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Genetic variation in selected acorn and seedling characteristics of northern red oak (Quercus rubra L.).

Mark Alexander Remaley

To the Graduate Council:

I am submitting herewith a thesis written by Mark Alexander Remaley entitled "Genetic variation in selected acorn and seedling characteristics of northern red oak (Quercus rubra L.).." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Scott E. Schlarbaum, Major Professor

We have read this thesis and recommend its acceptance:

Arnold Saxton, Paul P. Kormanik, George Hopper

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

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We have read this thesis
and recommend its acceptance

Accepted for the Council:

Associate Vice Chancellor
and Dean of the Graduate School

Genetic variation in selected acorn and seedling characteristics of northern red oak (*Quercus rubra* L.).

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Mark Alexander Remaley

August 1998

DEDICATION

This thesis is dedicated to my parents Tom and Carol Remaley

and

Laurin Remaley

who have given me love and support through my graduate program.

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I wish to express my gratitude to Professor Scott E. Schlarbaum, for his guidance and mentoring through my graduate program. The experience, wisdom and teachings over the past five years gives me the foundation to succeed in my professional career.

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Thanks to my parents, Tom and Carol, for the opportunity and endless support through my ten years of undergraduate and graduate programs.

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ABSTRACT

Three separate studies were conducted to evaluate genetic variation in selected acorn and seedling characteristics of northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.). The objective of the studies were to: (1) evaluate sources of genetic variation and genotype-environmental interaction in seedling characteristics, (2) determine occurrence and frequency of polyembryony within and among half-sib families of northern red oak and relationships between acorn size and polyembryony, and (3) determine the maximum length of time northern red oak acorns can be left under simulated orchard conditions and collection procedures and remain viable.

For the first objective, seedlings from 12 genetic families of both species were grown at locations in Tennessee and Georgia. White oak was found to be very sensitive to early growing season water stress that occurred at the Tennessee location, causing cessation of seedling growth following initial germination and growth. Following increased soil moisture levels, the seedlings generally failed and set a terminal bud to recommence growth and development. The northern red oak seedlings were subjected to the same water stress, but responded to the increase in soil moisture levels. However, the seedlings failed to reach the same size as the other location. Northern red oak families exhibited wide variation between family means. A distribution analysis on number of first-order lateral roots, indicated that most seedlings will fail to meet minimum standards for planting on highly competitive upland sites. Single tree and family heritability estimates for growth characteristics were relatively similar at both locations and generally lower than combined location estimates.

Acorn germination and dissections were used to determine the occurrence of polyembryony in eight open-pollinated families of northern red oak. Relationships between acorn size and polyembryony was determined between collections of two mother trees. Only seed sources from Overton County, Tennessee, produced polyembryonic acorns. Acorn germination tests revealed more embryos per acorn than acorn dissections. As acorn size increased, the number of embryos increased in families predisposed to polyembryony. The occurrence of polyembryony in northern red oak open pollinated families indicated that seed sources should be screened for polyembryony occurrence.

A two year study of the relationship between acorn moisture content, weather and the number of days following natural seed fall under simulated orchard conditions. Northern red oak acorns were collected from 10 trees and were subjected to five levels of shading for a thirty day period and at two day intervals, acorn moisture content was determined. It was found that acorn moisture content did not desiccate below 25 percent under all shading regimes, indicating that viability was not affected. Results of the experiment generally indicated that other factors such as predation should be of greater importance to overall viability of acorn crops than acorn desiccation.

TABLE OF CONTENTS

CHAPTER PAGE

PART 1: GENERAL INTRODUCTION

1. INTRODUCTION....2

2. OBJECTIVES....4

3. LITERATURE REVIEW....5
Description of the genus....5
Range and silvical characteristics of northern red oak....5
Range and silvical characteristics of white oak....6
Silvicultural management of oak....7
Shelterwood regeneration method....8
Artificial oak regeneration....11
Phenotypical graded nursery stock for quality....13
Reproductive biology of oak....14
Pistillate flower formation....15
Staminate flower formation....16
Flower fertilization....16
Polyembryony....17
Acorn maturation and collection....18
Acorn production....20
Genetic variation of northern red oak....21
Studies related to nursery seedling production....22
Studies related to acorn phenotype....22
Importance of seed source....24
Tennessee Valley Authority northern red oak seed source study....25
Conversion of the Watuaga progeny test to a seedling seed orchard....26

LITERATURE CITED....29

Part 2: Genetic variation and heritability of seedling characteristics in northern red oak (*Quercus rubra* L.) 1-0 seedlings.

1. ABSTRACT....37

2. INTRODUCTION....38

3. MATERIALS AND METHODS....40

4. STATISTICAL ANALYSIS....43

5. RESULTS....45
Early growing season results....45
Tennessee location....45
Analyses of Tennessee seedlings....46
General differences....46
Replication differences....46
Correlation coefficients....47
Variation in family means....47
Seedling distribution analysis....48
Analyses the Georgia seedlings....49
General differences....49
Replication differences....50
Correlation coefficients....50
Variation in family means....51
Seedling distribution analysis....51
Combined location analyses....52
General differences....52
Replication differences....53
Variation in family means....54
Seedling distribution analysis....54
Field grading criteria....56
Heritability estimates....56
Tennessee location....56
Georgia location....57
Combined locations....57
General combining ability....58
Tennessee location....58
Georgia location....58
Combined locations....59

6. DISCUSSION....60
Tennessee location....60
White oak....60
Individual location analyses....62
General differences....62
Replication differences....63
Correlation coefficients....65
Variation in family means....66
Distribution analysis....67
Combined analysis....68
Comparisons between locations....68
Seedling distribution analysis....69
Field grading criteria....70

Evaluation of VIGOR....71
Heritability estimates and general combining abilities....72

LITERATURE CITED....74

APPENDIX....76

PART 3: Polyembryony occurrence and variation between genetic families in northern red oak (*Quercus rubra* L.).

1. ABSTRACT....133

2. INTRODUCTION....134

3. MATERIALS AND METHODS....136

4. STATISTICAL ANALYSIS....139

5. RESULTS....140
Germination test....140
Acorn dissection....141

6. DISCUSSION....143

LITERATURE CITED....146

APPENDIX....147

PART 4: Relationships between acorn moisture content and time of collection after natural seed fall in northern red oak (*Quercus rubra* L.).

1. ABSTRACT....158

2. INTRODUCTION....159

3. MATERIALS AND METHODS....161

4. STATISTICAL ANALYSIS....164

5. RESULTS....165

6. DISCUSSION.....167

LITERATURE CITED.....169

APPENDIX.....170

VITA.....184

LIST OF TABLES

TABLE PAGE

Part 2: Genetic variation and heritability of seedling characteristics in northern red oak (*Quercus rubra* L.) 1-0 seedlings.

