedling stands of *E. grandis*. The increase in mean tree size was also slower in clonal stands than in seedling stands. Despite the lower mortality in clonal stands, these stands still had lower volume growth. However, Sale (2005) concluded that "...clone could increase production per hectare without any change in survivorship, which is contrary to popular theory." This conclusion suggests that within stand competition or its effects could be lower in clonal stands. Boyden et al. (2008) modeled competition interactions in clonal stands of *E. grandis* x *E. urophylla* than in seedling stands of *E. grandis* using the formula

$$NI_{focal} = \sum_{i=1}^n \frac{M_i^\alpha}{d_i^\beta} \quad (2.8)$$

where  $NI_{focal}$  is the neighborhood competitive interaction for the focal tree,  $M_i$  is the mass of the  $i^{th}$  neighboring tree within a given radius,  $d_i$  is the distance between the focal tree and the  $i^{th}$  neighbor, and  $\alpha$  and  $\beta$  are parameters fitted by maximum likelihood with simulated annealing. Based on the comparisons of the parameters  $\alpha$  and  $\beta$  in clonal and seedling stands, they concluded that competitive interactions among trees were higher in clonal stands than in seedling stands. This conclusion is contrary to what the conclusion by Sale (2005) implies. The effects of propagule type in these studies were however confounded by species differences between the clones and seedlings used. In the study by Boyden et al. (2008), the effects are further

confounded by the differences in planting program for the two types of stands. Trees in seedling plots were planted on the same day while the planting of those in the clonal stands was staggered over a 90-day period to increase variability among the trees in the clonal stands. In effect, the results of this study do not provide accurate information on effect of propagule type on competition within a forest stand.

It is generally known that individually trees from clones do not grow differently from trees from seedlings. However, it is not fully known whether the growth of trees in stands of clones is different from the growth in stands of trees from seedlings. Theoretically, there is a difference, but reported research has not provided undisputable evidence of the difference or nature of the difference. Research in this area is needed to provide information to be used to manage clonal stands especially in conifers where clonal forestry is recent and most of the experience is with management of seedling stands.

### **2.3. Incorporating effects of genetic improvement and clonal forestry in existing growth and yield models**

#### ***2.3.1. Incorporating effects of genetic improvement in growth and yield models***

The general approach of incorporating effects of genetic improvement into existing growth and yield models has been to investigate how growth of the genetically improved varieties differs from that of the unimproved varieties then using the observed differences to make changes in the growth and yield models developed using data from unimproved stands. Given that most genetic improvement information is from early age data, Hamilton and Rehfeldt (1994) recommended that to provide a more accurate prediction of the performance of the

improved genetic varieties during the rotation, differences observed from the early-age data should be combined with expert assumptions on how the observed differences carry on during the rotation. Two approaches have been commonly used to incorporate genetic gain information into existing growth and yield models; a) site index adjustment approach, and b) genetic gain multiplier approach.

Site index adjustment approach involves adjusting the site index equation to reflect the height growth of the genetically improved variety. The assumption in this approach is that there are no significant changes in stand dynamics, with genetic improvement, beyond those that can be explained by the observed site index change. The common practice with this approach has been to assume that the early age gains in site index are maintained during the rotation (Andersson et al. 2003; Dhakal et al. 1996; Li et al. 1999; Matziris 2005; Newton 2003; Talbert et al. 1985). Assumptions of gains that change in the course of the rotation have been reported in actual genetic gain incorporation work (Xie and Yangchuk 2003) and also in simulation studies (Nance and Bey 1979). In an apparent test of the accuracy of the site index approach; Adams et al. (2006), using the loblolly pine whole stand growth and yield simulator of Matney and Farrar (1992), observed that modifying the survival function, diameter function, and stem profile, in addition to modifying site index, reduced age 17 volume estimate error from 30% to 6% compared to when site index alone was modified. Thus, site index approach may fail to accurately incorporate genetic gain effects into growth and yield models.

Genetic gain multiplier approach involves the use of a multiplier that adjusts the height increment or dbh increment by the number of times that the genetically improved variety grows faster than the unimproved. The multipliers may be calculated from field measurements e.g. in Carson et al. (1999) or from breeding values as demonstrated by Gould et al. (2008). Carson et

al. (1999) used genetic gain multiplier approach to incorporate effects of genetic gain in a whole stand growth and yield model for radiata pine in New Zealand. The authors argued that given that the effect of genetic improvement on height growth was different from the effect on dbh growth, site index adjustment could not accurately account for the changes observed in dbh growth. Percentage increase in rate of height growth resulting from genetic improvement was much smaller than the percentage increase in rate of basal area growth. Genetic gain multipliers have also been used to incorporate observed or hypothetical effects of genetic improvement into the individual tree model Prognosis and its variant SORNEC (Du 1990; Hamilton and Rehfeldt 1994; Rehfeldt et al. 1991). Genetic gain multiplier approach is a good alternative to the site index approach where the effect of genetic improvement on height growth is different from the effect on diameter growth. However, the multipliers should be used with caution as interrelationships among model components may cause multipliers to be propagated through the model system producing biologically illogical predictions (Hamilton 1994; Westfall and Burkhardt 2001). In addition, genetic gain multiplier approach requires information on genetic gains in diameter growth, which are not reliable when data is from single-tree or row plot genetic trials or from genetic trial stands with significant mortality.

### ***2.3.2. Incorporating effects of clonal forestry in growth and yield models***

There are no reported studies on the incorporation of effects of using clonal planting stock in forest growth and yield models for conifers. Clonal forestry has been practiced only recently with conifers and clonal stands are likely to have stand dynamics that are different from the dynamics in seedling stands. Incorporation of effects of clonal forestry in growth and yield

models is likely to follow the same approach as incorporation of the effects of genetic improvement – determine differences between clonal stands and seedling stands then adjust model components to reflect the observed differences. Due to the absence of genetic variability in clonal stands, focus is likely to be on the distributional properties of stem characteristics in these stands and the within stand changes in competition that are likely to come with the genetic similarity among trees in clonal stands. Clonal forestry is accompanied by genetic improvement as higher genetic gains are possible with clonal deployment than with the other forms of deployment (White et al. 2007). This may also be a factor to consider when incorporating gains from cloning in forest growth and yield models.

## **2.4. Conclusions**

Genetic improvement activities have been an integral part of pine plantation forestry in southern United States for approximately 60 years. These activities have resulted in a wide selection of pine planting material ranging from the genetically heterogeneous half-sib seedlings to intensively selected clones. Theoretically, the wide selection of available planting stock also means a wide range of stand dynamics with potentially different effects on forest growth and productivity. Stand level dynamics of the different genetic material available have not been studied in breadth and depth. Estimates of growth and yield of genetically improved southern pines and the comparison of the performance of seed versus clonal pines has mostly been done under single-tree or row-plot designs where stand level dynamics due to trees of the same genetics competing with each other may not be experienced. There have been concerns that estimates of genetic gain in yield that have been reported with these approaches that do not take

into account stand level dynamics of the genetic varieties do not provide strong evidence, at plantation level, that genetic improvement has resulted in higher yields (South 2010). Studies on genetic improvement and clonal forestry effects, under stand level conditions, from other species similar to southern pines have been few hence evidence from trends in other species is limited. There is evidence that genetic improvement results in faster height growth but there has been no agreement among various researchers on the nature of the relationships among the height growth trajectories of different genetic varieties of loblolly pine. There is need to further investigate this aspect of stand dynamics to sort out some of the disagreements and also to provide information on the relationships among the height trajectories in genetic varieties from advanced methods of breeding, selection, and propagation. There has been very little research on the effect of genetic improvement on stand level height development in loblolly pine as it relates to the accompanying stand level dbh development. There is evidence that some of the assumptions that have been made regarding this relationship may be erroneous. Further studies in this aspect of stand dynamics are necessary for accurate predictions of height growth and basal area growth due to genetic improvement. Clonal forestry in southern pines is taking root but dynamics of clonal conifer stands are not well known especially as it pertains to the variability of tree size distributions and the effects of genetic uniformity on stand dynamics. Studies in this area are needed to correctly assess the effect of clonal forestry on stand economic values and on within stand competition dynamics.

## 2.5. Literature cited

Adams, J.P., S.B. Land Jr, K.L. Belli, and T.G. Matney. 2008. Comparison of 17-year realized plot volume gains with selection for early traits for loblolly pine (*Pinus taeda* L.). *For. Ecol. Manage.* 255:1781-1788.

Adams, J.P., T.G. Matney, S.B.L. Jr., K.L. Belli, and H.W.D. Jr. 2006. Incorporating genetic parameters into a loblolly pine growth-and-yield model. *Can. J. For. Res.* 36:1959 - 1967.

Allen, H.L., T.R. Fox, and R.G. Campbell. 2005. What is ahead for intensive pine plantation silviculture in the south? *South. J. Appl. For.* 29:62-69.

Andersson, B., B. Elfving, T. Ericsson, T. Persson, and B. Gregorsson. 2003. Performance of improved *Pinus sylvestris* in Northern Sweden. *Scand. J. For. Res.* 18:199-206.

Andersson, B., B. Elfving, T. Persson, T. Ericsson, and J. Kroon. 2007. Characteristics and development of improved *Pinus sylvestris* in northern Sweden. *Can. J. For. Res.* 37:84-92.

Binkley, D., J.L. Stape, M.G. Ryan, H.R. Barnard, and J. Fownes. 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems* 5:58-67.

Boyden, S., D. Binkley, and J.L. Stape. 2008. Competition among Eucalyptus trees depends on genetic variation and resource supply. *Ecology* 89:2850-2859.

Buford, M.A. 1986. Height-diameter relationships at age 15 in loblolly pine seed sources. *For. Sci.* 32:812 - 818.

Buford, M.A., and H.E. Burkhart. 1985. Dynamics of improved loblolly pine plantations and the implications for modeling growth of improved stands. P. 170 - 177 in *Proceedings of the 18th*

Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Long Beach, MS.

Buford, M.A., and H.E. Burkhart. 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci.* 33:707 - 724.

Carson, S.D., O. Garcia, and J.D. Hayes. 1999. Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *For. Sci.* 45:186 - 200.

Carson, S.D., and J.D. Hayes. 1998. Diameter and height distributions in genetically improved *Pinus radiata*. *Can. J. For. Res.* 28:248 -258.

Dhakal, L.P., T.L. White, and G.R. Hodge. 1996. Realized genetic gains from slash pine tree improvement. *Silvae Genet.* 45:190-197.

Du, W. 1990. Incorporating genetic effects into a forest growth and yield model. PhD Dissertation, University of Idaho, Moscow, ID. 155 p.

Fielding, J.M. 1970. Trees grown from cuttings compared with trees grown from seed *Pinus radiata* D. Don. *Silvae Genet.* 19:54-63.

Foster, G.S., C.C. Lambeth, and M.S. Greenwood. 1987. Growth of loblolly pine rooted cuttings compared with seedlings. *Can. J. For. Res.* 17:157-164.

Foster, G.S., H.E. Stelzer, and J.B. McRae. 2000. Loblolly pine cutting morphological traits: effects on rooting and field performance. *New For.* 19:291-306.

Frampton, J., B. Li, and B. Goldfarb. 2000. Early field growth of loblolly pine rooted cuttings and seedlings. *South. J. Appl. For.* 24:98-105.

- Gaspar, M.J., N. Borralho, and A.L. Gomes. 2005. Comparison between field performance of cuttings and seedlings of *Eucalyptus globulus*. *Ann. For. Sci.* 62:837-841.
- Gemmel, P., G. Örländer, and K.A. Högberg. 1991. Norway spruce cuttings perform better than seedlings of the same genetic origin. *Silvae Genet.* 40:198-202.
- Gould, P., R. Johnson, D. Marshall, and G. Johnson. 2008. Estimation of genetic-gain multipliers for modeling Douglas-fir height and diameter growth. *For. Sci.* 54:588 - 596.
- Hamilton, D.A., Jr. 1994. Uses and abuses of multipliers in the stand prognosis model. USDA For. Serv. Gen. Tech. Rep. INT-GTR-310. 9 p.
- Hamilton, D.A., Jr., and G.E. Rehfeldt. 1994. Using individual tree growth projection models to estimate stand-level gains attributable to genetically improved stock. *For. Ecol. Manage.* 68:189-207.
- Karlsson, I., and J. Russell. 1990. Comparisons of yellow cypress trees of seedling and rooted cutting origins after 9 and 11 years in the field. *Can. J. For. Res.* 20:37-42.
- Klomp, B.K., and S.O. Hong. 1985. Performance of *Pinus radiata* seedlings and cuttings to age 15 years. *N. Z. J. For. Sci.* 15:281-297.
- Knowe, S.A., and G.S. Foster. 1989. Application of growth models for simulating genetic gain of loblolly pine. *For. Sci.* 35:211-228.
- Kroon, J., B. Andersson, and T.J. Mullin. 2008. Genetic variation in the diameter-height relationship in Scots pine (*Pinus sylvestris*). *Can. J. For. Res.* 38:1493-1503.

- Li, B., S.E. McKeand, and R.J. Weir. 1999. Tree Improvement and sustainable forestry-Impact of two cycles of loblolly pine breeding in the USA. *For. Genet.* 6:229 - 234.
- Libby, W.J., and M.R. Ahuja. 1993. The Genetics of Clones. P. 5-13 in *Clonal Forestry I: Genetis and Biotechnology*, Ahuja, M.R., and W.J. Libby (eds.). Springer-Verlag, Berlin, Germany.
- Lindgren, D. 2002. Advantages of clonal propagation. P. 98-109 *in* Proceedings of the workshop on high quality birch August 27-28, 2001. Swedish University of Agricultural Sciences, Department of Crop Science, Ronneby, Sweden.
- Magnussen, S., and A. Kremer. 1993. Selection for an optimum tree growth curve. *Silvae Genet.* 42:322-335.
- Martin, S.W., and B.D. Shiver. 2002. Impacts of vegetation control, genetic improvement and their interaction on loblolly pine growth in the Southern United States - age 12 results. *South. J. Appl. For.* 26:37-42.
- Matney, T.G., and R.M. Farrar, Jr. 1992. A thinned/unthinned loblolly pine growth and yield simulator for planted cutover site-prepared land in the Mid-Gulf South. *South. J. Appl. For.* 16:70-75.
- Matziris, D. 2005. Genetic variation and realized genetic gain from black pine tree improvement. *Silvae Genet.* 54:96-103.

- McKeand, S.E., B.J. Zobel, T.D. Byram, and D.A. Huber. 2007. Southern pine tree improvement-A living success story. P. 3 - 5 *in* Proceedings of the 29th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Galveston, TX.
- Mitchell, K.J. 1975. Dynamics and simulated yield of Douglas-fir. Forest Science Monograph. No. 17. 39 p.
- Namkoong, G., and M.T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. For. Sci. 22:2-12.
- Nance, W.L., and C.F. Bey. 1979. Incorporating genetic information in growth and yield models. P. 140-148 *in* Proceedings of the 15th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Starkville, MS.
- Nance, W.L., and O.O. Wells. 1981. Site index models for height growth of planted loblolly pine (*Pinus taeda* L.) seed sources. P. 86 - 96 *in* Proceedings of the 16th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Blacksburg, VA.
- Newton, P.F. 2003. Systematic review of yield responses of four North American conifers to forest tree improvement practices. For. Ecol. Manage. 172:29-51.
- Niskanen, A.M., N. Stenvall, A. Pakkanen, and P. Pulkkinen. 2008. Comparison of growth and stem form characters of *Pinus sylvestris* clones and seedlings of the same origin in a 10-year field trial. Scand. J. For. Res. 23:484-490.

Park, Y.S., J.D. Barrett, and J.M. Bonga. 1998. Application of somatic embryogenesis in high-value clonal forestry: deployment, genetic control, and stability of cryopreserved clones. *In Vitro Cell. Dev. Biol. Plant* 34:231-239.

Rehfeldt, G.E., W.R. Wykoff, R.J. Hoff, and R.J. Steinhoff. 1991. Genetic gains in growth and simulated yield of *Pinus monticola*. *For. Sci.* 37:326-342.

Richards, F.J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10:290 - 300.

Sabatia, C.O., H.E. Burkhart, and P.M. Dougherty. 2009. Height-age relationships in a loblolly pine varietal screening trial: implications for stand yields. P. 70 - 72 in *Proceedings of the 30th Southern Forest Tree Improvement Conference*. Southern Forest Tree Improvement Committee, Blacksburg, VA.

Sale, G. 2005. A comparison of between-tree competition effects in separate stands of *Eucalyptus grandis* seedling and a single *Eucalyptus grandis* x *urophylla* hybrid clone. Masters thesis, University of the Witwatersrand, Johannesburg, South Africa. 97 p.

South, D. 2010. "Letter". Do realized volume gains equal estimates? *J. For.* 108:266 - 266.

Sprinz, P.T., C.B. Talbert, and S.M. R. 1989. Height-Age trends from an Arkansas seed source study. *For. Sci.* 35:677 - 691.

St. Clair, J.B., L.M. Nancy, and J.S.J. Keith. 2004. Early realized genetic gains for coastal Douglas-fir in the northern Oregon cascades. *West. J. Appl. For.* 19:195-201.

Stelzer, H.E., G.S. Foster, D.V. Shaw, and J.B. McRae. 1998. Ten-year growth comparison between rooted cuttings and seedlings of loblolly pine. *Can. J. For. Res.* 28:69-73.

Struve, D.K., and S.E. McKeand. 1990. Growth and development of eastern white pine rooted cuttings compared with seedlings through 8 years of age. *Can. J. For. Res.* 20:365-368.

Struve, D.K., J.T. Talbert, and S.E. McKeand. 1984. Growth of rooted cuttings and seedlings in a 40-year-old plantation of eastern white pine. *Can. J. For. Res.* 14:462-464.

Sutton, B. 2002. Commercial delivery of genetic improvement to conifer plantations using somatic embryogenesis. *Ann. For. Sci.* 59:657-661.

Talbert, J.T., R.J. Weir, and R.D. Arnold. 1985. Costs and benefits of a mature first-generation loblolly pine tree improvement program. *J. For.* 83:162 - 166.

Tang, S., F.R. Meng, and C.P.A. Bourque. 2001. Analyzing parameters of growth and yield models for Chinese fir provenances with a linear mixed model approach. *Silvae Genet.* 50:140-145.

Weng, Y.H., J. Kershaw, K. Tosh, G. Adams, and M.S. Fullarton. 2008. Height-diameter relationships for jack pine seedlots of different genetic improvement levels. *Silvae Genet.* 57:276-282.

Weng, Y.H., Y. Park, D. Simpson, K. Tosh, and M. Fullarton. 2010. Tree improvement effects on tree size distributions for *Picea glauca* and *Picea mariana* in New Brunswick, Canada. *Scand. J. For. Res.* 25:10-20.

Westfall, J.A., and H.E. Burkhart. 2001. Incorporating thinning response into a loblolly pine stand simulator. *South. J. Appl. For.* 25:159 - 164.

White, T.L., W.T. Adams, and D.B. Neale. 2007. *Forest Genetics*. CAB International, London. 682 p.

Xie, C.-Y., and A.D. Yangchuk. 2003. Breeding values of parental trees, genetic worth of seed orchard seedlots, and yields of improved stocks of British Columbia. *West. J. Appl. For.* 18:88 - 100.

Zeide, B. 1993. Analysis of growth equations. *For. Sci.* 39:594-616.

Zobel, B.J., and J.T. Talbert. 1984. *Applied Forest Tree Improvement*. Bruce Zobel and John Talbert, Raleigh, NC. 505 p.

## Chapter 3

### Genetic effects on height-age relationships in clonal loblolly pine

#### Abstract

Knowledge of the effect of genetics on height-age relationships may be used to localize a species-wide height-age or site index equation to a given genetic variety. The effect of genetic variety on height-age relationships in loblolly pine was investigated for 86 loblolly pine clonal genetic varieties, growing in a single-tree plot clonal screening trial, using mixed-effects modeling approach. Akaike information criterion and likelihood ratio tests were used to compare competing model forms. Height growth trajectories for the different genetic varieties were modeled using the Chapman-Richards (C-R) and the Korf height-age functions. The type of model used was found to have an effect on the conclusion about the type of relationship among the height-age trajectories of the clonal genetic varieties. The anamorphic assumption was not rejected when the Korf equation was used. Polymorphism among the height-age trajectories, resulting from clone affecting the asymptote and shape parameters of the equation, was detected with the C-R equation. Coefficient of variation values of the random asymptote and random shape parameters of the C-R equation showed that there was greater variability due to clone in the asymptote than in the shape parameter. Fit index, root mean square residual, and mean bias values of the random asymptote only equation (anamorphic) and those of the random asymptote and shape equation (polymorphic) showed that the polymorphic assumption was probably not biologically significant. Prediction of the future height trajectory of a new clone, from early-age height measurements, was demonstrated with the C-R equation for mixed-effects model and least

squares calibration approaches using 25 of the 86 clones. Mixed-effects model predictions were biased for the observations at the extremes of the group distribution but were more accurate than the estimates from least squares calibration. Least squares calibration approach did not exhibit the type of bias observed with the mixed-effects model approach. Use of either approach to calibrate height-age models to new genetic varieties should consider the tradeoffs between bias and accuracy and the quantity and appropriateness of available prior information.

**Keywords:** *Pinus taeda*, mixed-effects model calibration, least squares calibration, site index prediction

### 3.1. Introduction

Height growth is the commonly preferred measure of forest growth due to its relative stability over a wide range of non-extreme stand densities. Height growth is modeled as a function of age and parameters that describe the overall shape of the height-age curve. Commonly used height-age functions have an upper asymptote parameter and a rate parameter that determines how fast the upper asymptote is reached. Others have additional parameters for more flexibility in curve fitting. In a review of height-age functions, Zeide (1993) identified functions that have been commonly used to describe height growth in loblolly pine as the two parameter Korf function

$$H_{iA} = \beta_1 \times \exp(-\beta_2 A^{-1}) + \varepsilon_{iA} \quad (3.1)$$

and the three parameter Chapman-Richard's function

$$H_{iA} = \beta_1 (1 - \exp(-\beta_2 A))^{\beta_3} + \varepsilon_{iA} \quad (3.2)$$

(Richards 1959). In equations 3.1 and 3.2,  $H_{iA}$  is the total height of the  $i^{\text{th}}$  clone at age  $A$ ,  $\beta_1$  is the asymptote parameter,  $\beta_2$  is the rate parameter,  $\beta_3$  is the shape parameter, and  $\varepsilon_{iA}$  is a random error due to the observed total height at age  $A$  ( $\varepsilon_{iA} \sim N(0, \sigma_{\varepsilon A}^2)$ ). Height-age relationships are useful in growth and yield modeling for predicting future heights of stands or for predicting site index that is then used as a predictor in a growth and yield model.

Stands of different genetic varieties growing in a similar location grow along different height growth trajectories (Buford and Burkhart 1987; Magnussen and Kremer 1993; Tang et al. 2001). The effect of genetic variety has been studied by investigating how the parameters of height-age relationships differ among stands of different genetic varieties of different height

growth potentials. Changes in the parameters indicate the type of change in the height trajectory and how differences among the genetic varieties, at early ages, relate to the differences at rotation age. Studies using seed source and first generation half-sib genetic varieties of loblolly pine led to different conclusions on the effect of genetic improvement on height growth trajectory. Nance and Wells (1981) and Buford and Burkhart (1985, 1987), using equation 3.1, concluded that genetic improvement affected only the asymptote parameter. This type of effect implies that proportional gains in height growth, due to genetic improvement, are maintained throughout the rotation. This assumption has been used widely in estimating gains in yield due to genetic improvement (Li et al. 1999; McKeand et al. 2006; Newton 2003). Sprinz et. al. (1989) reported that genetic variety only affected the shape parameter of equation 3.2 and argued that different genetic varieties grew towards a common asymptote following different trajectories, which could be explained by differences in the shape parameter. Under this assumption, height differences among genetic varieties increase with age to a maximum around mid-rotation then decrease as stands approach rotation age (Figure 8 of Sprinz et al. 1989). The assumption allows for disjoint polymorphism among height-age curves of genetic varieties. Using equation 3.2, Knowe and Foster (1989) concluded that genetic variety affected the asymptote and the rate parameters and hence different genetic varieties grew to different asymptotes at different rates. This assumption allows for both disjoint and non-disjoint polymorphism among height-age curves of different genetic varieties. In a study with Chinese fir (*Cunninghamia lanceolata* Lamb.) seed source genetic varieties, Tang et al. (2001), using equation 3.1, concluded that genetic variety affected the asymptote parameter but not the rate parameter.

The differences in the conclusions by the different researchers could be due to the differences in the model forms used or the differences in the ages of the stands sampled.

Investigations based on equation 3.1 arrived at the conclusion of anamorphic height growth trajectories for different genetic varieties. Those based on equation 3.2 did not agree with the anamorphic conclusion. The age range of the stands used in the investigations could also have led to differences in the conclusions. Other than the stands used in the study by Sprinz et al. (1989), which were 29 years of age, those used in the studies by the other authors were 15 to 25 years old. Data from the 29-year old stands pointed to a single asymptote parameter for all genetic varieties while data from the younger stands pointed to different asymptotes for different genetic varieties with either anamorphic or polymorphic height growth trajectories. There is a need to understand if the model form and the age of the stands used in a study have any effect on the conclusions that could be reached.

Genetic improvement for pines of southern United States has progressed considerably since the late 1980's when most of the studies on effect of genetic variety on height growth trajectories were done. Currently, more advanced techniques of breeding and propagation are being used. The breeding program is in its third cycle with second and third generation seed orchards supplying over 80% of seed used in planting the approximately 2 million acres of pine plantations established annually in this region (McKeand et al. 2003; Virginia Department of Forestry 2009). The more highly selective control pollination (CP) and cloning are also being used to produce pine planting material. Over 100 million full-sib CP seedlings and over 10 million somatic embryogenesis clones have been used in plantation establishment in the last ten years (McKeand et al. 2007). Marker-assisted selection and breeding and genetic engineering are also being applied in the genetic improvement of southern pines (White et al. 2007, p. 553 – 591). These are likely to increase the differences among loblolly pine varieties planted in southern United States as trees get “designed” to meet certain specific objectives such as

biomass, pulp and paper, saw timber, etc. With these rapid changes, it is important to understand the height growth relationships among different genetic varieties to provide a means of accurately adjusting an overall loblolly pine height-age curve to a specific genetic variety.

Gains from genetic improvement programs are normally measured at early ages (about 6 to 8 years old) and the differences among the genetic varieties at the early age projected to obtain differences at rotation age. Gains in height growth are normally reported as gains in site index. With the anamorphic relationship that has been commonly assumed, site index gains due to genetic improvement may be estimated through proportional increases in site index values using the proportional differences at the early age (Lambeth 2000; Matziris 2005; Vergara et al. 2004). With the highly selective tree breeding and propagation techniques currently being applied in southern pines, polymorphism in height-age trajectories may become more pronounced than is the case in stands composed of a mix of genotypes. Proportional adjustments of site indices based on selection age proportional differences in observed heights may not give accurate estimates of site index gain. Methods that are capable of incorporating both disjoint and non-disjoint polymorphism in the prediction of future heights of genetic varieties may be required. Empirical Bayes approach of calibration, commonly known as mixed-effects model calibration approach (Vonesh and Chinchilli 1997 Chapter 7), is one possible method of calibration that has the flexibility of incorporating polymorphism of the height-age relationships in future height predictions. The applicability of this technique to forestry problems has been demonstrated for height-dbh equations (Lappi 1997; Lynch et al. 2005; Robinson and Wykoff 2004); volume equations (Lappi 1991); taper equations (Trincado and Burkhart 2006); diameter distributions (Fortin et al. 2006); and height-age/site index equations (Fang and Bailey 2001; Wang et al. 2008; Wang et al. 2007). Mixed-effects model approach of calibration, however, requires an

estimate of the covariance matrix of the random effects and an assumption that the random effects follow a certain distribution mostly the normal distribution. Information on the covariance matrix of the random effects may not be available or the matrix may not be appropriate for a given application. It may also not be appropriate to assume some probability distribution for a given application. An alternative method, which does not require knowledge of the covariance matrix of the random effects and an assumption that the subject-specific effects follow a certain probability distribution, is the least squares (LS) approach. With this approach the height-age equation containing estimates of the global parameters is calibrated by ordinary least squares regression, using the available early-age height data, to estimate the genetic variety-specific parameters. Wang et al. (2008) demonstrated this approach with plot-specific site index equations. An evaluation of the performance of the alternative methods is necessary to provide an understanding of their strengths and weaknesses.

The objectives of this study were 1) to determine the effect of clone on the parameters of the height-age relationship of loblolly pine and 2) to determine the accuracy of predicting the future height trajectory and site index of a new loblolly pine clone from early-age height measurements, using MM and LS calibration techniques. Under objective 1, we tested the hypothesis that genetic variety had no effect on the parameters of loblolly pine height-age relationship except the asymptote parameter. We also investigated the effect of the type of height-age model on the conclusions on the effect of clone on model parameters.

## 3.2. Methods

### 3.2.1. Study material, study area, and data

The study material was made up of 120 clonal genetic varieties developed by MeadWestvaco Company from a controlled cross between two half-sibling (half-sib) genetic varieties identified within MeadWestvaco and ArborGen® as WV3 and WV5. Each of the 120 clones had 10 rooted cutting ramets at the start of the study. The study was planted in the spring of 1994 on an old-field site near Summerville in Berkeley County, South Carolina (33°17' N, 80°14' W) in the Atlantic Coastal Plain physiographic region of the United States. It was a single-tree plot genetic screening trial. Site preparation included sub soiling and chemical weed control. The setup of the study was a randomized complete block design of 10 contiguous blocks with 1 ramet of the 10 per clone planted in a random position in every block. The ramets were spaced at 9 ft by 9ft. Two rows of buffer trees were established around the study. Total height and dbh, in addition to other measurements not used here, were measured on every surviving tree at ages 1 to 10, 13, and 15. Fertilizer application was done every 3 years until age 12 and there was complete control of competing vegetation for the duration of the study. Selection thinning was done in 5 of the ten blocks at the end of the 8<sup>th</sup> growing season during which damaged trees and those badly infested with fusiform rust were removed.

Clones that had at least 5 undamaged surviving ramets at age 15 provided the height data that was used here. The arithmetic mean height of the 5 or more trees of a given clone at a given age was considered as the height for the clone at that age. Only the trees available for measurement at age 15 were the ones that provided the height measurements for the earlier ages even if the clone had more trees at the earlier ages. Eighty-six of the 120 clones in the study

satisfied this criterion and hence were used to investigate the effect of genetic variety on the height growth trajectory of clonal loblolly pine. The clone average total height growth trajectories for the 86 clones are shown in Figure 3.1.

In single tree genetic screening trial experiments like the one used in this study, genetic varieties that start off with fast height growth could overgrow those that start off at a slow pace resulting in effect of competition on height growth confounding the effect of genetic variety (Cappa and Cantet 2008; Foster 1989; Magnussen 1989). Thus, data from a single tree genetic trial may not be suitable for investigating effect of genetic variety on parameters of height growth trajectory. The possibility of within stand competition affecting height growth in the study was investigated using the Pearson correlation coefficients between annual height increment of the trees in the study and a modification of the Hegyi (1974) competition index

$$CI_i = \sum_{j=1}^n \frac{Vol_j}{Vol_i} \times \frac{1}{d_{ij}} \quad (3.3)$$

where,  $CI_i$  the competition index for the  $i^{\text{th}}$  subject tree,  $Vol_i$  is the volume of the  $i^{\text{th}}$  subject tree,  $Vol_j$  is the volume of its  $j^{\text{th}}$  competitor, and  $d_{ij}$  is the Euclidean distance between the  $i^{\text{th}}$  subject tree and its  $j^{\text{th}}$  competitor. The  $n$  competitors for the  $i^{\text{th}}$  subject tree were selected using the basal area factor 10 angle with the vertex centered at the subject tree approach of Daniels (1976). Tree volumes were estimated as  $dbh^2 \times \text{total height}$ . Correlation coefficients were computed for each of the growing seasons 5<sup>th</sup> to 11<sup>th</sup>, and 14<sup>th</sup>. The correlations between annual height growth and the competition index in equation 3.3 were only significant at  $\alpha = 0.05$  for the 11<sup>th</sup> and the 14<sup>th</sup> growing seasons (Pearson correlation coefficients = 0.4064 and 0.3560 for the 11<sup>th</sup> and 14<sup>th</sup> growing seasons respectively). Competition from neighboring trees, therefore, had no significant effect on height growth in the study for at least ten growing seasons. It is therefore unlikely that

the competition from the taller growing clones had a major effect on the height growth of the shorter growing clones, and the data were judged suitable to be used to gain insights into the effect of clone on parameters of the height growth trajectory of genetically enhanced loblolly pine.

Thinning has been found to have some effect on height growth trajectory of loblolly pine with height growth slowing down slightly during the period immediately after thinning (Sharma et al. 2006). Whether thinning at age 8 in some of the blocks of the study had a significant impact on the height growth trajectories of the clones or not was investigated using 41 of the 86 clones selected for height-age relationship analysis. The 41 clones are those represented, at age 15, in at least 3 unthinned blocks and in at least 3 thinned blocks. The effect of thinning was investigated using graphical techniques to compare average height growth trajectories of the same clones in the thinned and the unthinned portions of the study. For a given clone, the height growth trajectory, after thinning, for the trees in the thinned portion of the stand did not appear to differ significantly from the trajectory of the trees in the unthinned portion. The effect of thinning was tested using an expanded form of equation 3.2 in which a thinning effect variable was associated with each of the model parameters

$$H_{iA} = (\beta_{10} + \beta_{11}T + b_{10i}) \times \{1 - \exp(-[\beta_{20} + \beta_{21}T + b_{20i}]A)\}^{(\beta_{30} + \beta_{31}T + b_{30i})} + \varepsilon_{iA} \quad (3.4)$$

and that without the thinning variable

$$H_{iA} = (\beta_{10} + b_{10i}) \times \{1 - \exp(-[\beta_{20} + b_{20i}]A)\}^{(\beta_{30} + b_{30i})} + \varepsilon_{iA} \quad (3.5)$$

In equations 3.4 and 3.5,  $H_{iA}$  is the mean height of the  $i^{\text{th}}$  clone at age  $A$ ;  $\beta_{10}$ ,  $\beta_{20}$ , and  $\beta_{30}$  are the fixed-effect parameters;  $\beta_{11}$ ,  $\beta_{21}$ , and  $\beta_{31}$  are fixed thinning effect parameters;  $b_{10i}$ ,  $b_{20i}$ , and  $b_{30i}$

are random effect parameters due to the  $i^{\text{th}}$  clone ( $i = 1, 2, \dots, 41$ ) with each of the random effect parameters being normally distributed with mean zero;  $\varepsilon_{iA}$  is the random within clone error due to the height observation for clone  $i$  at age  $A$ ; and  $T$  is the thinning dummy variable with value 0 for the trees in unthinned blocks and 1 for those in thinned blocks. Heteroscedasticity in the error term  $\varepsilon_{iA}$  was modeled as a power function of age and correlations among the values of  $\varepsilon_{iA}$ , due to repeated height measurements on the same trees, were modeled by assuming an autoregressive order 1 (AR(1)) error correlation structure. The equations were fitted to the height and age data of the 41 clones by nonlinear mixed-effects regression and their likelihood fit statistics compared using the likelihood ratio test (LRT). There was no significant difference between the likelihood fit statistics of the two models (LRT p-value = 0.1612). Thus, the thinning in some of the blocks of the study at age 8 did not significantly affect the height growth trajectories of the clones. Height data for the individual clones was therefore used without consideration of whether the clone was from the thinned or from the unthinned blocks.

