REALIZED GENETIC GAINS AND VALIDATION OF BREEDING VALUES FOR SLASH PINE

By

LOKENDRA PURUSH DHAKAL

A THESIS PRESENTED TO THE GRADUATE SCHOOL OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

1995

UNIVERSITY OF FLORIDA LIBRARIES
ACKNOWLEDGEMENTS

I greatly appreciate the assistance of all those who helped to make this research a success. I would like to express my deepest gratitude to my major advisor Dr. Timothy L. White for his constant support, encouragement, and guidance for all these years. It has been a wonderful learning experience working under his direct supervision. I am especially grateful to Dr. Gary Hodge. I have learned much from his creative approach to problem solving, and at a personal level, I am particularly thankful for his encouragement and unwavering confidence in my abilities. I would like to thank my committee member Dr. Donald Rockwood for his advisement and contributions to this research.

I wish to express my sincere appreciation to Mr. Greg Powell for his continuous support of me in data extraction, data cleaning and statistical programming. I would like to thank Dr. Mark Dieters for his support on acquainting me with the data sets that I am working with. I also thank my friend Steven Parker for his help in creating graphs and figures for this thesis.

This project was partially funded by His Majesty’s Government of Nepal and the Cooperative Forest Genetics Research Program of University of Florida. I am appreciative of their support and would like to thank the latter for allowing me to use their data.

I extend my love and appreciation to my wife Usha for her encouragement, understanding, and patience throughout my graduate program. Finally, I sincerely thank my parents, Mr. and Mrs. Bhupendra P. Dhakal, for a lifetime of love and moral support.
# TABLE OF CONTENTS

ACKNOWLEDGEMENTS ................................................................. ii

LIST OF TABLES ................................................................. v

LIST OF FIGURES ................................................................. vi

ABSTRACT ................................................................. vii

CHAPTERS

1. INTRODUCTION ................................................................. 1

2. REALIZED GENETIC GAINS FROM SLASH PINE TREE IMPROVEMENT .... 5

   Introduction ................................................................. 5
   Materials and Methods ........................................................ 9
      Plant Material and Genetic Tests ........................................... 9
      Checklots and Groupings of Families in Controlled-pollinated Tests 10
      Estimation of Region-wide Realized Gains ................................ 13
      Influence of Age and Site Characteristics on Realized Gains ...... 15
   Results and Discussion ......................................................... 19
      Regionwide Gains for Tree Volume and Rust Resistance .......... 19
      Influence of Age and Site Characteristics on Volume Gains .... 21
         Volume Gains for Volume Groups ........................................ 21
         Volume Gains for Rust Groups ........................................... 24
      Influence of Age and Site Characteristics on Gains in Rust Resistance 26
         Rust Gains for Rust Groups .............................................. 26
   General Discussion and Conclusions ....................................... 28

3. VALIDATION OF BREEDING VALUES FOR SLASH PINE ................. 32

   Introduction ................................................................. 32
   Materials and Methods ........................................................ 35
      Plant Material and Genetic Tests ........................................... 35
      The Breeding Value Information ............................................ 35
      Breeding Values of Full-sib Families .................................... 36
      Pollen Contamination Assumption ......................................... 37
      Realized Genetic Gain Calculation ....................................... 38
      Calculation of Expected Genetic Gain Ratios for Rust Resistance 39
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calculation of Expected Genetic Gain Ratios for Volume</td>
<td>40</td>
</tr>
<tr>
<td>Comparison of Realized and Expected Percent Gains</td>
<td>41</td>
</tr>
<tr>
<td>Results and Discussion</td>
<td>42</td>
</tr>
<tr>
<td>VX and RX groups versus CHECK</td>
<td>42</td>
</tr>
<tr>
<td>Comparisons Among VX groups and RX groups</td>
<td>44</td>
</tr>
<tr>
<td>Hypotheses for Inflation of Breeding Value Variance</td>
<td>46</td>
</tr>
<tr>
<td>Adjustment of Expected Genetic Gains</td>
<td>47</td>
</tr>
<tr>
<td>Conclusions</td>
<td>48</td>
</tr>
<tr>
<td>4. CONCLUSIONS AND APPLICATIONS</td>
<td>50</td>
</tr>
<tr>
<td>REFERENCE LIST</td>
<td>52</td>
</tr>
<tr>
<td>BIOGRAPHICAL SKETCH</td>
<td>56</td>
</tr>
<tr>
<td>Table</td>
<td>page</td>
</tr>
<tr>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td>2-1. Groups of full-sib families for tree volume (vol) and rust resistance (rust) based on their Expected genetic value calculated from mid-parental breeding values predicted from OP progeny tests</td>
<td>13</td>
</tr>
<tr>
<td>3-1. Breeding Value for volume and rust and the number of full-sib families for 1001 and 1002 checklots, V1-V5, and R1-R5 groups</td>
<td>37</td>
</tr>
<tr>
<td>3-2. Average Breeding value for volume (BVVOL) and rust (BVR50) for unimproved check, first-generation unrogued and first-generation rogued CFGRP slash pine seed orchards</td>
<td>38</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1.</td>
<td>Volume ratios compared to CHECK of different genetic entries, estimated</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>by ratio and regression approaches</td>
<td></td>
</tr>
<tr>
<td>2-2.</td>
<td>Infection ratio of different genetic entries, estimated by ratio and</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>regression approaches</td>
<td></td>
</tr>
<tr>
<td>2-3.</td>
<td>Volume gain ratios (compared to CHECK) of volume groups for full-sib</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>families grouped according to the family levels of tree volume</td>
<td></td>
</tr>
<tr>
<td>2-4.</td>
<td>Volume gain ratios (compared to CHECK) for full-sib families grouped</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>according to the family levels of rust resistance</td>
<td></td>
</tr>
<tr>
<td>2-5.</td>
<td>Rust incidence ratios (compared to CHECK) plotted against the</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>family groupings of different rust resistance levels</td>
<td></td>
</tr>
<tr>
<td>3-1.</td>
<td>Comparison of realized versus expected gain for volume where volume ratio</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>is genetic entry compared with CHECK</td>
<td></td>
</tr>
<tr>
<td>3-2.</td>
<td>Comparison of realized versus expected gain for fusiform rust resistance</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>where infection ratio is genetic entry compared with CHECK</td>
<td></td>
</tr>
<tr>
<td>3-3.</td>
<td>Comparison of realized versus expected genetic gain ratios for tree volume</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>and rust resistance for unadjusted (BLP predicted) BV and adjusted BV</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(three-fourths of unadjusted BV)</td>
<td></td>
</tr>
</tbody>
</table>
Abstract of Thesis Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirement for the Degree of Master of Science

REALIZED GENETIC GAINS AND VALIDATION OF BREEDING VALUES FOR SLASH PINE

By

Lokendra Purush Dhakal

December 1995

Chairperson: Timothy L. White
Major Department: School of Forest Resources and Conservation

This study determines realized genetic gains and examines the validation of breeding value (BV) predictions of slash pine (*Pinus elliottii* Englem. var *elliottii*) made by best linear prediction (BLP) using 367 open-pollinated (OP) tests data for tree volume and rust resistance. The study utilizes the independently predicted BVs for tree volume and rust resistance to rank 2051 controlled-pollinated (CP) families grown in 175 CP tests (age classes centered at ages 5, 8, and 11 with 144, 120, and 120 measured tests, respectively (some tests were measured at more than 1 age)) to determine realized gains. All CP families were divided into five groups for volume, according to BV for volume (groups V1-V5) and five groups for rust based on BV for rust (groups R1-R5). For each variable the five groups represent the expected performance range from best to worst. Using simple linear regression analysis realized genetic gains were determined by comparison among these groups and also by comparison of improved materials to unimproved materials (called CHECK) included in the test. The ranking of realized gain ratios for volume and
Rust of the five groups corresponded exactly to the order predicted by the *a priori* classification based on the BLP predicted BVs.

Regression analyses were used to examine how age and site characteristics (e.g., site index, rust hazard) and their interactions with the two types of genetic groupings (V1-V5, R1-R5) affected genetic gains in the two traits, volume and rust. The results suggest that superior families for tree volume express increased gain in volume compared to the CHECK on better quality sites, and the genetic differences among genetic groups were greater on better sites (SIclass 3, 4 and 5) relative to poorer sites (SIclass 1 and 2). Similarly, it was found that genetically superior families for rust resistance have higher tree volume advantage on the high hazard sites, and on these sites the most resistant families also had the highest volume gains relative to the CHECK.

Expected genetic gains were calculated using mid-parental BVs for the full-sib families of groups (V1-V5 and R1-R5). For comparison of realized and expected gain ratios, two kinds of approaches were used to examine how well expected genetic gain ratios agreed with realized genetic gain ratios. First, all genetic groups (V1-V5, R1-R5) were compared to the unimproved CHECK, and the realized and expected genetic gain ratios were examined graphically. Second, all possible comparisons among the genetic groups were made. The relationship between the realized percent genetic gain ($\Delta G_r$) versus expected percent genetic gain ($\Delta G_e$) for both volume and rust groups were examined using the model: $\Delta G_r = b \Delta G_e$. The expected and realized gain comparisons for both traits, tree volume and rust resistance, revealed that genetic gain using BLP BVs is over-predicted relative to the gains realized. In other words, the variance of BLP predicted BVs is too large for both tree volume and rust resistance. This discrepancy is worse for tree volume than it is for rust resistance. Based on both theoretical and empirical grounds, the BLP BVs were multiplied by three-fourths to reduce the range and the adjusted expected gains agreed much more closely with the observed realized gains.
CHAPTER 1
INTRODUCTION

Realized genetic gains are important in tree improvement programs establishing genetically-improved tree plantations. The Cooperative Forest Genetics Research Program (CFGRP) of the University of Florida, with over 10 million acres of genetically improved slash pine plantation, is one of them. It is important to note that for a large scale tree improvement program even a small genetic gain justifies the costs incurred in the selection and breeding of superior phenotypes (Porterfield 1975, Row and Dutrow 1975), and appropriately designed genetic tests are needed for evaluating those realized genetic gains (Lowerts 1986). Quite often, realized genetic gains from a selection or breeding program are determined by a comparison of performance of improved materials with unimproved materials (Zobel and Talbert 1984, La Farge 1993) using 1) row or single-tree plots and 2) large block plots (Lowerts 1986). In general, large block plots of improved and unimproved (commercial checks) materials provide unbiased estimates of realized genetic gain for growth traits on a per unit area basis (Lowerts 1986); however, these large block plots suffer from large block (replication) sizes which in effect contribute to low statistical precision. Therefore, a large number of sample sites are needed to determine statistically significant differences (Tankersley et al. 1983). Because of these problems very few realized gain studies are conducted in large block plots. Using row or single-tree plot designs has some important statistical and logistical advantages; however, these designs can provide biased estimates of realized gain for growth traits if dominant phenotypes gain early competitive advantage (Wright 1975, Cannell 1982).
Realized genetic gain experiments using any statistical design require a long time partially because of the time required for tree growth and the experimental complexities associated with it. Because of these problems, there are very few published results from realized gain studies (Lowerts 1987), and the majority of the estimates are realized gains from first-generation mass selection. Reliable results from later stages of breeding are not available. The reported results from first-generation mass selection have suggested genetic gains of increased total volume, better and uniform quality of timber production and disease resistance (Goddard et al. 1975, Lowerts 1986, Hodge et al. 1989, Hodge et al. 1990, La Farge 1993).