2.1. Weight of 100 acorns for the northern red oak and white oak genetic families used for the Tennessee and Georgia studies.....77

2.2. Amounts of fertilizer used to adjust soil levels to comparable levels of fertility at the Tennessee location. Beds 1 and 2 were planted with northern red oak. Beds 3 and 4 were planted with white oak.....78

2.3. Fertilizer amounts applied to the raised nursery beds during the 1994 growing season at the Tennessee location. Beds 1 and 2 were planted with northern red oak. Beds 3 and 4 were planted with white oak.....79

2.4. Replication, family, characteristic, number of seedlings, mean, standard deviation, minimum and maximum for the seedling characteristic measured for the Tennessee data.....80

2.5. Arithmetic means for family characteristics in replication 2 by planting order from east to west at the Tennessee location.....84

2.6. Correlation coefficients for seedlings grown in replication 1 and 2 and combined replications at the Tennessee location. All correlations were significant at p = .001.....85

2.7. BLUP mean estimates and standard errors for seedling characteristics of different families grown in Tennessee by replication.....86

2.8. BLUP mean estimates and standard errors for combined replications of seedling characteristics of different families grown in Tennessee.....88

2.9. Percentage of seedlings by family within and across replications with a first-order lateral root number equal to or greater than the combined replication first-order lateral mean for each respective family.....89

TABLE PAGE

2.10. Percentage of seedling by family within and across replications with 7 or more first-order lateral roots 90

2.11. Replication, family, characteristic, number of seedlings, mean, standard deviation, minimum and maximum for the seedling characteristics measured for the Georgia data..... 91

2.12. Correlation coefficients for seedlings grown in replication 1 and 2 and combined replications at the Georgia location. All correlations were significant at p = .001..... 95

2.13. BLUP mean estimates and standard errors for family and seedling characteristics for Georgia by replication..... 96

2.14. BLUP mean estimates and standard errors for the combined replications of seedling characteristics of different families grown in Georgia..... 98

2.15. Percentage of seedlings by family within and across replications with the family BLUP mean or greater number of first-order lateral roots from the Georgia location..... 99

2.16. Percentage of seedlings by family within and across replications with five or more first-order lateral roots from the Georgia location..... 100

2.17. Correlations coefficients for seedling characteristics from the combined location analysis. All correlations were significant at p = .001..... 101

2.18. Overall BLUP mean estimates and standard errors by location and location by replication for seedling characteristics from the combined location analysis..... 102

2.19. BLUP mean estimates for family by replication for the seedling characteristics from combined location analysis..... 103

2.20. BLUP mean estimates for family by location for the seedling characteristics from the combined location analysis..... 106

2.21. BLUP mean estimates for family by seedling characteristics from the combined location analysis..... 108

TABLE PAGE

2.22. Percentage of seedlings by family within replication at the Tennessee location with equal to or greater than six first-order lateral roots....109

2.23. Percentage of seedlings by family within replication at the Georgia location with equal to or greater than six first-order lateral roots....110

2.24. Percentage of seedlings with the BLUP mean or more first-order lateral roots by location and combined locations....111

2.25. Percentage of seedlings within families with the BLUP mean or more first-order lateral roots by location and combined locations....112

2.26. Number of seedlings by family with 6 or more first-order lateral roots and 1 meter or greater in height by location and combined locations....113

2.27. Family heritability estimates and associated standard errors for seedling characteristics grown at the Tennessee location....114

2.28. Single tree heritability estimates and associated standard errors for seedling characteristics grown at the Tennessee location....115

2.29. Family heritability estimates and associated standard errors for seedling characteristics grown at the Georgia location....116

2.30. Single tree heritability estimates and standard errors for seedling characteristics grown at the Georgia location....117

2.31. Family heritability estimates and standard errors for seedling characteristics for the combined location analysis....118

2.32. Single tree heritability estimates and standard errors for seedling characteristics for the combined location analysis....119

2.33. General combining ability estimates of families grown in Tennessee by replication....120

TABLE PAGE

2.34. General combining ability estimates of families grown in Tennessee across replications....121

2.35. General combining ability estimates of families grown in Georgia by replication....122

2.36. General combining ability estimates of families grown In Georgia across replications....123

2.37. General combining ability estimates of families for first-order lateral roots by location and replication within location....124

2.38. General combining ability estimates of families for root collar diameter by location and replication within location....125

2.39. General combining ability estimates of families for height by location and replication within location....126

2.40. General combining ability estimates of families for flush by location and replication within location....127

2.41. General combining ability estimates of families by location and replication for VIGOR by location and replication within location....128

2.42. General combing ability estimates of families across locations and replications....129

PART 3: Polyembryony occurrence and variation between genetic families in northern red oak (*Quercus rubra* L).

3.1. Genetic family, parent tree number, parent origin, seedlot type, and number of acorns used in the germination and dissection analysis for polyembryony....148

3.2. Genetic family, seedlot type, number of acorns and resulting number of polyembryonic acorns from the germination test....149

3.3. Mean number of seedlings and standard deviation for genetic families that produce multiple seedlings in the germination test....151

TABLE PAGE

3.4. Pooled data from families 850-2-23 and 856-6-19 for the number of embryos per size class from the germination test....152

3.5. Number of embryos per acorn as detected by acorn dissection....153

3.6. Mean number of embryos and standard deviation for genetic families which produce multiple embryos, as detected by acorn dissections....154

3.7. Pooled data from families 850-2-23 and 856-6-19 for the number of seedlings per size class, as detected by acorn dissections....155

3.8. Origin of TVA parent trees that produced more seedlings than acorns planted....156

PART 4: Relationship between acorn moisture content and time of collection after natural seed fall in northern red oak (*Quercus rubra* L).

4.1. Seed sources from the Watuaga northern red oak seed orchard used for the acorn quality study....171

4.2. Pearson correlation coefficients among moisture content and study variables for the 1994 study....172

4.3. Pearson correlation coefficients among moisture content and study variables for the 1995 study....172

4.4. Pearson correlation coefficients for moisture content among study variables by year and treatment....173

4.5. Pearson correlation coefficients among moisture content and study variables across years....174

4.6. 1994 Pearson correlation coefficients for interval change in moisture content among study variables across years....174

4.7. 1995 Pearson correlation coefficients for interval change in moisture content among study variables across years....175

TABLE PAGE

4.8. Pearson correlation coefficients for interval change in moisture content among study variables by year and treatment.....176

4.9. Change in moisture content correlations across years for study variables.....177

LIST OF FIGURES

FIGURE PAGE

PART 4: Relationship between acorn moisture content and time of collection after natural seed fall in northern red oak (*Quercus rubra* L).