### ***3.2.2. Effect of clone on parameters of height-age relationship***

The effects of genetic variety on the parameters of the height-age relationship were investigated using the models in equation 3.1 and 3.2. Due to the large number of clones involved, the effect of genetic variety on the parameters was treated as random with mean zero and a finite variance. To facilitate the analysis, equation 3.1 with the random effects for clone included was expanded to

$$H_{iA} = (\beta_1 + b_{1i}) \times \exp(-[\beta_2 + b_{2i}]A^{-1}) + \varepsilon_{iA} \quad (3.6)$$

where  $H_{iA}$ ,  $\beta_1$ ,  $\beta_2$ , and  $\varepsilon_{iA}$  are as defined in equation 3.1 and  $b_{1i}$  and  $b_{2i}$  are random-effect parameters due to the  $i^{\text{th}}$  clone ( $b_{1i} \sim N(0, \sigma_{b_1}^2)$  and  $b_{2i} \sim N(0, \sigma_{b_2}^2)$  with no correlations between them). Heteroscedasticity in the error term  $\varepsilon_{iA}$  was modeled as a power function of age and the correlations among the errors, due to repeated height measurements on the same trees, were modeled by assuming an autoregressive order 1 (AR(1)) error correlation structure. Equation 3.2 with random effects for clone on the model parameters appears as shown in equation 3.5. The random effect parameters in equation 3.5 were assumed to be distributed as  $b_{10i} \sim N(0, \sigma_{b_{10}}^2)$ ,  $b_{20i} \sim N(0, \sigma_{b_{20}}^2)$ , and  $b_{30i} \sim N(0, \sigma_{b_{30}}^2)$ ; with no correlations among the three random effect parameters.

The full models equation 3.5 and 3.6 were separately fitted to the height and age data from the 86 clones by nonlinear mixed-effects regression using the “nlme” package in R software (R Development Core Team 2010). The effect of genetic variety on model parameters were investigated by excluding the random effect parameters from the model one at a time and observing the effect of the exclusion on overall model fit. The significance of the change in model fit was investigated by looking at the significance of the differences in the Akaike Information Criterion (AIC) statistic value between the more parameterized model and the less parameterized one, using LRT statistic. The significance of any parameters beyond only the asymptote parameter was subjected to further tests of significance that were based on prediction accuracies. Prediction accuracies used were model fit index (FI), root mean square residual (RMSR), and mean absolute bias (MAB) calculated as

$$FI = 1 - \frac{\sum_{i=1}^N \sum_{j=1}^{n_i} (H_{ij} - \hat{H}_{ij})^2}{\sum_{i=1}^N \sum_{j=1}^{n_i} (H_{ij} - \bar{H})^2} \quad (3.7)$$

$$RMSR = \sqrt{\sum_{i=1}^N \sum_{j=1}^{n_i} \frac{(H_{ij} - \hat{H}_{ij})^2}{n_1 + n_2 + \dots + n_N}} \quad (3.8)$$

$$MAB = \frac{1}{N} \sum_{i=1}^N \left| \frac{\sum_{j=1}^{n_i} (\hat{H}_{ij} - H_{ij})}{n_i} \right| \quad (3.9)$$

respectively, where  $N$  is the number of clones,  $n_i$  is the number of height-age pairs for the  $i^{\text{th}}$  clone,  $H_{ij}$  is the  $j^{\text{th}}$  observed height for the  $i^{\text{th}}$  clone for  $j = 1 \dots n_i$ ,  $\hat{H}_{ij}$  is the  $j^{\text{th}}$  predicted height for the  $i^{\text{th}}$  clone, and  $\bar{H}$  is the mean of all the  $N \times n_i$  observations. Absolute value instead of actual bias was used to avoid positive and negative values for different clones cancelling out when averaged across clones. These prediction-based measures of fit for subject-specific parameter estimation have been recommended and applied in forestry (Huang et al. 2009; Wang et al. 2008). Graphical plots of bias trends were used to complement the prediction based measures of fit.

### ***3.2.3. Predicting future height growth trajectory and site index of a new loblolly pine clone from early-age height measurements***

#### ***3.2.3.1. Predicting future height growth trajectory by mixed-effects model calibration***

The prediction of future heights and site index of a new clone from early-age height data by MM calibration was investigated for 25 clones selected randomly out of the 86 clones used in the investigation in section 3.2.2. The 25 clones, hereinafter referred to as “New” clones, were representative of the range of observed heights at age 15 of the 86 clones (Table 3.1). The 61 remaining clones, hereinafter referred to as “Fitting” clones, were used to re-fit the parameters of

equation 3.2 in a mixed-effects model formulation with random effects for clone on the parameters identified in section 3.2.2 as those significantly affected by clone. The parameters were estimated by nonlinear mixed-effects regression by maximum likelihood using “nlme” package in R software (R Development Core Team 2010). For each of the 25 New clones, the empirical Bayes estimator of the random effect  $\hat{\mathbf{b}}_{ik}$  for the  $i^{\text{th}}$  clone was calculated as

$$\hat{\mathbf{b}}_{ik} \cong \hat{\mathbf{D}}\hat{\mathbf{Z}}_k' [\hat{\mathbf{Z}}_k \hat{\mathbf{D}}\hat{\mathbf{Z}}_k' + \hat{\mathbf{R}}_k]^{-1} (\mathbf{y}_k - f(\mathbf{A}_k \hat{\boldsymbol{\beta}}, \mathbf{x}_k)) \quad (3.10)$$

where  $k$  is the number of early-age height measurements used in the estimation;  $\hat{\mathbf{D}}$  is the  $q \times q$  covariance matrix for the random-effect parameters estimated when equation 3.2 with significant random-effect parameters for clone was fitted to the data from the Fitting clones, with  $q$  as the number of random-effect parameters;  $\hat{\mathbf{Z}}_k$  is a matrix computed as  $\hat{\mathbf{F}}_k \cdot \mathbf{B}$  where  $\hat{\mathbf{F}}_k$  is the  $k \times p$ , with  $p$  as the number of parameters in equation 3.2, matrix of partial derivatives

$$\left. \frac{\partial f(\mathbf{A}_k \boldsymbol{\beta}, \mathbf{x}_k)}{\partial \boldsymbol{\beta}_k'} \right|_{\boldsymbol{\beta}=\hat{\boldsymbol{\beta}}} \quad (3.11)$$

and  $\mathbf{B}$  is the  $p \times q$  design matrix for the random effects;  $\hat{\mathbf{R}}_k$  is a  $k \times k$  covariance matrix for the within clone error terms estimated as

$$\hat{\mathbf{R}}_k = \sigma_e^2 [\text{diag}[A_{ik}^{2\hat{\delta}}]^{0.5} \cdot \Gamma_{k \times k} \cdot \text{diag}[A_{ik}^{2\hat{\delta}}]^{0.5}] \quad (3.12)$$

where  $\sigma_e^2$  is the residual variance,  $A_{ik}$  is the  $k^{\text{th}}$  age for the  $i^{\text{th}}$  new clone,  $\hat{\delta}$  is the power variance function parameter,  $\Gamma_{k \times k}$  is the  $k \times k$  correlation matrix for the  $k$  early-age measurements;  $\mathbf{y}_k$  is a  $k \times 1$  vector of the  $k$  early-age height measurements;  $\mathbf{A}_k$  is the  $k \times p$  design matrix of the

population average parameters;  $\hat{\boldsymbol{\beta}}$  is the  $p \times 1$  vector of the population average parameters estimated from the Fitting clones data; and  $\mathbf{x}_k$  is the  $k \times 1$  vector of the  $k$  early ages at which the early-age height measurements were taken (Vonesh and Chinchilli 1997 Chapter 7). The maximum early age used in this investigation was age 5. This maximum was chosen based on the findings of Lambeth (1980) that optimum selection age for rotations of 30 years would be 6 years. We considered age 5 to be an optimum selection age for height growth given that there have been advances in genetic improvement and that current loblolly pine plantations of the southern United States have fast growth rates that have made shorter rotations (approximately 25 years) possible (Fox et al. 2007). The combinations of early age height measurements used were a single measurement at age 5; two measurements – an age 5 measurement and 1 earlier measurement at age 1, age 2, or age 3; and five measurements from each of the ages 1 to 5. For the 2 early age height measurements, we did not use an age 4 and 5 combination as we considered the two ages too close to each other that they might not capture the height growth trajectory accurately. The portion  $(\mathbf{y}_k - f(\mathbf{A}_k \hat{\boldsymbol{\beta}}, \mathbf{x}_k))$  in equation 3.10 is sometimes simply denoted as  $\mathbf{e}_k$ , the vector of the  $k$  error terms.

The predicted vector of random effects  $\hat{\mathbf{b}}_{ik}$  for the  $i^{\text{th}}$  New clone, for  $i = 1, \dots, 25$ , was used to adjust the population average parameters vector  $\hat{\boldsymbol{\beta}}$  to obtain clone-specific vector of parameter estimates  $\hat{\boldsymbol{\beta}}_{ik}$  as

$$\hat{\boldsymbol{\beta}}_{ik} = \hat{\boldsymbol{\beta}} + \hat{\mathbf{b}}_{ik} \tag{3.13}$$

The clone-specific vector of parameter estimates  $\hat{\beta}_{ik}$  was used with equation 3.2 to obtain the predicted height trajectory of the  $i^{\text{th}}$  New clone. The error of prediction for each New clone was the root mean square error (RMSE) calculated as

$$\text{RMSE}_i = \sqrt{\bar{e}_i^2 + \sigma_{e_i}^2} \quad (3.14)$$

where,  $\bar{e}_i$  is the mean and  $\sigma_{e_i}^2$  the variance of the residuals for the  $i^{\text{th}}$  New clone. The residuals for each New clone were calculated as the difference between the height observed at a given age and that estimated using the clone-specific parameter estimates from equation 3.13. Bias due to prediction of site index (base age 15) from early-age measurements was evaluated for each New clone as the predicted height at age 15 less the height observed at this age. The values of RMSE and those of site index base age 15 ( $\text{SI}_{15}$ ) bias were used to compare the performances of the different combinations of early-age measurements in predicting future height trajectories and hence site index for each New clone and also to compare the MM approach of predicting the future height trajectory of a new clone to the LS calibration approach explained in section 3.2.3.2

### *3.2.3.2. Predicting future height growth trajectory by least squares calibration*

The prediction of the future height trajectory and site index of a new loblolly pine clone from early-age height measurements, by LS calibration approach, was demonstrated using the same Fitting and New clones described in section 3.2.3.1. The data from the 61 Fitting clones were used to estimate the global and the clone specific parameters of equation 3.2 by nonlinear least squares regression; with dummy variables associated with the clone-specific parameters

identified in section 3.2.2. The dummy variables were  $D_i = 1$  if the  $i^{\text{th}}$  clone and 0 otherwise. The clone-specific parameters estimated for the 61 Fitting clones were just nuisance parameters and were not used in the calibration work. Their role was to provide a means of accounting for clone-specific effects in the estimation of the parameters not affected by clone (the global parameters). The estimates of the global parameters were substituted into equation 3.2 and the equation fitted separately to the early age height data of each New clone, by nonlinear least squares, to estimate the clone-specific parameters for each New clone. The early age height measurement combinations used were the same as those used in the MM approach in section 3.2.3.1 above. The clone-specific parameter estimates for each New clone were used, with equation 3.2, to predict the height trajectory of that clone. The prediction error for each New clone was then calculated using equation 3.14. Bias in predicting  $SI_{15}$  was calculated using the same procedure used for the MM approach. Errors due to prediction of the future height trajectory and the  $SI_{15}$  of a new clone by the LS approach were compared to those by MMA by graphical and parametric techniques.

### **3.3. Results**

#### ***3.3.1. Effect of clone on parameters of the height-age relationship***

The AIC measures of model fit for the height-age equations with different combinations of clone specific parameters are given in Table 3.2. Overall, the Chapman-Richards (C-R) equation 3.2 and its variations of clone specific parameters fitted the data better than the Korf equation 3.1. Varying the asymptote parameter randomly with clone significantly improved model fit for both the C-R and the Korf equations compared to the model that did not take into

account variation of any of the parameters by clone (LRT p-value < 0.0001). Varying the rate or shape parameter randomly with clone, in addition to varying the asymptote parameter, significantly improved model fit of the CR-equation (LRT p-value < 0.0001) but the improvement was greater with addition of the random effect parameter for clone on the shape parameter than with the addition of random effect parameter for clone on the rate parameter. Addition of the second random effect parameter on the Korf model did not improve model fit. For cases with only one random parameter for clone, varying the asymptote parameter randomly with clone gave better model fit than varying only the rate parameter or only the shape parameter. For the two random parameter cases with the C-R equation, varying the shape and rate parameters randomly with clone did not give as good a model fit as varying the asymptote and shape or the asymptote and rate parameters. The C-R equation with all 3 parameters varying randomly with clone was not considered as the parameter estimation algorithm would not converge. The best fitting clone specific height-age equation was the C-R equation with asymptote and shape parameters varying randomly with clone. For this equation, the variability due to effect of clone on the asymptote parameter was larger (coefficient of variation = 4.21%) than the variability in shape parameter (coefficient of variation = 2.84%). The C-R equation with only the asymptote parameter varying randomly with clone was the second best fitting equation.

Table 3.3 gives the parameter estimates and prediction fit statistics for the two best fitting clone-specific height-age equations. The prediction accuracy of the model with random-effect for clone on asymptote parameter alone did not appear to differ greatly from the accuracy of the model with random-effect for clone on the asymptote and shape parameters. The FI values of the two models were not different and the model root mean square values differed by approximately

0.1 ft. The mean MAB value indicated that the model the 2 random parameter for clone model was 5 times more precise than the model with only 1 random parameter model but the precision were both within 0.5 ft. The higher precision of the 2 random parameter model and the effect of clone size on the sign of the bias are shown in Figure 3.2. The random-effect parameters of the two model forms did not appear to violate the assumption that the random effect parameters came from a normal distribution with mean zero (Figure 3.3). The residual plots (Figure 3.4) indicated that modeling of the residual variance as a power function of age took care of the heteroscedasticity in the model fitting.

The C-R height-age model described the height-age trajectories of the different clones better than the Korf model. Statistical tests indicated that the polymorphic model with asymptote and shape parameters varying with clone fitted the data better but prediction accuracies indicated that the polymorphism, due to the shape parameter varying randomly with clone, may not be biologically significant.

### ***3.3.2. Predicting future height growth trajectory and site index of a new loblolly pine clone from early-age height measurements***

#### ***3.3.2.1. Mixed-effects model calibration results***

From section 3.3.1, the C-R equation with random effects for clone on the asymptote and shape parameters was the most appropriate height-age model for the data. The demonstration of the application of MM approach in predicting the future height trajectory of a new clone was based on this equation. The population average parameters vector  $\hat{\beta}$  estimated from the height

and age data of the 61 Fitting clones was  $[92.99, 0.145, 1.866]^T$ . The estimated covariance matrix of random effects  $\hat{\mathbf{D}}$  was a  $2 \times 2$  diagonal matrix  $diag[14.57, 0.0023]$ . The error vector  $\mathbf{e}_k$  was a scalar when only the age 5 height measurement was used in the calibration, a vector of length 2 when two early-age height measurements were used, and a vector of length 5 when the ages 1 to 5 height measurements were used. The derivative in equation 3.11 for estimating the matrix  $\hat{\mathbf{F}}_k$  solved to

$$\begin{bmatrix} (1 - \exp(-\beta_2 A_k))^{\beta_3} | \beta_1 \beta_3 (1 - \exp(-\beta_2 A_k))^{\beta_3 - 1} \cdot A_k \cdot \exp(-\beta_2 A_k) | \beta_1 (1 - \exp(-\beta_2 A_k))^{\beta_3} \cdot \ln(1 - \exp(-\beta_2 A_k)) \\ \vdots \\ (1 - \exp(-\beta_2 \cdot 5))^{\beta_3} | \beta_1 \beta_3 (1 - \exp(-\beta_2 \cdot 5))^{\beta_3 - 1} \cdot 5 \cdot \exp(-\beta_2 \cdot 5) | \beta_1 (1 - \exp(-\beta_2 \cdot 5))^{\beta_3} \cdot \ln(1 - \exp(-\beta_2 \cdot 5)) \end{bmatrix} \quad (3.15)$$

where  $A_k$  is the  $k^{\text{th}}$  early age for  $k = 1$  and/or 2 and/or 3 and 4,  $\exp$  is exponential function  $\ln$  is natural logarithm, 5 stands for age 5, and the parameter estimates in the vector  $\hat{\boldsymbol{\beta}}$  substituted  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$ . The vertical bars in matrix 3.15 mark where one element of the matrix ends. When two early age measurements were used in the calibration, matrix 3.15 was a  $2 \times 3$  matrix. The matrix was of dimension  $5 \times 3$  when the ages 1 to 5 height measurements were used, and a  $1 \times 3$  matrix made up of only the last row of the matrix 3.15, when only the age 5 height measurement was used in the calibration. Given that there were 2 random effects for clone in the C-R equation used, the design matrix of the random effects  $\mathbf{B}$  was

$$\begin{bmatrix} 1 & 0 \\ 0 & 0 \\ 0 & 1 \end{bmatrix} \quad (3.16)$$

The matrix  $\hat{\mathbf{R}}_k$  in equation 3.10 was a  $2 \times 2$  matrix when 2 early-age height measurements were used. With at least 1 height measurement separating the 2 early age measurements used, and a small (0.131) AR(1) correlation parameter estimated from the 61 Fitting clones, the correlation

between the 2 early age height measurements used was assumed to be zero. Thus, the correlation matrix  $\Gamma_{k \times k}$  in equation 3.12 reduced to an identity matrix and hence  $\hat{\mathbf{R}}_k$  reduced to the  $2 \times 2$  diagonal matrix  $\sigma_e^2 \cdot [diag[A_k^{2\hat{\delta}}, 5^{2\hat{\delta}}]]$ . In the case where only the age 5 measurement was used in the calibration, the matrix  $\hat{\mathbf{R}}_k$  was reduced to a scalar  $\sigma_e^2 \cdot 5^{2\hat{\delta}}$ . For the calibration with height measurements from ages 1 to 5,  $\hat{\mathbf{R}}_k$  was a  $5 \times 5$  diagonal matrix  $\sigma_e^2 \cdot [diag[A_k^{2\hat{\delta}}]]$ . The correlation of 0.131 between the errors from adjacent height measurements was judged very small as not to be included in the matrix.

The prediction accuracies for the future height trajectory and  $SI_{15}$  for the 25 New clones, based on MM calibration and different combinations of early-age height measurements, are compared in Figure 3.5. Generally, there were no major differences in the prediction accuracies of the different combinations of calibration ages, across the 25 New clones with the exception of the fastest growing 4 clones where the calibration with 5 early-age height measurements resulted in more accurate predictions compared to the calibration with 1 or 2 early-age height measurements. For the rest of the clones, there was generally no difference in the prediction accuracies for the different combinations of calibration ages. For all the 25 New clones, calibration with a single height measurement at age 5 predicted the future height trajectory and  $SI_{15}$  with accuracy that was equivalent to that of calibration 2 early-age height measurements that included an age 5 height measurement. The average prediction accuracies (Table 3.4) indicated only minor differences in the overall accuracies of the predictions. From the Table, calibration with height measurements from ages 1 and 5 was the most accurate for both the prediction of the future height trajectory and for prediction of  $SI_{15}$  when 2 early-age height measurements were used. The calibration using all the 5 early-age height measurements from ages 1 to 5, as

expected, resulted in the lowest error in prediction of the future height trajectory of a new clone but, unexpectedly, resulted in the highest mean absolute error in the prediction for SI<sub>15</sub>. The prediction accuracies changed predictably with size of the New clone with the trends of change being similar for all the combinations of calibration ages investigated. Root mean square error was larger for clones at the extremes (Figure 3.5 (a)) and predicted SI<sub>15</sub> became increasingly biased upwards with decrease in clone size away from the median clone and increasingly biased downwards with increase in clone size away from the median clone (Figure 3.5 (b)). Thus, with the clone of median height growth potential as the reference, the calibrated height-age curves generally overestimated site index for the slower growing clones and underestimated it for the faster growing ones.

### 3.3.2.2. Least squares calibration results

The C-R height-age equation, whose asymptote and shape parameters vary with clone, was identified in section 3.3.1 as the most appropriate for the height growth trajectories of the clones. This equation, with dummy variables for clone on asymptote and shape parameters, fitted to the Fitting clones height and age data resulted in the clone-specific height-age equation

$$H_{iA} = \alpha_{1i}(1 - \exp(-0.145178 \times A))^{\alpha_{2i}} + \varepsilon_{iA} \quad (3.17)$$

where  $\alpha_{1i}$  and  $\alpha_{2i}$  are, respectively, the clone-specific asymptote and shape parameters for the  $i^{\text{th}}$  clone and the rest are as defined for equation 3.2. Only the New clones' early-age height data that had the ages 1 through 5 height measurements were the ones used to estimate the parameters of equation 3.17. The data that had only 1 height measurement at age 5 and those that had 2

height measurements were not used. Model convergence issues made it impossible to fit equation 3.17 to early-age height data with only 2 observations. With two parameters to be estimated, equation 3.17 could not be easily fitted to the data with only 1 height measurement.

The prediction accuracies for the future height trajectory and for  $SI_{15}$  of each of the New clones, from the clone-specific parameter estimates obtained using equation 3.17, are compared in Figure 3.6. This figure also compares the prediction accuracies of LS calibration with 5 early-age height measurements to those of MM calibration with the same number of early-age height measurements. The overall prediction accuracies of the LS approach are given in Table 3.4 where they are also compared to the prediction accuracies of the MM approach. The results in Table 3.4 and Figure 3.6 (a) show that the LS approach was generally less accurate in predicting the future height trajectory across all the 25 New clones. The root mean square error values for the individual clones were in most of the cases higher for the LS approach than for the MM approach (Figure 3.6 (a)) and its average root mean square error value was the highest of all the calibration ages tested (Table 3.4). The approach resulted in an average root mean square error larger than even when only one early-age height measurement was used with MM approach. The LS approach also gave a mean absolute  $SI_{15}$  prediction error that was larger than that from any of the MM approach calibrations (Table 3.4). The LS approach, however, did not exhibit a clone size-related bias as seen with the MM approach (Figure 3.6 (b)). The accuracies of LS and MM calibration approaches in predicting the future height trajectories of clones at the extremes of the New clone size distribution are compared in Figure 3.7.

### 3.4. Discussion

#### 3.4.1. *Effect of clone on parameters of height-age relationship*

The less flexible Korf equation 3.1 indicated that the height-age relationships among the clones studied were a series of anamorphic height-age curves while the more flexible C-R equation 3.2 detected polymorphism among the curves due to differences in the shape parameters of the height-age curves for different clones. Thus, the type of equation used to model the height-age relationship can have an effect on the conclusion on the existence of polymorphism among the height-age curves for different genetic varieties. Both models, however, indicated that there was a significant effect of clone on the asymptote parameter. This agreed with the trends of the height-age trajectories (Figure 3.1). However, with the maximum age of the data used for the current study being 15 years, the data were not suitable for testing the hypothesis of the height-age trajectories converging to a common asymptote at advanced ages. This hypothesis was rejected for these data given the higher AIC values associated with the equations that had the asymptote parameter not varying with clone (Table 3.2). Height data for ages up to 25 years or more will be required to confirm whether there is a tendency of the height trajectories to converge to a common asymptote and whether that tendency affects the relationship among the trajectories at age 25. However, with rotations of about 25 years, the relationship among the height growth trajectories at 30 or more years may not be of importance if they have no effect on the relationships at age 25. It may be appropriate to assume height-age trajectories with different asymptotes for such shorter rotations even if the height growth trajectories of different genetic varieties will at some point in future converge to a common asymptote. Assuming a common asymptote for all genetic varieties for such rotations may result in height-age trajectories that poorly mimic the observed growths as seen in Figure 3.8. The height growth trajectories in this

figure are a poor representation of the observed height growth trajectories (Figure 3.1). Even though it may be biologically appropriate, the assumption of a common asymptote for height growth trajectories of different genetic families may not be practically appropriate especially in most forest plantation studies where height and age data used in fitting rarely have height and age measurements close to asymptotic age.

By the results with the Korf model, the conclusions of this study were similar to those of previous studies that used this model (Buford and Burkhart 1987; Nance and Wells 1981; Tang et al. 2001) where it was concluded that height growth trajectories of different genetic varieties growing in the same location were anamorphic. From the results of the C-R model, the findings of the current study are similar to those of the study by Knowe and Foster (1989) who concluded that there was polymorphism among height-age trajectories of different genetic varieties, which they attributed to the effect of genetic variety on the rate parameter of the C-R equation. In the current study, the polymorphism was found to be due to the effect of genetic variety on the shape parameter. This difference in the conclusion on which parameter is responsible for the polymorphism could be due to the asymptote and shape parameter combination not having been investigated in the study by Knowe and Foster (1989). With the shape parameter being the possible cause of polymorphism among the height growth trajectories modeled by the C-R equation, it is possible that the absence of a shape parameter in the Korf equation is the reason why polymorphism in the height growth trajectories of the clones could not be detected by this equation.

The results of the mixed-effects model calibration of the mean C-R height-age curve using early-age height measurements from “new” clones (Table 3.4 and Figure 3.5) appeared to support the conclusion of an anamorphic relationship among the height growth trajectories of the

different clones. Calibrating the population average height-age curve to a “new” clone using only one height measurement at age 5 predicted the future height trajectory of the “new” clone with accuracy that was equivalent to that obtained from multiple measurements. This would only happen if there was an anamorphic relationship among the height-age trajectories.

### ***3.4.2. Predicting future height growth trajectory and site index of a new loblolly pine clone from early-age height measurements***

Mixed-effects model calibration approach resulted in calibrations that were biased upwards for the groups below the population average mean and those that were biased downwards for the clones above the population mean. This happened because the empirical Bayes procedure used to predict the group level random-effects results in shrinkage parameter estimates (Pinheiro and Bates 2000 p. 152). The shrinkage is greatest for the group-specific parameters furthest from the population average parameter estimates. A similar trend was evident, though not emphasized, in the study by Wang et al. (2008). Previous studies that have demonstrated the application of the mixed-effects model approach of calibration only compared the performance of the calibrated model to the population average model (Lynch et al. 2005; Trincado and Burkhart 2006; Wang et al. 2007). The performance of the mixed-effects model approach across different subjects from the same population was never done.

Other than the bias, MM approach was superior to the LS approach in terms of prediction accuracy even when only 1 or 2 early age height measurements were used in calibration. This observation is different from that by Wang et al. (2008) who, using plot-specific random effects in calibration of site index curves, observed that LS calibration with multiple measurements was

similar in accuracy to the MM approach with the same number of measurements. The higher accuracy obtained with the MM approach in the current study and generally when measurements are few is probably due to the fact that this approach of calibration utilizes more information from the population, in terms of the covariance matrix of the random-effects and the variance matrix of the error terms, than the LS approach. It is likely that if this information is not available or is inappropriate for the application, then MM approach may produce undesirable results.

### **3.5. Conclusions and recommendations**

For the data used in this study, we determined that loblolly pine clone had no significant biological effect on rate and/or shape parameters of the C-R or Korf height-age equations but a significant effect on the asymptote parameter in these equations. The hypothesis of no effect of clone on parameters other than the asymptote parameter was therefore not rejected. Thus the height growth trajectories of the different clones were series of anamorphic height-age curves. A conclusion of significant effects of genetic variety on some of the parameters, that may not have a significant biological consequence, may be reported if the prediction differences of the different model formulations are not evaluated. Similar studies should incorporate analyses that look into differences among prediction accuracies of different model formulations where significant differences have been detected by the inference approaches used. We also determined that the type of equation used to model the height-age relationship could have an effect on the conclusions about the nature of the relationship among the height-age trajectories of the different clonal genetic varieties. We recommend that a more flexible height-age equation should be used

in such analyses especially with the highly specific genetic selection techniques currently used in loblolly pine.

The results of this study may not be generalized. The 86 clones used had common parents and hence similarities due to common parentage could have played some role in bringing about similarity in the height-age trajectories. Screening trials with clones of diverse parentage may exhibit somewhat different trends than observed in the current study. The results of this study may apply to clones from a common breeding line. For such clones, their height growth trajectories are likely to be a series of anamorphic height-age curves and the trajectory of any one clone in the breeding line can be estimated by proportional adjustment of the average height-age trajectory of the breeding line. Another limitation of the study was that the maximum age available for analysis was 15 years. Given that the common rotation age for pine plantations of southern United States is currently 25 years (Fox et al. 2007), this study did not have the complete data to do a rotation length analysis of effect of clone on parameters of loblolly pine height-age relationship. Age 15 to 25 height growth trajectories for the different clones can, however, be predicted by extrapolating the age 1 to 15 trajectories. Analysis with rotation length data may improve the parameter estimates and provide a rotation length assessment of the effects of clone on loblolly pine height growth.

We demonstrated how the future height trajectory and site index of a new genetic variety could be predicted from early-age height measurements using either the simpler LS approach that requires more current data but less prior information or the MM approach, which requires more prior information but is less demanding on the amount of currently available data. We also highlighted the possible prediction weaknesses of either approach. The choice of the technique to use will depend on what amount of early-age data available, the appropriateness of the prior

information available, and possibly whether the user is willing to sacrifice accuracy or bias. The idea of bias with MM approach due to shrinkage parameter estimates with empirical Bayes predictor of the subject-specific random effect was not addressed in most studies that applied or demonstrated this approach in forestry. We recommend that apart from highlighting the improved estimates resulting from calibration with mixed-effects over the use of the population average model, the performance of the technique especially at the limits of the distribution of the subjects should be evaluated. Mixed-effects model calibration approach is a promising calibration technique but any calibration with it should be done with awareness of its limitations.

### 3.6. Literature cited

Buford, M.A., and H.E. Burkhart. 1985. Dynamics of improved loblolly pine plantations and the implications for modeling growth of improved stands. P. 170 - 177 *in* Proceedings of the 18th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Long Beach, MS.

Buford, M.A., and H.E. Burkhart. 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci.* 33:707 - 724.

Cappa, E.P., and R.J.C. Cantet. 2008. Direct and competition additive effects in tree breeding: Bayesian estimation from an individual tree mixed model. *Silvae Genet.* 57:45-56.

Daniels, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. *For. Sci.* 22:454-456.

Fang, Z.X., and R.L. Bailey. 2001. Nonlinear mixed effects modeling for slash pine dominant height growth following intensive silvicultural treatments. *For. Sci.* 47:287-300.

Fortin, M., C. Ung, L. Archambault, and J. Bégin. 2006. Calibrating a generalized diameter distribution model with mixed effects. *For. Sci.* 52:650-658.

Foster, G.S. 1989. Inter-genotypic competition in forest trees and its impact on realized gain from family selection. P. 21 - 35 *in* Proceedings of the 20th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Charleston, SC.

Fox, T.R., E.J. Jokela, and H.L. Allen. 2007. The development of pine plantation silviculture in the southern United States. *J. For.* 105:337 - 347.

Hegy, F. 1974. A simulation model for managing jack-pine stands. P. 74-90 in Growth Models for Tree and Stand Simulation. Res. Notes No. 30. Royal College of Forestry, Stockholm, Sweden.

Huang, S., S.X. Meng, and Y. Yang. 2009. Assessing the goodness of fit of forest models estimated by nonlinear mixed-model methods. *Can. J. For. Res.* 39:2418-2436.

Knowe, S.A., and G.S. Foster. 1989. Application of growth models for simulating genetic gain of loblolly pine. *For. Sci.* 35:211-228.

Lambeth, C. 2000. Realized genetic gains for the first generation improved loblolly pine in 45 tests in coastal North Carolina. *South. J. Appl. For.* 24:140 - 144.

Lambeth, C.C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. *For. Sci.* 26:571-580.

Lappi, J. 1991. Calibration of height and volume equations with random parameters. *For. Sci.* 37:781 - 801.

Lappi, J. 1997. A longitudinal analysis of height/diameter curves. *For. Sci.* 43:555-570.

Li, B., S.E. McKeand, and R.J. Weir. 1999. Tree Improvement and sustainable forestry-Impact of two cycles of loblolly pine breeding in the USA. *For. Genet.* 6:229 - 234.

Lynch, T.B., A.G. Holley, and D.J. Stevenson. 2005. A random-parameter height-dbh model for cherrybark oak. *South. J. Appl. For.* 29:22 - 26.

Magnussen, S. 1989. Effects and adjustments of competition bias in progeny trials with single-tree plots. *For. Sci.* 35:532-547.

Magnussen, S., and A. Kremer. 1993. Selection for an optimum tree growth curve. *Silvae Genet.* 42:322-335.

Matziris, D. 2005. Genetic variation and realized genetic gain from black pine tree improvement. *Silvae Genet.* 54:96-103.

McKeand, S.E., R.C. Abt, H.L. Allen, B. Li, and G.P. Catts. 2006. What are the best loblolly pine genotypes worth to land owners? *J. For.* 104:352 - 358.

McKeand, S.E., T.J. Mullin, T.D. Byram, and T.L. White. 2003. Deployment of genetically improved loblolly and slash pines in the south. *J. For.* 101:32 - 37.

McKeand, S.E., B.J. Zobel, T.D. Byram, and D.A. Huber. 2007. Southern pine tree improvement-A living success story. P. 3 - 5 *in* Proceedings of the 29th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Galveston, TX.

Nance, W.L., and O.O. Wells. 1981. Site index models for height growth of planted loblolly pine (*Pinus taeda* L.) seed sources. P. 86 - 96 *in* Proceedings of the 16th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Blacksburg, VA.

Newton, P.F. 2003. Systematic review of yield responses of four North American conifers to forest tree improvement practices. *For. Ecol. Manage.* 172:29-51.

Pinheiro, J.C., and D.M. Bates. 2000. *Mixed-Effects Models in S and S-Plus*. Springer Verlag, New York, NY. 528 p.