Reliable genetic gain estimates can be achieved only when large amounts of data representing many tests and locations are available. None of the previously published realized gain studies have utilized large data sets from many experimental locations, nor have previous studies investigated impacts of site characteristics (e.g., site index) on realized gains. This thesis utilizes data from 175 controlled-pollinated (CP) tests of slash pine (Pinus elliottii Englem. var elliottii) measured for volume and the incidence of fusiform rust (Cronartium quercuum (Berk.) Miyabe ex Shirai f. sp. fusiforme) from ages 4 to 20 in the CFGRP to quantify realized gains. There are altogether 669 first-generation slash pine parents in these 175 CP tests, which had been used to create 2051 full-sib families. The breeding values (BVs) of each parent used to create the CP slash pine families in these tests had been previously predicted from an independent set of 367 open-pollinated (OP) slash pine tests. In this study the independently predicted BVs were used to rank each CP family so that realized gains could be determined for different segments of the population (corresponding to different levels of predicted genetic gain).

The 367 OP slash pine progeny tests of the CFGRP planted during the 1960s were not well balanced (data with different ages, insufficient replication, and tests in different sites with different soil quality and rust hazard). Hence, best linear prediction (BLP), a statistical method
able to analyze unbalanced progeny test data, was used by White and Hodge (1988) to develop BLP of the BVs for volume and rust-resistance of 2245 mass-selected slash pine parents. The BV predictions were calculated for rust incidence in a 50% rust incidence environment and tree volume at age 15 (White and Hodge 1988). These BV predictions are being used in many ways by the 12 members of the CFGRP: 1) choosing better parents to graft into new seed orchards, 2) roguing poor genotypes out of existing seed orchards, 3) increasing genetic gains by deploying rust-resistant genotypes to high hazard sites, and 4) selecting parents with high BVs for future breeding.

Accurate and precise estimates of realized genetic gain are very much important, first, because a small percentage gain (2.5 to 4.0%) is enough to justify an entire tree improvement program (Davis 1967) and second, because the ranking of parents from any progeny tests are critical to genetic progress (McKinley 1983, Lindgren 1986, White and Hodge 1987, 1988, Hodge and White 1992). Hence, there are two types of validation to be examined in this study: 1) relative precision of the BVs and 2) their absolute accuracy. Accurate prediction of BVs will give the correct ranking of the parents, hence any selection of top parents will be generally correct, and thus maximize genetic gain from selection decisions. Chapter 3 of this thesis discusses this topic. Additionally BLP theory says that the BV predictions should be absolutely predictive (accurate) of the amount of genetic gain to be expected from any seed orchard or other use. For example, if there are 30 parents in a seed orchard, then each parent should have a predicted BV. If the average of these 30 BVs is 15% above the average of all 2245 parents, then we expect the progeny from the seed orchard to yield 15% more volume than use of average seed at a specified age. This information would further enable the forest manager to analyze the economic viability of a tree improvement program.
It is not the focus of this thesis to test in detail the mathematical and statistical assumptions underlying BLP. Rather, the goal is to use the BLP BVs predicted from the 367 OP tests to estimate gains for tree volume and rust resistance in independent data sets (175 CP tests). If there is a high degree of correspondence between expected (based on the BLP BVs) and realized (based on performance in the CP tests) gains, then we will assume that either the underlying assumptions of BLP were met, or that the BLP method is robust to violation of these assumptions.

This thesis has been divided into two parts. The first part (chapter 2) examines the realized genetic gains with these objectives: (1) to quantify realized gains for tree volume and rust resistance of improved and unimproved mixed-family lots compared to commercial checklots; (2) to quantify realized gains of slash pine for volume gain and rust resistance of CP families of varying genetic quality based on their parental performance in independent OP tests; and (3) to determine whether characteristics (such as age, site index class and rust hazard of the site) influence realized gain of slash pine in volume and rust resistance. The second part (chapter 3) focuses on validation of the slash pine BV predictions (made using 367 OP tests) for volume and rust resistance using independent data set (175 CP tests). These data will be used to assess if the BLP BV predictions from OP data accurately predict performance in CP tests. The specific objective of the second part of this thesis will be therefore to validate accuracy of genetic gain predictions made using BLP of BVs for volume and rust resistance in slash pine.
CHAPTER 2
REALIZED GENETIC GAINS FROM SLASH PINE TREE IMPROVEMENT

Introduction

Tree improvement programs produce genetic gains in specific traits of interest, and even small genetic gains can have enormous economic returns in a large scale tree improvement program (Weir 1973). It is the genetic progress achieved which justifies the costs incurred in the selection and breeding of superior phenotypes (Porterfield 1975, Row and Dutrow 1975). Thus, estimates of realized genetic gains are an important means of evaluating the performance of a tree improvement program (Hodge et al. 1989). However, precise estimates of realized genetic gain are difficult to obtain, and are infrequently found in the tree improvement literature.

Generally, realized gains from a selection or breeding program are determined by a comparison of performance of improved materials with unimproved materials (Zobel and Talbert 1984, La Farge 1993). Normally, two kinds of genetic test designs are used to assess the performance of the improved and unimproved materials: 1) Row or single-tree plots, and 2) large block plots (Lowerts 1986). Large block plots of improved and unimproved (commercial checks) materials provide unbiased estimates of realized genetic gain for growth traits on a per unit area basis (Lowerts 1986); however, large block plots suffer from large block (replication) sizes which contribute to low statistical precision. Therefore, a large number of experimental locations are needed to determine statistically significant differences (Tankersley et al. 1983). There are many statistical and logistical advantages of using row or single-tree plots; however, they can provide
biased estimates of realized gain for growth traits if dominant phenotypes gain early competitive advantage (Wright 1975, Cannell 1982). Studies on estimating realized genetic gains suggest that the net effect of predicting performance of selected genotypes over a full rotation on the basis of individual tree performance, using traits such as height, growth, and stem volumes at certain ages, may result in an overestimate of the true genetic gain (Cannell 1982).

In general, very few realized gain studies have been published (Lowerts 1987) and of those published studies, estimates often are from a small number of parents and genetic tests. This may be due to the experimental complexities and the long time required for the growth of the tree. Most published studies are estimates of realized gains from first-generation mass selection (not from later stages of a breeding program), and have reported genetic gains of increased total volume, better and more uniform quality of timber production and increased disease resistance (Goddard et al. 1975, Lowerts 1986, Hodge et al. 1989, Hodge et al. 1990, La Farge 1993). One study done by Tankersley et al. (1983) comparing "improved" (unrogued clonal seed orchard) and "unimproved" (commercial checklot) 15-year-old plantations of slash pine in 10 locations in Georgia suggests no significant differences for tree volume and rust resistance characteristics. However, the analytical method used to estimate realized gain in their study was insensitive and only able to detect differences greater than 10% in volume and 23% in rust infection.

Butcher (1988) published the results of full-sib P. pinaster Ait. tested at two locations in West Australia in which 11-year-old seed orchard progeny produced an extra 20 m³/ha total wood volume (40% more) compared with a routine seed source. Additionally, he found that 83 and 62% of the trees raised from the orchard seeds were reasonably straight and had acceptable branching pattern compared with 58% and 46% for routine seed sources. Another realized gains studies in Australia on radiata pine (P. radiata D. Don) tested in three locations revealed the
orchard seed lot (with 30 parents) produced 20% more total wood volume, with about twice as many trees of excellent stem and branch quality than a control seedlot (Eldridge 1982).

In slash pine, Hodge et al. (1989) estimated realized genetic gains from mass selection as 10% for individual tree volume at 15 years. Also in slash pine, mass selection of uninfected trees in stands with high levels of fusiform rust (Cronartium fusiforme Berk. Miyabe ex. Shirai f. sp. fusiforme) incidence (> 80%) has resulted in significant realized genetic gain. Goddard et al. (1975) compared open-pollinated (OP) seed from slash pine seed production areas developed by roguing out all infected trees to unimproved material in three geographic locations and showed a remarkable reduction in infection (approximately one half) relative to the check. Furthermore, substantial genetic gain in rust-resistance was observed for three independent slash pine populations developed through mass selection in highly infected stands (Hodge et al. 1990). These authors compared the offspring from a total of 592 rust-free selections of slash pine to unimproved material in 46 progeny tests. These progeny tests also indicated substantial genetic gain: selected material had approximately two-thirds the amount of infection observed in the unimproved materials across all sites.

Lowerts (1986) reported the results of a realized gains study of 6-year-old block plot loblolly (P. taeda L.) and slash pine in a single location in Georgia compared with their respective commercial checks. When a rogued first-generation loblolly seed orchard mix was compared with unimproved checks he found 20% volume gain and 40% reduction in fusiform rust. Similarly, in slash pine the author found volume gain and rust resistance of 14 and 8%, respectively, when two types of orchard mix were compared with commercial checks. In a study done by Gladstone et al. (1987), a comparision of the same loblolly pine families in a 22-year-old full-sib row-plot progeny test and in an 8-year-old yield trial showed quite similar realized gain (24% compared to 20% gain). In other studies of 8-year and 4-year loblolly pine at five locations
Lowerts (1987) reported relatively lower genetic gains of the first-generation orchard mixes compared to the commercial check seed lots (-3 to +6 percent). He also suggested that the level of genetic gain realized is dependent on the choice of commercial check lots.

La Farge (1993), using unrogued clonal seed orchard materials for volume in shortleaf pine (*P. echinata* Mill.), eastern white pine (*P. strobus* L.), and loblolly pine, estimated gain of 31, 8, and up to 23%, respectively. The total number of parents for shortleaf, white and loblolly pine were 78, 60 and 51 and the number of progeny tests were 12, 14 and 10 for shortleaf, white and loblolly pine, respectively.

As stated earlier, a large amount of data representing many tests and locations is needed in order to get useful and reliable genetic gain estimates. Also, none of the previously reported studies have investigated impacts of site characteristics (such as site index) on realized gains. This study, therefore, utilizes data from 175 genetic tests of slash pine measured for volume and rust resistance from ages 4 to 20 in the CFGRP to quantify and investigate the nature of realized gains.