4.1. 1994 replication 1 moisture content by day and treatment....178

4.2. 1994 replication 2 moisture content by day and treatment....179

4.3. 1995 replication 1 moisture content by day and treatment....180

4.4. 1995 replication 2 moisture content by day and treatment....181

4.5. 1994 average moisture content in percent and temperature data in degrees Fahrenheit....182

4.6. 1995 average moisture content in percent and temperature data in degrees Fahrenheit....183

PART 1:

GENERAL INTRODUCTION

1. INTRODUCTION

Upland oaks (*Quercus* sp.) are an important component of the eastern hardwood forests by providing a valuable timber resource and the periodic production of acorns for wildlife. Commercial species are used for lumber, veneer, furniture, flooring, cabinets, and many other products. Since the demise of the American chestnut (*Castanea dentata* (Marsh) Borkh.) from chestnut blight (*Cryphonectria parasitia* (Murr.) Barr.), oaks have become increasingly important to the forest products industry and for wildlife as a source of hard mast.

Across the eastern United States, problems in maintaining a desired level and composition of oak following harvest exist on the high quality upland sites (site index 70 or greater). Upland oak species such as northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.), and chestnut oak (*Q. primus* L.) often are unable to regenerate successfully or compete with more tolerant or faster growing species (*cf.* Smith 1993). Natural or artificial regeneration of these upland oaks have proven to be very difficult (McGee and Loftis 1993). Due to regeneration failures, species composition of many stands is shifting to species other than oak. This species composition shift has the potential to impact the productivity and utility of the forest resource for aesthetic, timber, wildlife (mast production), or a combination of resource values.

The hardwood lumber industry has identified the need to successfully regenerate oak following harvest and also desires to incorporate genetically improved stock for improved

growth and quality (National Hardwood Lumber Association 1996). Artificial regeneration affords the opportunity to incorporate improved seedlings for both timber and wildlife. Improved seedlings also could have the potential to overcome regeneration problems following harvest and may offer the option to manage the type and amount of oak in the future stand (Pope 1993).

Prior to establishment of oak plantings, seedlings procured from a nursery should be geographically matched to the site. To meet future seedling demands, nurseries require an annual source of acorns. Currently, procurement of acorns for seedling production is often problematic. Nursery managers rely on collections from natural stands, trees located in urban settings and to a limited extent, oak seed orchards to meet production goals. Acorn production is often cyclic in nature and when local or regional mast failures occur, nursery managers are forced to procure seed from other states or regions. The resulting seedlings may or may not be adapted to local planting sites and survival and subsequent growth can be negatively impacted.

Acorns from oak seed orchards will match seed source to planting site based on performance data and will provide acorns that produce genetically improved seedlings in terms of growth and quality. Furthermore, oak seed orchards offer the ability to evaluate genetic variation in selected reproductive traits. For example, studies in oak seed orchards can further identify trees that have early acorn production, which is important for wildlife management.

2. OBJECTIVES

This thesis research was conducted to provide information on intraspecific variation of northern red oak seedling and acorn characteristics and development of management protocols for northern red oak seedling seed orchards. There are three main objectives:

(1) Determine the patterns of genetic variation of certain seedling traits in 1+0[1] seedlings of northern red oak and white oak open-pollinated families;

(2) Determine the occurrence and genetic variation of polyembryonic acorns within and among open-pollinated genetic families of northern red oak;

(3) Determine the relationship between acorn moisture content and the number of days following natural seed fall under simulated orchard conditions.

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[1] Classification system of nursery stock based on its age and treatment. The first number refers to the number of years plants were grown as seedlings, and the second the number of years grown as transplants.

3. LITERATURE REVIEW

Description of the genus:

The genus *Quercus* (family *Fagaceae*), contains the most species within North America. The genus contains both deciduous and evergreen trees and shrubs. In North America, there are approximately 58 native trees and about 10 native shrubs in the genus (Little 1979). Oaks found in North America are divided into two subgenera: *Leucobalanus* (white oaks) and *Erythrobalanus* the (red or black oaks).

The primary taxonomic differences between the two subgenera are: *Leucobalanus* - leaves without spinose teeth or bristle-tipped lobes, fruit maturing in one season, and no embryo dormancy; *Erythrobalanus* - leaves are mostly bristle-tipped lobes or if unlobed, margins, apices, or both are often with spines or bristles, fruit maturing in two seasons, and embryonic dormancy exhibited (Nixon 1993).

Range and silvical characteristics of northern red oak:

Northern red oak is an important species in the upland oak hardwood forests type of the eastern United States. It is a moderate to fast growing tree, grows to a relative large size, and is distributed over a large area in the eastern United States. Northern red oak is a major component of four Society of American Foresters forest cover types and is an associated

species in 24 cover types (Eyre 1980). The native range of northern red oak is from Nova Scotia in southeast Canada, west to the Great Plains and as far south as the Gulf Coast.

In the upland hardwood forests of southern Appalachia, northern red oak grows on a wide range of topographic positions and sites. The best growth is attained on lower mesic slopes with a northerly or easterly aspect containing a deep A soil horizon (Sander 1990). The species has been rated as intermediate to intolerant of shade, yet optimal growth rates are often attained in full sunlight (Sander 1957, Kormanik, P.P. 1997. USDA Forest Service Athens, GA. Personal Communication to M.A. Remaley).

Range and silvical characteristics of white oak:

White oak is the most important timber tree of the *Leucobalanus* group in North America. It is a relative slow growing tree, but capable of achieving a large size. The species is distributed across a large portion of the eastern United States ranging from southern Canada, west to the Great Plains, and as far south as the Gulf Coast. It is a major component of three forest cover types, and a minor component of 28 cover types (Eyre 1980).

Optimal growing conditions are found on the western slopes of the Appalachian Mountains (Rogers 1990). White oak has the ability to grow on a variety of soils, slopes and topographic positions. Seedlings have been found to be relatively drought resistant except under unusually dry conditions (Rogers 1990). For optimal growth and survival, white oak seedlings need full sunlight (Rogers 1990).

Silvicultural management of oak:

The silvicultural mangement of oaks for increased productivity and utilization is important to the hardwood lumber industry and to landowners (National Hardwood Lumber Association 1996). Abundant oak stands in the eastern hardwood forest are thought to have originated by a combination of: intense fires, cessation of repeated fires, natural regeneration underneath pine stands, repeated and intensive clear cutting, and the effect of chestnut blight (Lorimar 1993).

Many oak dominated stands paradoxically fail to adequately regenerate after harvest (Smith 1993). This problem has been apparent to foresters since the 1930's (Clark 1993). Regeneration failure has been attributed to: poor seed production, consumption of acorns by predators, damage of regeneration seedlings, adverse weather conditions, poor growth and development of seedlings, excessive shade and competition, and fire exclusion (*cf.* Lorimar 1993). The problem of oak regeneration can be separated into two areas: sites where biological and site conditions indicates regeneration is highly unlikely following harvest, and sites in which biological and site conditions where regeneration should, but does not occur (Smith 1993). Smith (1993) qualitatively rated the scope of the problem of regenerating by species and site. He concluded that the overall regeneration problem is more severe on high quality sites, i.e., site index 70 or greater, compared to lower quality sites.