R Development Core Team. 2010. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Richards, F.J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10:290 - 300.
- Robinson, A.P., and W.R. Wykoff. 2004. Imputing missing height measures using a mixed-effects modeling strategy. *Can. J. For. Res.* 34:2492-2500.
- Sharma, M., M. Smith, H.E. Burkhart, and R.L. Amateis. 2006. Modeling the impact of thinning on height development of dominant and codominant loblolly pine trees. *Ann. For. Sci.* 63:349-354.
- Sprinz, P.T., C.B. Talbert, and S.M. R. 1989. Height-Age trends from an Arkansas seed source study. *For. Sci.* 35:677 - 691.
- Tang, S., F.R. Meng, and C.P.A. Bourque. 2001. Analyzing parameters of growth and yield models for Chinese fir provenances with a linear mixed model approach. *Silvae Genet.* 50:140-145.
- Trincado, G., and H.E. Burkhart. 2006. A generalized approach for modeling and localizing stem profile curves. *For. Sci.* 52:670 - 682.
- Vergara, R., T.L. White, D.A. Huber, B.D. Shiver, and D.L. Rockwood. 2004. Estimated realized gains for first-generation slash pine (*Pinus elliottii* var. *elliottii*) tree improvement in southeastern United States. *Can. J. For. Res.* 34:2587 - 2600.
- Virginia Department of Forestry. 2009. Forest Research Review April 2009. Virginia Department of Forestry. 12 p.
- Vonesh, E.F., and V.M. Chinchilli. 1997. Linear and Nonlinear Models for Analysis of Repeated Measures. Dekker Inc., New York, NY. 560 p.

Wang, M., B.E. Borders, and D. Zhao. 2008. An empirical comparison of two subject-specific approaches to dominant heights modeling: The dummy variable method and the mixed model method. *For. Ecol. Manage.* 255:2659-2669.

Wang, Y., V.M. LeMay, and T.G. Bake. 2007. Modeling and prediction of dominant height and site index of *Eucalyptus globulus* plantations using a nonlinear mixed-effects model approach. *Can. J. For. Res.* 37:1390 - 1403.

White, T.L., W.T. Adams, and D.B. Neale. 2007. *Forest Genetics*. CAB International, London. 682 p.

Zeide, B. 1993. Analysis of growth equations. *For. Sci.* 39:594-616.

**Table 3.1:** Summary statistics for the heights at age 15 for the 61 clones used in model fitting and the 25 “New” clones used in model calibration.

Data	Statistic (ft)					
	Minimum	1 <sup>st</sup> Quartile	Mean	Median	3 <sup>rd</sup> Quartile	Maximum
Fitting Clones’ Data	66.3	72.0	74.2	74.8	76.8	81.7
“New” Clones Data	67.6	72.4	74.6	75.2	77.5	81.8

**Table 3.2:** Akaike Information Criterion (AIC) fit statistics for the different combinations of random clone-specific parameters in the Chapman-Richards and the Korf height-age equations fitted to the height and age data used in the study

Model	AIC Value for the Model with the Random Parameter Combination						
	None	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_1$ and $\beta_2$	$\beta_1$ and $\beta_3$	$\beta_2$ and $\beta_3$
C-R	2826	2663	2718	2828	2623	2572	2720
Korf	5052	3790	3822	-	3791	-	-

**Note:** C-R stands for the Chapman-Richards height-age equation

$H_{iA} = \beta_1(1 - \exp(-\beta_2 A))^{\beta_3} + \varepsilon_{iA}$ . Korf is equation  $H_{iA} = \beta_1 \times \exp(-\beta_2 A^{-1}) + \varepsilon_{iA}$ . In both equations  $H_{iA}$  is the total height at age  $A$  and  $\varepsilon_{iA}$  is the random error, with zero expectation, due to the total height measurement at age  $A$ ; and  $\beta_1$  is the asymptote parameter,  $\beta_2$  is the rate parameter, and  $\beta_3$  is the shape parameter

**Table 3.3:** Parameter estimates and prediction measures of fit for the Chapman-Richard (C-R) height- age equation, with random parameters for clone, fitted to the height and age data used in the study

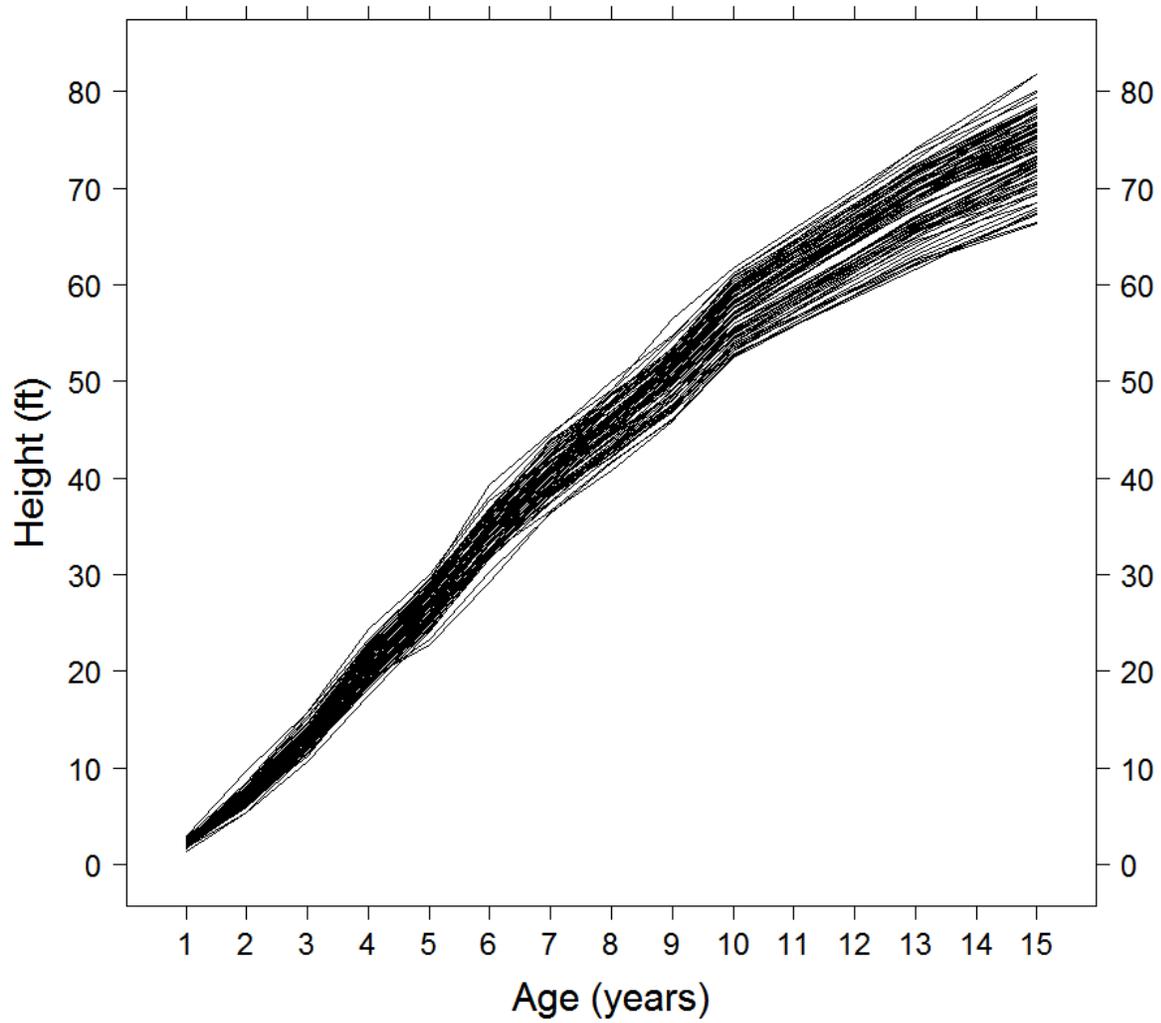
Random Parameter in Model	Parameter Estimates						Prediction Measures of Fit		
	$\beta_1$	$\beta_2$	$\beta_3$	$\sigma_{b_1}^2$	$\sigma_{b_3}^2$	$\sigma_{\epsilon}^2$	FI	RMSR (ft)	MAB (ft)
Asymptote	92.97	0.145	1.862	16.62	-	0.1190	0.999	0.828	0.15
Asymptote, Shape	93.04	0.145	1.860	15.37	0.0028	0.0611	0.999	0.690	0.03

**Note:** The estimates for the fixed-effect parameters  $\beta_1, \beta_2$ , and  $\beta_3$  were all significant ( $p < 0.0001$ ). FI stands for fit index, RMSR for root mean square residual, and MAB for mean absolute bias. The C-R equation with random asymptote and shape is the equation  $H_{iA} = (\beta_1 + b_{1i}) \times \{1 - \exp(-\beta_2 A)\}^{(\beta_3 + b_{3i})} + \epsilon_{iA}$  with  $b_{1i}$  and  $b_{3i}$  as the random-effect parameters for asymptote and shape respectively. The random-effect parameters and the random error term  $\epsilon_{iA}$  were each assumed to be normally distributed with mean zero.

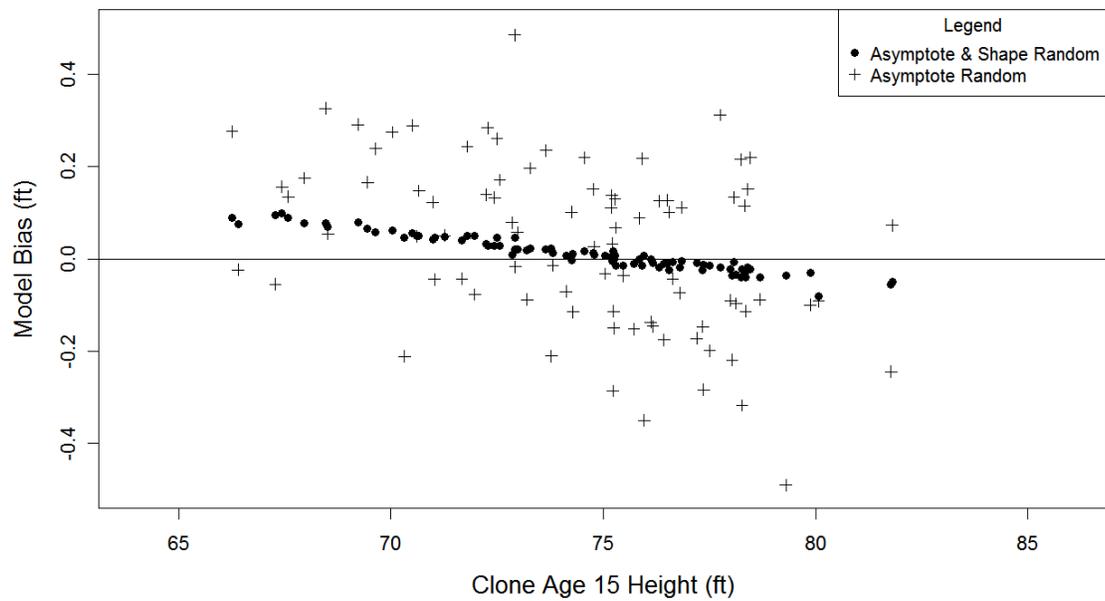
**Table 3.4:** Average prediction accuracies for the future height growth trajectories and for site index (base age 15) for the 25 “new” loblolly pine clones when the Chapman-Richards height-age equation, with the rate parameter assumed to be known, was calibrated to these clones using the clones’ early-age height measurements

Number of Early-age Height Measurements	Age(s) of the Early-age Height Measurement(s)	Mixed Model Calibration		Least Squares Calibration	
		Av. RMSE (ft)	MAPE (ft)	Av. RMSE (ft)	MAPE (ft)
One Measurement	5	1.30	1.79	-	-
	1 and 5	1.27	1.76	-	-
Two Measurements	2 and 5	1.28	1.78	-	-
	3 and 5	1.30	1.82	-	-
Five Measurements	1, 2, 3, 4, and 5	1.20	1.86	1.56	2.82

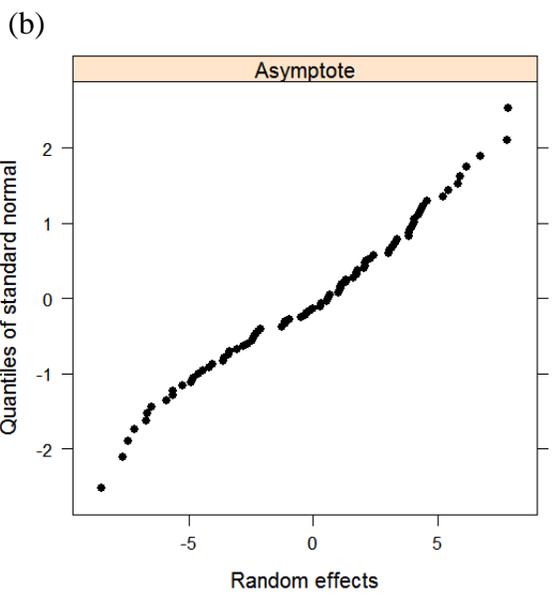
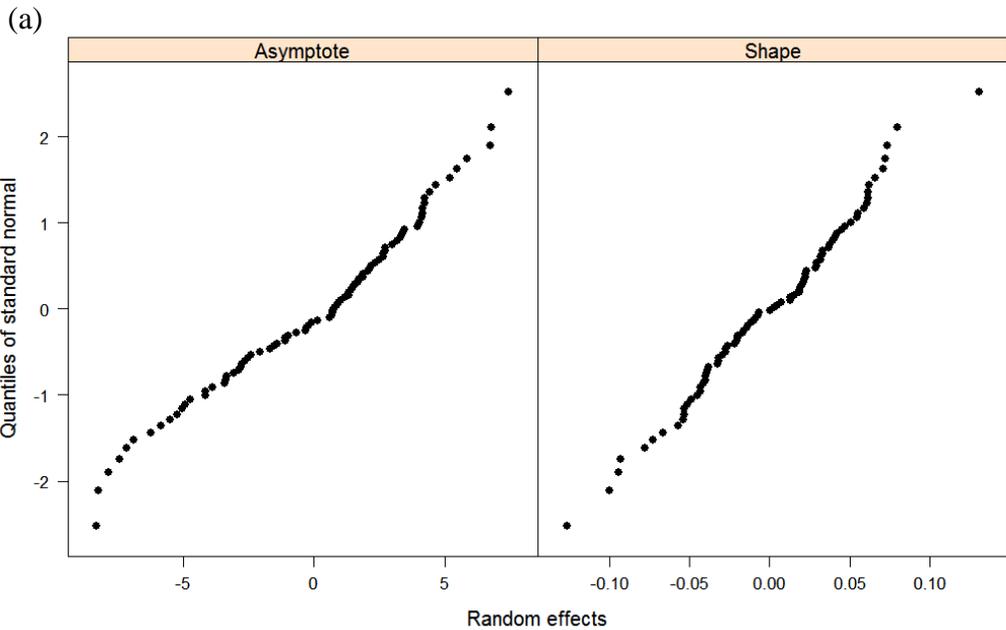
**Note:** Av. RMSE stands for average root mean square error and MAPE stands for mean absolute prediction error for site index (base age 15). The averages are arithmetic averages of these values from the 25 “new” clones used in the calibration.



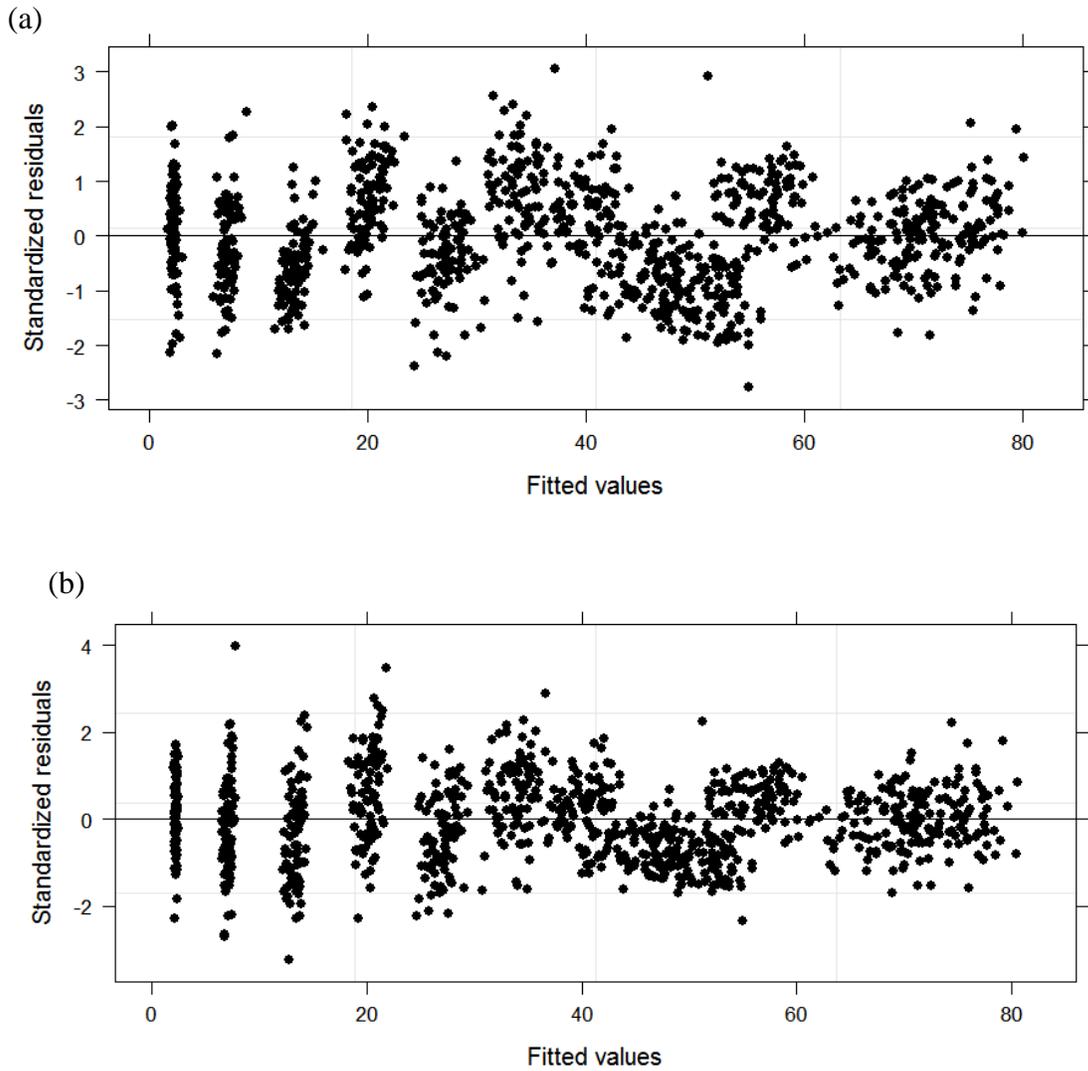
**Figure 3.1:** Height growth trajectories of the 86 rooted cutting loblolly pine clones with 5 or more undamaged surviving trees at age 15 in the single-tree plot genetic screening trial study of the 120 clones from a WV3  $\times$  WV5 control cross.



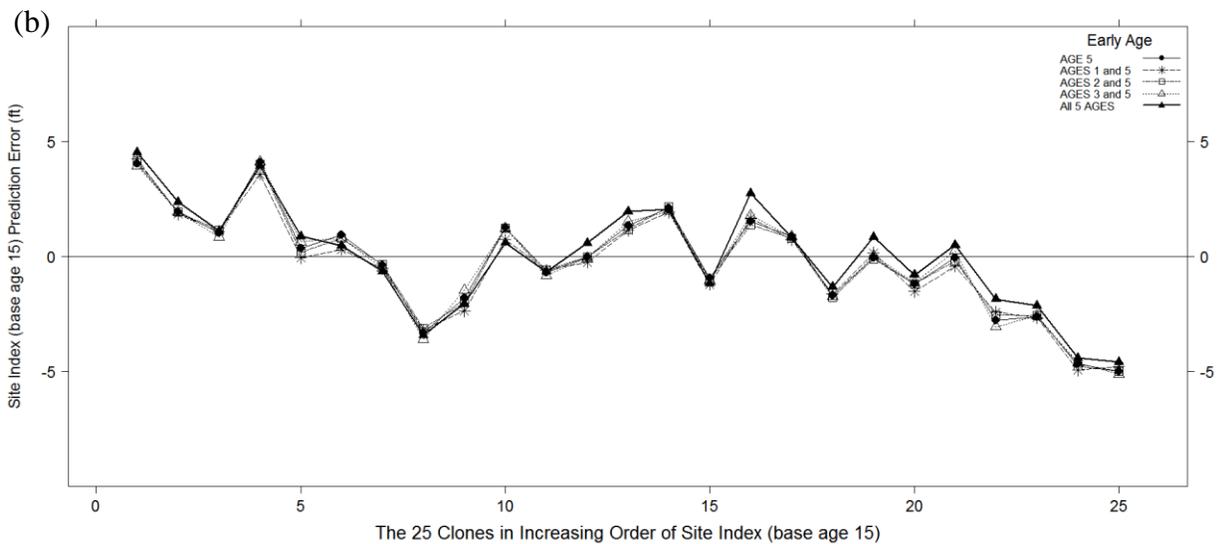
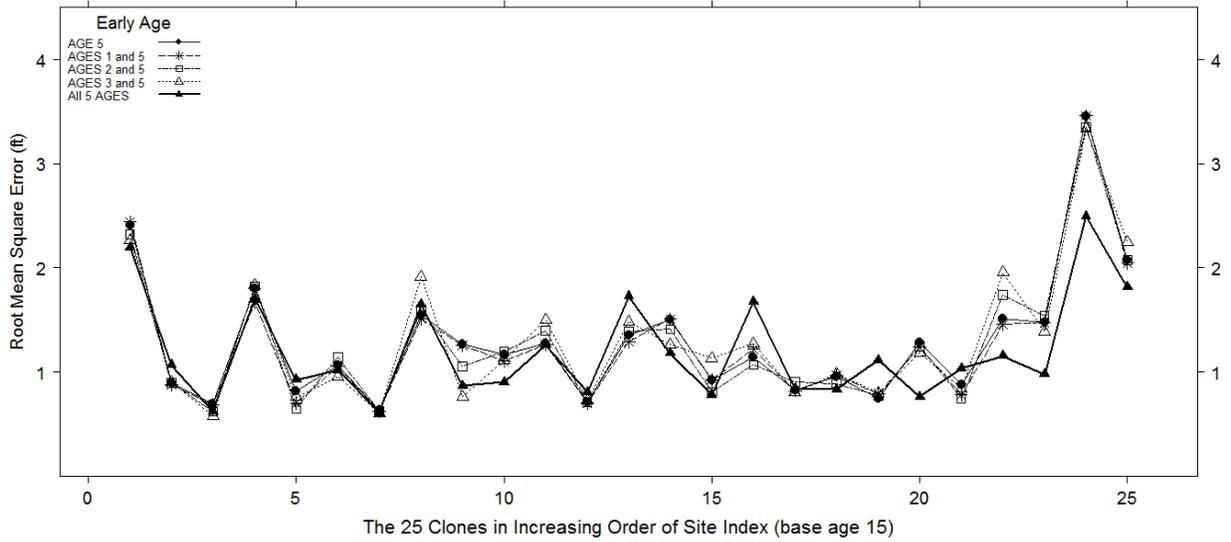
**Figure 3.2:** Plots of model bias when the Chapman-Richards height-age equation with random effects for clone on asymptote parameter only and on asymptote and shape parameters was fitted to the height and age data from the loblolly pine trees of different clonal genetic varieties in the clonal genetic screening trial experiment.



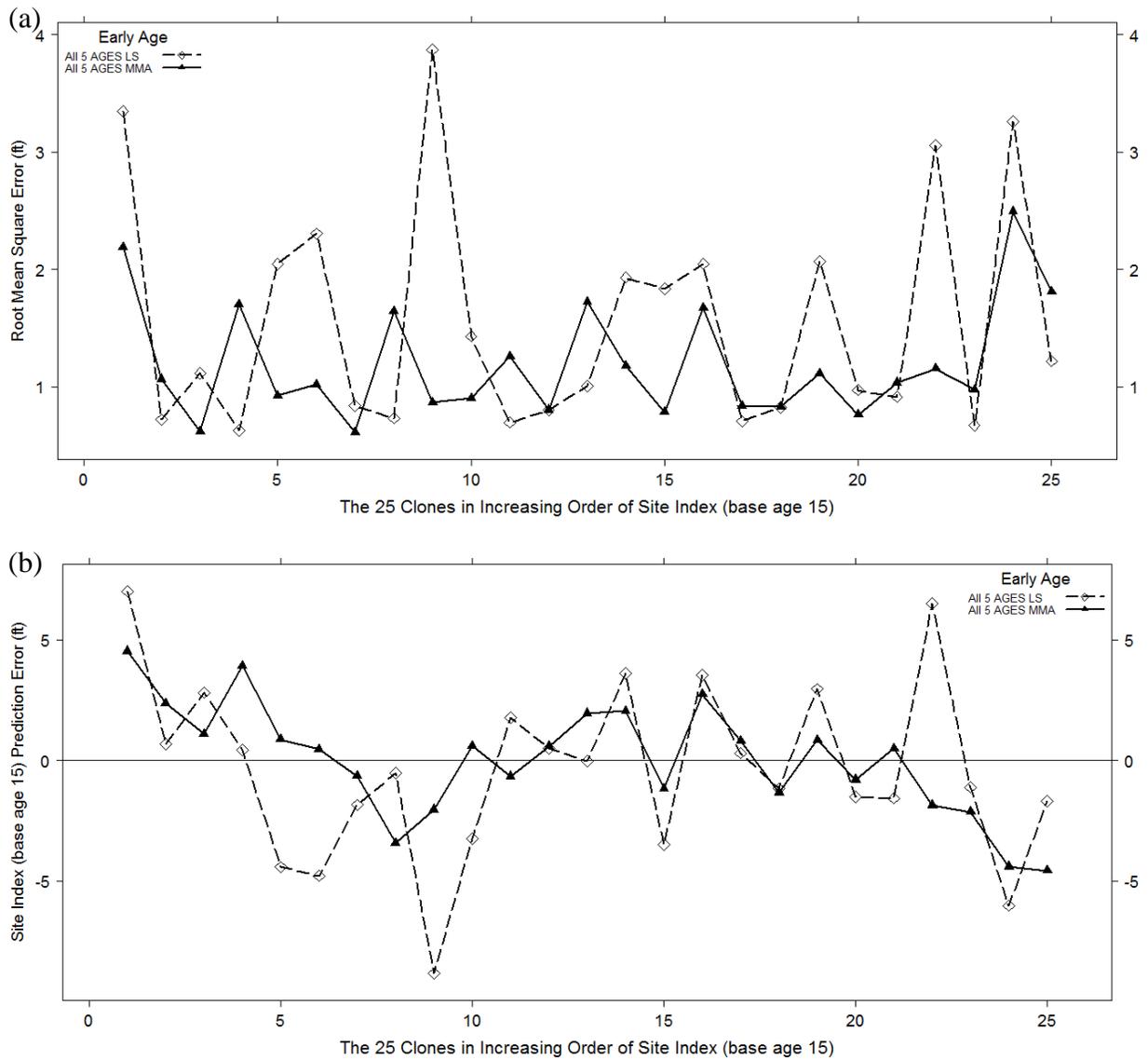
**Figure 3.3:** Normal QQ plots for the random effects in the Chapman-Richards height-age equation with random effects for clone (a) on asymptote and shape parameters and (b) on asymptote parameter only, when the equations were fitted to the height and age data from the loblolly pine clonal genetic screening trial study.



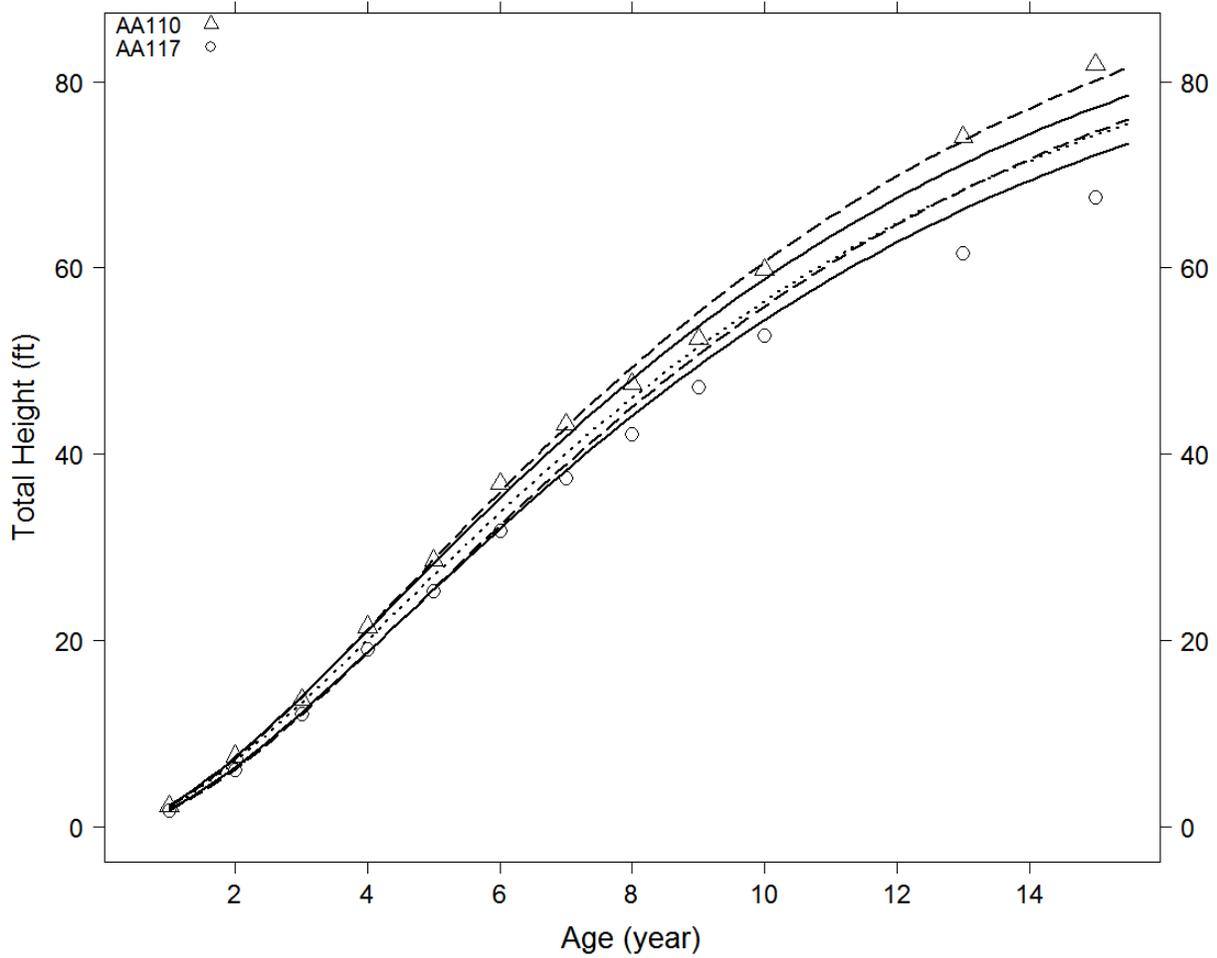
**Figure 3.4:** Residual plots for the Chapman-Richards height-age equation (a) with random asymptote and shape parameters for clone and (b) with random asymptote parameter for clone, fitted to the height and age data from the loblolly pine clonal genetic screening trial study.



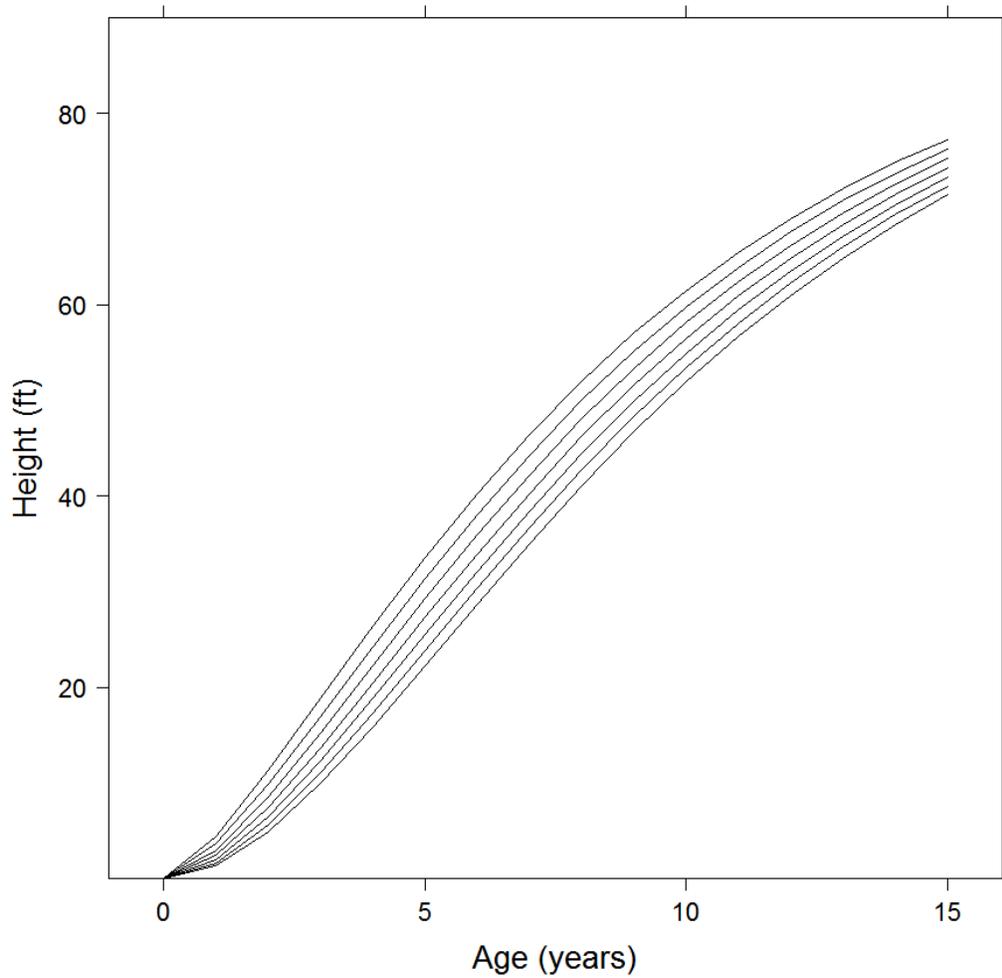
**Figure 3.5:** Plots of (a) model root mean square errors and (b) site index (base age 15) prediction error when a Chapman-Richards height-age equation calibrated from 1, 2, or 5 early-age height measurements by mixed-effects model approach was used to predict the height growth trajectory of a “new” loblolly pine clone. The root mean square errors are based on the observed heights and heights predicted by the calibrated equation, for each of the 25 “new” clones used in the calibration. The site index (base age 15) prediction errors were computed as height predicted at age 15 less the height observed at this age.