The specific objectives of this work were (1) to quantify realized gains for tree volume and rust resistance of improved and unimproved mixed-family lots compared to commercial checklots; (2) to quantify realized gains of slash pine for tree volume and rust resistance of CP families of varying genetic quality based on their parental performance in independent OP tests; and (3) to determine whether characteristics (such as age, site index class and rust hazard of the site) influence realized gain in volume and rust resistance.
Materials and Methods

Plant Material and Genetic Tests

From 1954 to 1963, the CFGRP selected over 2500 superior slash pines from across the species' range. Subsequent to selection, clones were grafted into seed orchards and all of them were progeny tested with orchard OP seed, beginning from 1960. Data from over 300 of these OP progeny tests were used to predict BVs for original selections for tree volume at 15 years and fusiform rust resistance (White and Hodge 1988). The initial mass selections of superior slash pine candidates were concentrated in low rust incidence areas and their selection was based mostly upon phenotypic superiority for volume (Hendrickson 1976, White et al. 1988). Therefore, to secure trees with a high probability of rust resistance, candidates from heavily infected stands (>70% infection) were selected in 1973 to 1975 and these were called rust-free selections (Hendrickson 1976, Hodge et al. 1991).

In addition to OP progeny tests, the CFGRP established two separate series of full-sib tests. The first series was established during 1966 to 1973, and is comprised of 78 tests in a factorial crossing scheme; each test contains from 6 to 86 full-sib families (mean = 30) created by crossing some of the mass selected parents (from the population of over 2500 first-generation selections). The second series, established during 1975 to 1989, is comprised of 187 tests and utilizes either potentially-superior first-generation parents chosen from very early OP progeny test data mated in diallels or factorial mating designs or rust-free selections (as male) and first-generation parents (as females) in factorial mating designs (Dieters 1994).

A randomized complete block design was used for all tests in both series, and each full-sib family was represented either in a single row plot or non-contiguous plot with 5 to 10 trees in each block with 3 to 10 blocks per test. Trees in these tests were measured between ages 4 and
20 years. The measured traits were height, diameter at breast height (DBH) (4.5 ft above ground), and rust incidence. Rust incidence was evaluated by eye and scored 0 for no rust and 100 for trees infected with at least one rust gall. Inside bark tree volume (bole) was calculated by using the volume equations provided by Goddard and Strickland (1968) for DBH ≤7 inch (VOL = -0.0852 + 0.1454 DBH - 0.05839 DBH^2 + 0.003102 DBH^2* HT), and Rockwood (1981) for DBH > 7 inch (ln VOL = -6.3219 + 1.9160 ln DBH + 1.0702 ln HT).

In 1994 measurements from 175 tests were available for analysis. These 175 CP tests included 669 slash pine parents, which had been used to create 2051 full-sib families. In each test, a subset of these families were planted along with various commercial, improved, and unimproved checklots that were used in calculating and comparing realized gains. The BVs of each parent used to create the CP slash pine families in these tests had been previously predicted from an independent set of 367 OP slash pine tests. For the purpose of analysis, age measurements were grouped into three age classes centered at ages 5, 8, and 11 with 144, 120, and 120 measured tests, respectively (some tests were measured at more than 1 age). The mean percentage of rust infection in a test varied from 0 to 100%. Tests with rust infection of ≤10 % were not used to examine realized gains for rust since low levels of infection do not provide reliable information on rust resistance (White and Hodge 1989). Therefore, 79, 86, and 84 tests at age 5, 8, and 11, were used in the analysis of rust resistance.

Checklots and Groupings of Families in Controlled-pollinated Tests

The genetic gains in this study were determined by the comparison of performance of improved materials versus unimproved materials. All the 175 CP tests included some kind of checks which were (1) commercial checks (CC); (2) a University of Florida checklot (UC); (3) bulk mix (1001); and (4) a second bulk mix (1002). The CC are various woods-run unimproved
checks planted by the individual cooperators in progeny tests established on their land. The UC is seed collected from a single unimproved stand in southeast Georgia and has been used by the CFGRP as a standard check across most progeny tests to compare with family performances. The checks 1001 and 1002 were bulk mixes included in many of the CP tests. The mixes were constructed in the mid 1960's based on early OP progeny test results, and were intended to represent "improved" and "unimproved" materials, respectively. The "improved" check, 1001, is a bulk mix of OP seed from 22 families collected in 1.0 and 1.5 generation rogued orchards. The "unimproved" check, 1002, is a bulk mix of OP seed from 20 families from an unrogued 1.0 generation orchard (Horticulture Unit at Gainesville, Florida). Subsequent analyses of OP progeny tests have shown these two checklots to be less distinct than originally thought (see next section).

The UC and CC are both thought to represent unimproved slash pine as it existed before domestication, and these two checks were compared to examine if they were of similar genetic quality. The UC and CC consistently performed similarly, in terms of genetic gains, against each other and against other genetic entries and were never more than 2.7% different for volume and 7% different in rust resistance. All statistical analyses done using SAS® (SAS® Institute Inc. 1988) indicated that these two types of checklots were not statistically different across the 155 total observations (51, 43, and 61 tests at age 5, 8, and 11, respectively) in which they occurred together. Since there was little apparent difference, and since both types were samples of unimproved material used prior to improvement activities, these checks were pooled together and treated as one throughout the remainder of the study. Hereafter, this pooled checklot of unimproved material is called CHECK.

The BVs for tree volume and rust resistance had been previously predicted with Best Linear Prediction (BLP) using data from OP row-plot progeny tests for 2245 of the parents used
to create these full-sib families (White and Hodge 1988). These BVs predicted from independent OP data sets were used to calculate an expected value for each of the three OP checklots (CHECK, 1001 and 1002). Based on OP data, CHECK has a mean BV volume = - 0.38 (where the mean of all 2500 first-generation selections has BV = 0) and mean BV R50 = 50 (the amount of rust to be expected on a site with a rust hazard of 50%, i.e. an area where unimproved material will incur 50% infection). The 1001 had mean BV volume = 0.32 ; mean BV R50 = 35. The 1002 had mean BV volume = 0.01 ; mean BV R50 = 50. On this basis, the expected genetic quality for tree volume is 1001 > 1002 > CHECK. For rust, low values are more

Table 2-1. Groups of full-sib families for tree volume (vol) and rust resistance (rust) based on their expected genetic value calculated from mid-parental breeding values predicted from OP progeny tests. For vol, the parental breeding values are in units of cubic feet at 15 years with mean = 0. For rust, the parental breeding values represent expected rust incidence in a site in which unimproved material gets 50% rust.

<table>
<thead>
<tr>
<th>Group</th>
<th>Level</th>
<th>Number of tests</th>
<th>Breeding value range</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Age 5</td>
<td>Age 8</td>
<td>Age 11</td>
</tr>
<tr>
<td>V1</td>
<td>worst</td>
<td>45</td>
<td>39</td>
<td>48</td>
</tr>
<tr>
<td>V2</td>
<td>poor</td>
<td>106</td>
<td>95</td>
<td>108</td>
</tr>
<tr>
<td>V3</td>
<td>average</td>
<td>144</td>
<td>120</td>
<td>120</td>
</tr>
<tr>
<td>V4</td>
<td>good</td>
<td>138</td>
<td>115</td>
<td>117</td>
</tr>
<tr>
<td>V5</td>
<td>best</td>
<td>89</td>
<td>74</td>
<td>70</td>
</tr>
<tr>
<td>R1</td>
<td>best</td>
<td>59</td>
<td>63</td>
<td>47</td>
</tr>
<tr>
<td>R2</td>
<td>good</td>
<td>79</td>
<td>86</td>
<td>78</td>
</tr>
<tr>
<td>R3</td>
<td>average</td>
<td>75</td>
<td>81</td>
<td>81</td>
</tr>
<tr>
<td>R4</td>
<td>poor</td>
<td>33</td>
<td>35</td>
<td>58</td>
</tr>
<tr>
<td>R5</td>
<td>worst</td>
<td>5</td>
<td>4</td>
<td>19</td>
</tr>
</tbody>
</table>
improved (indicating less infection), thus 1001 is expected to be better than both 1002 and CHECK.

The independently-predicted BVs were also used to calculate an expected genetic value for each full-sib family as the mid-parent of the two parental BVs. All families were then divided into five groups according to the expected BV for volume (groups V1-V5) and into five groups according to BV for rust (groups R1-R5). For each variable the five groups represent the expected performance range from best to worst based on the independent ranks calculated from OP progeny tests (Table 2-1).

Estimation of Region-wide Realized Gains

The unit of observation for all analyses of realized gains was the mean of a given type of genetic entry in a given progeny test location. This was calculated in two steps. First a least square mean (LSmean) of each full-sib family and check was calculated in each test. LSmeans were used in order to take account of unequal representation of families in blocks. Second, the mean of the LSmeans for each type of genetic entry was calculated (CHECK, 1001, 1002, V1, V2, ... V5, R1, R2, ... R5). Thus, in general there was one value for each type of genetic entry in each test, although some types of genetic entries were not represented in some tests.

To estimate realized genetic gain across all tests, two kinds of approaches were used: (1) Ratio (hereafter called ratio approach), and (2) Separate variable regression (hereafter called regression approach). In each approach, each test in the data set described above provided at most one observation to estimate the realized gain for a particular type of genetic entry. In both approaches, all realized gains were estimated relative to the CHECK (the pooled UC and CC checks believed to be representative of unimproved slash pine). In the ratio approach, the ratio of the genetic entry divided by the CHECK was calculated in each test. For example, if in a
given test, \( \text{VOL}_{v5}/\text{VOL}_{\text{CHECK}} = 1.25 \), this indicates that the V5 group had 25% more volume than the unimproved check. These ratios were then averaged across all tests to estimate realized gains for each type of genetic entry (such as the V5 group). Average ratios were calculated for both tree volume and rust resistance.

In the regression approach, a linear regression for each type of genetic entry was fit using the following model:

\[
X_{\text{ENTRY}} = b \cdot X_{\text{CHECK}}.
\]

For all regression analyses, the regression approach was first investigated with an intercept, and intercept terms were never significantly different from zero. Therefore, all models were forced through the origin. Since the regression line is fit through the origin, the slope coefficient \( b \) estimates the average ratio of performance of the genetic entry versus the unimproved check across all tests. If \( b = 1.25 \) for volume of the V5 group, this indicates 25% improvement for volume of this group. Similar regressions were fit for all VX groups (V1,.....V5), RX groups (R1,.....R5), 1001, and 1002 all against the CHECK as the regressor variable.