Many studies have been conducted to develop guidelines to achieve successful regeneration of oak species (McGee and Loftis 1993). For example, recommendations have

been developed for upland oaks in the Central States (Sander and Graney 1993), the southern and central Appalachian region (Loftis 1993, Smith 1993), and the northeast New England States (Marquis and Twery 1993). All these recommendations are based upon advanced regeneration of oak being present on site. Advanced regeneration is defined as oak seedlings over 4.5 feet in height (Sander 1971). Currently all recommendations for regions specified above, prescribe that advanced regeneration needs to be present in adequate stocking levels for successful regeneration to occur following harvest. If advanced regeneration is not present, the only method advocated to increase advanced regeneration is the shelterwood method.

Shelterwood regeneration method:

The shelterwood system, in theory, will increase the growth and development of advanced oak regeneration (Loftis 1993). Basal area reductions are made in the stand to allow oak seedlings already present to grow to advanced regeneration size. This often is coupled with the control of the tolerant sub-canopy with the suppression of competitors. The final overstory cut is made only after adequate stocking of advanced regeneration is established. The primary advantages of this method are that advanced regeneration is developed on sites where it is deficient, and mast and browse production is prolonged (Clark and Watt 1971).

For high quality Appalachian oak sites, Loftis (1990) showed that mature stands can

be manipulated to increase the amount of advanced regeneration, thereby increasing the probability of successful oak regeneration. The treatment does not establish new seedlings, but only stimulates the small oak seedlings already established on the site (Loftis 1990). Loftis (1990) recommended that if oak regeneration is absent, underplanting of oak seedlings may be feasible.

Although current recommendations indicate that the shelterwood method can be successfully applied, many studies have also shown the inadequacy of applying the method. Sander and Graney (1993) in the Missouri Ozarks, reported that an increase in oak regeneration occurred 10 years after a shelterwood treatment. However, when stocking values for advanced reproduction evaluation criteria were applied, the stocking levels were less than one-half the recommended levels. Sander and Graney (1993) also reported a similar shelterwood study in southern Indiana, where in all treatments failed to increase the number of oaks to advanced regeneration size. The reasons cited were the lack of acorn production for the first 3 years following treatment, extremely rapid growth of competing understory species, and nine years after treatment, a major windstorm caused all study plots to be destroyed.

Johnson and Jacobs (1981) used two variations of the shelterwood system in southwestern Wisconsin and found that neither approach attained the minimum stocking levels to regenerate the stand after 27 years. In one shelterwood that received a light first cut (basal area reduction from 123 to 103 sq. ft.), most seedlings were less than 1 foot tall after ten years. The area was subjected to a second cut (basal area reduction to 75 sq. ft.) and

a third cut (basal area reduction to 60 sq. ft.) with overstory removal occurring six years later. Five years after the final overstory cut, inventory results found that the average largest red oak in each plot was 8.8 feet tall. The average largest competitor, however, averaged 10.3 feet tall. Minimum stocking levels required for successfully regenerating the stand were never attained.

Kuenzel and McGuire (1942) investigated the degree of cutting on the survival and growth of chestnut oak (*Quercus primus* L.) seedings in southern Indiana and found similar results. They concluded that an overstory of chestnut oak is necessary for seedling establishment, but the seedlings grew very slowly and do not develop beyond the seedling stage. After a fifty percent reduction in the basal area, seedlings grew from an average of 0.3 feet to 0.8 feet in ten years.

McGee (1981) studied the release of overtopped pole sized white oaks on lower quality sites (60 to 70; base age 50) in the Cumberland Plateau region of Tennessee. McGee found that these overtopped white oaks of advanced age and size were unable to respond to release. Fifteen year observations of this study revealed that the majority of trees had not responded to release (Clatterbuck 1993).

In northern Arkansas, Graney (1988) initiated a study of overstory thinning and understory control in an upland hardwood forest. Five year results showed that the small oak regeneration (<1.1 feet) grew relatively slowly (average growth 0.1 feet per year), and the larger oaks grew somewhat faster (average growth 0.2 to 0.3 feet per year). While the study did have a severe drought impact, ten year growth projection showed that many oaks would

be taller than 5 feet. However, many of the competing understory trees (4,000 stems per acre) were already taller than 5 feet by the fifth year.

McGee and Loftis (1993) summarized the best available technology on oak regeneration and concluded that if a stand or site has inadequate oak regeneration (advanced regeneration), different harvest/management options are available. Either postpone harvest until adequate regeneration is favorable, install a shelterwood treatment to enhance the size of existing oaks, or plant seeds or seedlings to increase oak numbers.

McGee and Loftis (1993) stated that while the opportunity to successfully regenerate by planting or direct seeding is good, certain requirements need to be addressed for an area or species. These requirements include: matching species to site, adequate site preparation, using seedlings that meet known physical and physiological requirements, provide adequate competition control, anticipate slow early growth, and consider use of fertilizers or other soil amendments. Even with careful attention to these recommendations, successful regeneration still remains uncertain, artificial regeneration may offer the best solution to oak regeneration problems (McGee and Loftis 1993).

Artificial oak regeneration:

Nursery-grown 1+0, 1+1, and 2+0 bareroot and containerized seedlings are widely available to foresters and land owners for planting. In 1994, southern nursery production of oak species was approximately 54 million seedlings (Moulton 1996 U.S.D.A. Forest Service

Washington, D.C., Personal Communication to M.A. Remaley). The reason for the high demand for oak seedlings is the continued failures of natural regeneration, reforestation, and to increase species diversity (Pope 1993). In addition to cultural preparation of the planting site, two factors are important in planting oak: (1) the physical quality of nursery stock based on stem form, buds, roots, and seed source, and (2) the physiological quality of nursery stock having the potential for rapid root and shoot growth (Pope 1993).

Artificial regeneration of oaks has never been a widely successful regeneration option (Russell 1971, Pope 1993). In stark contrast to nursery demand and current production levels, research studies have found that planting oak seedlings is not reliable (Wendel 1979, Farmer 1981). Planted oak seedlings of standard size and quality usually have good early survival, but resulting early growth is seldom more than a few inches per year (Olson and Hopper 1968, Russell 1971, Farmer 1981, Tworkoski *et. al.* 1986). Planting small seedlings with low vigor often results in suppression by more competitive species (Russell 1971).

To compensate for poor seedling performance, many studies have applied cultural remedies to enhance the competitive ability of planted oaks (Larson 1975, Johnson 1976, Wendel 1979, Farmer 1981, Johnson 1984, Johnson *et al.* 1986, Tworkoski *et. al.* 1986, Johnson 1988, Johnson 1992, Miller 1993, Teclaw and Isebrands 1993, Walters 1993). These include the suppression of competing regeneration through mechanical or chemical means, underplanting under shelterwoods, interplanting, nursery manipulation (root pruning and top clipping), the use of tree shelters, and manipulating after nursery cultivation through root pruning and/or top clipping.