**Figure 3.6:** Plots of (a) model root mean square errors and (b) site index (base age 15) prediction errors when a Chapman-Richards height-age equation calibrated from 5 early-age height measurements by mixed-effects model approach and by least squares method were used to predict the height growth trajectory of a “new” loblolly pine clone. The root mean square errors are based on the observed heights and heights predicted by the calibrated equation, for each of the 25 “new” clones used in the calibration. The site index (base age 15) prediction errors were computed as height predicted at age 15 less the height observed at this age.



**Figure 3.7:** Plots of the observed and the predicted future height trajectories for the extreme top (AA110) and the extreme bottom (AA117) of the 25 “new” clones used in the calibration. The lines represent the predicted height trajectories. The continuous lines are the trajectories predicted by the mixed-effects model calibration approach and the long-dash lines the trajectories predicted by the least squares calibration. For each set of lines, the top line represents the predicted trajectory for clone AA110 and the bottom line the trajectory for clone AA117. The dotted line is the trajectory predicted by the model that assumes no effect of clone (the population average height growth trajectory).



**Figure 3.8:** Height-age trajectories of 7 clones selected from the range of the site indices exhibited by the clones in the clonal screening trial. The trajectories were modeled under the assumption that the 7 clones grow to a common asymptote

## Chapter 4

### **Height and diameter relationships and distributions in loblolly pine stands of enhanced genetic material**

#### **Abstract**

The effect of genetic improvement and clonal forestry on loblolly pine height-dbh relationships and height and dbh distributions were investigated using four loblolly pine genetic varieties - an open-pollination family, a controlled-pollination family, and 2 rooted-cutting clones; each growing at 2 different levels of stand density. Height-dbh relationships were modeled using the Korf height-dbh function and height and dbh distributions were described using the mean, variance, and skewness moments of the distributions. The fixed effect of genetic variety on height-dbh relationship was tested using likelihood ratio test and root mean square error statistics. Moments of height and dbh distributions were compared using analysis of variance techniques. Genetic variety affected only the asymptote parameter of the height-dbh relationship. A height-dbh equation with the asymptote parameter expressed as a function of the site index exhibited by a genetic variety, and stand density, accurately predicted height for a given dbh in stands of different genetic varieties growing at different stand densities. Variance of the height-dbh relationship decreased with increase in genetic uniformity among trees in a stand. Higher levels of genetic improvement resulted in an increase in the mean of the height distribution but had no effect on the mean of the dbh distribution. Thus, modeling the effect of genetic selection on loblolly pine growth and yield may not assume a gain in the mean of the height distribution that is accompanied by a corresponding gain in the mean of the dbh distribution. Variance and

skewness of both height and dbh distributions were not affected by level of genetic improvement. Use of clones had no effect on variance of height and dbh distributions except for the dbh distributions at the higher stand density where the variance in non-clonal stands was larger. Thus, differences in variance of dbh distribution between clonal and non-clonal stands of loblolly pine may depend on stand density.

**Keywords:** *Pinus taeda*, growth and yield models, genetic selection, clonal forestry

## 4.1. Introduction

Height-dbh relationships are useful in forestry for estimating heights of trees where only the dbh is given and subsequently for tree volume or biomass calculation. In forest inventory height-dbh relationships help to make timber cruises faster and cheaper as only dbh, which is less difficult and more accurate to measure, is the only variable measured on all the trees. In growth and yield modeling, height-dbh relationships are useful in diameter distribution growth and yield models where they are used to estimate heights and hence tree volume from the predicted diameter distributions (Avery and Burkhart 2002, p. 361 - 371; Clutter et al. 1983, p. 125 - 131). Height-dbh relationships have also been used in individual tree growth and yield models to estimate tree heights from tree dbh (e.g. Lynch et al. 1999) or tree dbh from tree heights (e.g. Westfall et al. 2004). Diameter distributions have been used to assign value to forest stands that are ready for harvest as the distributions determine the proportions of the various product classes such as saw timber, chip and saw logs, pulp wood, biomass, etc. Height and dbh distributions of forest stands may be used to make management and planning decisions on activities such as thinning, selection harvesting, or habitat improvement activities that may require manipulation of tree size distributions.

Genetic improvement may affect height-dbh relationship in trees of a selected species depending on the way the improvement process affects height growth relative to dbh growth. Andersson et al. (2007) and Kroon et al.(2008) using data from Scots pine (*Pinus sylvestris* L.) observed that that selection based on height growth resulted in trees with a higher height/dbh ratio. They concluded that such trees allocated more biomass to height growth than basal area growth and as such they were more slender. A similar observation was made by Vergara et al. (2004) in slash pine (*Pinus elliottii* Engelm.). Genetically improved slash pine had a significantly

higher height/dbh ratio than the genetically unimproved variety. These observations suggest that genetic improvement through selection for height growth may change the height-dbh relationship and the height distributions but leave the dbh distribution unaffected or with a lower mean if the trees are more slender. Genetic selection for growth improvement in forest trees has mainly been based on height growth (White et al. 2007; Zobel and Talbert 1984) hence the possibilities of genetic improvement resulting in trees that allocate more biomass to height growth is high. Studies using provenance varieties and first generation open-pollination (OP) varieties have shown that height growth differences between the shorter and the taller varieties only affect the asymptote parameter of the height-dbh relationship and that the effect could be accounted for by including the site index, exhibited by the genetic variety, in the height-dbh equation (Buford 1986; Buford and Burkhart 1987; Lynch et al. 2010). However, the effect of a change in the height-dbh relationship due to genetic improvement/selection for height growth on height and diameter distributions has, in our knowledge, never been investigated fully. Buford and Burkhart (1987) concluded that genetic improvement did not affect the variance of the distributions of dbh and height in loblolly pine (*Pinus taeda* L.) and hence the effect of genetic improvement on growth and yield could be accounted for by adjusting the site index to that exhibited by the improved genetic variety. Weng et al. (2010) showed that site index exhibited by black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* Moench.) stands of different levels of genetic improvement was linearly related to the parameters of the 2-parameter Weibull probability distribution of the stand heights at age 15. The effect of the genetically induced differences in site index, on diameter distributions, was not reported.

A number of studies have provided evidence of genetic improvement affecting height growth differently from the way it affected dbh growth. Carson et al.(1999) reported a

percentage genetic gain in basal area growth of radiata pine (*Pinus radiata* D. Don.) that was approximately 5 times the percentage gain in height growth. In loblolly pine, results from a number of studies suggest that genetic improvement changes in height growth may not necessarily be accompanied by significant changes in dbh growth. Martin and Shiver (2002) reported non-significant differences (p-value = 0.0601) in the age 12 mean dbh among the different levels of genetic improvement (unimproved, first generation mixed variety open pollinated, and first generation single variety open pollinated) but highly significant differences in mean dominant heights (p-value < 0.0001). Adams et al. (2008) reported non-significant differences (p-value > 0.05) in mean dbh at age 17 for loblolly pine varieties, including a commercial check, grown at a spacing of 5ft by 5ft. However, the differences in mean heights were significant (p-value < 0.05). Will et al. (2010) showed that the mean diameters at age 25 in two loblolly pine provenance varieties, growing at 4 different densities, were not significantly different while the mean heights were different (Figures 3 and 4 in Will et al. 2010). It is therefore evident that if site index is used to incorporate the effect of genetic improvement in a height-dbh relationship and the site index value used in a stand level basal area growth model that has site index as a predictor (e.g. Hasenauer et al. 1997; Sullivan and Clutter 1972), the model may estimate a genetic improvement in basal area growth that might not have been realized. The extent to which there may be genetic improvement in height growth that may not be accompanied by a corresponding improvement in basal area growth, among enhanced loblolly pine genetic material, is not well established.

The effect of genetic improvement on the stand dbh distribution may affect stand economic value. Given that phenotypic variability is the sum of variance due to effect of genetics and the variance due to environmental factors, it is thought that selection for genetic

improvement would result in an increase in the average tree size due to selection for larger size and a decrease in the variability due to decreased genetic variability in the selected population. Mitchell (1975) and Nance and Bey (1979), through simulation, observed that decreased variability would lower stand economic value as there would be increased competition among the trees that would curtail the progression of the trees into the larger diameter classes. Studies with provenance varieties, first generation OP varieties, and first generation seed orchard control pollination (CP) varieties did not find evidence of an effect of genetic improvement on the variability of dbh distribution (Buford and Burkhart 1985; Carson and Hayes 1998). Carson and Hayes (1998) reported an increase in the mean of dbh distribution of radiata pine with, genetic improvement. Weng et al. (2010) on studies in black spruce reported some cases where there was an increase in the mean of dbh distribution, with genetic improvement, and other cases where the mean of dbh distribution did not change with genetic improvement. Advances in tree improvement and propagation techniques have made it possible to carry out more highly specific genetic selection. Currently, genetic improvement for southern pines of the United States is in its third cycle with over 80% of seed for plantation establishment coming from second and third generation seed orchards (Virginia Department of Forestry 2009). Over 100 million seedlings from control crosses and over 10 million clones have been planted in the last ten years (McKeand et al. 2007). The effect of these advances in genetic improvement and techniques of propagating planting material, on dbh and by extension height distributions in loblolly pine, need to be more thoroughly studied and quantified.

The objectives of this study were to determine the effect of genetic improvement and clonal forestry on 1) the parameters of the height-dbh relationship of loblolly pine trees and 2) the mean, variance and skewness of the dbh and height distributions in loblolly pine plantations.

We tested the hypotheses that 1) genetic improvement has no effect on parameters height-dbh relationship of loblolly pine other than the asymptote parameter and 2) genetic improvement and clonal forestry have no effect on the mean, variance, and skewness of the stand height and dbh distributions of loblolly pine. We also examined the relationship between any change in height distribution, with genetic improvement, and the corresponding change in dbh distribution. The variability of heights at a given dbh in the height-dbh relationships for trees in the different varieties was also examined.

## **4.2. Methods**

### ***4.2.1. Study material, study area, and data collection***

The study material was made up of 4 loblolly pine genetic varieties developed by Westvaco Company. The genetic varieties were WV3, an open-pollination variety hereafter referred to as OP; MCP317, a controlled-pollination variety whose mother tree was WV3, hereafter referred to as CP; Clone AA32 a clonal variety from a control cross between WV3 as the mother tree and WV5 as the father tree; and Clone AA93, a clonal variety also from a control cross between WV3 as the mother tree and WV5 as the father tree. Despite being offspring of the same parents, Clone AA32 is a broad crown ideotype while Clone AA93 is a narrow crown ideotype selected for fast height growth. Planting material for the clonal varieties was containerized rooted cuttings while that of the OP and the CP varieties was bare root seedlings. According to genetic theory, the study material represented 3 levels of genetic improvement with the OP variety having the lowest level of genetic improvement and the two clonal varieties having the highest level (White et al. 2007, p. 443 – 472). The material can also be classified into

clonal and non-clonal material with Clone AA32 and Clone AA93 being the clonal material and OP and CP being the non-clonal material.

Data for the current study were obtained from a study established with the 4 genetic varieties in spring of 2002 to investigate the effect of initial spacing density (ISD) on stand level growth and development. The study was established near Summerville in Berkeley County, South Carolina (33°15' N, 80° 7' W), in the Atlantic Coastal Plain physiographic region of the United States, on a cutover site. The experiment was a completely randomized factorial design with 4 levels of genetic variety treatment – OP, CP, Clone AA32, and Clone AA93; and 2 levels of ISD treatments – 275 TPA and 550 TPA. It was made up of 24 contiguous 0.44-acre plots as experimental units on which the inner 0.13 acre was the measurement plot with the rest of the area around the 0.13 acre plot being occupied by buffer trees. Management of competing vegetation and nutritional deficiencies on the plots was done according to operational management prescriptions. Site preparation included shear, spot raking, chemical competition control, and bedding. Phosphorus fertilizer was applied in late summer of 2002 at the rate of 40 lbs/ac elemental phosphorus. Herbaceous weed control was done for the first two years and competition from hardwoods had been controlled as needed. Each 0.44-acre experimental plot had 10 beds each 158 ft long and spaced 12 ft apart. Trees along the beds were 13 ft from each other in the 275 TPA ISD treatment and 6.5ft from each other in the 550 TPA plots. The 0.13 acre measurement plot was made up of the inner 6 beds with the inner 6 trees per bed in the 275 TPA ISD and with the inner 12 trees per bed in the 550 TPA density.

The data were collected during the 2009/10 dormant season when the stands were 8 years old. Each tree was measured for dbh at 4.5 ft from the ground level and total height, in addition to other measurements that do not form part of the current study. Diameter was measured in

inches using a diameter tape while total height was measured in feet using a laser hypsometer. Some of the age 8 stand characteristics of the plots are given in Table 4.1.

#### ***4.2.2. Effect of genetic improvement on parameters of height-dbh relationship***

Scatter plots of height versus dbh for the different genetic variety by ISD combinations are shown in Figure 4.1. Given the trends in the scatter plots, the effect of genetic improvement on height-dbh relationship was investigated using the height-dbh equation

$$H_i = \beta_0 \times \exp(\beta_1 D_i^{-1}) + \varepsilon_i \quad (4.1)$$

where  $H_i$  is the total height and  $D_i$  the dbh of the  $i^{\text{th}}$  tree;  $\beta_0$  is the upper asymptote parameter; and  $\beta_1$  is the rate parameter; and  $\varepsilon_i$  is the random stochastic error due to the  $i^{\text{th}}$  tree ( $\varepsilon_i \sim N(0, \sigma_\varepsilon^2)$ ). Equation 4.1 is the type known as the Korf equation (Zeide 1993) and it is an equation form that has been found to be satisfactory for loblolly pine (Arabatzis and Burkhart 1992). The trends of the scatter plots in Figure 4.1 suggested a possible effect of ISD on the parameters of the height-dbh relationship. The trends of the plots at 550 TPA ISD appeared slightly steeper than the trends of the plots at 275 TPA ISD. A decision on whether to fit equation 4.1 separately to the trees in the different initial densities was made based on the significance of the effect of ISD on the parameters  $\beta_0$  and  $\beta_1$ , which were each expressed as a function of the dominant height of the genetic variety and ISD. The dominant heights of the genetic varieties were used to reflect the genetic differences in the growth potentials of the different varieties as the different genetic varieties exhibited different dominant heights (Table 4.1). Dominant height for a genetic variety was estimated as the average of the dominant heights at the two ISDs 275 TPA and 550 TPA.

Equation 4.1 with the parameters  $\beta_0$  and  $\beta_1$  expressed as functions of dominant height and ISD was expanded to

$$H_{ijk} = [\alpha_0 + \alpha_1 HD_i + \alpha_2 N_j] \times \exp( [\gamma_0 + \gamma_1 HD_i + \gamma_2 N_j] D_{ijk}^{-1} ) + \varepsilon_{ijk} \quad (4.2)$$

where  $H_{ijk}$  is the total height and  $D_{ijk}$  the dbh of the  $k^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety in the  $j^{\text{th}}$  ISD;  $HD_i$  is the dominant height of the  $i^{\text{th}}$  genetic variety;  $N_j$  is the  $j^{\text{th}}$  ISD;  $\alpha_0$ ,  $\alpha_1$ ,  $\alpha_2$ ,  $\gamma_0$ ,  $\gamma_1$ , and  $\gamma_2$  are parameters; and  $\varepsilon_{ijk}$  is the random stochastic error due to the  $k^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety in the  $j^{\text{th}}$  ISD ( $\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$ ). Equation 4.2 was fitted to the data by maximum likelihood using the “*gnls*” package in R software (R Development Core Team 2010). The outliers/possible data errors were excluded from the analysis. Genetic variety was found to have a significant effect on both the rate and asymptote parameters. Initial spacing density was found to have a significant effect on the rate parameter but not on the asymptote parameter. Due to the effect of ISD on the parameter  $\beta_1$ , the effect of genetics on the parameters was investigated separately for the two ISDs. Data from the 3 replicates of each genetic variety in an ISD level were combined for use in fitting the equations.

The investigation of the effect of genetic variety on the parameters of the height-dbh equation was done using the model

$$H_{ij} = [\beta_{0A} + \sum_{i=1}^3 \beta_{0i} G_i] \times \exp( [\beta_{1A} + \sum_{i=1}^3 \beta_{1i} G_i] D_{ij}^{-1} ) + \varepsilon_{ij} \quad (4.3)$$

where  $H_{ij}$  is the total height in feet and  $D_{ij}$  the dbh in inches for the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety;  $G_i$  is the dummy variable for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$  with a value of 1 if the  $i^{\text{th}}$  genetic variety and zero otherwise;  $\beta_{0A}$  and  $\beta_{1A}$  are global parameters and were associated with the OP genetic variety;  $\beta_{0i}$  and  $\beta_{1i}$  are dummy variable

coefficients for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$ ; and  $\varepsilon_{ij}$  is the random error due to the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ij} \sim N(0, \sigma_{\varepsilon}^2)$ ). Equation 4.3 was fitted to the data by maximum likelihood using the “*gnls*” package in R software (R Development Core Team 2010). The significance of the effects of the different genetic varieties on the asymptote and rate parameters was investigated by comparing the likelihood fit statistics of equation 4.3 to the fits of its reduced forms with the dummy variables associated with  $\beta_{0i}$  and  $\beta_{1i}$  dropped out of the model one at a time, using likelihood ratio tests.

The genetic variety – specific parameters obtained from fitting reduced forms of equation 4.3 to the data from the genetic variety by ISD experiment were used to estimate the fitted regression line for each genetic variety in each ISD treatment. The root mean square residual about the fitted regression lines was then calculated for each genetic variety in each ISD treatment as

$$RMSR_{ij} = \sqrt{\frac{(H_{ijk} - \hat{H}_{ijk})^2}{n_{ij} - 2}} \quad (4.4)$$

where  $RMSR_{ij}$  is the root mean square residual in the  $j^{\text{th}}$  genetic variety in the  $i^{\text{th}}$  ISD treatment;  $H_{ijk}$  is the observed total height and  $\hat{H}_{ijk}$  the predicted total height, for the  $k^{\text{th}}$  tree of the  $j^{\text{th}}$  genetic variety in the  $i^{\text{th}}$  ISD treatment; and  $n_{ij}$  is the number of trees of the  $j^{\text{th}}$  genetic variety in the  $i^{\text{th}}$  ISD treatment. The absolute values of the root mean square residuals were compared across the different genetic varieties to give an idea of how the variability of the heights at a given diameter differed with level of genetic improvement and between clonal and non-clonal varieties of loblolly pine.

#### 4.2.3. Effect of genetic improvement and clonal forestry on height and dbh distributions

The effect of genetic improvement on height and dbh distributions was investigated for the mean, variance, and skewness moments of the distributions. These moments were chosen due to ease of interpretation and because they are related to the parameters of the Weibull probability distribution commonly used to describe dbh and height distributions of forest stands. Weibull probability distribution parameters can be obtained from the mean and variance of a dbh or height distribution by the parameter recovery method of Hyink and Moser (1983). The mean, variance, and skewness of the diameter and height distributions were calculated for each of the replicate plots of the genetic variety by ISD experiment. The variance was standardized to coefficient of variation (CV). The value of the moments from each replicate plot was treated as one observation from a sample of size 3. The moments were compared across the different levels of genetic improvement by carrying out a one-way analysis of variance (ANOVA) on the values of the moments using the GLM procedure in SAS software (SAS Institute Inc. 2000 - 2004). An ANOVA was done separately for each of the ISDs as the interest was in the effect of genetic improvement and not in genetic improvement by ISD interaction. The ANOVA method of estimating the effect of genetic improvement on moments of dbh and height distributions has been used before in forestry (Carson and Hayes 1998). The linear model for the current analysis was

$$y_{ij} = \mu + \alpha_i + \varepsilon_{ij}, i = 1, 2, \dots, 4; j = 1, 2, 3 \quad (4.5)$$

where  $y_{ij}$  is the  $j^{\text{th}}$  value of the moment for the  $i^{\text{th}}$  genetic variety;  $\mu$  is the overall mean value of the moment;  $\alpha_i$  is the effect of the  $i^{\text{th}}$  genetic variety; and  $\varepsilon_{ij}$  is the random error due to the  $j^{\text{th}}$  value of the moment for the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$ ). The moment means were each

compared to the mean of the OP genetic variety, which theoretically was at the lowest level of genetic improvement, as the control. The adjustment of p-values to maintain an overall error rate of 0.05, due to the multiple comparisons, was done by the Dunnett (1955) method.

The effect of clonal forestry on the moments was investigated using contrasts between moment means of clonal varieties and those of non-clonal varieties. The contrasts were estimated separately for each level of ISD as

$$c = \frac{1}{2}(\bar{y}_{OP} + \bar{y}_{CP}) - \frac{1}{2}(\bar{y}_{Clone AA32} + \bar{y}_{Clone AA93}) \quad (4.6)$$

where  $c$  is the estimate of the contrast and  $\bar{y}_i$ ; for  $i = OP, CP, Clone AA32,$  and  $Clone AA93$ ; are the sample means of the moments. Each contrast was tested, as to whether it was significantly different from zero, by carrying out a t-test on the estimate of the contrast. Estimation of the contrasts and the testing of their significance were done within the ANOVA procedure used to estimate the effects in the linear model 4.5.

#### ***4.2.4. Comparing changes in height distribution, with genetic improvement, to the corresponding changes in dbh distribution***

A comparison of the changes in height distribution, with genetic improvement, to the corresponding changes in dbh distribution, was done by graphical techniques. The dbh and height distribution in each genetic variety by density combination was modeled by the Weibull probability density function

$$f(x) = \left(\frac{\gamma}{\beta}\right) \left(\frac{x}{\beta}\right)^{\gamma-1} \exp\left(-\left(\frac{x}{\beta}\right)^{\gamma}\right) \quad (4.7)$$

where  $x$  is the diameter or height value,  $\beta$  is the scale parameter and  $\gamma$  is the shape parameter. Data from the 3 replicate plots of each genetic variety in an ISD were combined for use in the estimation of the parameters of equation 4.7. The parameters were estimated by maximum likelihood. A test of the fitted distribution using the Kolmogorov-Smirnov (K-S) test did not find sufficient evidence to reject the hypothesis that the height or diameter data for the given genetic variety in a given ISD were Weibull distributed ( $p > 0.1662$  in all cases). The parameters of the Weibull distribution for the height and dbh distributions were used to plot the distributions on the same axes to display the changes in the distributions, with genetic improvement.

### 4.3. Results

#### 4.3.1. Effect of genetic improvement on parameters of height-dbh relationship

The reduced forms of equation 4.3 that best fit the data from the 275 TPA ISD treatment and that which best fit the data from the 550 TPA initial spacing treatment were, respectively,

$$H_{ij} = [\beta_{0A} + \sum_{i=1}^3 \beta_{0i} G_i] \times \exp(\beta_{1A} D_{ij}^{-1}) + \varepsilon_{ij} \quad (4.8)$$

and

$$H_{ij} = [\beta_{0A} + \sum_{i=1}^2 \beta_{0i} G_{2i}] \times \exp([\beta_{1A} + \sum_{i=1}^2 \beta_{1i} G_{2i}] D_{ij}^{-1}) + \varepsilon_{ij} \quad (4.9)$$

In equations 4.8 and 4.9,  $H_{ij}$  is the total height in ft and  $D_{ij}$  the dbh in inches for the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety;  $G_i$  is a dummy variable with value 1 if the  $i^{\text{th}}$  genetic variety and 0 otherwise for  $i = \text{CP}$ , Clone AA32, and Clone AA93;  $G_{2i}$  is a dummy variable with value 1 if the  $i^{\text{th}}$  genetic variety and 0 otherwise for  $i = \text{Clone AA32}$  and Clone AA93;  $\beta_{0A}$  and  $\beta_{1A}$  are global parameters

and were associated with the OP genetic variety;  $\beta_{0i}$  and  $\beta_{1i}$  are genetic variety-specific dummy variable coefficients for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$  in equation 4.8, and  $i = \text{Clone AA32 and Clone AA93}$  in equation 4.9; and  $\varepsilon_{ij}$  is the random error due to the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ij} \sim N(0, \sigma_{\varepsilon}^2)$ ). The genetic variety – specific parameter estimates obtained from fitting equations 4.8 and 4.9 to the age 8 data, from the genetic variety by ISD study, are given in Table 4.2. Plots of the height and dbh data, and the regression lines that best fitted the data from the different genetic varieties, are shown in Figure 4.2.

At 275 TPA ISD genetic variety did not affect the rate parameter  $\beta_1$  of equation 4.1 but affected it at the 550 TPA treatment (equations 4.8 and 4.9 and Table 4.2). The difference in the rate parameters at the higher spacing density only involved the OP and the CP genetic varieties. The values of rate parameters for these two varieties, at 550 TPA ISD, were significantly less negative than they were at the 275 TPA ISD. For Clone AA32 and Clone AA93, the values of their rate parameters at 550 TPA ISD were not different from the values of these parameters at 275 TPA ISD. This can be seen from Table 4.2 where the 95% confidence intervals of the rate parameters for Clone AA32 and Clone AA93, at the two densities, overlapped.

Genetic variety affected the asymptote parameter  $\beta_0$  in equation 4.1 at both ISDs (Table 4.2). However, the effect was not similar at both initial densities. At 275 TPA ISD, the value of the asymptote parameter increased with level of genetic improvement. At 550 TPA ISD the value of the asymptote parameter generally increased with genetic improvement except that the value for the CP genetic variety was unexpectedly equal to that of the OP genetic variety. With the exception of the CP genetic variety, the values of the asymptote parameters for a genetic

variety at the two ISDs were not different as there was overlap in the 95% confidence intervals of the asymptote parameter estimates at the two ISDs in all except the CP genetic variety. The value of the asymptote parameter for the CP genetic variety at 550 TPA density was significantly smaller than the value at the 275 TPA density. Generally, the values of the asymptote and the rate parameters for the clonal genetic varieties did not change between the lower and the higher densities. Those of the non-clonal genetic varieties generally decreased in magnitude with increased density. Average height of a tree of a given dbh increased with genetic improvement/clonal forestry (Figure 4.2).

The root mean square residuals for the genetic variety-specific height-dbh lines of best fit, shown in Figure 4.2, are given in Table 4.3 as the root mean square error for model A. At both ISDs, the average variability of the observed heights about the fitted regression line decreased with genetic improvement. Considering clonal and non-clonal genetic varieties, the average variability about the fitted regression line in stands of non-clonal genetic varieties was approximately 2 times that observed in the stands of clonal genetic varieties.

#### ***4.3.2. Effect of genetic improvement and clonal forestry on height and dbh distributions***

##### ***4.3.2.1. Diameter at breast height (dbh) distributions***

The histograms of the dbh distributions for the trees from the different genetic variety plots are shown in Figure 4.3. With the exception of the exception of the distribution for the CP variety, which appeared slightly more spread out than the others, the dbh distributions at a given density did not appear to differ significantly. The ANOVA comparisons of the mean, variance,

and skewness moments of the dbh distributions are given in Table 4.4. At 275 TPA ISD, dbh distributions for the CP, Clone AA32, and Clone AA93 genetic varieties were not significantly different in mean, variance, and skewness from the dbh distribution of the OP variety (the assumed control) ( $p \geq 0.3849$ ). The same was the case at 550 TPA ISD ( $p \geq 0.3225$ ) except that the mean of the dbh distribution for the CP genetic variety was significantly smaller than that of the OP variety ( $p = 0.0123$ ). Generally, genetic improvement did not result in an increase in mean of dbh distribution.

Contrasts to compare the moments of the dbh distributions in clonal versus non-clonal varieties did not detect a difference in the moments of the 2 groups of genetic varieties at the 275 density ( $p \geq 0.2848$ ). Thus, the mean, variance, and skewness of the clonal genetic varieties at 275 density were not different from those of the non-clonal varieties. At 550 density, the mean of the dbh distribution for the non-clonal varieties was smaller than that for the clonal varieties ( $p = 0.0037$ ) while the variance of the distribution was larger for the non-clonal than for the clonal varieties ( $p = 0.0445$ ). However, the skewness of the distributions did not differ between clonal and non-clonal genetic varieties ( $p = 0.4114$ ).

#### *4.3.2.2. Height distributions*

The histograms of the height distributions for the trees from the different genetic variety plots of the genetic variety by ISD experiment are shown in Figure 4.4. Just like in the case of dbh distributions, the height distributions for the CP family appeared slightly spread out compared to the others. There appeared to be general rightward shift in the distribution, with genetic improvement. The ANOVA comparisons of the mean, variance, and skewness moments

of the height distributions are given in Table 4.4. At both densities, height distributions for the CP, Clone AA32, and Clone AA93 genetic varieties were not significantly different in variance and skewness from the height distributions of the OP variety ( $p \geq 0.1596$ ). However, there were significant differences in the means of the distributions. At 275 TPA density, the height distribution means for Clone AA32 and Clone AA93 were significantly larger than that of the OP variety ( $p \leq 0.0002$ ) while the height distribution mean for the CP variety was not significantly different ( $p = 0.0808$ ). At 550 TPA density, the height distribution mean for the CP genetic variety was significantly smaller than that of the OP variety ( $p = 0.0351$ ) while the distribution means of Clone AA32 and Clone AA93 were significantly larger than that of the OP variety ( $p < 0.0001$ ). Generally, the effect of genetic improvement on height distribution was that it resulted in an increase in the mean of the distribution.

Contrasts to compare the moments of the height distributions did not detect significant differences in the variance and skewness of the distribution at both 275 TPA and 550 TPA densities ( $p \geq 0.0709$ ). However, means of height distributions for the clonal varieties were significantly larger than those for the distributions of the non-clonal varieties at both densities ( $p < 0.0001$ ). Thus, clonal forestry could result in taller stands.

#### ***4.3.3. A comparison of the changes in height distribution, with genetic improvement, to the corresponding changes in dbh distribution***

Comparisons of the changes in the height distribution with genetic improvement, to the corresponding changes in the dbh distributions, are shown in Figure 4.5 for the 275 TPA ISD treatment and in Figure 4.6 for the 550 TPA ISD treatment. At 275 TPA ISD, height distribution

shifted to the right with genetic improvement, given the distribution of the OP genetic variety as the reference. There was no obvious change in the spread of the distribution with genetic improvement except for the apparent slight increase in spread of the distribution for the CP genetic variety. The changes in dbh distribution generally did not follow the pattern of change in the height distribution with the exception of the dbh distribution of the CP genetic variety. The dbh distribution of this genetic variety had a wider spread as was the case with its height distribution, but the dbh distribution did not have the rightward shift observed in the height distribution. At 550 TPA treatment, there was a rightward shift in the height distribution, with genetic improvement, except for the contradictory leftward shift observed with the CP genetic variety. The dbh distribution of the CP genetic variety also exhibited the contradictory leftward shift. With the exception of the contradictory shift observed in the dbh distribution of the CP genetic variety, the changes in dbh distribution, with genetic improvement, at 550 TPA density did not follow the same trend as the changes in height distribution.

#### **4.4. Discussion**

##### ***4.4.1. Effect of genetic improvement on parameters of height-dbh relationship***

Genetic variety only affected the asymptote parameter of the height-dbh relationship at 275 TPA density but affected both the asymptote and the rate parameter at 550 TPA density. The results for the 275 TPA density are consistent with findings from previous studies on the effect of genetic or seed source variety on height-dbh relationship of forest trees at a given stand density, age, and location (Buford and Burkhart 1987; Lynch et al. 2010; Weng et al. 2008). The results for the 550 TPA density were consistent with expectation for the clonal genetic varieties

but inconsistent for the non-clonal varieties in as far as the changes in the asymptote parameters were concerned. Previous studies that have examined the role of stand density in height-dbh relationships, using equations similar to those used in this study, have indicated that the asymptote parameter increases with increase in stand density (Burkhart 1971; Lynch et al. 2010). The asymptote parameters for the clonal varieties were as expected larger (though not statistically significant) at the 550 TPA density but those of the non-clonal genetic varieties were smaller (Table 4.2), which was contrary to the expected trend. This could be due to a genetic variety by stand density interaction effect on the asymptote parameters or it could be due to the effect of the rate parameters, which changed significantly between the two planting densities. Asymptote and rate parameters in the height-dbh equation used in this study are known to be highly correlated and changes in one set of parameters could affect the changes in the other set. The changes in the rate parameters could also, like the changes in the asymptote parameters, be due to a genetic variety by stand density interaction or they could be due to effects of random error.

To rule out the effect of stochastic differences in data on the rate parameters, model 4.8 was fitted to the combined data from the 2 planting densities with the asymptote parameter being allowed to vary with genetic variety and planting density and the rate parameter fixed across genetic varieties and planting densities. Equation 4.8 with the asymptote parameter also varying by ISD was expanded to

$$H_{ijk} = [\beta_{0A} + \sum_{i=1}^3 \beta_{0i}G_i + \beta_{04}N_j] \times \exp(\beta_1 D_{ijk}^{-1}) + \varepsilon_{ijk} \quad (4.10)$$

where  $H_{ijk}$  is the total height in ft and  $D_{ijk}$  the dbh in inches for the  $k^{\text{th}}$  tree in the  $j^{\text{th}}$  ISD with the  $i^{\text{th}}$  genetic variety;  $G_i$  is a dummy variable with value 1 if the  $i^{\text{th}}$  genetic variety and 0 otherwise

for  $i = \text{CP, Clone AA32, and Clone AA93}$ ;  $N_j$  is the ISD in TPA,  $\beta_{0A}$  is the global asymptote parameter and was associated with the OP genetic variety;  $\beta_{0i}$  is the genetic variety-specific dummy variable coefficient for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$ ;  $\beta_{04}$  is the ISD coefficient;  $\beta_1$  is the rate parameter; and  $\varepsilon_{ijk}$  is the random error due to the  $k^{\text{th}}$  tree in the  $j^{\text{th}}$  ISD with the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$ ). The genetic variety by ISD – specific root mean square errors (RMSEs) calculated using equation 4.4 with  $\hat{H}_{ijk}$  estimated using the parameters estimated with equation 4.10 (Table 4.3) were not very different from the RMSEs obtained using the parameters estimated with equations 4.8 and 4.9. Plots of the genetic variety by ISD – specific residuals (Figure 4.7) did not indicate cases of gross model misfits at genetic variety by ISD level except for the CP genetic variety at 275 TPA ISD where the residuals indicated that the model was biased downwards. The model with a common rate parameter for all densities was therefore sufficient to describe the height-dbh relationship for the 4 genetic varieties. The differences in the rate parameter between 275 TPA ISD and 550 TPA ISD observed in Table 4.2 were probably mostly due to stochastic differences in the data between the two densities.