The two approaches (ratio and regression) were used to examine the same questions, but provided different weights to different data points. The regression approach provides more weight on higher values of the independent variable \( (X_{\text{CHECK}}) \) because the regression is fit through the origin (and hence values nearer the origin cannot strongly influence the slope). In contrast, the ratio approach gives equal weight to all observations. In this thesis both ratio and regression approaches were used, and the results of the two approaches are slightly different. Final results presented are always the averages of the two approaches (ratio and regression).
Influence of Age and Site Characteristics on Realized Gains

Influence of age and site characteristics on realized gains was investigated using only the five volume and five rust groups. The 1001 and 1002 checks were not used because they were bulk mixture of many families that might buffer some influences and because the five groups for each trait were linear relative to predicted BVs.

One of the site characteristics investigated in this study was site index, which was estimated for each test following the approach used by Dieters (1994). The mean height of the largest 43.5% trees ranked by diameters was used to estimate dominant height (Bailey and Brooks 1994), and then the formulae developed by Pienaar et al. (1990) was utilized to estimate site index using the dominant height. Dieters (1994) found that data less than eight years of age over-estimated site index, but data older than eight-year provided site index estimates not significantly different from those obtained with eight-year data. Therefore, the estimated site index was adjusted to that estimated from eight-year data, when necessary.

Using this approach, each test was assigned to one of five site index classes (siclass 1-5, 1 = poor, 5 = good) using this eight-year adjusted site index (SI) (SI predicted at a base age of 25 years): Siclass 1, SI < 62 ft; Siclass 2, 62 ≤ SI < 68; Siclass 3, 68 ≤ SI < 73; Siclass 4, 73 ≤ SI < 78; Siclass 5, SI ≥ 78.

The influences of age on realized gains was investigated using the three previously defined age classes of 5, 8 and 11 years. To investigate impact of rust hazard levels, each test was assigned to one of five rust hazard (rushaz) levels (rushaz 1 to 5 with 1 indicating low rust and 5 indicating high rust) on the basis of rust incidence observed in the CHECK (ruschk); rushaz 1, ruschk < 20%; rushaz 2, 20 ≤ rushk < 40; rushaz 3, 40 ≤ rushk < 60; rushaz 4, 60 ≤ rushk < 80; rushaz 5, rushk ≥ 80. Only tests with rushk values ≥ 10 were used for the
purpose of analysis since tests with low or high incidence of rust provides little information on rust resistance (White and Hodge 1989).

The influences of age and site characteristics were examined using four types of analyses which examined how these test characteristics and their interaction with the two types of genetic groupings (V1-V5, R1-R5) affected genetic gains in the two traits, volume and rust. In other words, one analysis examined how realized genetic gains in volume were affected by the test characteristics and their interactions with the volume groups V1-V5 (the V/V analysis). A second analysis examined realized genetic gains in volume as affected by the test characteristics and interactions with the rust groups R1-R5 (V/R analysis). The third analysis examined realized gains in rust, test characteristics and interaction with rust groups R1-R5 (R/R analysis), and the fourth examined gains in rust affected by test characteristics and interaction with volume groups V1-V5 (R/V analysis).

For each of the four analyses, both the ratio and regression approaches were conducted with groups (R1-R5 or V1-V5), ages (5, 8, and 11), site index classes (1,...5) and rust hazard levels (1,...5) used as class variables in the analysis. For the ratio analysis, the unit of observation was gain ratio (R) of a given group to the CHECK in a given test. A full linear model with all effects and 2- and 3-way interactions was first fit.

\[
R_{ijklm} = \mu + G_i + A_j + S_k + H_l + GA_{ij} + GS_{jk} + GH_{il} + AS_{jk} + AH_{jl} + SH_{kl} + GAS_{ijk} + \]
\[
GAH_{ijl} + GSH_{ikl} + ASH_{jkl} + e_{ijklm}
\]

where:

\[ R_{ijklm} = \text{gain ratio (for volume or rust) of a given group (R1,...R5, or V1,...V5) relative to CHECK from a given test location m; } \]
\[ \mu = \text{the population mean}; \]
\[ G_i = \text{group effect of the } i^{\text{th}} \text{ group (} i = R1, \ldots, R5 \text{ or } V1, \ldots, V5); \]
\[ A_j = \text{age effect of } j^{\text{th}} \text{ class (} j = 5, 8, \text{ or } 11 \text{ years}); \]
\[ S_k = \text{effect of } k^{\text{th}} \text{ site index class (} k = 1, 2, \ldots, 5); \]
\[ H_l = \text{effect of } l^{\text{th}} \text{ rust hazard class (} l = 1, 2, \ldots, 5); \]
\[ GA_{ij} = \text{effect of the interaction of } i^{\text{th}} \text{ group and the } j^{\text{th}} \text{ age class}; \]
\[ GS_{ik} = \text{effect of the interaction of } i^{\text{th}} \text{ group and the } k^{\text{th}} \text{ site index class}; \]
\[ GH_{il} = \text{effect of the interaction of } i^{\text{th}} \text{ group and the } l^{\text{th}} \text{ rust hazard class}; \]
\[ AS_{jk} = \text{effect of the interaction of } j^{\text{th}} \text{ age class and the } k^{\text{th}} \text{ site index class}; \]
\[ AH_{jl} = \text{effect of the interaction of } j^{\text{th}} \text{ age class and the } l^{\text{th}} \text{ rust hazard class}; \]
\[ SH_{kl} = \text{effect of the interaction of } k^{\text{th}} \text{ site index class and the } l^{\text{th}} \text{ rust hazard class}; \]
\[ GAS_{ikj} = \text{effect of the interaction of } i^{\text{th}} \text{ group, } j^{\text{th}} \text{ age class and the } k^{\text{th}} \text{ site index class}; \]
\[ GAH_{ijl} = \text{effect of the interaction of } i^{\text{th}} \text{ group, } j^{\text{th}} \text{ age class and the } l^{\text{th}} \text{ rust hazard class}; \]
\[ GSH_{ilk} = \text{effect of the interaction of } i^{\text{th}} \text{ group, } k^{\text{th}} \text{ site index class and the } l^{\text{th}} \text{ rust hazard class}; \]
\[ ASH_{jkl} = \text{effect of the interaction of } j^{\text{th}} \text{ age class } k^{\text{th}} \text{ site index class and the } l^{\text{th}} \text{ rust hazard class}; \]
\[ e_{ijklm} = \text{error effect of the } ijklm^{\text{th}} \text{ observation.} \]

The regression (or covariance) approach was also employed for each of the four analyses (V/V, V/R, R/R, R/V) with a full-model as follows:
\[ Y_{ijklm} = \mu + X_m + X_mG_i + X_mA_j + X_mS_k + X_mH_l + X_mGA_{ij} + X_mGS_{ik} + X_mGH_{jl} + X_mAS_{jk} + X_mAH_{jl} + X_mSH_{kl} + X_mGAS_{ijk} + X_mGAH_{ijkl} + X_mGSH_{iklj} + X_mASH_{ijkl} + e_{ijklm} \]

Where:

- \( Y_{ijklm} \) = The observed volume (in V/V and V/R analyses) or rust (in R/R and R/V analyses) of a given genetic group from the \( m^{th} \) test location;
- \( X_m \) = The observed volume or rust for the CHECK from the \( m^{th} \) test;
- and all other terms are as previously defined for the ratio approach.

In the regression approach, the goal was to determine whether a different slope (and hence a different ratio) is needed for each group and all of the other factors in the model. If a factor is significant in the regression or ratio approach (such as \( S_k \)), it implies that realized gains are impacted by that factor.

After fitting the above full models for both the ratio and regression approaches to a given analysis (such as the V/V analysis), the following steps were employed to determine the final model: (1) All statistically-significant two-way interactions and three-way interactions were examined graphically to determine the biological importance; (2) The influence of main-effects and interactions were examined for consistency in direction and magnitude across the two approaches (ratio and regression); (3) Many types of reduced models were fit and examined graphically; and (4) A final model was chosen in which all effects in the model were statistically significant (at \( \alpha = 0.05 \)), biologically interpretable, and consistent across both approaches.
Results and Discussion

Regionwide Gains for Tree Volume and Rust Resistance

The rankings of the realized gains for volume of the genetic entries corresponds exactly to the order predicted by the *a priori* classification based on the predicted genetic quality from the BLP predicted BVs from the OP data. The V1 group, the designated worst volume group on the basis of the BVs (Table 2-1), had the poorest tree volume, performing slightly worse than the unimproved CHECK (ratio = 0.97 in Figure 2-1 indicates that V1 had 97% of the volume of the check averaged over the ratio and regression methods). All other genetic entries (V2, V3, V4, V5, 1001 and 1002) performed significantly (p=0.05) better than the check as indicated by ratios and regression coefficients significantly different than 1.0 in the two different approaches. The V2, V3 and V4 groups performed increasingly better relative to the unimproved CHECK, and the best volume group, the V5 group, produced over 22% more volume than the unimproved CHECK (ratio = 1.22, Figure 2-1). In addition, the 1001 bulk check produced slightly more volume than the 1002 check (approximately 18% gain versus 16% gain above unimproved) the same order predicted by their rankings based on OP breeding values.

Although the realized gain ratios presented for volume in Figure 2-1 (and for rust in Figure 2-2) are averages of the ratio and regression approach, the two methods produced very similar estimates and trends. Using the ratio approach, it was possible to partition the sums of squares for the volume groups into components due to a linear and quadratic relationship with BV. The linear term accounted for 90% of the group sums of squares, indicating a nearly linear increase in realized gain with increasing volume BV. Thus, the CP families predicted to perform better based on the BLP-predicted BVs of the parents in OP progeny tests actually did grow faster in nearly linear fashion with predicted performance.
Figure 2-1. Volume ratios compared to CHECK of different genetic entries, estimated by ratio and regression approaches. The value presented is the average of the two approaches for each entry. In both the ratio and regression approaches all genetic entries (except V1) were significantly different than 1 indicating statistically-significant gain above CHECK.

Figure 2-2. Infection ratio of different genetic entries, estimated by ratio and regression approaches. The value presented is the average of the two approaches for each entry. Note that for rust infection, a ratio greater than 1.0 indicates the genetic group had more rust than the CHECK.
The trends in realized gain ratios for rust were similar to those for volume (Figure 2-2). The realized gain ratio for rust infection for the R1 group (the most resistant group according to the OP breeding value predictions) incurred approximately half the infection incurred by the unimproved checks (ratio = 0.53, Figure 2-2). The R2 group had a higher ratio than R1 (ratio = 0.69), followed by the R3 group which averaged approximately the same amount of infection as the unimproved CHECK (ratio = 0.94). The most susceptible group, R5, did in fact have the poorest realized gain ratio (ratio = 1.37) indicating that if the unimproved checks incurred 50% infection, the R5 families would incur approximately 70% infection (1.37 x 50). Also as expected, the 1001 check showed significantly more resistance than the 1002 check, (ratio = 0.81 versus 1.24, respectively). Using the analysis of variance (ANOVA), the partitioning of group sums of squares indicated that the linear trend with rust BV accounted for over 96% of the sums of squares. Thus, as in volume, there is a nearly perfect linear relationship between expected group performance based on OP breeding values and actual realized gains of the five groups.