Phenotypical graded nursery stock for quality:

Few studies have used graded seedlings for planting. Olson and Hooper (1968) evaluated a 1964 planting of graded nursery seedlings. The authors graded seedlings based upon root collar diameter and used local seed sources. Second year results found that the highest grade seedlings grew better than the lower grades (Olson and Hopper 1968). Five year results indicated that competition control had to be done annually, and the overall mortality rate indicates that the seedlings never became fully established. Eleven year results reported by Loftis (1979), found a survival of 43 percent, and poor height growth (less than 1 foot per year). Loftis (1979) concluded that the effort to establish the plantation was an unqualified failure, despite the intensive competition control.

Research into first-order lateral roots may lead to a new criteria for grading of nursery seedlings for reforestation (Kormanik and Ruehle 1986). The grading system is partially based on the number of first-order lateral roots, which are lateral roots arising in normal morphogenetic sequence from a primary (tap) root (Sutton and Tinus 1983). Roots 1 mm in diameter at the proximal end and occur within 25 to 30 cm of the root collar are identified and counted as first-order lateral roots (Kormanik, P.P. 1997. USDA Forest Service Athens, GA. Personal Communication to M.A. Remaley). First- order lateral roots are important because the roots support other lateral roots in sequence up to 7th order which in turn support feeder or absorption roots (Sutton and Tinus 1983, Kormanik, P.P. 1997. USDA Forest Service Athens, GA. Personal Communication to M.A. Remaley).

A standard nursery fertility protocol has been developed which stratifies seedlings into identifiable grades and thereby enables the identification of superior individuals (Kormanik *et al.* 1989, Kormanik *et al.* 1993b, Kormanik *et al.* 1993c). In addition to first-order lateral roots, seedlings are selected for height, root collar diameter, and overall form of the tap root.

Results from this research has shown that seedlings with high numbers of first-order lateral roots compete better and have higher growth rates compared to seedlings with low numbers of first-order lateral roots (Kormanik 1986, Teclaw and Isebrands 1993). Mother tree evaluation of first-order lateral roots has indicated that first-order lateral roots is a highly heritable trait (Kormanik *et al.* 1990, Kormanik *et al.* 1993a), although the heritability estimates were only calculated for a single location. When fully implemented, the nursery fertility protocols coupled with a seedling grading system, based in part on first-order lateral root number, may enable the establishment of oak seedlings on sites where natural regeneration has failed or increase the oak component on sites with poor stocking levels.

Reproductive biology of oak:

Oaks species flower in the spring of the year usually shortly before leaves appear. Time of flowering varies by latitude and species, yet occurs between April and late May. Flowering is monecious, and following pollination and fertilization, acorns fully develop and mature in the fall. Cecich (1993) published a comprehensive literature review on the floral biology of North American oaks.

Pistillate flower formation:

Oak pistillate flowers are initiated when the meristemetic tissue of the bud is stimulated by an unknown process to direct axillary primordia in some of the leaves to become an inflorescence stalk. The inflorescence primordia remain relatively naked with only one or two bracts and are somewhat larger than the vegetative bud. In late March, the axis begins to elongate and several additional bracts are formed in a spiral. Following further growth, three outer and then three inner perianth primordia are initiated. Three gynoecial (carpel) primordia appear on the apex opposite the three outer perianth primordia and grow together laterally to form stigmas.

As stigma growth continues, the area beneath the stigmas becomes the ovary wall. As the young ovary closes, the base of the gynoecial primordia initiates the septa. Three septa are formed and become appraised at their upper, inner margins. Two placentae form initially along the base and on each side of the septa. In each locule, two placentae are found, one from each septum. The ovule is a structure that bears the megaspore mother cell. Following meiosis, one surviving haploid cell becomes a functional megaspore. By a series of mitotic divisions, the megaspore forms the megagametophyte or embryo sac at the tip of the nucellus. The nucellus is partly covered forming a micropyle, where the pollen tube approaches the embryo sac.

Staminate flower formation:

Differentiation of the staminate inflorescence occurs from late May to early June in the year prior to pollen dispersal. The inflorescence is found inserted in the axil of a bud scale, in contrast to that of the pistillate found in a leaf scale. On the flank of the floral apex, the perianth primordia develops, fusing into a single perianth. The stamen primordia arise on the apex opposite the perianth members in mid to late July. Through late summer and fall, the stamen primordia grow into immature anthers and filaments.

Anther development occurs from early March to late April. The parenchymatous mass differentiates into the sporogenous mass and parietal layers. The number of sporogenous cells increases mitotically to become microspore mother cells, then microspores and finally pollen grains. The inflorescence, bearing numerous staminate flowers, elongate and emerge from the bud scales in catkins just prior to full leaf out expansion.

Following dehiscence of the pollen and pollination of the pistillate flower, pollen tube growth and behavior on the stigmatic surface is affected by environment and genetic factors specific to each *Quercus* subgenus.

Flower fertilization:

Following full development of the embryo sac, fertilization of the egg takes place via the germinating pollen. Following fertilization, the first division of the zygote occurs. The

endosperm becomes cellular, and the embryo begins to differentiate. At maturity, acorns have a small embryo axis surrounded by a well-developed cotyledon and a continuous layer of epidermis. The pericarp (outer shell), has three distinct layers: a sclerfied exocarp, a striated mesocarp, and a thin coriacous endocarp.

Polyembryony:

Quercus is taxonomical classified as a 1-seeded nut. The staminate flower ovary is 3-celled, 6-ovuled, in which 2 of the cells and 5 of the ovules abort (Wood 1866, Mogensen 1975). It is hypothesized that five of six ovules will abort by an unknown chemical signal between developing ovules ensuring a single embryo per acorn (Cecich, R. 1997 U.S.D.A. Forest Service Columbia, MO. Personal Communication to M.A. Remaley). However, acorns with more than one embryo have been reported. In North American oaks, the occurrence of acorns producing more than one seedling per acorn has been reported in cherrybark oak (*Q. falcata* var. *padodifolia* Ell.), shumard oak (*Q. shumardii* Buckl.), northern red oak, black oak, pin oak (*Q. palustris*), bur oak (*Q. macrocarpa* Michx.), chestnut oak (*Q. prinus*), and white oak (Coker 1904, Smith 1914, Harvey 1917, Hosner 1959, Garrison and Augspurger 1983).

Garrison and Augspurger (1983) evaluated the possible selection pressures that maintain multi-seeded acorns. Double-seeded acorns were suggested to have an advantage in having at least one seed escaping insect damage. However, the authors noted that

polyembryony is also a disadvantage as the resulting growth rate and biomass accumulation are reduced due to the smaller seed size

Garrison and Augspurger (1983) found the frequency of double-seeded acorns in *Q. macrocarpa* Michx. ranged from 0-20 percent among 17 individual trees. Stevens and Matthew (1989) studied *Q. costaricensis* Liebm. in Costa Rica and found that 42 percent of an acorn crop were multi-seeded acorns. The authors hypothesized that the production of multi-seeded acorns was not related to insect predation selection pressures, and is therefore selectively neutral. To date, the frequency of occurrence, the genetic inheritance of polyembryony in *Quercus,* and more specifically, variation within and among genetic families has not been determined.