The model with only the asymptote parameter varying with genetic variety and ISD (equation 4.10) resulted in equivalent model accuracy to the models where both the rate and asymptote parameters were allowed to vary with genetic variety and with ISD (equations 4.8 and 4.9). This indicated that genetic variety and ISD had no significant effect on the rate parameter of the height-dbh equation 4.1. It also indicated that the effect of genetic variety by ISD interaction on both the asymptote and rate parameters of equation 4.1 was not significant. The only significant effect that was apparent from the analysis was that of genetic variety and ISD on the

asymptote parameter. Lynch et al.(2010) got similar results with age 25 loblolly pine seed source variety data in a provenance by initial spacing density experiment.

The average variability of the height-dbh relationship decreased with genetic improvement and the highly selective clonal forestry had a greater reduction effect on the variability. This was in line with expectation from genetic theory that the selected population has individuals that are more similar. Trees similar in dbh were more similar in heights where there was greater genetic similarity than where there was less genetic similarity.

#### ***4.4.2. Effect of genetic improvement and clonal forestry on height and dbh distributions***

While statistical tests indicated that the variability of the dbh and height distributions in the CP, Clone AA32, and Clone AA93 genetic varieties were not significantly different from the variability in the OP variety, visual inspection of Figures 4.3 and 4.4 and the CV values in Table 4.4 suggested that the height and dbh distributions of the clonal genetic varieties were generally less variable than those of the OP variety while the distributions of the CP genetic variety were more variable than those of the OP variety. The variability of the height and dbh distributions did not exhibit a decreasing trend from OP, CP, and clonal genetic varieties as was expected if genetic improvement resulted in decreased variability of the distributions. The changes observed in variance of the distributions, with genetic improvement, did not support the hypothesis that genetic improvement would result in a decrease in the variability of height and dbh in loblolly pine plantations. The contradictory trend exhibited by the CP genetic variety suggested that the decreased genetic variability due to control crossing of tested genetically improved parents could result in increased phenotypic variability. Similar observations were made by Carson and Hayes

(1998) in radiata pine. Stands of the CP genetic varieties exhibited dbh and height distributions that were wider in spread than those of OP genetic varieties (Figures 1 and 2 of Carson and Hayes 1998). The CP variety in the study by Carson and Hayes (1998), however, was a result of control crosses between 1 tested genetically improved mother tree and 10 genetically improved pollen trees.

The results of the contrasts to test whether the variability of dbh and height distributions in clonal stands differed from the variability in non-clonal stands suggested a possibility of a clonal forestry by ISD interaction. There was no significant difference in the variability of both dbh and height distributions at 275 ISD but dbh distribution of clonal stands at 550 TPA ISD was less variable than that of the non-clonal stands. The height distribution of clonal stands was also less variable but with marginal statistical insignificance ( $p = 0.0776$ ). The smaller variability in the dbh and height distributions of the clonal varieties was expected given the logic that a significant decrease in genetic variability could result in an observable decrease in phenotypic variability. Trees in the clonal genetic varieties had zero genetic variability, assuming that the physical conditions during propagation and in the field did not change some of them genetically. The increased concentration of dbh values about the mean, observed in the dbh distributions of clonal stands (Figure 4.3), could be an indicator that the greater uniformity of clonal stands was probably curtailing the progression of the trees into the larger dbh classes as hypothesized by Mitchell (1975) and Nance and Bey (1979). This is especially so given that the concentration of the dbh values about the mean was more evident in the stands at the higher density.

The trend in the means of height distributions were in line with the expectations of the effect of genetic selection except for the mean of the CP genetic variety at 550 TPA density, which was unexpectedly smaller than the mean of the OP genetic variety. This out of trend

behavior of the height distribution mean of the CP genetic variety could be due to genetic variety by stand density interaction. The increase in stand density from 275 TPA to 550 TPA probably had impacted height growth of the CP genetic variety. The same could be the reason for the out of trend behavior of the mean of the dbh distribution for the CP genetic variety at the 550 TPA density. The out of trend behavior of the height and dbh distribution means of the CP variety at 550 TPA density could also be due to natural variation. With the exception of the mean of the CP genetic variety at 550 TPA density, the means of dbh distribution at a given density were not significantly different and did not have a trend that suggested that the mean of the distribution increased with genetic improvement or even with clonal forestry. The observed trend is probably not a desirable outcome of a tree genetic improvement program as such a trend would imply that genetic improvement would not necessarily result in improvement of stand value due to the improvement process not producing the trees of larger dbh. The trend is however not unexpected given that genetic selection for faster growth in forest trees has been based on height and studies have shown that trees selected based on height growth may not be the type that put so much photosynthates into basal area growth (Andersson et al. 2007; Kroon et al. 2008; Vergara et al. 2004). Previous studies that have reported changes in the mean of dbh distribution with genetic improvement have indicated that the mean could increase (Knowe et al. 1994), remain unchanged (Will et al. 2010), show both no change and also an increase depending on level of genetic improvement or geographic region (Martin and Shiver 2002; Weng et al. 2010), or show both an increase and a decrease depending on level of genetic improvement (Carson and Hayes 1998). Martin and Shiver (2002) reported that genetic improvement did not have a significant effect ( $p = 0.0601$ ) on mean diameter for the Coastal Plain location but a significant one for the Piedmont location ( $p = 0.0102$ ). Weng et al. (2010) reported 2-parameter Weibull dbh

distribution parameters that indicated that genetically improved black spruce from seed collected from a rouged seed orchard did not have a dbh distribution different from that of the check variety. In the same publication, the authors also reported 2-parameter Weibull distribution parameters that indicated that black spruce from seed collected from plus trees had a dbh distribution whose mean was larger than that of the check variety. In the study by Carson and Hayes(1998), the mean of the diameter distribution appeared to increase with genetic improvement up to the OP genetic variety level but decreased with the improvement from OP to CP variety. Thus, changes in the mean of the dbh distribution, with genetic improvement, are probably not consistent. Results of genetic selection should be tested through field trials to verify genetic improvement effects on height and dbh growth.

Height distribution shifted to the right with genetic improvement or clonal forestry while dbh distribution generally did not change (Figures 4.5 and Figure 4.6 with exception of the case for the CP genetic variety). These results indicated that the effect of genetic improvement on height development in loblolly pine was probably different from the effect on basal area development. These results are similar to those reported by Carson et al. (1999) in radiata pine and by Johnson (2002) in Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco).

#### **4.5. Conclusions and recommendations**

This study highlighted the effects of varying levels of genetic selection on dbh and height aspects of tree size for loblolly pine trees growing in monoculture stands under operational silviculture. The study did not find sufficient evidence to reject the hypothesis that genetic variety has no effect on parameters of the height-dbh relationship of loblolly pine other than the

asymptote parameter. Heights of trees of different genetic varieties, growing in stands of different densities, can be estimated accurately by expressing the asymptote parameter as a function genetic variety and stand density. The effect of genetic variety in the height-dbh relationship may be represented by the site index exhibited by the genetic variety. The study did not find sufficient evidence to reject the hypothesis that genetic improvement has no effect on the mean, variance, and skewness of dbh distribution and the variance and skewness of height distribution in loblolly pine. However, there was sufficient evidence to reject the hypothesis that genetic improvement has no effect on the mean of height distribution. For the clones included here, there was sufficient evidence to reject the hypothesis of no effect of clonal forestry on the mean and variance of height distributions, and the variance of dbh distributions. The evidence against no significant effect of clonal propagation on variance of height distribution was, however, marginal. The impact of the difference in the variability between clonal and non-clonal genetic varieties on growth and yield estimates was not evaluated. The hypothesis that clonal forestry had no effect on the mean of the dbh distribution and on skewness of height and dbh distributions was not rejected. Thus, tree breeding and cloning in loblolly pine affected only the mean of height distribution and to a small extent the variance of dbh and height distributions for the OP, CP, and clonal material included in this study. The effect on variance is probably dependent on stand density. The study was however limited in the range of stand densities, study locations, silvicultural treatments, and genetic varieties. A wider range of stand densities, genetic varieties, and regions could help resolve the impact of genetic varieties and densities and confirm some of the observed trends. A similar study under intensively managed silvicultural regimes is necessary to gauge the applicability of these results to stands under intensive silviculture.

The study found that the increase in height growth, with genetic improvement, did not result in a corresponding increase in dbh growth. This finding underscores the need to re-evaluate the way genetic improvement effects are incorporated into loblolly pine growth and yield models. Currently, the effect of genetic improvement is incorporated in the models by adjusting the site index variable to that exhibited by the genetic variety (Li et al. 1999; McKeand et al. 2006; Newton 2003). In the models used by the cited authors, basal area growth is predicted as a function of site index among other variables. The results of the current study suggest that site index increase due to effects of genetic selection may not result in an increase in basal area growth. Thus, the portion of site index that can be attributed to genetic improvement should not necessarily find its way into the basal area growth component of a loblolly pine growth and yield model. Otherwise basal area growth, yield, and stand value may be overestimated. Carson et al. (1999) proposed and showed how genetic gain multipliers could be used in a situation like this one. The genetic multiplier approach has also been applied to some extent in growth and yield models for the Pacific Northwest region of the US (Gould and Marshall 2010; Hamilton and Rehfeldt 1994; Rehfeldt et al. 1991). This approach, however, could easily give erroneous estimates of growth and yield if the interrelationships among various model components cause the multiplier and its possible interaction effects to be propagated through the model system (Hamilton 1994; Westfall and Burkhart 2001). Adams et al. (2006) proposed an approach that involves the modification of the survival function, the dbh function, and the stem profile. Another possible approach is to predict the dbh distribution using the unimproved variety site index (baseline site index) then assigning the heights to the predicted diameters using a height-dbh equation that has the site index exhibited by a genetic variety as one of the predictors. We recommend that unless the stand level basal area growth dynamics of a

genetic variety are known, realized genetic gain estimates from single tree or row plots should not assume that trees that show better height growth will also show better stand level basal area growth. Research on stand level basal area growth dynamics of genetic varieties in single tree plot or row plot genetic trials will be helpful in providing information that can be used to accurately incorporate the effect of genetic improvement and clonal forestry in forest decision support systems.

#### 4.6. Literature cited

- Adams, J.P., S.B. Land Jr, K.L. Belli, and T.G. Matney. 2008. Comparison of 17-year realized plot volume gains with selection for early traits for loblolly pine (*Pinus taeda* L.). *For. Ecol. Manage.* 255:1781-1788.
- Adams, J.P., T.G. Matney, S.B.L. Jr., K.L. Belli, and H.W.D. Jr. 2006. Incorporating genetic parameters into a loblolly pine growth-and-yield model. *Can. J. For. Res.* 36:1959 - 1967.
- Andersson, B., B. Elfving, T. Persson, T. Ericsson, and J. Kroon. 2007. Characteristics and development of improved *Pinus sylvestris* in northern Sweden. *Can. J. For. Res.* 37:84-92.
- Arabatzis, A.A., and H.E. Burkhart. 1992. An evaluation of sampling methods and model forms for estimating height-diameter relationships in loblolly pine plantations. *For. Sci.* 38:192-198.
- Avery, T.E., and H.E. Burkhart. 2002. *Forest Measurements*. McGraw Hill Inc., New York, NY. 456 p.
- Buford, M.A. 1986. Height-diameter relationships at age 15 in loblolly pine seed sources. *For. Sci.* 32:812 - 818.
- Buford, M.A., and H.E. Burkhart. 1985. Dynamics of improved loblolly pine plantations and the implications for modeling growth of improved stands. P. 170 - 177 *in* Proceedings of the 18th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Long Beach, MS.
- Buford, M.A., and H.E. Burkhart. 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci.* 33:707 - 724.

Burkhart, H.E. 1971. Slash Pine plantation yield estimates based on diameter distribution: an evaluation. *For. Sci.* 17:452-453.

Carson, S.D., O. Garcia, and J.D. Hayes. 1999. Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *For. Sci.* 45:186 - 200.

Carson, S.D., and J.D. Hayes. 1998. Diameter and height distributions in genetically improved *Pinus radiata*. *Can. J. For. Res.* 28:248 -258.

Clutter, J.L., J.C. Fortson, L.V. Pienaar, G.H. Brister, and R.L. Bailey. 1983. *Timber Management-A Quantitative Approach*. John Wiley and Sons Inc., New York, NY. 333 p.

Dunnett, C.W. 1955. A multiple comparison procedure for comparing several treatments with a control. *J. Am. Stat. Assoc* 50:1096-1121.

Gould, P.J., and D.D. Marshall. 2010. Incorporation of genetic gain into growth projections of Douglas-fir using ORGANON and the forest vegetation simulator. *West. J. Appl. For.* 25:55-61.

Hamilton, D.A., Jr. 1994. Uses and abuses of multipliers in the stand prognosis model. USDA For. Serv. Gen. Tech. Rep. INT-GTR-310. 9 p.

Hamilton, D.A., Jr., and G.E. Rehfeldt. 1994. Using individual tree growth projection models to estimate stand-level gains attributable to genetically improved stock. *For. Ecol. Manage.* 68:189-207.

Hasenauer, H., H.E. Burkhart, and R.L. Amateis. 1997. Basal area development in thinned and unthinned loblolly pine plantations. *Can. J. For. Res.* 27:265-271.

Hyink, D.M., and J.W. Moser, Jr. 1983. A generalized framework for projecting forest yield and stand structure using diameter distributions. *For. Sci.* 29:85-95.

Johnson, G. 2002. Modeling the effects of genetic improvement on diameter and height growth. Available online at [www.westernforestry.org/wmens/m2002/gpjohnson.ppt](http://www.westernforestry.org/wmens/m2002/gpjohnson.ppt); last accessed Feb. 23, 2011.

Knowe, S.A., G.S. Foster, R.J. Rousseau, and W.L. Nance. 1994. Eastern cottonwood clonal mixing study: predicted diameter distributions. *Can. J. For. Res.* 24:405-414.

Kroon, J., B. Andersson, and T.J. Mullin. 2008. Genetic variation in the diameter-height relationship in Scots pine (*Pinus sylvestris*). *Can. J. For. Res.* 38:1493-1503.

Li, B., S.E. McKeand, and R.J. Weir. 1999. Tree Improvement and sustainable forestry-Impact of two cycles of loblolly pine breeding in the USA. *For. Genet.* 6:229 - 234.

Lynch, T.B., K.L. Hitch, M.M. Huebschmann, and P.A. Murphy. 1999. An individual-tree growth and yield prediction system for even-aged natural shortleaf pine forests. *South. J. Appl. For.* 23:203-211.

Lynch, T.B., R.E. Will, T.C. Hennessey, R.A. Heinemann, and R.T. Holeman. 2010. Relationships among diameter at breast height and loblolly pine attributes from local and nonlocal seed sources near the western edge of the natural range of loblolly pine. *South. J. Appl. For.* 34:149-153.

Martin, S.W., and B.D. Shiver. 2002. Impacts of vegetation control, genetic improvement and their interaction on loblolly pine growth in the Southern United States - age 12 results. *South. J. Appl. For.* 26:37-42.

McKeand, S.E., R.C. Abt, H.L. Allen, B. Li, and G.P. Catts. 2006. What are the best loblolly pine genotypes worth to land owners? *J. For.* 104:352 - 358.

McKeand, S.E., B.J. Zobel, T.D. Byram, and D.A. Huber. 2007. Southern pine tree improvement-A living success story. P. 3 - 5 *in* Proceedings of the 29th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Galveston, TX.

Mitchell, K.J. 1975. Dynamics and simulated yield of Douglas-fir. *Forest Science Monograph*. No. 17. 39 p.

Nance, W.L., and C.F. Bey. 1979. Incorporating genetic information in growth and yield models. P. 140-148 *in* Proceedings of the 15th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Starkville, MS.

Newton, P.F. 2003. Systematic review of yield responses of four North American conifers to forest tree improvement practices. *For. Ecol. Manage.* 172:29-51.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G.E., W.R. Wykoff, R.J. Hoff, and R.J. Steinhoff. 1991. Genetic gains in growth and simulated yield of *Pinus monticola*. *For. Sci.* 37:326-342.

SAS Institute Inc. 2000 - 2004. SAS 9.2 Help and Documentation. SAS  
Institute Inc., Cary, NC.

Sullivan, A.D., and J.L. Clutter. 1972. A simultaneous growth and yield model for loblolly pine.  
*For. Sci.* 18:76-86.

Vergara, R., T.L. White, D.A. Huber, B.D. Shiver, and D.L. Rockwood. 2004. Estimated  
realized gains for first-generation slash pine (*Pinus elliottii* var. *elliottii*) tree improvement in  
southeastern United States. *Can. J. For. Res.* 34:2587 - 2600.

Virginia Department of Forestry. 2009. Forest Research Review April 2009. Virginia  
Department of Forestry. 12 p.

Weng, Y.H., J. Kershaw, K. Tosh, G. Adams, and M.S. Fullarton. 2008. Height-diameter  
relationships for jack pine seedlots of different genetic improvement levels. *Silvae Genet.*  
57:276-282.

Weng, Y.H., Y. Park, D. Simpson, K. Tosh, and M. Fullarton. 2010. Tree improvement effects  
on tree size distributions for *Picea glauca* and *Picea mariana* in New Brunswick, Canada.  
*Scand. J. For. Res.* 25:10-20.

Westfall, J.A., and H.E. Burkhart. 2001. Incorporating thinning response into a loblolly pine  
stand simulator. *South. J. Appl. For.* 25:159 - 164.

Westfall, J.A., H.E. Burkhart, and H.L. Allen. 2004. Young stand growth modeling for  
intensively-managed loblolly pine plantations in Southeastern U.S. *For. Sci.* 50:823-835.

White, T.L., W.T. Adams, and D.B. Neale. 2007. *Forest Genetics*. CAB International, London. 682 p.

Will, R., T. Hennessey, T. Lynch, R. Holeman, and R. Heinemann. 2010. Effects of planting density and seed source on loblolly pine stands in southeastern Oklahoma. *For. Sci.* 56:437-443.

Zeide, B. 1993. Analysis of growth equations. *For. Sci.* 39:594-616.

Zobel, B.J., and J.T. Talbert. 1984. *Applied Forest Tree Improvement*. Bruce Zobel and John Talbert, Raleigh, NC. 505 p.

**Table 4.1:** Age 8 least square means for some of the stand characteristics of the plots in the genetic variety by initial spacing density experiment

Stand Characteristic	Genetic Variety	Initial Spacing Density	
		275 TPA	550 TPA
Quadratic Mean DBH (inch)	OP	6.8 <sup>a</sup>	5.9 <sup>ab</sup>
	CP	7.0 <sup>a</sup>	5.5 <sup>a</sup>
	Clone AA32	6.8 <sup>a</sup>	6.0 <sup>b</sup>
	Clone AA93	6.9 <sup>a</sup>	5.9 <sup>ab</sup>
Dominant Height (ft)	OP	35.6 <sup>a</sup>	37.8 <sup>a</sup>
	CP	38.7 <sup>b</sup>	36.5 <sup>a</sup>
	Clone AA32	43.2 <sup>c</sup>	43.4 <sup>b</sup>
	Clone AA93	45.9 <sup>c</sup>	46.0 <sup>b</sup>
Basal Area (ft <sup>2</sup> /ac)	OP	69.2 <sup>a</sup>	102.1 <sup>ab</sup>
	CP	72.3 <sup>a</sup>	89.7 <sup>a</sup>
	Clone AA32	70.1 <sup>a</sup>	104.3 <sup>b</sup>
	Clone AA93	70.9 <sup>a</sup>	103.9 <sup>b</sup>
Survival (%)	OP	98.1 <sup>a</sup>	97.2 <sup>a</sup>
	CP	98.1 <sup>a</sup>	97.2 <sup>a</sup>
	Clone AA32	99.1 <sup>a</sup>	94.9 <sup>a</sup>
	Clone AA93	99.1 <sup>a</sup>	98.6 <sup>a</sup>

**Note:** The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. TPA is trees per acre. Dominant height was calculated as the average height of the trees whose dbh was equal to or greater than the plot quadratic mean dbh. Means in the same column, for a given stand characteristic, with the same letter a, b, or c are not significantly different at  $p = 0.05$  with Tukey HSD adjustment procedure for multiple comparisons.

**Table 4.2:** Genetic variety-specific parameter estimates when the model

$H_{ij} = [\beta_{0A} + \sum_{i=1}^3 \beta_{0i}G_i]\exp([\beta_{1A} + \sum_{i=1}^3 \beta_{1i}G_i]D_{ij}^{-1}) + \varepsilon_{ij}$  was fitted to age 8 height and dbh data from the genetic variety by initial spacing density experiment.

Parameter	Initial Spacing Density (trees/ac)	Parameter Estimate for the Genetic Variety			
		OP	CP	Clone AA32	Clone AA93
$\beta_{0G}$	275	52.29 (50.51, 54.08)	55.87 (53.84, 57.90)	63.09 (61.04, 65.14)	66.94 (64.86, 69.01)
	550	50.97 (49.76, 52.17)	50.97 (49.76, 52.17)	64.00 (60.98, 67.01)	68.28 (65.35, 71.21)
$\beta_{1G}$	275	-2.88 (-3.10, -2.67)	-2.88 (-3.10, -2.67)	-2.88 (-3.10, -2.67)	-2.88 (-3.10, -2.67)
	550	-2.09 (-2.21, -1.96)	-2.09 (-2.21, -1.96)	-2.59 (-2.88, -2.30)	-2.59 (-2.86, -2.32)

**Note:** In the equation,  $H_{ij}$  is the total height in ft and  $D_{ij}$  the dbh in inches for the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety;  $G_i$  is the dummy variable for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$  with a value of 1 if the  $i^{\text{th}}$  genetic variety and 0 otherwise;  $\beta_{0A}$  and  $\beta_{1A}$  are global parameters and were associated with the OP genetic variety;  $\beta_{0i}$  and  $\beta_{1i}$  are dummy variable coefficients for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$ ; and  $\varepsilon_{ij}$  is the random error due to the  $j^{\text{th}}$  tree of the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$ ). The genetic variety – specific height-dbh equation based on the Table entries is of the form  $H_{Gj} = \beta_{0G} \times \exp(\beta_{1G}D_{Gj}^{-1})$  where  $H_{Gj}$  is the total height and  $D_{Gj}$  the dbh, of the  $j^{\text{th}}$  tree in the  $G^{\text{th}}$  genetic variety. The 95% confidence interval of each parameter estimate is indicated below the parameter estimate in parentheses.

**Table 4.3:** Root mean square residuals from two different model types for the genetic variety specific height-dbh relationships at age 8 for the trees in the genetic variety by initial spacing density experiment

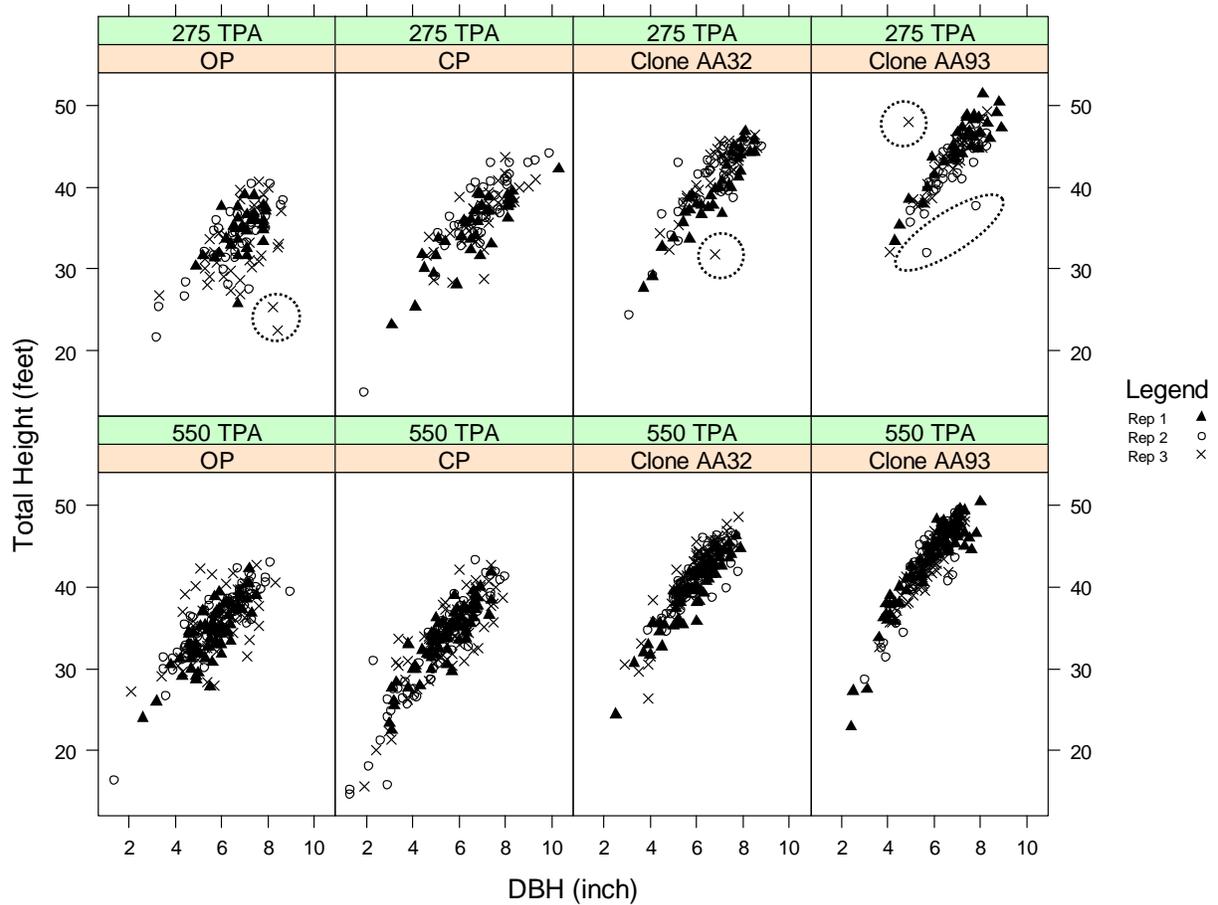
Initial Spacing Density (trees/ac)	Model	Root Mean Square Residual (in ft) for the Genetic Variety			
		OP	CP	Clone AA32	Clone AA93
275	A	2.9235	2.4168	2.1758	1.5782
	B	3.0254	2.5965	2.2762	1.7362
550	A	2.5002	2.4874	1.7359	1.5792
	B	2.6279	2.5965	1.7460	1.5918

**Note:** Model A allows both the asymptote and the rate parameter of the height-dbh relationship to vary with both the initial spacing density (ISD) and genetic variety. Model B allows only the asymptote parameter to vary with ISD and genetic variety. The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. OP and CP are non-clonal genetic varieties and Clone AA32 and Clone AA93 the clonal genetic varieties.

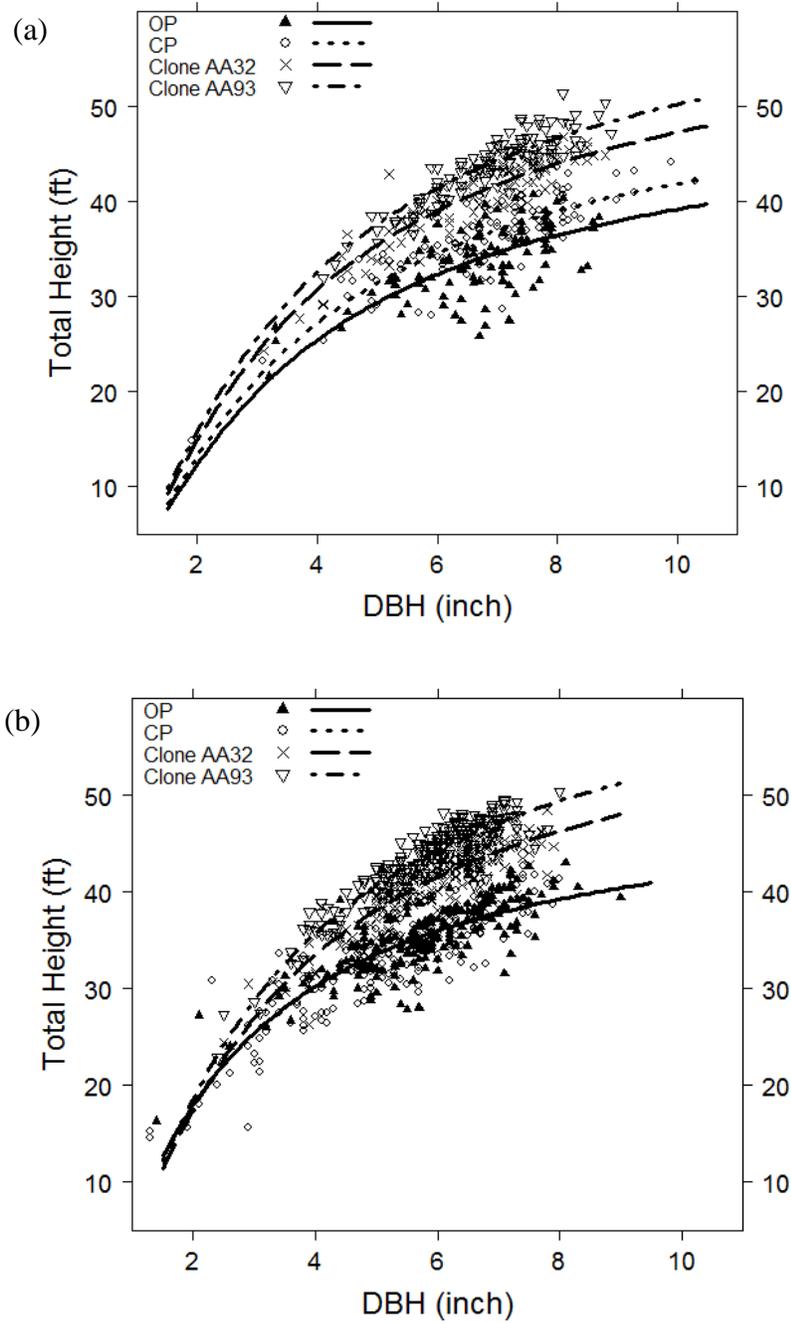
**Table 4.4:** Least square (LS) means and multiple comparisons of the moments of the age 8 total height and dbh distributions of the trees in the genetic variety plots of the genetics by initial spacing density (ISD) experiment.

Initial Spacing Density (trees per/ac)	Genetic Variety	Diameter Moments (inch)			Total Height Moments (ft)		
		MEAN	CV	Skewness	MEAN	CV	Skewness
275	OP	6.7 <sup>d</sup> (0.0820)	0.162 <sup>d</sup> (0.0280)	-0.651 <sup>d</sup> (0.0829)	33.7 <sup>d</sup> (0.5037)	0.110 <sup>d</sup> (0.0148)	-0.403 <sup>d</sup> (0.4007)
	CP	6.9 <sup>d</sup> (0.0893)	0.199 <sup>d</sup> (0.0149)	-0.466 <sup>d</sup> (0.2260)	36.1 <sup>d</sup> (0.6655)	0.122 <sup>d</sup> (0.0119)	-1.091 <sup>d</sup> (0.4935)
	Clone AA32	6.7 <sup>d</sup> (0.1127)	0.173 <sup>d</sup> (0.0138)	-0.732 <sup>d</sup> (0.0694)	40.6 <sup>e</sup> (0.7212)	0.107 <sup>d</sup> (0.0086)	-1.191 <sup>d</sup> (0.3312)
	Clone AA93	6.8 <sup>d</sup> (0.1686)	0.147 <sup>d</sup> (0.0099)	-0.470 <sup>d</sup> (0.1950)	43.6 <sup>e</sup> (0.7311)	0.082 <sup>d</sup> (0.0052)	-0.798 <sup>d</sup> (0.2166)
550	OP	5.8 <sup>d</sup> (0.0905)	0.198 <sup>d</sup> (0.0146)	-0.454 <sup>d</sup> (0.0206)	35.4 <sup>d</sup> (0.4321)	0.107 <sup>d</sup> (0.0045)	-0.742 <sup>d</sup> (0.4102)
	CP	5.4 <sup>c</sup> (0.0918)	0.248 <sup>d</sup> (0.0287)	-0.475 <sup>d</sup> (0.0833)	33.4 <sup>c</sup> (0.4010)	0.153 <sup>d</sup> (0.0244)	-0.916 <sup>d</sup> (0.1017)
	Clone AA32	5.9 <sup>d</sup> (0.0423)	0.169 <sup>d</sup> (0.0138)	-0.511 <sup>d</sup> (0.2528)	40.9 <sup>d</sup> (0.5879)	0.095 <sup>d</sup> (0.0123)	-0.956 <sup>d</sup> (0.3175)
	Clone AA93	5.8 <sup>d</sup> (0.0718)	0.170 <sup>d</sup> (0.0275)	-0.709 <sup>d</sup> (0.2039)	43.2 <sup>d</sup> (0.3284)	0.100 <sup>d</sup> (0.0142)	-1.235 <sup>d</sup> (0.3400)

**Note:** The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. OP and CP are non-clonal genetic varieties and Clone AA32 and Clone AA93 the clonal genetic varieties. CV stands for coefficient of variation and MEAN for the arithmetic mean of the distribution. The standard error of each LS mean is shown below the LS mean in parentheses. The LS mean for the OP variety, at a given ISD, is the LS mean for the control group and has a letter d on it. LS means in the same column, that are significantly greater than the control LS mean, are indicated by the letters e, f, or g in increasing magnitude of the difference. LS means significantly less than the control LS mean are indicated by the letters c, b, and a in increasing magnitude of the difference. LS means not significantly different from the control have the same letter d as the control.