Influence of Age and Site Characteristics on Volume Gains

Volume Gains for Volume Groups

The intent of this analysis was to examine the impact of site and age characteristics on realized gains in volume and to ascertain whether some volume groups (V1,...,V5) responded differently to these characteristics. The final model for this analysis included effects for the volume groups (V1-V5), SIclass, and group*SIclass interaction and is presented graphically in Figure 2-3. These factors significantly and consistently (across both approaches) impacted the realized gains ratios (compared to CHECK) for volume. The final model for this analysis did not include rust hazard (rushaz) or age class and their associated interactions. Rust hazard effects
were not included in the final model because: (1) The main effects for rushaz class were not consistent across the regression and ratio approaches; and (2) The interactions with other effects were uninterpretable biologically and graphically. Age class was not included in the final model, but there may be some marginally significant effect on realized gains for tree volume expressed as percentage gains as in this study. In some of the models examined, age was significant, but this varied depending on what other main effects and interactions were in the model, and on which analytical approach (ratio versus regression) was used. If age was significant, the realized gain ratio for tree volume was approximately 2-3% lower at age 11 than at ages 5 and 8. Thus, extrapolation of tree volume gain to the rotation age should be reduced by these percentages due to the fact that BV volumes were predicted for age 15.

The final model for volume gain ratio (Figure 2-3) indicates the following. First, there is increased volume gain (when expressed as a ratio to CHECK) on sites of better quality (note tendency of SIclass lines 1 and 2 to exhibit 5 to 10% less gain than other better sites). Secondly, on every site the volume groups ranked in the order predicted by their OP breeding values (V5 > V4 > V3 > V2 > V1 as indicated by upwardly sloping lines for all SIclasses). The only exception to this was the V1 group in SIclass 1 which had only 17 observations. Finally, genetic differences appear to be greater on better sites (3, 4 and 5) relative to poorer sites (1 and 2). Note that for SIclass 1 and 2, the curves are relatively flat, indicating little differences in realized gain across volume groups. The curves for siclass 3, 4 and 5 are much steeper indicating progressively larger realized gains on better sites with increasing genetic quality. Perhaps genetic differences in tree volume are poorly expressed on very poor sites, and better expressed as site quality improves. Graphical analysis of volume versus DBH suggested that the relative similarity of using two different volume equations (for \( \leq 7 \) and \( >7 \) inch DBH) does not bias the prediction of volume.
Figure 2-3. Volume gain ratios (compared to the unimproved CHECK) of volume groups for full-sib families grouped according to the BLP-predicted levels of tree volume (X axis; V1 = worst and V5 = best) and plotted for different site index classes (SIclass 1 = poor and 5 = good) of the test locations.
Taken together these results imply that the BVs accurately predict genetic rankings across all site qualities, but that more gain (expressed as ratio or %) is evidenced on better sites.

**Volume Gains for Rust Groups**

The intent of this analysis was to examine the impact of rust resistance (using the rust groups as independent class variables) on realized volume gains. In this analysis the main effect of age class and interactions associated with age class, SIclass, and rust group were not included in the final model. Age class effects were not significant in either analytical approach (ratio or regression). The associated interactions of age class, SIclass and group were found to be unimportant in various models investigated graphically.

The final model for both approaches contained rust group, SIclass, rushaz and rushaz*group. In both approaches all the terms were highly significant and biologically consistent across the two approaches.

Examination of the estimated realized gains averaged across both approaches (Figure 2-4) suggests that rust resistance does confer some tree volume advantage, but mainly on high hazard rust locations. This is evident for the most rust resistant groups (R1 and R2) where the rankings for rust hazard classes show progressively more volume gain with increasing rust hazard. For both of these groups containing resistant families, the gains are only evidenced in rust hazard classes 4 and 5 where the unimproved checklots incurred 60 to 80% rust incidence (class 4) or greater than 80% rust incidence (class 5). In these high hazard areas, the most rust resistant groups of families had volume gain ratios some 10 to 15% higher than on lower hazard sites. The competition effect in high hazard rust locations between the trees may not have accounted for these realized gains since the rust mortality observed in the randomly selected 6 tests revealed relatively low mortality (9-17%) due to rust.
Figure 2-4. Volume gain ratios (compared to CHECK) for full-sib families grouped according to the family levels of rust resistance [X axis; R1 = best (rust resistant) and R5 = worst] and plotted for different levels of rust hazard (rust hazard 1 = low rust and 5 = high rust) of the test location as measured by rust incidence of CHECK.
The same conclusions are supported by noting that for non-resistant family groups 4 and 5 the rankings of the hazard classes are basically random. Finally, the lines representing low hazard sites (classes 1, 2 and 3) (disregarding the data point of rushaz group 3 for rust group R5 since it had only 2 observations) are basically flat while those for high hazard classes (classes 4 and 5) are generally downward sloping (disregarding the data point of rushaz group 4 for rust group R5 since it has only 1 observation) group due to the progressively smaller volume gains with rust susceptible material (in the higher numbered RX groups) on these high hazard sites.

Influence of Age and Site Characteristics on Gains in Rust Resistance

Rust Gains for Rust Groups

In the examination of the impact of age and site characteristics and the family groups for rust resistance on realized gains in rust incidence, the final model included rust group, rushaz, group*rushaz interaction. In the final model all terms were significant in both the ratio and regression approaches with consistent trends for both approaches. Other main effects (age and siclass) and associated interactions were found not to be significant in both approaches (ratio and regression).

From the graphical display of the averaged values from the ratio and regression models (Figure 2-5), several inferences are possible. First, there is a steady increase in the observed incidence ratios (indicating more rust incidence relative to the check and therefore less gain) for the less resistant groups. This trend is true for all rust hazard levels as evidenced by the fact that all lines slope upward. The increasing spread of among the rust hazard lines for the R4 and R5 groupings reflects the statistically significant rust group*rushaz interaction probably due to a scale effect due to the fact that rust incidence is measured on a binomial scale.
Figure 2-5. Rust incidence ratios (compared to unimproved CHECK) plotted against the family groupings of different rust resistance levels [R1-R5; R1 = best (rust resistant) and R5 = worst] for different values of rust hazard class (rust hazard 1 = low rust and 5 = high rust).
For example, in sites with high rust hazard (rushaz = 5), commercial checks averaged greater or equal to 80% rust infection. Even the most susceptible group (group 5) has maximum ratio of $\frac{100}{\geq 80} = \approx 1.2$ if all the trees in the group are infected. On lower hazard sites (rushaz 1 and 2), the checks incur only 20 to 40% rust so that susceptible families can double this value (incidence ratios of 1.8 to 2.2 for susceptible group R5) without topping out the scale. As with all binomial variables the scale is important, but basically the more rust resistant families were more rust resistant for all site hazards, and neither age of the test nor site quality influence the realized gains observed.

The final analysis was done to examine whether realized gains in rust incidence ratio was affected by families predicted to grow at different rates (the volume groups). Generally, there were few significant terms in either the ratio or regression approach and little consistency across the approaches. Also, main effects or interactions that were significant seemed spurious and not directly related to the $a priori$ resistance groups for volume. Thus, while the previous analysis indicated higher volume gains from more rust-resistant families planted in high hazard sites, the converse is not true. In no situation did being a genetically-superior family for tree volume help reduce rust incidence.

**General Discussion and Conclusions**

The results of this study indicate that: (1) Families which are genetically superior for tree volume will express increased percentage gain in volume (relative to the CHECK) on better quality sites; and (2) The genetic differences appear to be better expressed on better sites (SIclass 3, 4 and 5) relative to poorer sites (SIclass 1 and 2). The maximum range among the VX groups for realized gains occurs on SIclass 4. Perhaps genetic differences in tree volume are poorly
expressed on very poor sites, and better expressed as site quality improves; however, beyond a certain site quality, conditions become somewhat "luxurious" and genetic differences again become obscured. An alternative explanation for this observation may reflect genotype and environment (GxE) interaction associated with site quality (Hodge and White 1992). The BV prediction process used with the OP data placed more weight on data from sites of quality similar to the target site, which was the "average" site for some 367 OP progeny tests (White and Hodge 1988). The target site for the OP BLP process appears to correspond most closely to the SIclass 4 in this study (the mean SIclass for the CP progeny test is 3). Thus, since the OP BVs may apply best on a "average" site (SIclass 4), and since these BVs were used to partition the VX groups, it would follow that the maximum range in realized gain would be observed on SIclass 4. The smaller ranges observed among the groups on other site classes occurs since the BVs which define the groups are less precise on those sites due to GxE interaction (i.e., a lower Type B genetic correlation, Burdon (1977)).

It was also found that a high degree of rust resistance confers a tree volume advantage, mainly on the high hazard locations. In high hazard areas, the most rust resistant groups of families had 10-15% higher volume gain ratios (compared to unimproved CHECK) than on the low rust hazard sites. Further, on the highest hazard sites, the most resistant families had the highest volume gains relative to the CHECK than less resistant families. Some authors have suggested there is genetic cost to having disease resistance genes (Vanderplank 1978, p.133). This study can not provide strong additional evidence supporting this idea; however, on the lowest rust hazard sites (rust hazard 1), the most resistant group (R1) had the lowest volume gain ratio, while the most susceptible group (presumably with the fewest resistance genes) had the highest volume gain ratio.
Compared to the unimproved checklots (CHECK), the 1001 check is approximately 18% better for volume, and incurs 81% (ratio = 0.81) of the rust infection. In comparison, the 1002 check is approximately 16% better for tree volume, incurs more rust (ratio = 1.25) than the unimproved checklots. The difference in gain between the 1001 and 1002 checks was not as great for volume as it was in rust resistance even though the original intent of these checklots was for the 1001 check to be better than 1002 for both volume and rust resistance. The lack of difference for volume may reflect that the younger age data and the genetic evaluations used by the CFGRP for volume were not as accurate and precise as for rust resistance. Heritabilities for volume in slash pine clearly increase with age (Hodge and White 1992, Dieters 1994), while age appears to have no effect on heritability for rust resistance (Dieters 1994).