Acorn maturation and collection:

Acorns increase in size and fresh weight from June through August and mature in the fall of the year (Bonner and Vozzo 1987). At maturity, the pericarp color changes from green to dark brown (Bonner 1976). Maturity indices have been developed for most species of oak, which aid collectors in the field (Bonner and Vozzo 1987). Acorns must be collected when fully mature, as they generally will not completely maturation if prematurely separated from the tree or cap (Bonner 1993). The best indices are: color of the pericarp, ease of separation of acorns from cups, cup scar color and cotyledon color (Bonner and Vozzo 1987). In red oaks, the pericarp should have lost the green color and be primarily dark brown, cups have

released the acorn from the tree or are removed easily and cleanly, the resulting cup scar is "bright" in color, and the cross-section of the acorn is white to light yellow (Bonner 1993).

Acorns are classified as a semi-recalcitrant seed and need to maintain a high moisture content for the cotyledons to maintain viability (Bonner 1993). Collected acorns should be protected against excessive desiccation, which will harm the embryo (Bonner and Vozzo 1987).

Acorns within a single tree mature at differing rates, but usually a large percentage of acorns will mature and fall in a relative short period of time. In general, acorns on the lower branches of the crown ripen before those in the upper crown (Bonner and Vozzo 1987) Acorns left of the ground prior to leaf fall are subject to heavy predation pressure and desiccation.

Various techniques have been devised to collect acorns from trees. Collectors usually separate the large debris and leaves from the acorns and then rake the acorns into piles. In areas of active timber harvesting, acorns are collected from tops of felled trees. Acorns collected in non-forest open areas, are often gathered from underneath trees with little effort. In seed orchards, nets or taurpins are placed under the tree crown, and acorns are gathered frequently from the nets by hand. Often a leaf blower is used to group the acorns into piles.

Following collection, acorns are usually immersed in water to remove trash (leaves, cups) and to separate floating acorns that have been heavily damaged by insects. The immersion will help maintain a high moisture content in the sound sinking acorns (Bonner and Vozzo 1987). In times of extremely dry conditions when acorns are collected from the

ground, many good acorns will initially float (Bonner and Vozzo 1987). Under such conditions, it is recommended that the acorns be kept in water for up to 24 hours to elevate the moisture content.

Acorn production:

Studies have been conducted into acorn production due to the importance of acorns for oak regeneration and wildlife (Cypert and Webster 1948, Burns *et al.* 1954, Christisen 1955, Beck and Olson 1968). Investigations have focused into the prediction of acorn crops, characteristics of acorn maturation as indicated by drop, relationships between tree or stand characteristics and acorn production, and the environmental effects on acorn production. The relationships among the patterns of acorn drop, weather, and seed sources has not been investigated.

Studies on acorn drop have identified the seasonal patterns of acorn drop. Generally, acorn drop will slowly increase to a peak in the fall then taper off (Burns *et al.* 1954, Christisen 1955). The peak period of acorn drop will vary from year to year (Cypert and Webster 1948), but will be between mid-September to mid-October (Beck and Olson 1968). A loss of undeveloped acorns through premature abscission occurs between early and late summer (Petrides *et al.* 1953, Sork and Bramble 1993). Acorn drop is virtually complete by mid-November, with occasional acorn drop until mid-December (Beck and Olson 1968). Unsound or parasitized developed acorns drop earlier than sound unparasitized acorns (Burns

et al. 1954, Christisen 1955, Beck and Olson 1968).

Environmental effects on acorn drop has been observed only in a few studies. High wind and heavy rains were found to temporarily increase acorn drop (Burns *et al.* 1954, Christensen 1955). The first killing frost in the fall also accelerates acorn drop (Burns *et al.* 1954, Christensen 1955).

Genetic variation of northern red oak:

Approximately 25 provenance tests of northern red oak have been established in North America (Kriebel 1993). Kriebel (1993) reviewed the results of these tests in which the primary objectives of these studies were to identify intraspecific variation of important commercial traits such as height, survival, and form from different families (Kriebel *et al.* 1976, Kriebel *et al.* 1988, MacKay 1993, Kriebel 1993). These studies have found variation in northern red oak related to geographic origin, stand and family origin, and in adaptive traits such a drought and cold hardiness. However, Kriebel (1993) noted that the information on variation in growth and adaptive traits in northern red oak was inadequately sampled for the species abundance and wide distribution. While Kriebel (1993) summarized the variation in growth rate and adaptive traits, a relative few studies have focused on genetic variation of performance of seed sources in nursery settings.

Studies related to nursery seedling production:

Genetic variation studies of seedling performance in nurseries has centered on the effects of red oak mother trees on nursery productivity and family performance (Kriebel 1965, Gall and Taft 1973, McGee 1973, Larson 1977, Kolb and Steiner 1989, Struve and McKeand 1994). Kriebel (1965) found a provenance effect on growth rate and within a limited range of collection, the female parent effect on growth was larger than the provenance effect. The study found a strong effect of geographical origin on seedling growth rate, and individual inheritance appeared to be the most important source of variation in juvenile growth rate. Struve and McKeand (1994) found significant family differences in height growth after one growing season in the nursery.

Studies related to acorn phenotype:

Changes in the species nomenclature for northern red oak has occurred since Linnaeus first described northern red oak from a species composite of red oaks and was first typified as the northern red oak by Du Roi (Little 1979). The changes in naming was caused by the natural variation in leaf and acorn shape. For a time, northern red oak was classified into two forms: *Q. borealis* Michx. f. and *Q. borealis maxima* (Marsh.) Ashe. based in part on acorn phenotype (Little 1979). Acorns from *Q. borealis* Michx. f. were considered to be oblong-ovoid, about 3/4" long; nut 1/3 enclosed in a bowl-like cup (*cf.* Harlow and Harrar

1941). Acorns from *Q. borealis maxima* (Marsh.) Ashe. being subglobose, about 1" long; nut enclosed only at the base by a flat, thick saucer-like cup (*cf.* Harlow and Harrar 1941). Even though some taxonomist rejected *Q. rubra* as a *nome ambiguum*, it was restored following Ferald (1950).

Variation of the acorn phenotype of *Quercus* has primarily focused on the relationship between acorn size and seedling performance. Variation in seedling performance of various tree species has been related to seed size and may have, in part, have a genetic basis (*cf.* Farmer 1997). The studies of variation of seed size in *Quercus* have been based on collections from naturally occurring trees, and not from genetic tests or seed orchards containing trees of the same age and at the same location.

Kriebel (1965) reported variation in the weight in the northern red oak collection from different provenances. Acorns from northern provenances were lighter in weight and of smaller size when compared to southern provenances. He reported that the effect of provenance on seed weight was greater than the effect of female parent.