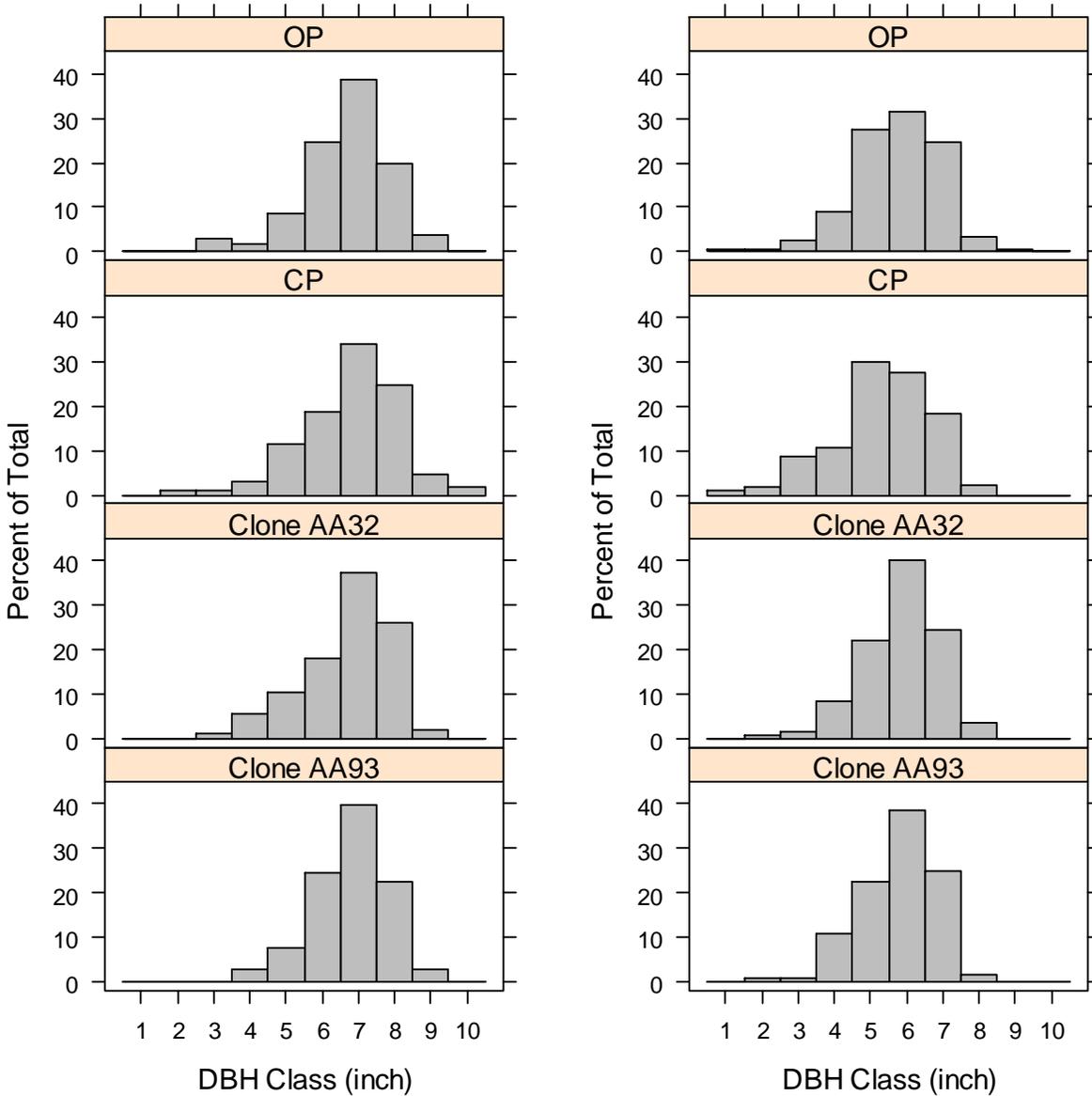
**Figure 4.1:** Height versus dbh scatter plots for the genetic variety by initial spacing density (ISD) combinations in the genetic variety by ISD experiment. The ISDs are 275 trees per acre (275 TPA) and 550 trees per acre (550 TPA). The genetic varieties are Clone AA32, Clone AA93, an open pollinated variety (OP), and a control pollinated variety (CP). Outliers or possible data recording errors are circled with dotted lines.



**Figure 4.2:** Scatter plots and the fitted height-dbh regression lines for the age 8 data for the different genetic varieties from (a) 275 trees per acre (TPA) and (b) 550 TPA treatments of the genetic variety by initial spacing density experiment. In the 550 TPA treatment plot (b) the fitted regression line for the CP genetic variety is concealed by the fitted regression line for the OP genetic variety.

(a) 275 TPA Initial Spacing Density

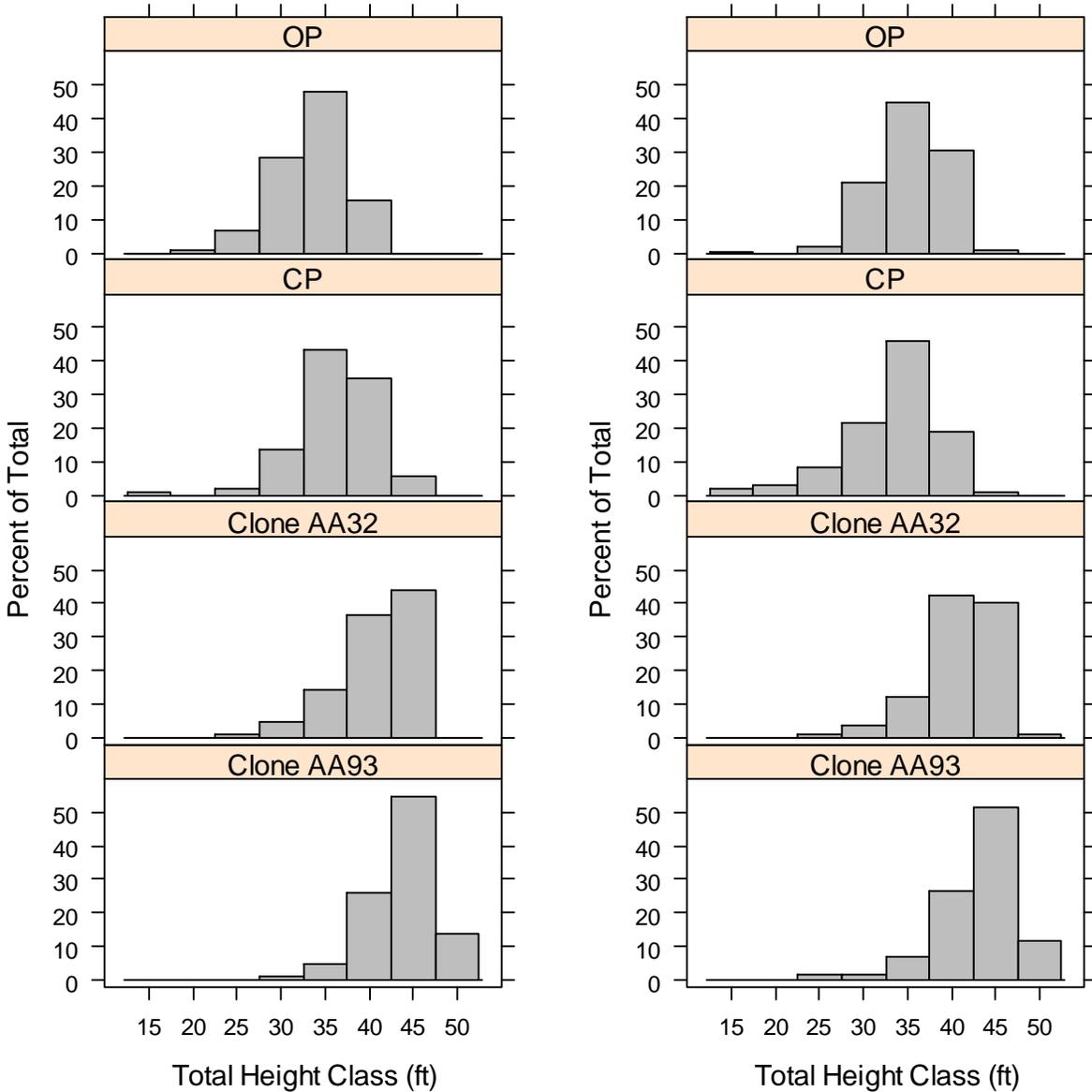
(b) 550 TPA Initial Spacing Density



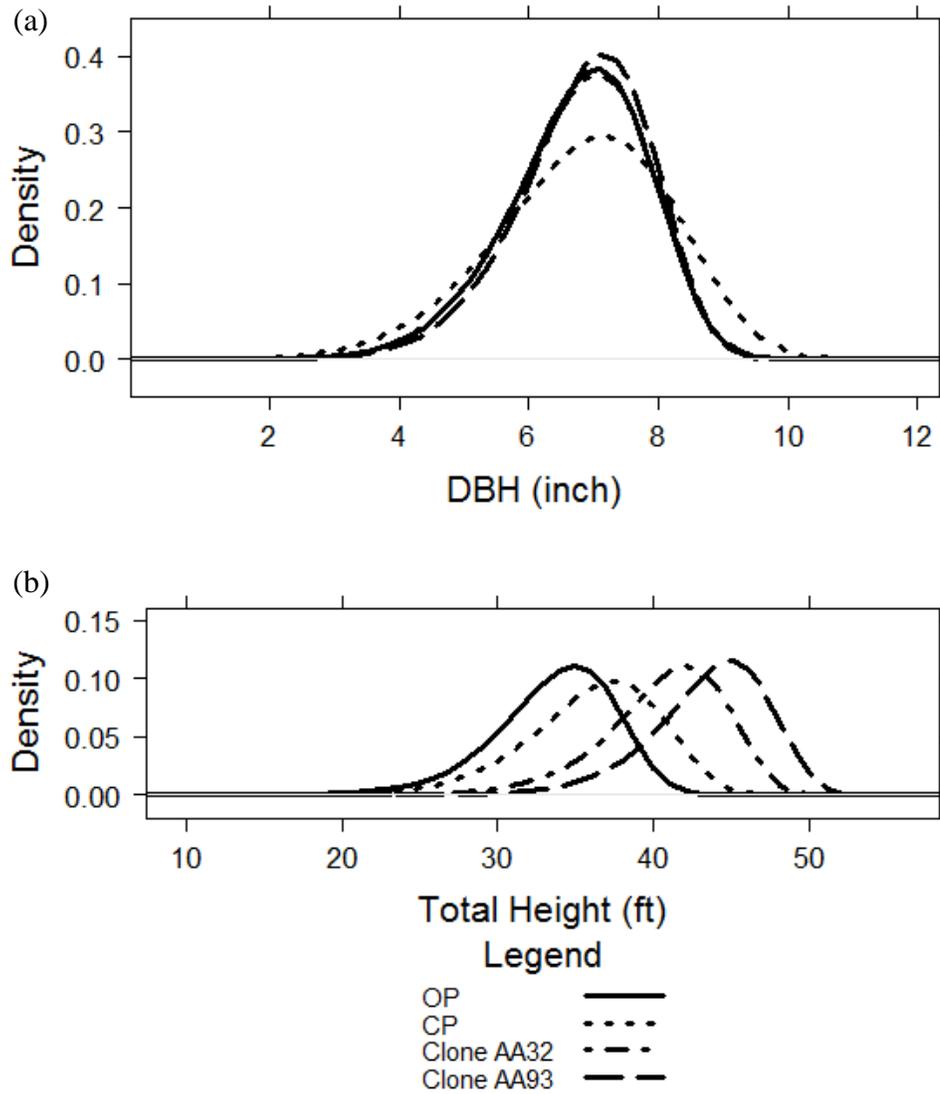
**Figure 4.3:** Histograms for the age 8 dbh distributions for the genetic varieties in (a) 275 trees per acre (TPA) and (b) 550 TPA plots, in the genetic variety by initial spacing density experiment. The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. Clone AA32 and Clone AA93 are clonal genetic varieties. A dbh class contains trees whose dbh values are within 0.5 inch of the class midpoint. A tree whose dbh was exactly 0.5 inch of the class midpoint was placed in the next lower dbh class.

(a) 275 TPA Initial Spacing Density

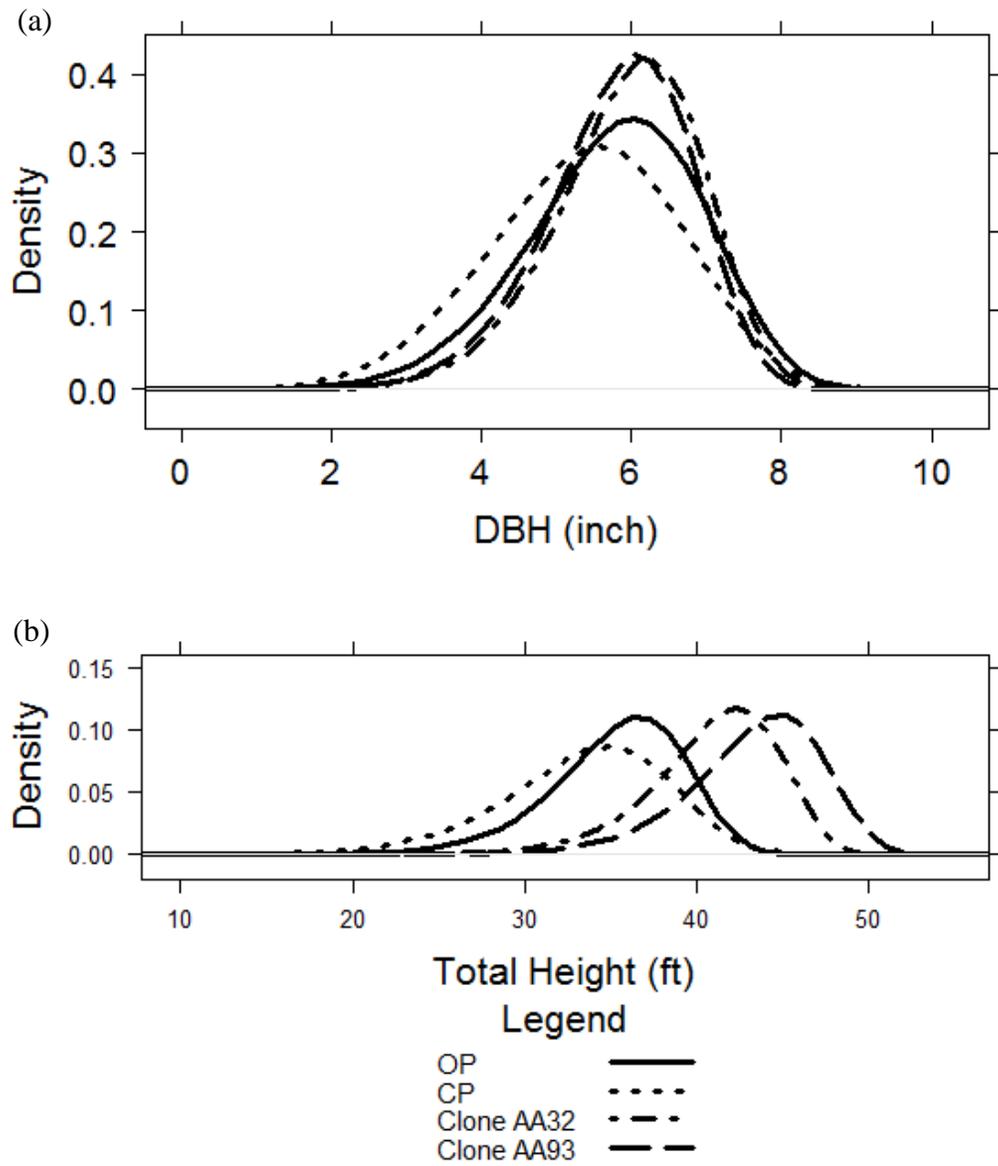
(b) 550 TPA Initial Spacing Density



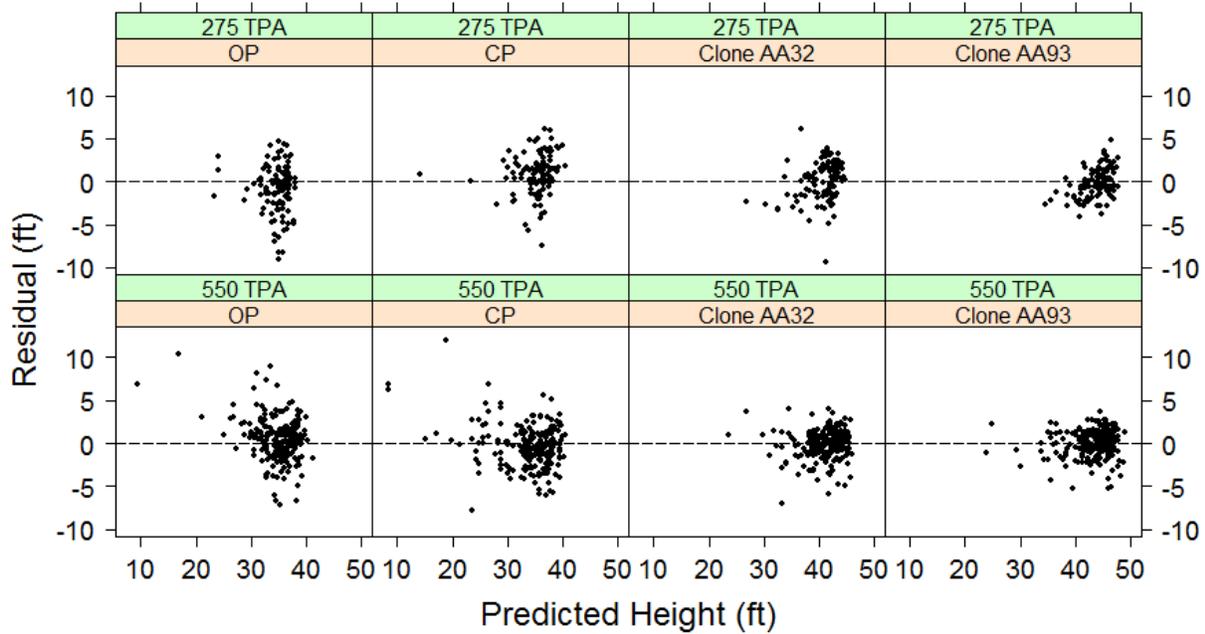
**Figure 4.4:** Histograms for age 8 height distributions for the genetic varieties in (a) 275 trees per acre (TPA) and (b) 550 TPA plots, in the genetic variety by initial spacing density experiment. The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. Clone AA32 and Clone AA93 are clonal genetic varieties. A height class contains trees whose heights are within 2.5 ft of the class midpoint. A tree whose height was exactly 2.5 ft of the class midpoint was placed in the next lower height class.



**Figure 4.5:** Fitted Weibull (a) dbh and (b) height distributions, at age 8, in the 275 trees/ac initial spacing density (ISD) treatment in the genetic variety by ISD experiment. The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. Clone AA32 and Clone AA93 are clonal genetic varieties



**Figure 4.6:** Fitted Weibull (a) dbh and (b) height distributions, at age 8, in the 550 trees/ac initial spacing density (ISD) treatment in the genetic variety by ISD experiment. The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. Clone AA32 and Clone AA93 are clonal genetic varieties



**Figure 4.7:** Plots of the genetic variety by initial spacing density (ISD) level residuals when the equation  $H_{ijk} = [\beta_{0A} + \sum_{i=1}^3 \beta_{0i} G_i + \beta_{04} N_j] \exp(\beta_1 D_{ijk}^{-1}) + \varepsilon_{ijk}$  was fitted to the height and dbh data from the genetic variety by ISD experiment. In the equation  $H_{ijk}$  is the total height in ft and  $D_{ijk}$  the dbh in inches for the  $k^{\text{th}}$  tree in the  $j^{\text{th}}$  ISD with the  $i^{\text{th}}$  genetic variety;  $G_i$  is a dummy variable with value 1 if the  $i^{\text{th}}$  genetic variety and 0 otherwise for  $i = \text{CP, Clone AA32, and Clone AA93}$ ;  $N_j$  is the ISD in trees per acre (TPA),  $\beta_{0A}$  is the global asymptote parameter and was associated with the OP genetic variety;  $\beta_{0i}$  is the genetic variety-specific dummy variable coefficient for the  $i^{\text{th}}$  genetic variety for  $i = \text{CP, Clone AA32, and Clone AA93}$ ;  $\beta_{04}$  is the ISD coefficient;  $\beta_1$  is the rate parameter; and  $\varepsilon_{ijk}$  is the random error due to the  $k^{\text{th}}$  tree in the  $j^{\text{th}}$  ISD with the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$ ).

## Chapter 5

### Competition among trees in loblolly pine stands: Does genetic variability of the trees in a stand matter?

#### Abstract

The intensity of intraspecific competitive interactions among trees in a stand was compared for seed origin versus clonal origin stands of loblolly pine using tree size-based competition indices. A method that uses maximum likelihood with simulated annealing (MLSA) and one that uses discrete radii with simple correlation coefficients (DRSC) were applied and their results compared to stand level observable effects of competition. DRSC was found to give estimates of competitor search radii that were reasonable and in line with observable stand level effects of intraspecific competition. MLSA appeared to overestimate the competitor search radii and had the potential to give estimates of the competitor search radius that were not unique. A comparison of competitor search radii in the different genetic variety stands and the observable stand level effects of competition did not find evidence to support the hypothesis that greater genetic uniformity among trees in loblolly pine stands would result in more intense intraspecific competition among the trees in the stand.

**Keywords:** *Pinus taeda*, competition indices, clonal forestry, maximum likelihood with simulated annealing, genetic uniformity

## 5.1. Introduction

Competition among trees in a forest stand is known to affect forest productivity. Prescriptions for optimum levels of spacing at planting time and thinning schedules in managed forest plantations are a response to the effects of competition among trees in a stand. Ecologically, competition among trees influences species composition in forest ecosystems and plays a role in evolution and speciation. With the advent of clonal forestry, there have been concerns that the genetic uniformity among trees in clonal stands could lead to greater intraspecific competition in such stands compared to stands of non-clonal trees (Lindgren 1993). Thus, clonal stands may require strategies of managing the effects of competition that are different from the strategies used in non-clonal stands.

Very few studies have compared inter-tree competition in clonal versus non-clonal stands. Boyden et al. (2008) mentioned that most studies on effect of genetic uniformity on the intensity of competition among plants have been in herbaceous plants with their findings not having concurred on whether genetic similarity among plants of the same species growing together increased, decreased, or had no effect on the intensity of competition among them. Studies that have compared effects of genetic uniformity on competitive interactions among trees in forest stands reached contradictory conclusions about the relationship between genetic uniformity of the trees in a stand and the intensity of the competition among the trees in that stand. Sale (2005), in a study in South Africa, concluded that competition among the trees in clonal stands of *Eucalyptus grandis* x *E. urophylla* was less intense than the competition among the trees in seed origin stands of *E. grandis*. Boyden et al. (2008), in a study in Brazil using the same species combination of clonal and seed origin stands as Sale (2005), concluded that the converse was the case. Competition among the trees in a stand was more intense in the clonal *E.*

*grandis* x *E. urophylla* stands than in the seed origin *E. grandis* stands. The contradicting conclusions could be due to the different methods that were used to “measure” competition in the stands. Sale (2005) reached his conclusion by comparing the density induced mortality and the per unit area volume production in the two stand types. Boyden et al. (2008) compared the effective competitor radius of the two stand types estimated from a functional relationship between tree growth and neighbor tree size-based competition index.

There is no known actual measure of the intensity of competition in a forest stand. Numerous indices that utilize the characteristics of the trees in a stand have been proposed and used to infer the amount of competition experienced by the trees in that stand. The indices include stand level indices such as trees per unit area, relative spacing, and Reineke’s stand density index (Reineke 1933) and a number of different tree level distance-independent and distance-dependent competition indices. Some of the existing tree level competition indices have been reviewed and compared e.g. in Daniels et al. (1986); Tomé and Burkhart (1989); Biging and Dobertin (1995). The distance weighted size ratio competition index of Hegyi (1974), or modifications of it, is probably the most widely applied tree level competition index. This could be due to the fact that it utilizes dbh, an easily measured attribute of tree size in forestry. The Hegyi (1974) competition index may be generally expressed as

$$CI_i = \sum_{j=1}^n \left( \frac{dbh_j}{dbh_i} \right)^\alpha \times \frac{1}{d_{ij}^\beta} \quad (5.1)$$

where  $CI_i$  is the competition index and  $dbh_i$  is the dbh, for the  $i^{\text{th}}$  tree;  $dbh_j$  is the dbh of its  $j^{\text{th}}$  competitor;  $d_{ij}$  is the Euclidean distance between the  $i^{\text{th}}$  tree and its  $j^{\text{th}}$  competitor; and  $\alpha$  and  $\beta$  are parameters. The parameter  $\alpha$  is a modifier parameter for the size ratio. The parameter  $\beta$  is the rate

of the exponential decrease of the competitive influence of a neighbor tree of a given size on the subject tree as distance increases. Larger values of  $\beta$  indicate a faster decline of the competitive influence of the neighbor tree. In the original Hegyi (1974) formulation, the parameters  $\alpha$  and  $\beta$  each have a value of 1. The assumption in this formulation is that the competitive influence of a neighbor tree decreases exponentially at rate = 1 as distance increases. With a value of  $\alpha = 1$ , Daniels (1976) observed, in loblolly pine, that a value  $\beta = 1$  resulted in a competition index with a higher correlation with height and dbh growth than a value of  $\beta = 2$ . Lorimer (1983) found  $\beta = 0.5$  to give the best indices for mixed hardwood stands. Methods that utilize maximum likelihood estimation combined with numerical optimization to estimate  $\alpha$  and  $\beta$  have been suggested and used e.g. Miina and Pukkala (2000); Canham et al. (2004); Richards et al. (2008). In addition, to estimating  $\alpha$  and  $\beta$ , these methods also estimate the competitor search radius and a number of other parameters in a growth – competition index (GR-CI) model that is used. It is however not known whether these methods uniquely estimate the search radius parameter and the other parameters in the competition index due to the possibility of high correlations among these parameters. None of the studies that have used these methods report the correlations among the parameters. It is known that maximum likelihood estimates may not be unique especially where parameters in the model are highly correlated. It is also doubtful whether the extra parameterizations make the competition index a significantly better indicator of the intensity of competition in a stand. In a comparison by Richards et al. (2008) the extra parameterization only reduced the model mean square error from 0.192 to 0.167. There was no mention whether this reduction was significant.

Competition indices have been used in different ways to compare the intensity of within stand competition among different stand types. Mäkinen (1997) compared the intensity of

competition in different Scots pine (*Pinus silvestris* L.) varieties by comparing the growth – tree level competition index trends for the different genetic varieties. With this approach, stands with steeper trends were considered to have more intense competition among trees in them. Brodie and DeBell (2004) used a similar approach, but with a different competition index, to compare the intensities of within stand competition in monoclonal versus clonal mixture stands of poplar (*Populus* species). Sale (2005) made a comparison of the competition intensities in clonal and non-clonal stands of Eucalyptus using stand level characteristics – maximum size-density lines and the per unit area volume production. Boyden et al. (2008) compared the competition intensities in a similar species combination of clonal and non-clonal stands by comparing the search radius parameters estimated for the different stand types by maximum likelihood with simulated annealing (MLSA), a numerical optimization technique. Thus, there has been no uniformity of approach in the comparison of the intensities of competition in different stand types. A comparison of the performance of some of the approaches has never been reported.

The objective of this study was to determine whether genetic uniformity among the trees in a loblolly pine stand would result in more intense competition among the trees in that stand. We tested the hypothesis that competition among trees in a loblolly pine stand is more intense in clonal than it is in seed origin stands. We compared the competition intensities in different stands using two different methods that use competition indices and compared the results of the two methods to the observed response of the different stand types to changes in competitive environment of the trees caused by a change in stand density. We also evaluated some of the size ratio competition indices that may be used to compare competition intensities among trees in a stand. Loblolly pine is an important commercial species in southern United States making up about 80% of the approximately 2 million acres of forest plantations established annually in this

region (McKeand et al. 2003). In the last ten years, over 10 million seedlings of clonal loblolly pine have been used in plantation establishment (McKeand et al. 2007). An understanding of how the competition dynamics in these stands compare to those of seed origin stands is necessary for appropriate density management of clonal stands.

## **5.2. Methods**

### ***5.2.1. Study material, study area, and data collection***

The study material was made up of 4 loblolly pine genetic varieties developed by Westvaco Company. The genetic varieties were WV3, a half-sib variety hereafter referred to as OP; MCP317, a full-sib variety whose mother tree was WV3 hereafter referred to as CP; Clone AA32 a clonal variety from a control cross between WV3 as the mother tree and WV5 as the father tree; and Clone AA93, a clonal variety also from a control cross between WV3 as the mother tree and WV5 as the father tree. Despite being offspring of the same parents, Clone AA32 is a broad crown ideotype while Clone AA93 is a narrow crown ideotype selected for fast height growth. Planting material for Clone AA32 and Clone AA93 was containerized rooted cuttings while that of the OP and the CP varieties was bare root seedlings. In summary, the study material was made up of 2 clonal and 2 non-clonal genetic varieties that were all related. The material can also be classified into 3 groups according to the level of genetic heterogeneity of the individuals in each genetic variety. The OP variety was theoretically the most genetically heterogeneous followed by the CP variety. The clonal varieties Clone AA32 and Clone AA93 each had genetically uniform individuals.

Data for the current study were obtained from a study established in spring of 2002, with the 4 genetic varieties, to investigate the effect of initial spacing density on stand level growth and development of the genetic varieties. The study was established near Summerville in Berkeley County, South Carolina (33°15' N, 80° 7' W), in the Atlantic coastal plain physiographic region of the United States, on a cutover site. The experiment was a completely randomized factorial design with 4 levels of genetic variety treatment – OP, CP, Clone AA32, and Clone AA93; and 2 levels of initial spacing density treatments – 275 trees/ac (TPA) and 550 TPA. It was made up of 24 contiguous 0.44-acre plots as experimental units on which the inner 0.13 acre was the measurement plot with the rest of the area around the 0.13 acre plot being occupied by buffer trees. Management of competing vegetation and nutritional deficiencies on the plots was done according to operational management prescriptions. Site preparation included shear, spot raking, chemical competition control, and bedding. Phosphorus fertilizer was applied in late summer of 2002 at the rate of 40 lbs/ac elemental phosphorus. Herbaceous weed control was done for the first two years and competition from hardwoods had been controlled as needed. Each 0.44-acre experimental plot had 10 beds each 158 ft long and spaced 12 ft apart. Trees along the beds were 13 ft from each other in the 275 TPA initial spacing density treatment and 6.5ft from each other in the 550 TPA one. The 0.13 acre measurement plot was made up of the inner 6 beds with the inner 6 trees per bed in the 275 TPA initial spacing density and with the inner 12 trees per bed in the 550 TPA density.

The data were collected during the 2009/10 dormant season (age 8 data) and during the 2010/11 dormant season (age 9 data). Each tree was measured for dbh at 4.5 ft from the ground level and total height, in addition to other measurements that do not form part of the current study. Diameter at breast height was measured in inches using a diameter tape while total height

was measured in feet using a laser hypsometer. Some of the age 8 and age 9 stand characteristics of the experimental plots are summarized in Table 5.1.

### 5.2.2. Evaluating tree level competition indices

An evaluation of some of the alternative size-based tree level competition indices was done to identify a competition index that would be most appropriate for use in comparing competition in the stands of the 4 genetic varieties. The competition indices evaluated were

$$CISR_i = \sum_{j=1}^n \frac{Size_j}{Size_i} \times \frac{1}{d_{ij}} \quad (5.2)$$

and

$$CINS_i = \sum_{j=1}^n Size_j \times \frac{1}{d_{ij}} \quad (5.3)$$

where,  $CISR_i$  and  $CINS_i$  are the competition indices for the  $i^{\text{th}}$  subject tree and  $d_{ij}$  is the Euclidean distance between the  $i^{\text{th}}$  subject tree and its  $j^{\text{th}}$  competitor. The competition index formula in equation 5.2 will hereinafter be referred to as CISR and that in equation 5.3 as CINS. CISR is a generalization of the Hegyi (1974) competition index formula to all aspects of tree size. CINS is a distance weighted size-based competition index formula that assumes that the size of the subject tree has no influence on competition from its neighbors. According to the competition interrelationship description of Weiner and Thomas (1986), this formula assumes that competition among the trees in the stand is symmetric. CISR is a mathematical transformation of

CINS obtained by scaling CINS by the reciprocal of the subject tree size. CINS was selected for evaluation due its previous applications in forest ecological studies (Canham et al. 2006; Coates et al. 2009; Perot et al. 2010) and also in studies in plantation forestry (Boyden et al. 2008).

CISR and CINS were computed from the age 8 data using only the trees in the 550 TPA initial spacing density treatment plots. The wider spacing in the 275 TPA initial density treatment plots (12 ft by 13 ft) made some of the analysis on CISR and CINS not possible hence the plots in this treatment were not used in the evaluation of the competition indices. The subject trees used in the computation of CISR and CINS were selected from the innermost 4 rows by 10 trees in each experimental plot. Thus each subject tree was at least 36 ft away from the boundary row of the 0.44-acre experimental plot, a distance that we had determined to be sufficient for the subject trees not to have potential competitors outside the experimental plot. The 4 rows by 10 trees subject tree plot was surrounded by one row of trees that had been measured during data collection and at least two rows of border trees that had not been measured. Measurements for the unmeasured border trees were generated by translation of the measurement plot into the eight plot positions around the measurement plot followed by a randomization of the translated tree measurements in the border tree positions. This method of imputing the measurements of the border trees, whose measurements are missing, has been shown to be accurate and unbiased (Pommerening and Stoyan 2006; Radtke and Burkhart 1998). CISR and CINS were computed using dbh and also using volume aspects of neighbor and subject tree size. Volume was estimated as  $0.42 \times 0.005454 \times dbh^2 \times total\ height$ . The same 4 rows by 10 trees subject tree plot was used for the investigations in sections 5.2.3 and 5.2.4. Selection of neighbor trees to be included in the computation of CISR and CINS was done using three different criteria 1) neighbor trees within a radius of one-third the dominant height of the plot, 2) neighbor trees

within a radius of one-half the dominant height of the plot, and 3) angle-gauge sampling with a basal area factor (BAF) 10 angle with the apex at the subject tree as proposed by Daniels (1976). Thus, each subject tree had 12 different competition indices computed for it from the different combinations of measures of tree size and competitor selection criteria. These procedures were implemented using a SAS (SAS Institute Inc. 2000 - 2004) macro program that was originally written by Jiping Liu for use in Liu and Burkhart (1994).

The relative performances of the competition indices were compared using the absolute value of the Pearson correlation coefficients between tree basal area growth and total height growth, during the 9<sup>th</sup> growing season, and the competition indices. The use of correlation coefficients to compare among competition indices is a common procedure in forestry research (Daniels et al. 1986; Holmes and Reed 1991; Maily et al. 2003). The 9<sup>th</sup> growing season tree basal area growth was obtained as the absolute difference between tree basal areas at ages 8 and 9. The Pearson correlation coefficients were estimated separately for each replicate plot using the CORR procedure in SAS software (SAS Institute Inc. 2000 - 2004). The 3 values of the correlation coefficient for each genetic variety were averaged to give a single value of the correlation coefficient for the genetic variety.