The examination of the impact of site characteristics and the family groups for rust resistance on realized gains in rust incidence indicates that more resistant family groups incur less rust across all site qualities and ages and that the realized gains (expressed as a ratio to the unimproved CHECK) are not impacted by these factors. The only interaction (that of rust resistance group with the rust hazard of the test location) is likely due to scale effect. The more resistant groups produced more realized gains in rust incidence (evidenced by smaller ratios to the CHECK) across all levels of rust hazard of the test location.

This study suggests that on sites where rust is essentially absent (rushaz 1), families which carry resistance genes may produce slightly less volume. On sites where rust hazard is moderate (rushaz 2 and 3), there is little relationship between rust resistance and tree volume, but on sites where rust hazard is high (rushaz 4 and 5), resistant families produce more volume (on an individual tree basis). Thus, on average across all rust hazard levels there appears to be no strong genetic correlation between volume and rust resistance. This agrees with the alternate
analysis of rust infection ratios as affected by the volume genetic groupings: no relationship was found.

Lastly, and most importantly, the *a priori* ranking based on the BLP predicted BVs for different genetic entries corresponded exactly to rankings in realized genetic gain observed both for tree volume and rust resistance. The linearity of gains across different groups also suggests that there is progressively more gain from families with higher OP BVs in volume gain and lower OP BVs in rust resistance. The fact that these groups of CP families ranked exactly as expected based on the independently predicted BVs should give the breeder confidence that the relative performance of individual families will also be accurately predicted by the BVs.
CHAPTER 3
VALIDATION OF BREEDING VALUES FOR SLASH PINE

Introduction

Breeding values evaluate the parental potential to transmit genetic traits to progeny. The additive genetic value of an individual, judged by the mean value of its progeny, is called breeding value (BV) of an individual (Falconer 1989). The prediction of BV of parents is based on performance of their offspring (Allard 1960, White and Hodge 1987, 1988). In forest tree breeding, BVs can be used in a number of ways: (1) Roguing poor genotypes out of existing seed orchards; (2) Choosing better parents to graft into seed orchards; (3) Increasing genetic gains by deploying specific genotypes to specific sites, e.g. by targeting fusiform rust-resistant genotypes to high hazard sites; (4) Selecting parents with high BVs for future breeding; and (5) Increasing the precision of the advanced generation BV predictions.

The CFGRP has been actively involved in slash pine breeding in the southeastern US since the mid-1950’s. Mass selections of slash pine were made throughout its natural range and grafted into seed orchards (Perry and Wu 1957, Goddard 1980). In the 1960’s, over 300 open-pollinated (OP) progeny tests were established using orchard seed to rank over 2500 mass-selected parents for their growth potential and rust resistance. Generally, these tests utilized a randomized complete block design, and an average test contained 33 families and 6 blocks with 7 to 10 tree row-plots representing each family in each block (White and Hodge 1988). Unfortunately, the data from the OP progeny tests were not well balanced, causing difficulties
in analysis because: (1) The 367 tests were established in different years making data from many different ages; (2) Some tests are well replicated, while others are not; (3) some parents have progeny in as many as 22 different test locations, while some are in only one test (White et al. 1987); and (4) The tests are on sites with different soil quality and rust hazard.

Best linear prediction (BLP), as a statistical tool for prediction of BV, was developed by Henderson (1973, 1977, 1984) to allow dairy cattle breeders to make accurate prediction of BVs from unbalanced, messy progeny test data. For the first time in forestry, White and Hodge (1988) applied this method to the data from the 367 OP progeny tests to develop BLP of the BVs for the volume and rust-resistance of 2245 slash pine parents. The BV predictions were calculated for two traits: rust incidence in a 50% rust incidence environment and tree volume at 15 years (White and Hodge 1988). These BV predictions have been used by the CFGRP to make important operational decisions, from roguing and establishing orchards to selecting an advanced-generation breeding population.

Since parental rankings from progeny tests are critical to genetic progress, the predicted BVs must be precise and accurate (McKinley 1983, Lindgren 1986, White and Hodge 1988, Hodge and White 1992). Hence, this thesis focuses on validating the relative precision of the BVs and their absolute accuracy. Although slightly different, both precision and accuracy are important. The BV predictions can be precise on a relative basis (one compared to another) which means that the rankings (and hence any selection of top parents) will be generally correct, and thus maximize genetic gain from selection decisions. Chapter 2 of this thesis discusses this topic, and indicates strongly that the BVs will correctly rank parental genotypes. However, in addition, BLP theory says that the BV predictions should be accurate, i.e. absolutely predictive of the amount of genetic gains to be expected from any seed orchard or other use. For example, if there are 30 parents in a seed orchard, then each parent should have a predicted BV. If the average of
these 30 BVs is 15% above the average of all 2245 parents, then we expect the progeny from the seed orchard to yield 15% more volume at a specified age than use of average seed. This information would further enable the forest manager to analyze the economic viability of a tree improvement program. This question of accuracy will be examined in this chapter.

It is important to note that it is not the focus of this thesis to validate or test the mathematical and statistical assumptions underlying BLP. Rather, the goal is to use an independent data set (175 CP tests) to validate the genetic gain predictions derived from BVs calculated from OP progeny test data. If there is a high degree of correspondence between predicted and realized gains, then we will assume that either the underlying assumptions of BLP were met, or that the BLP method is robust to violation of these assumptions.

Thus far, the BV predictions for tree volume have not been validated. However the BVs for rust-resistance have been validated using a relatively smaller data set (592 families, 46 tests) by Hodge et al. (1990). In this present work, a fairly large independent CP test data set will be used to validate the BV predictions for both tree volume and rust resistance. The data contain 175 CP tests with 2051 full-sib families from 669 parents. These data will be used to assess if the BLP predictions of the 669 parents from OP data accurately predict performance of their full-sib offspring in CP tests. The specific objective is therefore to validate the accuracy of genetic gain predictions made using BLP of BVs for volume and rust resistance in slash pine.
Materials and Methods

Plant Material and Genetic Tests

In this chapter the same 367 OP and 175 CP progeny test data, 1001 and 1002 checklot information and groupings of full-sib families (VX and RX groups) as described in chapter 2 are utilized. Briefly, they are described below:

a) CHECK = unimproved checks, including various commercial checks (woods-run unimproved checks) and the University of Florida checklot (seed collected from a single unimproved stand in southeast Georgia which has been used by the CFGRP as a standard check across most progeny tests),

b) 1001 check = a bulk mix checklot of OP seed from 22 families collected from 1.0 generation rogued or 1.5 generation orchards,

c) 1002 check = a bulk mix checklot of OP seed from 20 families collected from an unrogued 1.0 generation orchard (Horticulture Unit at Gainesville, Florida),

d) V1-V5 = five groups of full-sib families, classified on the basis of mid-parental volume BV, where V1 was the worst group and V5 was the best group (see Table 2-1), and

e) R1-R5 = five groups of full-sib families, classified on the basis of mid-parental rust BV, where R1 was the best, most resistant, group and R5 was the worst, least resistant, group (see Table 2-1).

The Breeding Value Information

The BLP-predicted BVs are the predicted additive genotypic values for parent trees expressed in the units of measurement for the two traits (ft³ for volume and % infection for
fusiform rust). The CFGRP has been using this BV information since the predictions were made (White et al. 1988). The BV predictions for volume (BVVOL) are for 15-year individual tree volume for 2245 first-generation parents, and are distributed approximately normally with a mean of 0 ft³ and standard deviation of 0.614 ft³. BVVOL ranges from -3.87 to 2.60 ft³, with approximately 98% of all predictions between -1.80 and 1.80 ft³. A BVVOL of zero represents an average first-generation selection, while an unimproved check would have a BVVOL of -0.38 ft³ (White et al. 1989). The difference of 0.38 ft³ is the genetic progress made for volume from the first-generation mass selection of good phenotypes, and is equivalent to 10% genetic gain over unimproved material because average 15-year volume for unimproved material is 3.82 ft³ (White et al. 1988).

For rust, the predicted BVs (BVR50) are in units of percentage infection. The BVR50 measures the percent infection expected in an environment where unimproved checks would incur 50% infection (defined as the 50% hazard environment), and thus low values of BVR50 are desirable since they indicate low infection (higher resistance) (White et al. 1988, White et al. 1989). The BVR50 values for 2245 first-generation selections are distributed approximately normally with a mean of 50% and a standard deviation of 25%. BVR50 ranges from -50 to 142%, with over 98% of the predictions between 0 and 100% (White et al. 1989).

Breeding Values of Full-sib Families

Since breeding values express additive genetic values, the expected mean BV of a full-sib family can be calculated simply by averaging the BVs of the female and male parents. Following this approach, BVs for all full-sib families were calculated, and then families were divided into groups [VX (V1-V5) and RX (R1-R5)] based on their predicted genetic values (Table 3-1).
Table 3-1. Breeding value for volume and rust and the number of full-sib families for 1001 and 1002 checklots, V1-V5, and R1-R5 groups. The V1-V5, and R1-R5 BV figures are the mean BV for the respective group. See Table 2-1 for more details.

<table>
<thead>
<tr>
<th>Genetic Entries</th>
<th>Number of Families</th>
<th>Breeding Value Volume (BVVOL)</th>
<th>Breeding Value Rust (BVR50)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1001</td>
<td>22*</td>
<td>0.73</td>
<td>25.3</td>
</tr>
<tr>
<td>1002</td>
<td>20*</td>
<td>0.21</td>
<td>50.6</td>
</tr>
<tr>
<td>V4</td>
<td>56</td>
<td>-0.92</td>
<td>42.4</td>
</tr>
<tr>
<td>V2</td>
<td>354</td>
<td>-0.45</td>
<td>39.7</td>
</tr>
<tr>
<td>V3</td>
<td>915</td>
<td>0.03</td>
<td>41.4</td>
</tr>
<tr>
<td>V4</td>
<td>541</td>
<td>0.96</td>
<td>39.3</td>
</tr>
<tr>
<td>V5</td>
<td>935</td>
<td>0.96</td>
<td>39.2</td>
</tr>
<tr>
<td>R1</td>
<td>164</td>
<td>0.13</td>
<td>13.0</td>
</tr>
<tr>
<td>R2</td>
<td>670</td>
<td>0.20</td>
<td>32.0</td>
</tr>
<tr>
<td>R3</td>
<td>940</td>
<td>0.22</td>
<td>48.0</td>
</tr>
<tr>
<td>R4</td>
<td>263</td>
<td>0.05</td>
<td>65.0</td>
</tr>
<tr>
<td>R5</td>
<td>14</td>
<td>-0.04</td>
<td>83.0</td>
</tr>
</tbody>
</table>

* Bulk mix of OP seed

Pollen Contamination Assumption

Since the two checklots 1001 and 1002 were bulk mixes of OP seed collected in seed orchards, and were not full-sib families, the quality of the male parents was unknown. Some assumptions about the average male parent in the orchard, as well as the amount of pollen contamination from outside the orchard, were necessary in order to calculate expected gain ratios (described later). Average BVs for CFGRP first-generation orchards (unrogued and rogued) were taken from Hodge et al. (1989) (Table 3-2). Research indicates that as much as 89% pollen contamination can occur in young conifer orchards (Fast et al. 1986), and even mature, fully productive orchards can have 30% or more contamination (El-Kassaby et al. 1989, Friedman and
Adams 1985a, 1985b). One study done by Squillace and Long (1981) suggests 83.5% pollen contamination in slash pine. However, in this study, we made the assumption that 50% of pollen (contributing to the fertilization of the females in the orchard) originated from outside the orchard (foreign). Pollen from outside the orchard was assumed equivalent to unimproved checks with BVVOL = -0.38 and BVR50 = 50. The average BV of the foreign pollen (from Table 3-2) and the orchard pollen was taken as the BV of the pollen cloud for the 1001 and 1002 checklots. Assuming equal fecundity, the average BV of the females in the mix was calculated. The male and female BVs were then averaged to calculate BVs for the bulk mix seed (Table 3-1).