Korstian (1927) determined the influence of acorn size upon germination, survival and early growth of northern red, black, white, and chestnut oak seedlings. He found that " an unmistakable advantage in total germination and survival in favor of the large acorn." He hypothesized that the increase in germination and survival was due to the greater food reserves in the larger acorns compared to the smaller ones.

Few studies have focused on variation in acorn shape of northern red oak. Kriebel (1965) reported variation of acorn shape related to different provenances. Acorns from the

northern provenances had the form of *Q. borealis* Michx. f. and other provenances were of the form *Q. borealis maxima* (Marsh.) Ashe.

Importance of seed source:

One tenant of artificial regeneration is that the establishment and productivity of a site depends upon the correct selection of species and seed source (*cf.* Zobel and Tallbert 1984). Tree improvement programs often began with the identification of good versus poor seed sources, as the largest, cheapest and fastest gains can often be made by the identification of the proper source. A problem associated with using a seed source not adapted to the locality can be good initial survival that is followed by an eventual reduction in growth and vigor and/or an increase in mortality.

Zobel and Tallbert (1984) advocated the use of local seed sources until tests have shown the suitability and advantage of using nonlocal seed sources. Once sufficient information is known, breeding or seed zones can be identified for seed collection. In species such as oak where conventional breeding is relatively unproductive, e.g., controlled pollinations in oak yield 1-2 seeds per cross, good gains can be made however if the proper race (e.g. attitudinal, climatic, physiological, physiographic, edaphic) is identified and developed through provenance and progeny test information (Zobel and Tallbert 1984).

Tennessee Valley Authority northern red oak seed source study:

In 1971, the Tennessee Valley Authority (TVA) began studies into developing genetic and geographical variation information on northern red oak seed sources. The primary objectives were to: (1) provide information about the patterns of genetic variation, particularly geographical variation, and (2) use the above information to develop seedling based seed orchards for reforestation (Farmer 1980).

Eleven progeny tests were established in 1973 throughout the Tennessee Valley region from the progeny of seed collected from 226 northern red oak seed trees. Twenty-two mother trees were graded phenotypic selections (Taft. 1966) and other mother trees were dominant or codominant trees of good or superior form (Taft, K. 1996. Retired Research Forester, Norris TN. Personnel Communication to M.A. Remaley.). The physiographic range of mother trees was between 81° to 88° latitude, 34° to 36° longitude and between 160 to 1500 meters in elevation.

Acorns from each seed source was equally divided and planted in two replicates at the TVA nursery located near Norris, TN. The seedlings were grown by genetic family for one year in the nursery under standard cultural practices at that time, at a seedbed density of approximately 100/m^2. The seedlings were then divided into eleven plantations according to an experimental design in the winter/spring 1973-1974.

Five year measurements were made of all plantations with the exception of three plantings with poor survival (Farmer 1980). Survival and height ranged from 34 to 86

percent and 0.4 meters to 1.8 meters in height. Significant differences were found among families. Variance estimates revealed that 2 to 20 percent of variance was related to family effects, depending on the plantation, and larger family effects were found in tests with better growth.

Conversion of the Watuaga progeny test to a seedling seed orchard:

Tree improvement research at TVA was suspended due to budgetary constraints in 1982. The TVA requested that the United States Department of Agriculture, Forest Service, Southern Region assume full responsibility for the plantation on the Watuaga Ranger District of the Cherokee National Forest. In 1983, Regional Geneticist James L. McConnell decided to convert the progeny test into a seedling seed orchard for production of acorns for reforestation needs.

The orchard is located near Elizabethton Tennessee, in the Dry Hill section of the Watuaga Ranger District on the former Greer and McKinney farms and consists of a broad ridge top with upper slopes of low lying intermountain ridges. The soil texture is a medium silty clay loam or clay loam that grades to clay at depths of .91 to 1.5 m. The depth to the underlying limestone bedrock ranges between 1.83 and 3.66 m. Slopes within the study range from 6 to 20 percent. Average annual precipitation for the area is 40 inches.

Prior to planting in 1973, the site was prepared first plowing, followed by discing. Planting was implemented by Forest Service personnel with a spacing of approximately 3 x

3 m. The plantation contained 220 genetic families planted in a randomized complete block with 8 replications using four tree plots. After planting, a pre-emergent herbicide, Simazinee, was applied around each seedling to reduce competing vegetation. The progeny test has been disced or mowed periodically since establishment for weed and competition control.

LaFarge and Lewis (1987) evaluated the progeny test prior to conversion into a research orchard that was intended for acorn production and reproductive biology research. Seven traits: height, diameter breast height, straightness, forking, diameter^2 x height, survival, and defoliation were analyzed. Due to the lack of flowering/fruiting information on northern red oak, only 21 families were rouged entirely from the orchard. All remaining families were thinned to include the tallest one or two trees (depending upon spacing and size). Selection differentials and genetic gains calculated at that time showed that positive gains could be obtained from both single tree selections and family selections.

The orchard has been the nexus of a concentrated research initiative studying the various aspects of reproductive biology and oak seed orchard management. With the replicated statistical design, the orchard can be used to evaluate genetic variation between families. Flower and acorn production has been studied in certain genetic families since 1985 (Schlarbaum *et. al.* 1993a, Schlarbaum *et. al.* 1993b). Periodic evaluation of male catkins, leaf flush, and acorn production related to genetic variation within and among genetic families has been conducted (Schlarbaum, S.E. 1996 Associate Professor, University of Tennessee Knoxville, TN. to M.A. Remaley.). The primary research objectives include: the development of management protocols for oak seed orchards, genetic studies of acorn and flower

production, insect diversity and impact assessments, and the production of acorns for reforestation and experimental needs. The importance of the orchard for these studies is that it provided genetic material in the form of acorns for the objectives of this thesis.

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PART 2:

Genetic variation and heritability of seedling characteristics in northern red oak (*Quercus rubra L.*) 1-0 seedlings.

1. ABSTRACT

In 1994, acorns from 12 genetic families of northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) were grown for a single year in a replicated study at two locations. Seedlings were grown in Athens, Georgia and Knoxville, Tennessee under nursery protocols developed by the U.S.D.A. Forest Service Institute of Tree/Root Biology. Five seedling characteristics were evaluated for the degree of genetic and genetic-environmental interaction. Additionally the heritability and general combining ability of these characteristics were determined. Early growing season water stress of seedlings grown at the Tennessee location resulted in the failure of the white oak seedlings to adequately develop and northern red oak seedlings attaining smaller size. Individual location analysis and the combined analyses indicated wide variation in family means for the seedling characteristics. Additionally families grown at the Tennessee location were more variable compared to the Georgia grown families. Family and individual tree heritability estimates for all characteristics varied from moderate to strong. Results indicates that sufficient variation is present among northern red oak families so that selection of families based on family means is possible. Families will need to be individually evaluated for their ability to produce adequate numbers of quality seedlings.