### ***5.2.3. Comparing competition intensities in different stands by maximum likelihood with simulated annealing (MLSA) method***

The comparison of the competition intensities in the stands of the different genetic varieties by maximum likelihood with simulated annealing (MLSA) was done using the approach explained in Canham and Uriarte (2006) and used by Boyden et al. (2008). In this

method, the intensities of the competition in the different stands are compared using estimates of the search radius parameter obtained when the parameters of a growth – competition index (GR – CI) model are fitted by maximum likelihood with simulated annealing. A stand with a smaller search radius parameter is considered to have more intense competition among the trees in it from the logic that in such a stand, the immediate neighboring trees affect the growth of the subject tree to a large extent that trees further away have no significant effect. Different GR – CI models have been used by different researchers e.g. Miina and Pukkala (2000) equation 1; Canham et al. (2004) equation 3; Uriarte et al. (2004b) equation 1. We used the model

$$\Delta BA_i = \alpha \times \exp(-\beta \times CI_i) + \varepsilon_i \quad (5.4)$$

where  $\Delta BA_i$  is the basal area increment for the  $i^{\text{th}}$  tree,  $\alpha$  is the maximum basal area increment parameter,  $\beta$  is the rate of the exponential decay parameter,  $\varepsilon_i$  is the random error due to the  $i^{\text{th}}$  tree ( $\varepsilon_i \sim N(0, \sigma_\varepsilon^2)$ ), and  $CI_i$  is the competition index for the  $i^{\text{th}}$  tree computed using the index that had better correlation with tree growth between CISR and CINS in equations 5.2 and 5.3. The size and distance components in these competition indices were parameterized as in equation 5.1 to take advantage of MLSA ability to fit these parameters instead of having them fixed e.g. in Daniels (1976) and in Perot et al. (2010). Basal area increment  $\Delta BA_i$  was calculated for each tree in the subject tree plot as the absolute difference between the age 8 and age 9 tree basal areas while  $CI_i$  was calculated from age 8 tree measurements. We chose model 5.4 as it had the best fit out of three models that we tested including one similar to 5.4 but with the parameter  $\alpha$  substituted with the potential diameter increment equation that was a function of tree dbh.

The MLSA procedure was implemented separately on each of the replicate plots of the 4 genetic varieties in the 550 TPA initial spacing density treatment using computer software code

that had been developed and compiled into an R package called '*neighlikeli*' by Charles Canham of Cary Institute of Ecosystem Studies, Millbrook, NY. The R code was obtained from [http://www.sortie-nd.org/lme/lme\\_R\\_code\\_tutorials.html](http://www.sortie-nd.org/lme/lme_R_code_tutorials.html) (last accessed February 5, 2011). For each experimental plot, the MLSA procedure was implemented 3 different times each time with different starting values for the parameters being estimated. Consistency in the final estimates of the parameters and the AIC fit statistic values, from the 3 different MLSA runs, were used as indicators of the procedure having converged correctly. The run with the median value of the search radius parameter, but within the 95% confidence limits of the estimates of this parameter from the 3 runs, was used to provide the parameter estimates for the experimental plot. In case of inconsistencies in the final parameter estimates, 3 more MLSA runs were executed for the experimental plot. Each MLSA run was set to have 50,000 model iterations, which were enough to provide evidence of the likelihood function having been maximized. We settled on 50,000 iterations after initial test runs showed that no significant changes in model fit and parameter estimates occurred with a higher number of iterations. A plot of the log likelihood against the number of iterations was used to display the changes in the log likelihood values with increasing number of model iterations/decrease in the annealing temperature. An unchanging likelihood during the last 20,000 of the 50,000 iterations was used as an indicator of the likelihood having been maximized. The trend in the log likelihood during the 50,000 iterations, for one of the experimental plots, is shown in Figure 5.1.

#### ***5.2.4. Comparing competition intensities in different stands by discrete radii with simple correlations (DRSC) method***

Comparison of the competition intensities by the method we named “discrete radii with simple correlations” (DRSC) was motivated by the way MLSA searches the estimate of the competitor search radius parameter. During a single iteration of the process, the value of the search radius is randomly varied while keeping the values of the other parameters in the GR – CI model at their current levels. The associated change in model log likelihood is used to determine whether or not to keep the new search radius. The iteration completes with the variation of the other parameters one at a time while holding the others at their current values. This is repeated until the preset number of iterations is reached. Thus, at the end of the iteration process, the estimate of the competitor search radius obtained is conditional on the other parameters in the GR – CI model. Correlations among the parameters in the GR – CI model are likely to affect the estimate of the competitor search radius obtained. Previous studies that have used MLSA to investigate competitive interactions among trees in forest stands do not report the correlations among the parameters hence it is not known how the parameters could have been affecting each other during the MLSA parameter estimation process. In addition, previous studies that have investigated the correlation between tree growth and competition indices have shown that the maximum of the correlation – competitor search radius curve may not correspond to a unique value of the competitor search radius or the maximum of the curve may not be estimable within the range of data available (Luis et al. 1998 Figure 2; Pukkala and Kolström 1987 Figure 3). For this reason, Luis et al. (1998) determined the competitor search radius for their application to be the radius that corresponded to the correlation that was 95% of the maximum. With possibilities of parameter correlations and a maximum correlation that may not be reached in the range of

data available, it is possible for MLSA to give an erroneous estimate of the competitor search radius.

DRSC is not an entirely new technique. The technique or variations of it have been used to determine the appropriate competitor search radius in forestry research (Luis et al. 1998; Perot et al. 2010; Pukkala and Kolström 1987). However, the use of the technique to compare the competition intensities in different stand types has not, in our knowledge, been reported. For this application, the technique works on the same principle as MLSA as used by Boyden et al. (2008). The competitor search radii for different stands are estimated from the relationship between tree growth and competition index then compared. DRSC is different from MLSA in that DRSC uses simple correlation coefficients and hence avoids the issue of possible correlations among parameters in a GR – CI model affecting estimates of the competitor search radius. In addition, the competitor search radii in DRSC are varied discretely by the researcher and graphical techniques used to visually identify the optimum radius. The researcher can easily identify the point where further increases in the radius may not be of significance.

DRSC was implemented separately on each of the replicate plots of the 4 genetic varieties in the 550 TPA initial spacing density treatment on the same trees that were used in the MLSA procedure described in section 5.2.3. The best formulation of the competition indices CISR and CINS was used to compute the competition index for every tree in the in the 4 rows by 10 trees subject tree plot. The competition index was computed using age 8 data. Seven different competition indices were computed for each tree every time with a different competitor search radius. The search radii used covered the range 8 ft to 32 ft and were spaced at intervals of 4 ft. The range of radii and the intervals between the radii were chosen based on the spacing of the trees in the experimental plots and the distance between the border row and the subject tree

closest to the border row. For the trees in the subject tree plots, the closest neighbor tree was 6.5 ft away and the closest border row was at least 36 ft away. The selected range and interval insured that a change in competitor search radius resulted in a change in the number of competitor trees included in the calculation of the competition index and that border row trees would not be included in the calculation. The average number of competitor trees per subject tree, for the search radii used, is given in Table 5.2. The implementation of the described procedure was done using the same SAS (SAS Institute Inc. 2000 - 2004) macro program used in section 5.2.2. Pearson correlation coefficients between the 9<sup>th</sup> growing season tree basal area growth and the competition indices were then estimated, for each experimental plot-competitor search radius combination, using the CORR procedure in SAS software (SAS Institute Inc. 2000 - 2004). Each genetic variety had 3 values of the correlation coefficient estimated for every competitor search radius, one for every replicate plot. The value of the correlation coefficient for a genetic variety, at a given competitor search radius, was estimated by taking the arithmetic average of the three values of the correlation coefficient. The optimum competitor search radius for each of the 4 genetic varieties was then determined by visual inspection of the correlation coefficients – competitor search radius graphic plots. Observable absolute differences among the competitor search radii were used to deduce the differences in the intensity of competition in the stands of the different genetic varieties.

### ***5.2.5. Comparing competition intensities in different stands using the responses of the trees to changes in stand density***

Comparing the intensities of competition in the different stands using the responses of the trees to changes in stand density was motivated by the logic that if within stand competition was more intense in the stands of some of the genetic varieties, then a change in stand density would have a greater impact on growth in those stands than in the stands where there is less intense competition among the trees. The research question was whether there is more intense competition among trees in clonal stands; hence we tested the hypothesis that changes in within stand competition has a greater impact on growth in clonal stands than it has in non-clonal stands. To test this hypothesis the experimental plots in both the 275 TPA and the 550 TPA initial spacing density treatments were used. For each experimental plot, the average basal area increment was calculated as the absolute difference between the basal area of the plot at age 8 and that at age 9, weighted by the number of trees in the plot. The increment in dominant height was also calculated as the absolute difference between the dominant height of the plot at age 8 and that at age 9. Dominant height at each age was calculated as the average height of the trees in the plot whose dbh was equal to or greater than the quadratic mean dbh of the plot. The effect of within stand competition on the basal area and dominant height increments of trees in the different stand types was investigated by analyzing the effects of genetic variety, initial spacing density, and genetic variety by initial spacing density interaction. This was done by carrying out 4 by 2 factorial analysis of variance (ANOVA) on the basal area increment and dominant height increment data using the GLM procedure in SAS software (SAS Institute Inc. 2000 - 2004). The linear model for the analysis was

$$y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk}, i = 1, 2, \dots 4; j = 1, 2; k = 1, 2, 3 \quad (5.5)$$

where  $y_{ijk}$  is the  $k^{\text{th}}$  dominant height increment or basal area increment in the  $j^{\text{th}}$  initial spacing density with the  $i^{\text{th}}$  genetic variety;  $\mu$  is the overall mean basal area increment or mean dominant height increment;  $\alpha_i$  is the effect of the  $i^{\text{th}}$  genetic variety;  $\beta_j$  is the effect of the  $j^{\text{th}}$  initial spacing density;  $(\alpha\beta)_{ij}$  is the  $i^{\text{th}}$  genetic variety by  $j^{\text{th}}$  initial spacing density interaction effect; and  $\varepsilon_{ijk}$  is the random error due to the  $k^{\text{th}}$  basal area increment or dominant height increment in the  $j^{\text{th}}$  initial spacing density with the  $i^{\text{th}}$  genetic variety ( $\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$ ). Pairwise comparisons of the genetic variety by initial spacing density means was done with Tukey honest significant differences (HSD) adjustment of p-values to maintain an overall Type I error rate of 0.05. A test of the hypothesis on whether change in within stand competition had more impact on the growth in clonal stands was done by looking at the significance of the interaction effect in the linear model 5.5 and comparing the Tukey HSD adjusted genetic variety means at each of the two initial spacing densities. These analyses were complemented with the visual inspection of the graphical plots of the increment least square means of the different genetic varieties at the two initial spacing densities.

## 5.3. Results

### 5.3.1. Evaluation of tree level competition indices

The average Pearson correlation coefficients between tree growth and competition indices in the plots of the different genetic varieties for the different considerations of computing the competition indices in equations 5.2 and 5.3, are shown in Figures 5.2 and 5.3. For all the genetic types the size ratio competition indices CISR were better correlated with basal area growth than the neighbor size only competition indices CINS, which for most of the plots were

not significantly different from zero at  $p = 0.05$  (Figure 5.2). The size-ratio competition index computed from the dbh of the trees, hereinafter referred to as DBH Ratio, exhibited greater correlation with basal area growth in the clonal stands than it did in the non-clonal stands with the correlation being greatest in the stands of Clone AA93 genetic variety. The size-ratio competition index computed from tree volumes, hereinafter referred to as Volume Ratio, did not exhibit this trend. Competition indices from competitor trees selected within a radius of one-half the dominant height of the plot did not appear to give better correlation with basal area growth than the competition indices with competitor trees selected within a radius of one-third the dominant height of the plot. The correlations from the competitor selection based on a fixed radius did not appear to be very different from the correlations with competitors selected by the variable radius angle-gauge sampling with BAF 10 angle. The Volume Ratio competition index appeared to be the more versatile of the two size-ratio competition indices DBH Ratio and Volume Ratio. Its correlations did not trend with genetic variety and did not appear to change between fixed radius and the variable radius criteria of selecting competitors. The results in sections 5.3.2 and 5.3.3 are based on the Volume Ratio competition index.

All the competition indices evaluated had very low, mostly insignificant, correlations with tree total height increment (Figure 5.3). For all the formulations of the competition indices evaluated, the correlations between the increment in total height and competition index appeared to be highest or among the highest for Clone AA93 genetic variety.

### 5.3.2. Comparing competition intensities in different stands by maximum likelihood with simulated annealing (MLSA) method

The competitor search radii obtained by MLSA method, for the different plots of the 550 TPA initial spacing density, are given in Table 5.3. These estimates were obtained using the GR – CI model

$$\Delta BA_i = \alpha \times \exp \left( -\beta \times \left[ \sum_{j=1}^N \left( \frac{Vol_j}{Vol_i} \right)^\gamma \times \frac{1}{d_{ij}^\delta} \times I_{\{d_{ij} \leq \rho\}} \right] \right) + \varepsilon_i \quad (5.6)$$

where  $\Delta BA_i$  is the basal area increment for the  $i^{\text{th}}$  subject tree;  $Vol_i$  is the volume of the  $i^{\text{th}}$  subject tree and  $Vol_j$  is the volume of its  $j^{\text{th}}$  competitor;  $d_{ij}$  is the Euclidean distance between the  $i^{\text{th}}$  subject tree and its  $j^{\text{th}}$  competitor,  $N$  is the total number of trees in the experimental plot including those not in the subject tree plot;  $I$  is a 1, 0 indicator variable with a value of 1 if  $d_{ij} \leq \rho$  and zero otherwise;  $\alpha$  is the maximum basal area increment parameter;  $\beta$  is the rate of the exponential decay parameter;  $\gamma$  is the modifier parameter to the size ratio whose value was fixed at  $\gamma=1$ ;  $\delta$  is the rate of the exponential decrease of the effect of a competitor with distance and its value was also fixed at  $\delta=1$ ;  $\rho$  is the competitor search radius parameter;  $\varepsilon_i$  is the random error due to the  $i^{\text{th}}$  tree ( $\varepsilon_i \sim N(0, \sigma_\varepsilon^2)$ ). Equation 5.6 is a detailed version of equation 5.4. We included the indicator variable in equation 5.6 to explicitly show the competitor search radius parameter. Previous studies that have used a similar approach (e.g. Canham et al. 2006; Coates et al. 2009; Uriarte et al. 2004a), did not explicitly show this parameter in their model equations making it difficult for a reader to recognize it as a parameter in the models. We fixed the values of the parameters  $\gamma$  and  $\delta$  as these parameters, and the other parameters in equation 5.6, could not be estimated uniquely when  $\gamma$  and  $\delta$  were free to be estimated by the MLSA process. Some of the parameter estimates changed significantly from one MLSA run to another without a change in

the log likelihood and other measures of model fit. With the fixing of the parameters  $\gamma$  and  $\delta$  the estimates of the other parameters became consistent from one MLSA run to another except for replicate 1 plot of Clone AA93 genetic variety. In this plot, the estimates of the parameter  $\beta$  were 0.3612 and 0.9650 while the estimates of  $\rho$ , the competitor search radius parameter, were 26.8 and 13.1 with the smaller value of  $\beta$  being associated with the larger value of  $\rho$ .

From the absolute value comparison of the means in Table 5.3, MLSA identified the CP genetic variety as the one with the shortest competitor search radius hence the genetic variety with the most intense competition among trees in its stand. Clone AA32 was estimated to have the longest competitor search radius hence the genetic variety with the least competition intensity among the trees in its stand. The OP variety and Clone AA93 variety were estimated to have the same degree of competition in their stands. If the value 13.1 ft was chosen instead of 26.8 ft for the replicate plot 1 of Clone AA93 genetic variety, then the optimum competitor search radius of Clone AA93 would be the second shortest making it the variety with the second highest intensity of within stand competition out of the 4 varieties. In 4 of the experimental plots used namely OP replicate 1 and replicate 3, Clone AA32 replicate 2, and Clone AA93 replicate 3; MLSA procedure estimated a competitor search radius that was the maximum possible radius under the limits of the experiment. In the named plots, each subject tree had, according to Table 5.2, an average of approximately 40 competitor trees.

### ***5.3.3. Comparing competition intensities in different stands by discrete radii with simple correlations (DRSC) method***

Plots of the average Pearson correlation coefficient between basal area growth and competition index versus the competitor search radius, for the 4 genetic varieties, are shown in Figure 5.4. The correlation for the CP variety increased slightly with distance to a maximum then dropped gradually. The correlations of the other varieties increased to a maximum, then remained more or less constant at the maximum value. As shown by the dotted arrows, DRSC method identified the CP variety to have the shortest competitor search radius and Clone AA32 to have the longest. The OP and Clone AA93 varieties were identified as having equal competitor search radii. Thus, the method identified the CP genetic variety to have the most intense competition among trees in its stands and the Clone AA32 genetic variety to have the least intense within stand competition of the 4 genetic varieties. The OP and the Clone AA93 genetic varieties were identified to have equivalent intensities of competition in their stands, which were higher than that in the CP stands but less than that in the Clone AA32 stands.

### ***5.3.4. Comparing competition intensities in different stands using the responses of the trees to changes in stand density***

The changes in the tree level mean basal area increments in the 4 genetic varieties, with changes in stand density, are shown in Figure 5.5 (a). The overall 4 genetic levels by 2 initial spacing density levels factorial ANOVA detected a significant effect of genetics ( $p = 0.0254$ ) and initial spacing density ( $p < 0.0001$ ) but a marginally insignificant genetics by initial spacing density interaction effect ( $p = 0.0669$ ) in the average basal area increments. A comparison of the

means at the 550 TPA initial spacing density did not detect significant differences among the average basal area increments for the different genetic varieties ( $p \geq 0.9997$ ) but there appeared to be some differences at the 275 TPA initial spacing density. At this density, the OP and the Clone AA93 genetic varieties had average basal area increments that were significantly smaller than the increment that was observed in the CP genetic variety ( $p = 0.0236$  and  $p = 0.0382$  respectively) but that were not significantly different from the increment that was observed in Clone AA32 genetic variety ( $p = 0.2522$  and  $0.3629$  respectively). The average basal area increment in the CP variety was not significantly different from the increments observed in Clone AA32 genetic variety ( $p = 0.8737$ ). Likewise the increment in the OP genetic variety was not significantly different from the increment in the Clone AA93 genetic variety ( $p = 1.000$ ).

Change in stand density impacted the basal area growth in the 4 loblolly pine genetic varieties differently. The CP genetic variety exhibited the greatest change in average basal area growth with change in stand density while the OP and Clone AA93 exhibited the least change. Clone AA32 variety exhibited a greater change than OP and Clone AA93 but less than the CP variety. By the criterion of the amount of response with change in stand density, the CP variety was identified to have the most intense within stand competition and the OP and Clone AA93 varieties the least intense of the 4 varieties. Clone AA32 had a within stand competition intensity that was in between that of the CP variety and that of the OP and Clone AA93 varieties.

The changes in the mean dominant heights of the 4 genetic varieties, with changes in stand density, are shown in Figure 5.5 (b). The overall 4 genetic variety levels by 2 initial spacing density levels factorial ANOVA indicated that the effects of genetic variety, initial spacing density, and genetic variety by initial spacing density interaction were all not significant ( $p$  values = 0.5676, 0.8752, and 0.2144 respectively). Thus changes in within stand competition

did not appear to have a significant effect on the 9<sup>th</sup> growing season height increment of any of the genetic varieties. However, though not statistically significant, the changes in dominant height increment of the 4 genetic varieties with change in stand density suggested two contrasting effects of within stand competition on stand height development. Increased within stand competition could decrease height growth as suggested by the trends of the OP and Clone AA93 varieties or it could increase it as suggested by the trends of the CP and Clone AA32 varieties (Figure 5.5 (b)).

## **5.4. Discussion**

### ***5.4.1. Evaluation of tree level competition indices***

For the 4 genetic varieties in this study, the size of the subject tree was found to be important in the computation of the competition index for that tree. Thus, according to the description of Weiner and Thomas (1986), competition in the stands of these varieties can be described as asymmetric. This finding agrees with the findings of Lorimer (1983) in natural hardwood stands and Miina and Pukkala (2000) in mixed conifer stands but disagrees with that of Canham et al. (2004) in mixed conifer stands and Boyden et al. (2008) in Eucalyptus clonal and non-clonal stands. The conclusion of Canham et al. (2004) was based on the observation that the competition index with the size ratio component (Equation 1b in Canham et al. 2004) resulted in a competition model with a poorer likelihood ratio fit statistic than the competition index without the size ratio component (Equation 1a in Canham et al. 2004 ). However, the authors also observed that the insignificant contribution of the size ratio component could be due to the effect of shading in the stand having been accounted for by a shading effect variable in the two models used to compare the effect of the size ratio variable. It is generally accepted that

competition for light is the major cause of size asymmetry in the competition among plants (Schwinning and Weiner 1998; Weiner 1990; Weiner and Thomas 1986). It is therefore possible that without the shading effect variable in their models, the size ratio effect might have been important. Boyden et al. (2008) based their conclusion on the observation that the parameter associated with the size asymmetric component in their competition index equation was estimated to be not different from zero when the parameters of the competition model were fitted by MLSA. It is possible that correlation among the parameters in the model due to an attempt to estimate 2 different parameters as exponents of the same variable in the model could have influenced the parameter estimates. The competition index equation 1 in Boyden et al. (2008) can be written, in an expanded form, as

$$NI_{focal} = \sum_{i=1}^n M_i^{\alpha} \times \frac{1}{d^{\beta}} \times M_i^{\gamma} \times \frac{1}{M_{focal}^{\gamma}} \quad (5.7)$$

where  $NI_{focal}$  is the competition index for the focal/subject tree;  $M_i$  is the mass of its  $i^{\text{th}}$  competitor;  $d$  is the distance between the subject tree and its  $i^{\text{th}}$  competitor; and  $\alpha$ ,  $\beta$ , and  $\gamma$  are parameters. It is evident from this expanded formulation that the parameters  $\alpha$  and  $\gamma$  are fitted as exponents of  $M_i$ . This is equivalent to fitting a different parameter say  $\delta = \alpha + \gamma$  and, depending on the relationship between  $\alpha$  and  $\gamma$ , one of them may drop out of the model due to model compatibility reasons and not due to insignificance of the predictor variable.

In the 3 criteria of competitor selection tested, DBH Ratio competition indices appeared to have better correlation with basal area growth in the clonal stands than in the non-clonal stands with the highest correlation observed being that in the stands of Clone AA93. Volume Ratio competition indices did not show this trend. This could be attributed to the observation in

these stands (analysis and results not shown) that the variability of the total heights at a given dbh was smaller in the clonal than in the non-clonal stands. Thus the dbh of a tree was a more accurate estimate of the size of the tree in clonal stands than it was in non-clonal stands. This explanation is supported by the observation that the Volume Ratio competition index, which includes tree total height in its computation, did not appear to give better correlations for trees in clonal stands.

For a given genetic variety, competition indices computed using neighbors from a radius of one-third the dominant height of the stand and those computed using neighbors from a radius of one-half the dominant height of the stand did not differ a great deal in their correlation with basal area growth. A radius of one-half the dominant height of the stand as the competitor search radius was probably longer than would be required to provide an optimum number of competitors. This was expected as it is known that more neighbor trees beyond those within a certain radius do not significantly change the correlation (Figure 5.4; Pukkala and Kolström 1987 Figure 3).

From the work of Daniels (1976), the general notion has been that variable radius (angle-gauge) criterion of selecting competitor trees to include in a competition index is superior to fixed radius approach; for instance Biging and Dobbertin (1992) stated that:

“In this study fixed radii were not considered because recent studies have shown that correlations with growth were greater when competitors were chosen by angle gauge techniques than by fixed competition zone (Daniels 1976, Daniels et al. 1986).”

The results in Figure 5.2 show that either of the fixed radius approaches based on a portion of dominant height resulted in correlations that were as good as those obtained with the variable

radius approach. The concern of Daniels (1976) was that the approach of Hegyi (1974) did not allow for the inclusion of more competitor trees in the competition index as the stand grew. With the choice of a fixed radius based on stand height such as done in this study, the competition zone radius will increase with stand age.

The low correlations between the competition indices and height growth is expected as it is known that except under conditions of high stand density, within stand competition does not have a significant effect on height growth. However, the slightly higher correlation observed for Clone AA93 may be interesting. It suggests that height growth of this genetic variety may be affected earlier on by the competition in a stand than is the case for the other genetic varieties included.

#### ***5.4.2. Comparing MLSA and DRSC methods of comparing competition intensities in forest stands***

The observable changes in the stand level basal area growth, with changes in stand density (Figure 5.5 (a)), showed that the OP and Clone AA93 were affected in the same way and were the least impacted by density changes while the CP variety was the most impacted by the density changes. Both the MLSA and DRSC methods identified the CP variety to have the most intense within stand competition and also identified the OP and Clone AA93 varieties to have similar levels of within stand competition. While the observable changes indicated that Clone AA32 variety had a within stand competition intensity in between that of the CP and the OP and Clone AA93 varieties, MLSA and DRSC identified the Clone AA32 variety to have the least within stand competition. Thus, it appears like MLSA and DRSC did not get right the

competition intensity in Clone AA32 stands. However, if the procedure used by Luis et al. (1998) is applied to get the optimum competitor search radius instead of using the point where the curve flattens, then this point on a smoothed version of the Clone AA32 curve would put the competitor search radius between 12 ft and 16 ft (Figure 5.4). Thus DRSC would give an estimate of Clone AA32 within stand competition that agrees with the changes observed in Figure 5.5 (a).

MLSA generally gave longer estimates of competitor search radii. Of concern are the estimates that were at the maximum limit of the competitor tree – subject tree distance. The trends in Figure 5.4 show that it is possible for MLSA to overestimate the competitor search radius. For example, for all the 4 genetic varieties, competitors selected within a radius of 32 ft of the subject tree would not give correlations that are very different from those given by competitors selected within a radius of 20 ft. So, as long as there is some increase in the correlation between growth and the competition index with increase in competitor search radius, the MLSA algorithm can continue increasing the competitor search radius until it reaches the limit. Thus MLSA, needs to be constrained to identify when the competitor search radius estimated is just the optimum and a further increase in the radius is not making the competition index significantly better biologically. Incorporating appropriate constraints or stopping rules in MLSA algorithm may not be an easy task. DRSC appeared to give reasonable estimates of the competitor search radius and led to conclusions on the intensity of within stand competition that were in line with observable stand level changes. In addition, the method leaves the determination of the optimum competitor radius to the user. There may be subjectivity in the process but this shields the competitor search radius estimation process from attempts to satisfy a statistical criterion that may not meaningful.

Correlations among the parameters of the GR – CI model used in MLSA are another issue of concern regarding this method. Though we did not fully investigate this during the current study, the fact that we could not obtain unique estimates of the parameters with the full model formulation equation 5.6 and we had a case where we could not uniquely estimate some of the parameters even after fixing some of the possibly offending parameters in this equation (Table 5.3) points to a possible problem with the MLSA that has apparently been overlooked by previous users of this method e.g. Uriarte et al. (2004b); Canham et al. (2006); Coates et al. (2009).

#### ***5.4.3. Competition intensities in clonal versus seedling stands of loblolly pine***

The clonal stands in this study did not appear to have competition dynamics that differed from those of seed origin stands. All 3 methods used to investigate the competition dynamics identified the non-clonal CP variety as the one with the most intense within stand competition. The methods also indicated that the intensity of within stand competition in the OP and the Clone AA93 genetic varieties did not differ. These observations do not support the hypothesis that clonal loblolly pine stands have more intense within stand competition than seed origin stands. Thus, this hypothesis was rejected. From the results in Figure 5.5, within stand genetic uniformity could increase, decrease, or have no effect on the intensity of the competition within the stand. This agrees with the findings in herbaceous plants as observed by Boyden et al. (2008). Comparing the OP and Clone AA93 genetic varieties only, one would conclude that genetic uniformity has no effect on the intensity of within stand competition. However, if the CP variety was compared to Clone AA93, the conclusion would be that genetic uniformity decreases

the intensity of within stand competition. The differences in the responses of the clonal varieties Clone AA32 and Clone AA93, though not statistically significant, point to a hypothesis that different clones could have different levels of within stand competition intensity hence the existence of genotype by competitive environment interaction. Increased stand density appeared to impact the basal area growth of Clone AA32 more than it impacted the basal area growth of Clone AA93. The possible explanation to this difference is that Clone AA32 being a broad crown ideotype experienced greater within stand competition at higher stand densities due to the larger crowns of its trees having greater shading effects on each other. On the other hand, Clone AA93 being a narrow crown ideotype experienced less shading among trees in its stands at high stand densities hence was impacted less by increased stand density.

The possible effects of within stand competition on height increment (Figure 5.5 (b)) did not indicate a grouping by clonal or seed origin varieties further lending support to the rejection of the hypothesis that within stand competition is more intense in clonal than in non-clonal stands of loblolly pine.

## **5.5. Conclusions and recommendations**

The size ratio competition index of Hegyi (1974), or modifications of it, has been widely used in forestry. In this study, we showed that this competition index is superior to competition indices that are based only on size of the neighbor trees. We also showed that selecting competitors to be included in the competition index from a fixed radius that is one half or one third of the dominant height of the stand resulted in competition indices that were as good as those obtained when the competitors were selected by angle-gauge sampling with a BAF 10

angle. Either of the competitor selection approaches, fixed radius or angle-gauge selection can be applied. Tree size based competition indices that utilize the dbh of the tree alone were found to be as good as those based on tree volume but those based on tree volume would be the best to use for comparing competition across different genetic varieties. The addition of the height measurement to the competition index computation would help take into account the differences in the height/dbh ratio among different genetic varieties.

We highlighted some of the possible weaknesses of MLSA as a method of estimating parameters that are used to infer the degree of competitive interactions among trees in forest stands. Apart from the weaknesses of maximum likelihood estimation such as need to assume a probability distribution and flat or almost flat likelihood surfaces at the maximum, correlations among the parameters to be estimated and the fact that a distance weighted competition index approaches an upper asymptote as more competitors further away are included were found to be issues that could influence the results. This procedure requires a rigorous evaluation that will highlight how correlations among the parameters in a GR – CI model could affect the estimates of the other parameters in that model. We demonstrated how simple correlation coefficients from varying competitor search radius could be used to compare the competition intensity in different stands. The results from this procedure agreed with the changes observed at stand level which indicated that the procedure provided results that were consistent with other evidence. This procedure needs to be applied on other similar studies to test its applicability. It could be useful in comparing intensities in within stand competition in stands of different genetic varieties where there is only one stand density available for each of the genetic varieties being compared.

The genetic uniformity among trees in a stand appeared not to affect the intensity of competition within the stand. Thus, generalizations on the competitive interactions in clonal

versus seed origin stands may not be made. Even among the clonal stands, generalizations may also not be made. Modeling competition, effects of thinning, or effects of spacing for clonal stands therefore remains a challenge. Selection criteria for clones may need to be taken into account. A closer working relationship between tree breeders and forest biometricians may help provide the needed information. The different competitive abilities and behavior also call for the re-evaluation of the accuracy of using a common competition index to model growth in mixed variety stands. Competition ideotypes and isolation ideotypes (Cannell 1978) growing in the same stand may experience the effects of competition in different magnitudes that a common competition index may not reflect correctly.

Our study was limited by the range of the stand densities and genetic material. In addition, we had only one growing season of growth data that we used in the investigation. Further investigations in this subject area with data from several growing seasons, a wider range of stand densities and genetic material, and a wider site distribution could help confirm and/or generalize some of the conclusions reached in this study and help generate trends that could be used in modeling.

## 5.6. Literature cited

- Biging, G.S., and M. Dobbertin. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *For. Sci.* 38:695-720.
- Biging, G.S., and M. Dobbertin. 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* 41:360-377.
- Boyden, S., D. Binkley, and J.L. Stape. 2008. Competition among Eucalyptus trees depends on genetic variation and resource supply. *Ecology* 89:2850-2859.
- Brodie, L.C., and D.S. DeBell. 2004. Evaluation of field performance of poplar clones using selected competition indices. *New For.* 27:201-214.
- Canham, C.D., P.T. LePage, and K.D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* 34:778-787.
- Canham, C.D., M.J. Papaik, M. Uriarte, W.H. McWilliams, J.C. Jenkins, and M.J. Twery. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecol. Appl.* 16:540-554.
- Canham, C.D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecol. Appl.* 16:62-73.
- Cannell, M.G.R. 1978. Improving per hectare forest productivity. P. 120 - 148 *in* 5th N Am For Biol Workshop, Gainesville, FL.
- Coates, K.D., C.D. Canham, and P.T. LePage. 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. *J. Ecol.* 97:118-130.

- Daniels, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. *For. Sci.* 22:454-456.
- Daniels, R.F., H.E. Burkhart, and T.R. Clason. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. *Can. J. For. Res.* 16:1230-1237.
- Hegyí, F. 1974. A simulation model for managing jack-pine stands. P. 74-90 in *Growth Models for Tree and Stand Simulation*. Res. Notes No. 30. Royal College of Forestry, Stockholm, Sweden.
- Holmes, M.J., and D.D. Reed. 1991. Competition indices for mixed species northern hardwoods. *For. Sci.* 37:1338-1349.
- Lindgren, D. 1993. Population biology of clonal deployment. P. 34-49 in *Clonal Forestry I: Genetics and Biotechnology*, Ahuja, M.R., and W.J. Libby (eds.). Springer-Verlag, Berlin, Germany.
- Liu, J., and H.E. Burkhart. 1994. Modelling inter- and intra-specific competition in loblolly pine (*Pinus taeda* L.) plantations on cutover, site-prepared lands. *Ann. Bot.* 73:429-435.
- Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manage.* 6:343-360.
- Luis, M.d., J. Raventós, J. Cortina, M.J. Moro, and J. Bellot. 1998. Assessing components of a competition index to predict growth in an even-aged *Pinus nigra* stand. *New For.* 15:223-242.

Mailly, D., S. Turbis, and D. Pothier. 2003. Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce. *Can. J. For. Res.* 33:435-443.

Mäkinen, H. 1997. Possibilities of competition indices to describe competitive differences between Scots pine families. *Silva Fenn.* 31:43-52.

McKeand, S.E., T.J. Mullin, T.D. Byram, and T.L. White. 2003. Deployment of genetically improved loblolly and slash pines in the south. *J. For.* 101:32 - 37.

McKeand, S.E., B.J. Zobel, T.D. Byram, and D.A. Huber. 2007. Southern pine tree improvement-A living success story. P. 3 - 5 *in* Proceedings of the 29th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Galveston, TX.

Miina, J., and T. Pukkala. 2000. Using numerical optimization for specifying individual-tree competition models. *For. Sci.* 46:277-283.

Perot, T., F. Goreaud, C. Ginisty, and J.F. Dhôte. 2010. A model bridging distance-dependent and distance-independent tree models to simulate the growth of mixed forests. *Ann. For. Sci.* 67:502p501-502p511.