Table 3-2. Average Breeding value for volume (BVVOL) and rust (BVR50) for unimproved check, first-generation unrogued and first-generation rogued CFGRP slash pine seed orchards.

<table>
<thead>
<tr>
<th>Orchard</th>
<th>Breeding Value Volume (BVVOL)</th>
<th>Breeding Value Rust (BVR50)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unimproved Check</td>
<td>-0.38</td>
<td>50</td>
</tr>
<tr>
<td>1.0 Unrogued</td>
<td>0.00</td>
<td>50</td>
</tr>
<tr>
<td>1.0 Rogued</td>
<td>0.20</td>
<td>41</td>
</tr>
</tbody>
</table>

Realized Genetic Gain Calculation ($\Delta G_{R,\text{VOL}}$ and $\Delta G_{R,\text{RUST}}$)

Calculation of realized genetic gains for volume and rust across all tests was performed using two kinds of approaches: 1) a regression approach and 2) a ratio approach. The ratio approach and regression approach are described fully in chapter 2, but are briefly described below. In the ratio approach realized gain is estimated by calculating for each test the ratio of volume or rust infection for all pairs of volume and rust groups, and then averaging these ratios across all tests. Say for example if in a given test, $\text{VOL}_{V5}/\text{VOL}_{\text{CHECK}} = 1.25$, this indicates that the V5 group had 25% more volume than the unimproved check in that test. Then averaging the
VOL\textsubscript{V5}/VOL\textsubscript{CHECK} ratio across all tests gives the overall estimate of realized gain for these two groups from the ratio approach. These average ratios (b\textsubscript{i}) were calculated for ten pairs of volume group (e.g., V5 vs V4, ..., V5 vs V1, V4 vs V3, ..., V4 vs V1, V3 vs V2, V3 vs V1, V2 vs V1); and ten pairs of rust group (e.g., R1 vs R2, ..., R1 vs R5, R2 vs R3, ..., R2 vs R5, R3 vs R4, R3 vs R5, and R4 vs R5); and the checklots 1001 and 1002.

In the regression approach, a linear regression of two groups was calculated using a model with no intercept, e.g.,

\[ \text{VOL}_{V5} = b_2 \times \text{VOL}_{\text{CHECK}} \]

with no intercept, the slope coefficient \(b_2\) is the overall estimate of realized gain from this approach. For example, if \(b_2 = 1.25\), it indicates 25\% more gain for volume for V5 group than the CHECK. These regressions were done for all pairs of volume groups and rust groups in Table 3-1.

The average of these two estimates (\(b_1\) and \(b_2\) from the ratio and regression approach, respectively) was taken as the final estimate of realized volume and rust ratios (\(\beta\)) for any given pair of groups. The percent realized genetic gain for volume (\(\Delta G_{R, VOL}\)) was then calculated as:

\[ \Delta G_{R, VOL} = (\beta-1) \times 100\%. \]

Similarly, the percent realized genetic gain for rust (\(\Delta G_{R, RUST}\)) was then calculated as:

\[ \Delta G_{R, RUST} = (1- \beta) \times 100\%. \]

Calculation of Expected Genetic Gain Ratios for Rust Resistance (\(\Delta G_{R, RUST}\)).

Evidence from a realized gain study on rust resistance indicates that rust resistance is proportional, i.e., the same relative improvement in rust resistance is observed at all levels of rust hazard (White \textit{et al.} 1989, Hodge \textit{et al.} 1993). For example, progeny from a full-sib cross with mid-parental BVR50 = 40 would, by definition, be expected to incur 40\% infection on a 50\% hazard site; thus, the ratio of family infection to unimproved infection is 40/50 or 0.80. This
relative resistance appears to be constant at all hazard levels; therefore, this family would be expected to incur 32% infection on a 40% hazard site (0.80 x 40% = 32%), and 64% infection on a 80% hazard site (0.80 x 80% = 64%). Thus, following the assumption of the proportional resistance, the ratio of BVR50/50 expresses the expected ratio of infection for a particular genetic group at any hazard level. Similarly, the expected ratio of infection for any two genetically-distinct groups X and Y is expected to equal the ratio of their rust BVs, i.e., BVR50x/BVR50y.

For example the expected rust ratio for BVR50 R1 over BVR50 R2 is 13/32 = 0.41 (Table 3-1). Which means R1 group is expected to incur less than half of the infection incurred by the R2 group. These expected rust ratios for rust resistance were calculated for all pairs of the five rust resistance groups, there was total of 10 comparisons (e.g., R1 vs R2, ..., R1 vs R5, R2 vs R3, ..., R2 vs R5, R3 vs R4, R3 vs R5, and R4 vs R5) and each of the checklots (1001 and 1002) in Table 3-1. The expected percent genetic gain of group X relative to group Y for rust (ΔG_e,rust) was defined as one minus the expected rust ratio for groups X and Y times 100%. For example, ΔG_e,rust for group R1 relative to group R2 equals (1 - 0.41) * 100 = 59%.

Calculation of Expected Genetic Gain Ratios for Volume (ΔG_e,volume)

For volume groups, the same formula for calculation of expected genetic gain was used which has been used by CFGRP members (White et al. 1988). The ratio of tree volume for a particular genetic group from Table 3-1 relative to unimproved material is (BVVOL + 4.21)/3.83 (White et al. 1988).

Similarly the expected volume ratio for two particular groups X and Y is simply (BVVOLx + 4.21)/(BVVOLy + 4.21). For example the expected volume ratio for BVVOL V5 over BVVOL V3 will be (0.96 + 4.21)/(0.03 + 4.21) = 1.22, which means that the best group (V5) is expected to be 22% better than the average group (V3). These expected gains ratios were
calculated for all pairs of volume groups (e.g., V5 vs V4, ..., V5 vs V1, V4 vs V3, ..., V4 vs V1, V3 vs V2, V3 vs V1, V2 vs V1)(V1, ..., V5) and checklots (1001, and 1002) in the Table 3-1. The expected percent genetic gain for volume (ΔGₖ,vol) is defined as the expected volume ratio of groups X and Y minus one times 100%. For example ΔGₖ,vol for group V5 relative to group V3 equals (1.22 - 1) * 100 = 22%.

**Comparison of Realized and Expected Percent Gains**

The realized genetic gain data were derived from the 175 CP progeny tests. Two kinds of approaches were used to examine how well expected genetic gains agreed with realized genetic gains. First, all genetic groups (V1-V5, R1-R5) and the checklots 1001, and 1002 were compared to the unimproved checks, and the realized and expected genetic volume and rust ratios were examined graphically. Second, all possible comparisons among the genetic groups (V5 vs V4, ..., V5 vs V1, V4 vs V3, ..., V4 vs V1, V3 vs V2, V3 vs V1, V2 vs V1 for volume groups and R1 vs R2, ..., R1 vs R5, R2 vs R3, ..., R2 vs R5, R3 vs R4, R3 vs R5, and R4 vs R5 for rust groups) were made using expected and realized percent genetic gain (note that all the comparisons were made with the inferior groups in the denominators for both VX and RX groups).

The relationship between the realized percent genetic gain (ΔGᵣ) versus expected percent genetic gain (ΔGₑ) for both VX and RX groups was examined using the following model:

\[ ΔGᵣ = b ΔGₑ. \]

The 10 possible comparisons among VX groups, and among RX groups were fitted using this model. In this analysis, a model with an intercept term was tried originally, and the intercept terms were never significantly different from zero either for tree volume or rust resistance groups. Therefore, all models were forced through the origin. Since the regression line is fit
through the origin, the slope coefficient $b$ estimates the average ratio of realized genetic gain versus the expected genetic gain.

**Results and Discussion**

**VX and RX groups versus CHECK**

The comparison of expected and realized gain ratios for the VX groups compared to the unimproved CHECK is presented in Figure 3-1. Expected ratios for the five groups V1-V5 were 0.86, 0.98, 1.11, 1.22 and 1.35, respectively. Realized ratios of the VX groups were 0.97, 1.11, 1.16, 1.19 and 1.22, respectively. Although the ranks were correct, the most striking result is the discrepancy between the expected and realized ratios for the most extreme groups, V1 and V5. The V1 group was not nearly as poor as the BVs had predicted, with a predicted ratio of 0.86, but a realized ratio of 0.97. Similarly, the V5 group was not as good as expected, with a predicted ratio of 1.35 and realized ratio of 1.22.

The comparison of expected and realized gain ratios for the RX groups compared to the unimproved CHECK is presented in Figure 3-2. Expected ratios for the five groups R1-R5 were 0.26, 0.64, 0.96, 1.30 and 1.66, respectively. Realized ratios of the RX groups were 0.53, 0.69, 0.94, 1.22 and 1.37, respectively. Here also the rankings were correct, and again the most interesting result is the discrepancy between the expected and realized ratios for the most extreme groups, R1 and R5. The R1 group was not nearly as good as the BVs had predicted, with a predicted ratio of 0.26, but an realized ratio of 0.53. Similarly, the R5 group was not as poor as expected, with a predicted ratio of 1.66 and realized ratio of 1.37.

The patterns for volume and rust when compared to the CHECK are quite similar. The difference between the realized and expected genetic gain ratios are increasingly inflated at either
Figure 3-1 Comparison of realized versus expected gain for volume where volume ratio is genetic entry compared with CHECK.

Figure 3-2 Comparison of realized versus expected gain for fusiform rust resistance where infection ratio is genetic entry compared with CHECK.
extreme of the groups and are not very much different for the middle groups (V3 or R3). These results suggest that the BLP predicted BVs using OP data will give correct rankings, but are not absolutely accurate. It appears that the range of the predictions (i.e., variance of the BVs) is too large for both volume and rust resistance. For both traits, the worst group was not as bad as expected and best group was not as good as predicted.