Pommerening, A., and D. Stoyan. 2006. Edge-correction needs in estimating indices of spatial forest structure. *Can. J. For. Res.* 36:1723-1739.

Pukkala, T., and T. Kolström. 1987. Competition indices and the prediction of radial growth in Scots pine. *Silva Fenn.* 21:55-67.

- Radtke, P.J., and H.E. Burkhart. 1998. A comparison of methods for edge-bias compensation. *Can. J. For. Res.* 28:942-945.
- Reineke, L.H. 1933. Perfecting a stand density index for even-age forests. *J. Agri. Res.* 46:627 - 638.
- Richards, M., A.J.S. McDonald, and M.J. Aitkenhead. 2008. Optimisation of competition indices using simulated annealing and artificial neural networks. *Ecol. Model.* 214:375-384.
- Sale, G. 2005. A comparison of between-tree competition effects in separate stands of *Eucalyptus grandis* seedling and a single *Eucalyptus grandis* x *urophylla* hybrid clone. Masters thesis, University of the Witwatersrand, Johannesburg, South Africa. 97 p.
- SAS Institute Inc. 2000 - 2004. SAS 9.2 Help and Documentation. SAS Institute Inc., Cary, NC.
- Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113:447-455.
- Tomé, M., and H.E. Burkhart. 1989. Distance-dependent competition measures for predicting growth of individual trees. *For. Sci.* 35:816-831.
- Uriarte, M., C.D. Canham, J. Thompson, and J.K. Zimmerman. 2004a. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.* 74:591-614.
- Uriarte, M., R. Condit, C.D. Canham, and S.P. Hubbell. 2004b. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *J. Ecol.* 92:348-360.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5:360-364.

Weiner, J., and S.C. Thomas. 1986. Size variability and competition in plant monocultures.  
Oikos 47:211-222.

**Table 5.1:** Age 8 and age 9 least square means for some of the stand characteristics of the plots of the genetic variety by initial spacing density experiment

Stand Characteristic	Genetic Variety	275 TPA Initial Spacing		550 TPA Initial Spacing	
		Age 8	Age 9	Age 8	Age 9
Quadratic Mean dbh (inch)	OP	6.8 <sup>a</sup>	7.4 <sup>a</sup>	5.9 <sup>ab</sup>	6.4 <sup>a</sup>
	CP	7.0 <sup>a</sup>	7.7 <sup>a</sup>	5.5 <sup>a</sup>	6.1 <sup>a</sup>
	Clone AA32	6.8 <sup>a</sup>	7.6 <sup>a</sup>	6.0 <sup>b</sup>	6.5 <sup>a</sup>
	Clone AA93	6.9 <sup>a</sup>	7.5 <sup>a</sup>	5.9 <sup>ab</sup>	6.4 <sup>a</sup>
Dominant Height (ft)	OP	35.6 <sup>a</sup>	40.9 <sup>a</sup>	37.8 <sup>a</sup>	42.6 <sup>a</sup>
	CP	38.7 <sup>b</sup>	43.9 <sup>a</sup>	36.5 <sup>a</sup>	43.0 <sup>a</sup>
	Clone AA32	43.2 <sup>c</sup>	48.6 <sup>b</sup>	43.4 <sup>b</sup>	49.4 <sup>b</sup>
	Clone AA93	45.9 <sup>c</sup>	51.9 <sup>b</sup>	46.0 <sup>b</sup>	50.9 <sup>b</sup>
Basal Area (ft <sup>2</sup> /acre)	OP	69.2 <sup>a</sup>	82.3 <sup>a</sup>	102.1 <sup>ab</sup>	119.4 <sup>a</sup>
	CP	72.3 <sup>a</sup>	88.7 <sup>a</sup>	89.7 <sup>a</sup>	108.0 <sup>a</sup>
	Clone AA32	70.1 <sup>a</sup>	85.9 <sup>a</sup>	104.3 <sup>b</sup>	121.5 <sup>a</sup>
	Clone AA93	70.9 <sup>a</sup>	84.5 <sup>a</sup>	103.9 <sup>b</sup>	122.0 <sup>a</sup>
Survival (%)	OP	98.1 <sup>a</sup>	97.2 <sup>a</sup>	97.2 <sup>a</sup>	95.8 <sup>a</sup>
	CP	98.1 <sup>a</sup>	98.1 <sup>a</sup>	97.2 <sup>a</sup>	96.8 <sup>a</sup>
	Clone AA32	99.1 <sup>a</sup>	99.1 <sup>a</sup>	94.9 <sup>a</sup>	94.9 <sup>a</sup>
	Clone AA93	99.1 <sup>a</sup>	99.1 <sup>a</sup>	98.6 <sup>a</sup>	98.6 <sup>a</sup>

**Note:** The genetic variety OP is the half-sib WV5 and CP is the full-sib MCP317. TPA is trees per acre. Dominant height was calculated as the average height of the trees whose dbh was equal to or greater than the plot quadratic mean diameter. Means in the same column, for a given stand characteristic, with the same letter a, b, or c are not significantly different at  $p = 0.05$  with Tukey HSD adjustment procedure for multiple comparisons.

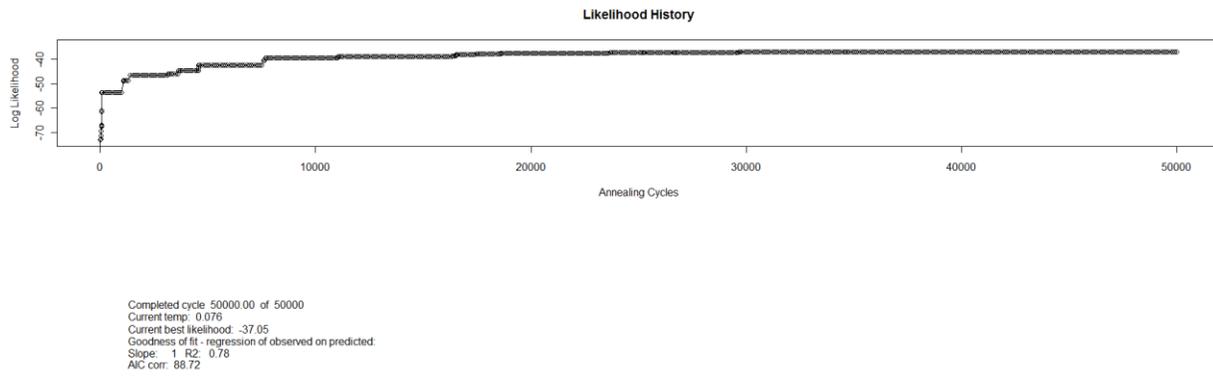
**Table 5.2:** Average number of competitor trees per subject tree for the selected competitor search radii in the 550 TPA plots of the genetics by initials spacing density experiment

Competitor Search Radius (ft)	8	12	16	20	24	28	32
Average Number of Competitors	2	4	10	16	21	31	39

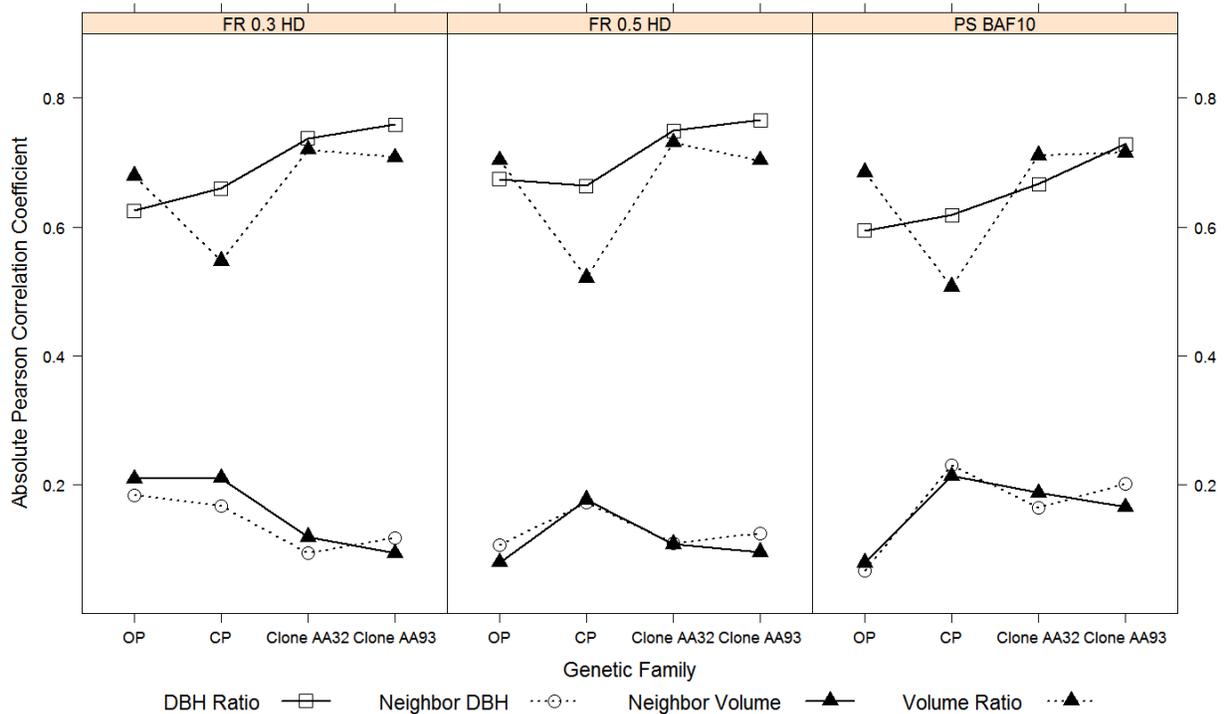
**Table 5.3:** Competitor search radii, estimated by maximum likelihood with simulated annealing (MLSA), for the trees in the 550 TPA plots of the genetics by initial spacing density experiment

Replicate	Competitor Search Radius for the Genetic Variety (ft)			
	OP	CP	Clone AA32	Clone AA93
1	36.0	18.9	27.0	26.8 (13.1)
2	12.0	26.0	36.0	26.5
3	36.0	19.8	28.2	36.0
Mean	29.0	21.3	33.7	29.8 (25.2)

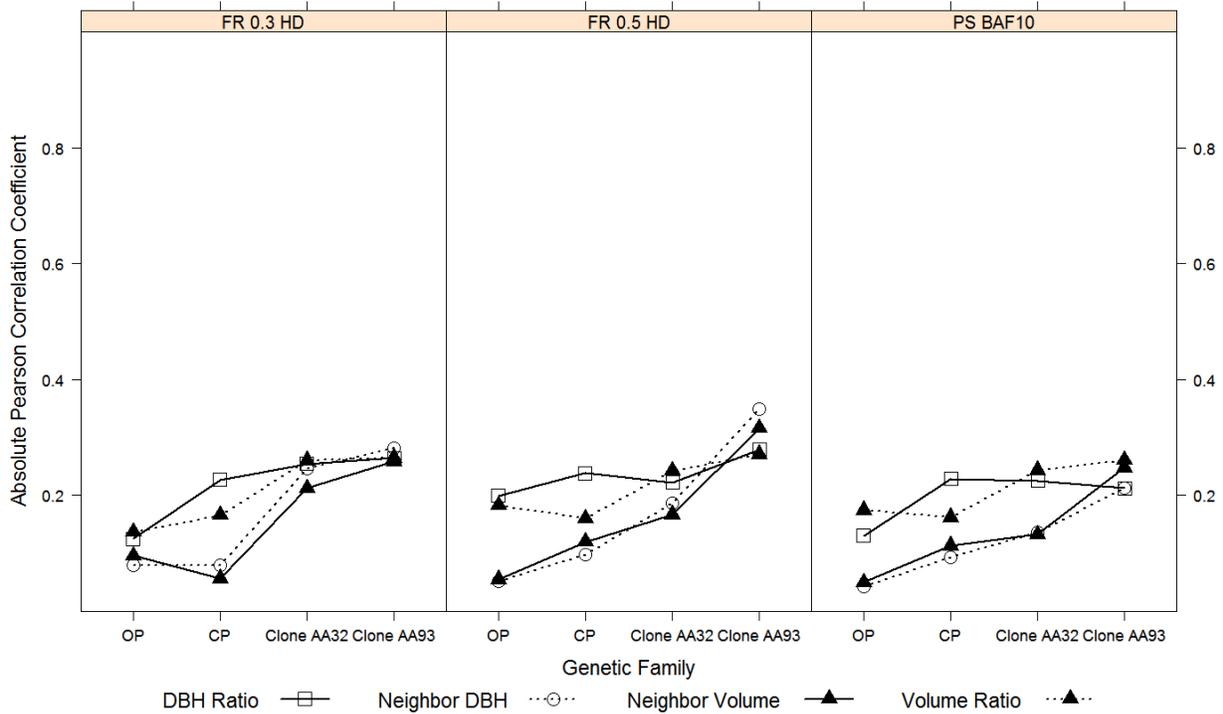
**Note:** The value of the search radius in parenthesis under Clone AA93 replicate 1 is the other competitor search radius value estimated by the MLSA procedure. The mean for Clone AA93 in parentheses was calculated using the estimate 13.1 ft for Clone AA93 replicate 1



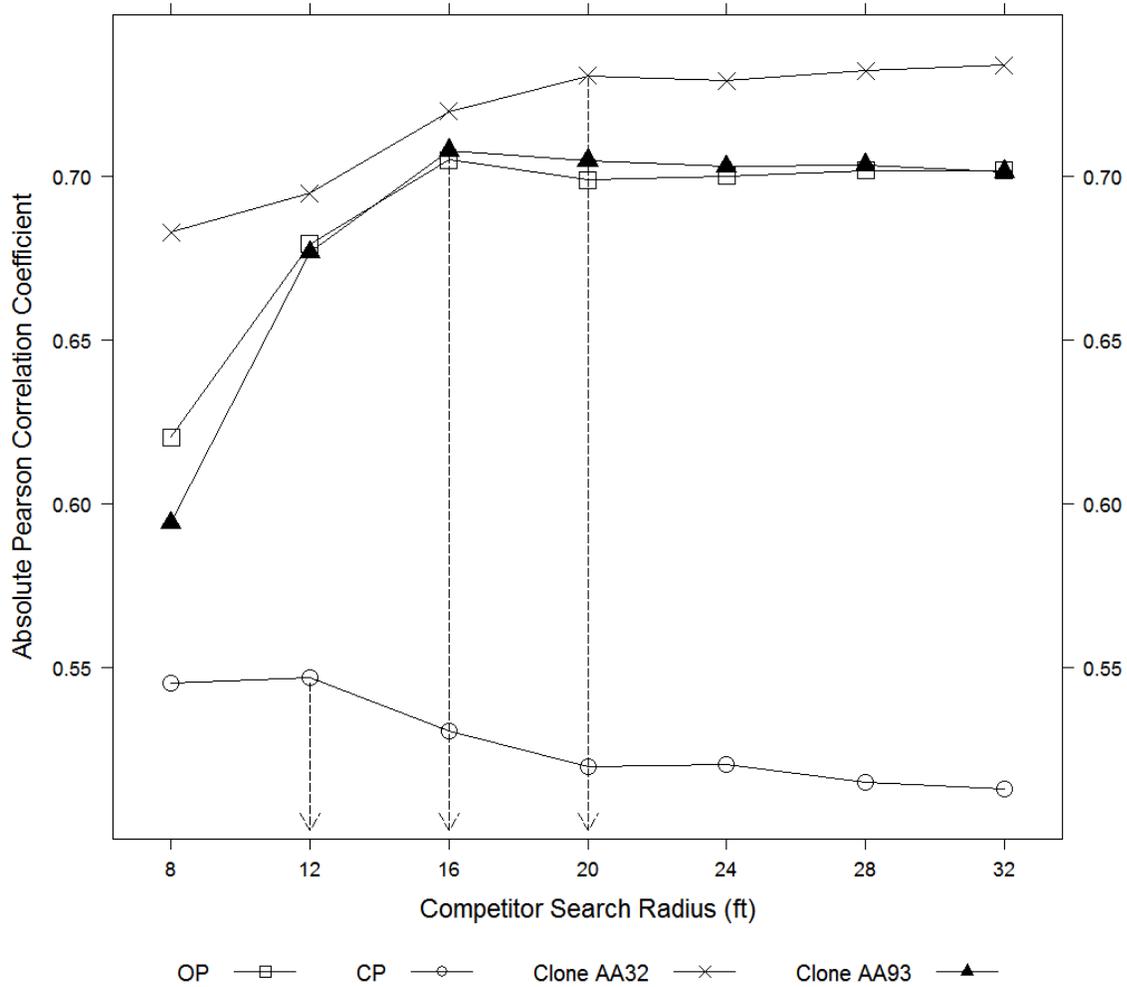
**Figure 5.1:** Trend in the model log likelihood for a maximum likelihood with simulated annealing run on the basal area increment-competition index data from one of the experimental plots in the 550 trees per acre initial spacing density treatment



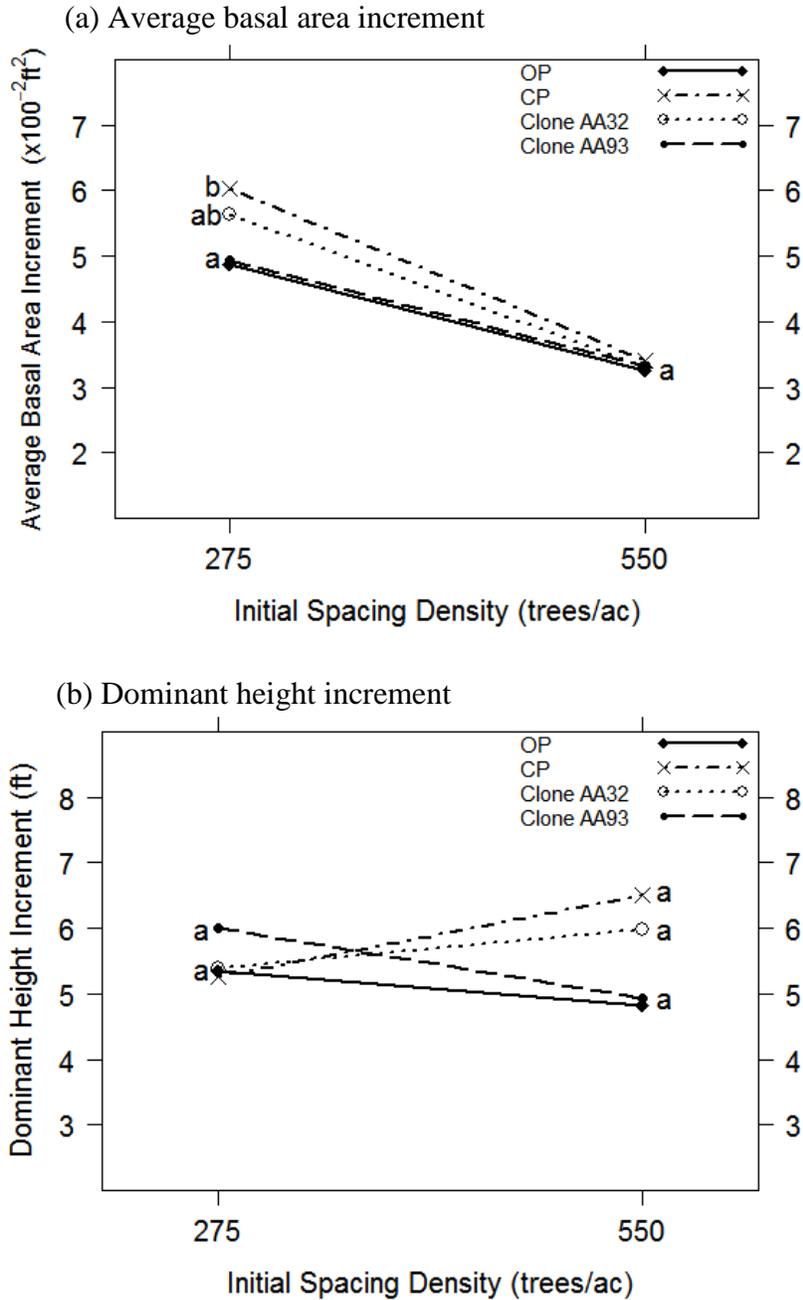
**Figure 5.2:** Plots of the absolute Pearson correlation coefficients between individual tree competition indices and tree basal area growth during the 9<sup>th</sup> growing season for the different genetic varieties in the 550 TPA plots of the genetic variety by initial spacing density experiment. FR 0.3 HD stands for fixed radius one-third of the plot dominant height, FR 0.5 HD for fixed radius one-half of the stand dominant height and PS BAF10 for angle-gauge sampling with basal area factor 10 angle with the apex at the subject tree. DBH Ratio and Volume Ratio are the distance weighted size ratio competition indices. Neighbor DBH and Neighbor Volume are competition indices that do not take the size of the subject tree into account.



**Figure 5.3:** Plots of the absolute Pearson correlation coefficients between individual tree competition indices and tree total height growth during the 9<sup>th</sup> growing season for the different genetic variety in the 550 TPA plots of genetic variety by initial spacing density experiment. FR 0.3 HD stands for fixed radius one-third of the plot dominant height, FR 0.5 HD for fixed radius one-half of the stand dominant height and PS BAF10 for angle-gauge sampling with basal area factor 10 angle with the apex at the subject tree. DBH Ratio and Volume Ratio are the distance weighted size ratio competition indices. Neighbor DBH and Neighbor Volume are competition indices that do not take the size of the subject tree into account.



**Figure 5.4:** Absolute Pearson correlation coefficients between tree basal area growth and competition indices for competition indices computed using neighbor trees from different radii from the subject tree. The dotted arrows point to the optimum competitor search radius for stands of the different genetic varieties OP, CP, Clone AA32, and Clone AA93.



**Figure 5.5:** Plots of the least square means of the 9<sup>th</sup> growing season (a) average basal area increments and (b) dominant height increments for the stands of the different genetic varieties in the genetic variety by initial spacing density experiment. OP stands for WV3 genetic variety and CP for MCP 317 genetic variety. The means at the same initial spacing density, with the same letter a or b are not significantly different at  $p = 0.05$  with Tukey HSD adjustment for multiple comparisons

## Chapter 6

### Summary, implications, and recommendations

#### 6.1. Summary and implications

The work done in this dissertation can be grouped into two main categories 1) investigation of the effects of genetic improvement and clonal forestry on stand characteristics and interrelationships among stand components that are used to model growth and yield of loblolly pine stands, and 2) evaluation of some of the methods that may be used to adjust loblolly pine growth and yield model components to new genetic families and those that may be used in the study of competitive interactions among trees in stands of genetically enhanced loblolly pine. The summary and implications of the findings in this dissertation follow.

##### *6.1.1. Effect of genetic improvement and clonal forestry on stand characteristics and within stand interrelationships*

Genetic improvement or clonal forestry had no practical effect on parameters of height-age and those of height-dbh relationships beyond the effect on the asymptote parameters of the relationships. These findings coincide with what has been observed in past studies with provenance or half-sib planting material. Thus, techniques currently used to adjust height-age and height-dbh relationships to different provenance and genetic family varieties can be used on clonal varieties. It was, however, observed that the variance of the height-dbh relationships decreased with decrease in genetic variability within a stand. This implies that the stands

established with open pollinated planting material (OP stands) will likely exhibit greater vertical crown differentiation compared to clonal stands, a difference that is likely to lead to differences in development of the two stand types after crown closure. The OP stands will likely exhibit higher degrees of dominance and suppression leading to greater suppression-driven mortality and faster progression of the dominant trees into the larger dbh classes. On the other hand, clonal stands might experience less suppression-driven mortality and hence slower progression of the trees into the larger dbh classes. These differences imply that whole stand mortality models that have number of trees per unit area as one of the predictors may need additional predictors to accurately reflect these hypothesized differences in after crown closure stand development. Individual tree mortality models that include size of the subject tree and a measure of the sizes of its neighbors as predictors may provide a better reflection of the hypothesized mortality differences between the two stand types. The hypothesized differences in future stand development may result in the diameter and height distributions of the OP stands being more variable than those of clonal stands despite there being no difference in the variances of these characteristics at age 8. This hypothesis is supported by the observation that non-clonal stands at the higher stand density had a dbh variance that was significantly larger than the dbh variance of clonal stands.

Trees in the stands exhibiting higher levels of genetic gains in site index were on average taller but not larger in average dbh than those exhibiting lower levels of genetic gain in site index. This suggests a modification of taper equations especially in growth and yield models that predict volume to different top diameters. Modification of tree volume equations may also be needed given the changes in tree form.

Genetic improvement had no effect on variance and skewness of height and dbh distributions. It also had no effect on the mean of dbh distribution but resulted in an upward shift in mean of height distribution. This finding indicated that there could be a genetic gain in height growth that is not accompanied by a gain in dbh growth. For improved genetic varieties that exhibit this kind of relationship with the genetically unimproved, growth and yield models in which the basal area growth equation is a function of site index or dominant height will overestimate the genetic gain in basal area. Economic gain due to genetic improvement will also be overestimated not only from the overestimated basal area but also from the fact that the model will predict a dbh distribution that has some higher in value larger dbh trees that may never develop in the stand. A simple analysis using the stand level basal area equation

$$\ln(BA) = -1.7525 - \frac{1.5902}{A} + 0.9880 \ln(HD) + 0.4522 \ln(N) \quad (6.1)$$

from the growth and yield model FASTLOB (Amateis et al. 2001) showed that a 25% increase in site index (base age 25) resulted in a 25% overestimation of basal area and volume at age 8 if the observed increase in site index did not result in a corresponding increase in basal area. Mortality estimates may also be erroneous where the mortality equation used is a function of site index, e.g. the mortality equations of Zhao et al. (2007).

Clonal stands did not exhibit decreased variance in height and dbh distributions as expected except for dbh distribution at the higher stand density where the variance of this distribution in clonal stands was smaller than it was in the non-clonal stands. The statistically significant difference in the variance of dbh distribution at the higher stand density was actually due to increased variance of dbh distribution of the non-clonal stands and not due to decrease in variance of dbh distribution of clonal stands when compared to coefficient of variation values for

dbh distribution at the lower stand density. This observation supports the hypothesis that increased within stand competition might cause variance of tree size distributions in non-clonal stands to become larger than the variance of the tree size distributions in clonal stands. The trend suggested by this observation is that at lower stand densities there may be no difference in the within stand tree size uniformity between clonal and non-clonal stands, but the uniformity in non-clonal stands may decrease with higher stand densities or after crown closure. Thus, modeling changes in within stand dbh or height variance due to clonal plantings in loblolly pine may require taking into consideration the stage of stand development and/or the stand density.

Competition among trees in stands was not necessarily more intense in the genetically similar clonal stands compared to the genetically heterogeneous non-clonal stands. This was not expected at least according to ecological resource partitioning theory, which expects genetically identical individuals to exhibit greater competition among them due to having identical ecological demands. Thus, generalizations of effects of stand density on stand growth, in the fashion of effect on clonal stands versus effects of non-clonal ones, may not be made.

With the exception of the increased height growth, higher levels of genetic improvement did not result in age 8 stands that were very different from the stands with lower levels of genetic improvement in as far as tree size characteristics are concerned. The same was the case with clonal forestry. Except in height, sizes of trees in clonal stands was not very different from the sizes of those in non-clonal stands. Thus, the major effect of loblolly pine genetic improvement and/or clonal forestry on tree size was the increased height growth. Economic benefits that may result from genetic improvement or clonal forestry increasing the proportion of the higher in value larger dbh trees, in the final harvest, may not be realized. This may be compounded by the hypothesized slower mortality in clonal stands, which may curtail the progression of the trees in

these stands into the larger dbh classes. The economic benefit of clonal forestry in loblolly pine will probably be mainly due to greater uniformity of tree quality characteristics such as stem straightness, smaller microfibril angle, more favorable branch angle, etc. It may also result from fewer incidences of fusiform rust where a rust resistant clone is deployed in a rust hazard area or from fewer incidences of traits such as forking. Fusiform rust and forking decrease the proportion of the saw timber size trees that finally get selected to be marketed for saw timber production. The benefits due to greater uniformity in quality characteristics and fewer incidences of fusiform rust and/or forking may be incorporated into growth and yield prediction systems by adjusting the proportions of the timber in the different dbh classes at rotation.

### ***6.1.2. Methodology evaluation***

An evaluation of alternative methods of assessing stand characteristics was done for mixed-effects model versus least squares approaches of calibrating height-age models to new genetic families. In addition, comparisons were carried out on dbh versus volume variables of tree size in competition index calculation, and the computationally intensive maximum likelihood with simulated annealing (MLSA) versus the simpler Pearson correlations-based methods of comparing within stand competition intensities. This dissertation demonstrated how the alternative methods could be used and highlighted some of the strengths and weaknesses of the methods.

Mixed-effects model approach of localizing a population-wide model to a specific group within the population has recently found a wide range of applications in forestry. For localizing a height-age equation to a new clone, this approach was found to be more accurate than using

ordinary least squares to estimate the clone-specific parameters. It can be applied to localize a region-wide loblolly pine height-age model to a new genetic variety. However, estimates with this approach may be biased especially if the new genetic family is an outlier or at the extremes of the assumed distribution of the groups. Its application may also be hampered by a prior covariance matrix that may not be appropriate to the application at hand or the absence of such a matrix.

Maximum likelihood with simulated annealing (MLSA) has been applied in ecological modeling to evaluate neighborhood interactions in forested ecosystems. It has been applied in plantation forestry to compare intensities of intraspecific competition in stands of different genetic varieties. This technique was found to have weaknesses in its application to loblolly pine plantations including the difficulty of incorporating stopping rules into the estimation algorithm and the potential to give non-unique estimates of the optimum competitor search radius. A simpler technique that works on the same principle as MLSA but using simple Pearson correlation coefficients and is under a greater degree of control by the researcher was proposed and evaluated. This simpler technique was found to perform better than MLSA. The technique can be applied to compare intraspecific competition intensities among stands where only one level of stand density is available.

Tree size-based competition indices are used in some distance-dependent individual tree growth and yield models. Tree size-based competition indices based on volume as an aspect of tree size were found to perform better than those based only on dbh, when the competition indices were used across different genetic varieties. Competition indices based only on dbh were found to be sufficient for competition indices to be used within one genetic variety. For certain management objectives where more than one genetic variety is planted in the same stand, a

volume based competition index should give tree size-based competition indices that are more accurate. Selection of competitor trees to be included in a tree size-based competition index for trees in loblolly pine plantations is mainly done using a basal area factor 10 angle with the vertex at the subject tree. Selection of competitor trees from a distance of one-third the dominant height of the stand gave competition indices were as good as those obtained with competitors selected by the angle gauge method in as far as correlations with tree height and basal area growth were concerned. The one-third of dominant height approach may be used where it is important to have all the competitors within a given distance included in a competition index e.g. in mixed genetic variety stands where the angle-gauge approach may disproportionately select some of the genetic varieties.

## **6.2. Recommendations for future research**

One of the limitations of this dissertation was the narrow genetic base of the loblolly pine varieties used in the studies. The varieties used were all siblings from a common mother tree identified by MeadWestvaco/ArborGen as WV3 and also as 7-56, one of the best growing loblolly pine half-sib genetic variety in southern United States. The findings of this study may be applicable to loblolly pine from the WV3 breeding line but further studies involving other breeding lines will be needed to develop a generalization and modeling framework with the information provided by this dissertation. However, the findings of this research provide useful indicators of stand behavior in genetically enhanced loblolly pine. Some of the observed and hypothesized differences in stand dynamics may be used in simulation studies to test different scenarios of the effects of genetic improvement and/or clonal forestry. This should however be

done with the awareness that the various aspects of stand dynamics are interrelated and that different model structures may give different results (Burkhart and Matney 1981).

Another limitation was the absence of rotation length (approximately 25 years) data for the height-age relationship studies and the relatively young ages of the stands used in the height-dbh relationships and distributions and competition interrelationships studies. With data only up to age 15 available for the former study, trends in height development of the clones between ages 16 and 25 could not be evaluated. In the latter studies, the age 8 and 9 data available was from stands that had not stayed in the closed crown stage long enough for some of the effects of intraspecific competition on stand development to be observed. Follow up studies with data from older ages will be useful in testing some of the hypotheses put forward in section 6.1.1 and also test the accuracy of using trends from early ages to predict later age development of new genetic varieties.

Propagation method by silviculture intensity interactions have been observed to occur (Stape et al. 2010) and hence there are possibilities of the results of the genetic variety by initial spacing study being different if the study was done on plots under intensive silviculture as opposed to plots under operational silviculture used in the current study. Future research under intensive silviculture may provide insights into how the stand dynamics between clonal and non-clonal stands may differ when intensive silviculture management is applied.

The observation that there may be a genetic gain in height growth that is not accompanied by a corresponding gain in dbh growth points to a genetic selection and/or breeding process that needs to be improved so that the process produces trees that not only grow taller but also have the potential to grow larger in dbh. Research in this area is required to avoid

developing tall slender trees that may be more prone to wind breakage. There is also need for a method to improve the way inferences about a stand are made from a single tree or a single row of trees in a genetic screening trial.

With rapid changes in tree breeding and selection technology, modeling genetic improvement effects remains a challenge and cooperation between forest biometricians and tree breeders will be needed. With such cooperation forest biometricians will have the information to model changes in tree and stand dynamics resulting from a given breeding strategy from which it can be seen whether the breeding strategy results in an overall desired consequence. Modifications in the strategy can then be made with an aim of preventing some of the undesired consequences that may result from a given breeding strategy.

### **6.3. Literature cited**

Amateis, R.L., H.E. Burkhart, H.L. Allen, and C. Montes. 2001. FASTLOB (A stand-level growth and yield model for fertilized and thinned loblolly pine plantations). Department of Forestry, Virginia Tech, Blacksburg, VA.

Burkhart, H.E., and T.G. Matney. 1981. Growth and yield modeling -- A place for genetic improvement effects. P. 6-17 *in* Proceedings of the 16th Southern Forest Tree Improvement Conference. Southern Forest Tree Improvement Committee, Blacksburg, VA.

Stape, J.L., D. Binkley, M.G. Ryan, S. Fonseca, R.A. Loos, E.N. Takahashi, C.R. Silva, S.R. Silva, R.E. Hakamada, J.M.d.A. Ferreira, A.M.N. Lima, J.L. Gava, F.P. Leite, H.B. Andrade, J.M. Alves, G.G.C. Silva, and M.R. Azevedo. 2010. The Brazil Eucalyptus Potential Productivity Project: influence of water, nutrients and stand uniformity on wood production. *For. Ecol. Manage.* 259:1684-1694.

Zhao, D.H., B. Borders, M.L. Wang, and M. Kane. 2007. Modeling mortality of second-rotation loblolly pine plantations in the Piedmont/Upper Coastal Plain and Lower Coastal Plain of the southern United States. *For. Ecol. Manage.* 252:132-143.