**Comparisons Among VX groups and RX groups**

Plots of the expected versus realized percent genetic gains for volume and rust (10 possible comparisons among the VX groups and 10 possible comparisons among the RX groups) are presented in Figure 3-3A and 3-3C.

For both traits, the trends are similar. For every comparison, the realized percent genetic gain was less than the expected genetic gain. This can be observed by noting that all points fall below the solid 45° line in the figures, which represents where the points should fall if realized is equal to the expected. The dashed lines in the figures represent the fitted regression line (no intercept) for realized gains versus expected gains. The slope coefficients (b) for these dashed lines are $b = 0.53$ and $b = 0.69$ for volume and rust, respectively. These indicates that realized genetic gain for volume was only 53% of expected genetic gain predicted by the BLP breeding values, while for rust 69% of the expected genetic gain was realized. The implications of these results are consistent with the comparisons of the VX and RX groups with the CHECK: the range of predictions is too large, the variance of BV predictions is too large, and differences between two genetic groups are always overestimated.

In the group comparison (VX and RX groups), the comparison of V5 group (the best volume group) with all other VX group always fell significantly below the expected. A nearly similar trend was true for the V4 group when it was compared against other VX groups.
Figure 3-3 Comparison of realized versus expected percent genetic gain for tree volume using unadjusted BVs (Figure A) and adjusted BVs (three-fourths of unadjusted BVs) (Figure B), and comparison of realized versus expected percent genetic gain for rust resistance for unadjusted BVs (Figure C) and adjusted BVs (three-fourths of unadjusted BVs) (Figure D). The solid line in each figure indicates where the points should fall if realized genetic gains equal those gains predicted by the BLP BVs; whereas, the dashed line is the regression of the actual realized gains on expected gain.
However, the difference was not as big as it was for the V5 group. A nearly identical trend was true for the rust resistance groups. Here the R1 group when compared to other RX group showed significantly smaller gains then predicted. Generally, in both cases (VX and RX groups) the best groups (top groups) did not realize the gains predicted.

Hypotheses for Inflation of Breeding Value Variance

BLP theory assumes that: (1) Fixed effects (e.g., site and block effects) are known, and (2) Second moments (variances and covariances) of the observations are known (White and Hodge 1989). In a Best Linear Unbiased Prediction (BLUP) application, fixed effects are estimated and BVs are predicted simultaneously. In BLP, where fixed effects are assumed known, the resulting BV predictions will have a slightly larger variance than BLUP predictions even given the same data and assumed second moments. In this case the effect is assumed small, because the fixed effects in the 367 CFGRP OP tests are precisely estimated; however, both of the assumptions could have attributed to the larger variance among predicted breeding values that was supported by the realized gains comparisons.

Another possible source of imprecision or error in the parameters used for BLP may be the assumption that all the families in the OP progeny tests were half-sibs. All genetic parameters used by White and Hodge (1988) in the BLP process were developed from OP progeny tests. Under this assumption, family variances were multiplied by the value of four to get an estimate of additive variance, and thus the heritability estimate (narrow sense heritability \( h^2 \)). This reasoning assumes there are no full-sib offspring in the OP families in the progeny tests which may not be true (Dieters 1994). The reported results from various authors suggests that multiplying the variance component for open-pollinated families by the value of four is too large
and that the value of three is more appropriate to account for the presence of full-sib families (Squillace 1974, Adams and Joyce 1990, Vargas-Hernandez and Adams 1991, Dieters 1994).

A comparison of heritability estimates in slash pine agrees with those assertions in the literature that there may be reason to multiply the family variance by 3 instead of 4 to obtain the additive variances. In one study, Hodge and White (1992) used 57 slash pine OP progeny test data from the CFGRP and calculated heritability estimates of 0.080, 0.156 and 0.161 at five, ten and fifteen years volume. In a study using full-sib families, Dieters (1994) used 171 slash pine tests from CFGRP and found heritability estimates of 0.072, 0.124 and 0.122 at five, eleven and fourteen years volume. The heritability estimates found by Dieters (1994) with full-sib data were 0.02 to 0.05 lower than the estimates from the OP data. Dieters (1994) also found that adjusted OP estimates (multiplying the variance component of OP families by the value of three instead of four to estimate additive variance) to agree closely to estimates obtained from the full-sib tests (0.060, 0.117 and 0.121 at five, ten and fifteen years, respectively).

Adjustment of Expected Genetic Gains

If it is in fact more appropriate to multiply by three than four when estimating additive variance from OP families of slash pines, then all BV predictions would be overestimated by 4/3. To illustrate this, consider the general BLP equation:

\[ \mathbf{g} = \mathbf{C}'\mathbf{V}^{-1} (\mathbf{Y} - \alpha) \]

Where:

\( \mathbf{Y} = \) vector of observations (in this case family means),
\( \alpha = \mathbb{E}(\mathbf{Y}) \), which is vector containing the expected values of the family means,
\( \mathbf{V} = \) a matrix containing variances and covariances of the observations,
C = covariances of observation with parental BVs, and
\( \mathbf{g} = \) a vector of predicted parental breeding values.

Assuming no inbreeding, the covariance of any family mean with \( \mathbf{g} \) (parental BV) equals \( 1/2 \sigma^2_A \), regardless whether the family is half-sib, full-sib, or open-pollinated (White and Hodge 1989, p.89, p.120). If \( \sigma^2_A \) is estimated by \( 4\sigma^2_r \), instead of \( 3\sigma^2_r \), then all elements in C will be inflated by \( 4/3 \), thus \( \mathbf{g} \) will also be inflated by \( 4/3 \). This could account for most of the observed inflation of expected gains compared to the observed realized gains. Under this assumption, BVs were multiplied by \( 3/4 \), and expected genetic gain ratios were recalculated using these adjusted BVs.

The comparison of these adjusted expected genetic gains and the realized gains are presented in Figure 3-3B and 3-3D for tree volume and rust resistance, respectively. There was a much closer correspondence between the predicted and the realized genetic gains, particularly for rust. The regression slope coefficients indicated that realized tree volume gain was about 74% of the expected gain, while realized rust resistance gain was about 89% of the expected gain (Figure 3-3 B and 3-3 D).

Conclusions

The comparison of expected and realized gain ratios for both tree volume and rust resistance suggests that the realized gains of the volume and rust groups is in the same order as was predicted by their rankings based on BLP predicted OP breeding values. The linearity of gains in different groups for both tree volume and rust resistance characteristics also suggests that there is progressively more gain from families with higher OP breeding values for volume gains and lower OP breeding values in rust resistance.
However, the range of predictions or the variance of BLP predicted BVs is too large for the two extreme groups for both tree volume (V1 and V5) and rust resistance (R1 and R5). Furthermore, the asymmetry of predictions indicates more discrepancy (impact) at the top (i.e., best families) for both tree volume and rust resistance characteristics and this discrepancy is worse for tree volume than it is for rust resistance groups. This large range means that very good families are predicted to be better than they really are. Based on both theoretical and empirical grounds, the BLP BVs were multiplied by three-fourths to reduce the range and the adjusted expected gains agreed much more closely with the observed realized gains.
CHAPTER 4
CONCLUSIONS AND APPLICATIONS

The realized gains for tree volume of improved and unimproved check compared to unimproved CHECK showed significant difference (18% and 16% gain, respectively) for tree volume. For rust, the improved check was found to be significantly more resistant compared to unimproved check.

The performance of CP families with different genetic quality (V1-V5 for volume and R1-R5 for rust) based on their parental performance in OP tests showed the exact correspondence of ranking of realized gain for tree volume and rust resistance of the genetic entries to the order predicted by the a priori classification based on the genetic quality.

Examining the impact of site characteristics on realized gains for volume indicated that the families superior for tree volume expressed more gain in volume (on a percent basis) compared the CHECK on better sites. Similarly, the genetic difference among genetic groups was greater on better quality sites (SIclass 3, 4 and 5) compared to poorer sites. It was also found that families with high degree of rust resistance have some tree volume advantage on high hazard locations compared to the CHECK.

On sites where rust is absent or low, families that are more resistant produced lesser volume this could indicate that there is a genetic cost in terms of volume production associated with maintaining resistance genes. On moderate rust hazard sites, there appears little relationship between rust resistance and tree volume, while on sites where rust hazard is high, the resistance families produce more volume.
The accuracy of genetic gain predictions using BLP of BVs for tree volume and rust resistance suggests that the magnitude of prediction is too large for the two extreme genetic entries for both tree volume (V1 and V5) and rust resistance (R1 and R5) groupings. The genetic gains of the best families are over predicted by BLP relative to the realized gains found in this study, and this discrepancy is worse for volume than rust resistance. However, when an adjustment of BLP predicted BVs was made based on both empirical and theoretical ground, by multiplying the values by three-fourths, the adjusted predicted gains were much closer to the observed gains.

Applications

1. Use BLP rankings for both tree volume and rust resistance with confidence for roguing, deployment and selection.

2. Reduce gain predictions for tree volume and rust resistance by 25% of BLP predicted BVs (and reduce another 26% and 11% for tree volume and rust resistance, respectively to get actual realized gains).

3. Deploy best tree volume growth material to better sites and expect at least 10% more volume (15% on S1class 1-2 and 25% on S1class 3-5).

4. Deploy most rust resistant material to high hazard sites.

5. Count on up to 10% more tree volume gain from use of resistant material on high hazard sites.

6. Reduce expected gain percentages when extrapolating gains to rotation realizing that there was a slight trend to lower percent volume gains at older ages (2-3% less gains in volume at age 11 compared to 5 and 8) and that BVs are predicted for age 15.
REFERENCE LIST


BIOGRAPHICAL SKETCH

Lokendra P. Dhakal was born May 21, 1961, in Kathmandu, Nepal. He was raised in Kopundole, Lalitpur, and received his high school degree from Padmodaya High School in 1977. He did his Bachelor of Science degree in botany and forestry in 1985 and 1987, respectively, and Master of Arts in psychology in 1989 from Tribhuvan University of Nepal. He enrolled in the School of Forest Resources and Conservation at the University of Florida on August 1993. He expects to receive his Master of Science degree in December, 1995. He is married with one daughter and plans to return his home country, Nepal, to assume his position as a tree improvement officer in existing tree improvement program.
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

Timothy L. White, Chairman
Professor of Forest Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

Donald L. Rockwood
Professor of Forest Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

Gary R. Hodge
Associate Scientist of Forest Resources and Conservation

This thesis was submitted to the Graduate faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Master of Science.

December 1995

Director, School of Forest Resources and Conservation

Dean, Graduate School