2. INTRODUCTION

Regeneration of oak (*Quercus* sp. L.) after harvest on good upland sites in eastern United States can be problematic (McGee and Loftis 1993). The reduction of the oak species component has been attributed to: poor seed production, poor growth and development of seedlings, excessive shade, competition, and fire exclusion (*cf.* Lorimar 1993). Studies on natural and artificial regeneration have been conducted to find solutions to the oak regeneration problem (McGee and Loftis 1993). In natural regeneration studies, research has focused on developing oak seedlings to advanced regeneration size (*sensu* Sander 1971)(>4.5 feet) in order to be competitive with other regeneration species (Sander 1971). For the upland hardwood forests in southeastern North America, the shelterwood method has been advocated to grow oak to advanced regeneration size (Loftis, 1990, Loftis 1993).

Artificial regeneration research has focused on planting seedlings that will compete with natural regeneration (Pope 1993, Russell 1971). Artificial regeneration on good upland sites (site index 70 or greater) is often considered to be unreliable due to the inability of planted seedlings to compete with natural regeneration (Russell 1971). To date, a satisfactory solution to the oak regeneration problem on these sites has not been found (McGee and Loftis 1993).

Studies on the frequency distribution of first-order lateral roots has shown a relationship between seedling growth under nursery conditions and competitive ability after field planting (Kormanik 1986, Teclaw and Isebrands 1993). Roots that occur within 25 to 30 cm of the root collar and are 1 mm in diameter at the proximal end are classified as first-

order lateral roots (Kormanik *et al.* 1993a). A standard nursery fertility and irrigation protocol has been developed that stratifies seedlings into identifiable grades and thereby enables the identification of superior individuals (Kormanik *et al.* 1989, Kormanik *et al.* 1993a, Kormanik *et al.*1993b).

The relationship between first-order lateral roots and seedling performance may be a new criteria for selection of superior genotypes within an open-pollinated family. Seedlings with higher numbers of first-order lateral roots have been found to perform better than those with lower numbers within an open-pollinated families, both in the nursery and under field conditions (Kormanik *et al.* 1989, Teclaw and Isebrands 1993). Heritability estimates for first-order lateral roots for oak and other species has been found to be high (Kormanik, P.P. 1997. U.S.D.A. Forest Service, Athens, Georgia Personnel Communication to M.A. Remaley). These estimates have been based on studies at a single location, so the estimate of genotype-environmental interaction was not possible. The following study was conducted to determine genetic variation and genetic-environmental interaction in 1-0 seedling characteristics from twelve open pollinated genetic families of northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) planted at two locations.

3. MATERIALS AND METHODS

In fall 1993, acorns were collected from 12 open-pollinated white oak and 12 open-pollinated northern red oak mother trees. The white oak mother trees were located at the USDA Forest Service, Beech Creek Seed Orchard on the Tusquitee Ranger District of the Nantahala National Forest in North Carolina. The northern red oak mother trees were located at a seedling seed orchard located on the Watauga Ranger District of the Cherokee National Forest in Tennessee. Following collection, acorns were subjected to a floatation test for quality (Olson 1974), with the floating acorns discarded, and the sinking acorns retained for study. The acorns were kept separate by individual tree, and the weight of 100 acorns was obtained (Table 2.1)[1]. Following weighing, 520 equally sized acorns were counted from each of the 24 trees. One half of the acorns from each family was sent to the USDA Forest Service, Institute for Tree Root Biology, Athens, Georgia to establish a duplicate test plot.

The acorns were sown in late fall 1994 at The University of Tennessee's Plant Sciences Farm, located south of Knoxville, Tennessee. For the experiment, four above-ground concrete block nursery beds were constructed in the same manner as described by Kormanik *et al.* (1990). Each bed measured 1.2 m wide by 1 m in height by 18.3 m long running east to west. Each bed is filled with a (1:1:1) mixture of loamy topsoil, sand, and finely ground bark mulch. Each bed was divided equally into 12 compartments comprising 10 rows, 15 cm apart arranged perpendicular to the long axis of the bed. Thirteen planting locations 9.5 cm apart were marked in each row to achieve a seed bed density of 62 m^2.

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[1] All Tables are located in the Appendix.

For each species, 130 acorns of each family was randomly assigned and planted into one of the 12 compartments in each of the two beds (replicates). Prior to planting, each bed was fumigated and soil fertility levels were tested and then adjusted to comparable levels (Table 2.2) (Kormanik *et al.* 1993). One acorn was planted in each planting location approximately 1 cm deep. After planting, all beds were lightly mulched to a depth of approximately 1 inch with fumigated pine straw and covered with screens to protect from predation.

A standardized nursery bed culture for fertilizer and irrigation was prescribed for the 1995 growing season (Kormanik *et al.* 1993a). Soil irrometers were used to estimate available soil moisture within each nursery bed. Two irrometers, a 15 cm and 30 cm irrometer were placed in each bed to determine available soil moisture. When the irrometer gauges reached 50 centibar's of available soil moisture, the bed was irrigated to increase the available soil moisture. Beds were watered as needed throughout the growing season.

Each nursery bed received equal fertilization treatment. Table 2.3 contains the fertilizer amounts and dates for each application. Granular fertilization was applied by hand, with the specified amount of fertilizer spread uniformly over each individual bed. Liquid fertilizer treatment consisted of thoroughly mixing the specific amount of fertilizer with water and evenly applying it to seedlings. Throughout the growing seasons, defoliating insects were controlled as needed by Liquid Seven™ applied to the seedling foliage of each bed.

The 1-0 seedlings were lifted in January 1996 following the 1995 growing season. Prior to lifting, outside border row seedlings and seedlings from polyembryonic acorns, i.e., seedlings with multiple sprouts, were identified. During lifting the roots of seedlings were

vertically cut between rows and undercut 30 cm deep with a shovel. The seedlings from each family and replication were labeled, bundled and placed into cold storage. Seedlings from each family and replicate were then measured for total height (in centimeters), root collar diameter (in millimeters) at 2.5 cm above the root collar, number of flushes from initial linear stem elongation (flush), and number of first-order lateral roots ($\geq$ 1.0 mm at proximal end) within 30 centimeters of the root collar. Border row and multiple seedlings were not included in the evaluation of seedling traits. Family 850-2-23 was deleted from the analysis because of the preponderance of polyembryonic acorns that produced multiple seedlings per acorn.

To evaluate seedling quality through a combination of multiple seedlings characteristics, a new variable VIGOR was calculated by the following formula: VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)]. This formula was derived from approximating seedling volume (root collar diameter^2 x height) then multiplied by the number of first-order lateral roots. Each individual VIGOR value was log transformed to normalize the distribution because of the extreme range in values between the highest and lowest value. This variable expresses large seedlings with many first-order lateral roots as high values and small seedlings with few first-order lateral roots with a corresponding low value.

4. STATISTICAL ANALYSES

Mixed model analysis of variance was used to evaluate family, replication and location differences pertaining to the number of first-order lateral roots, height, root collar diameter, flush, and VIGOR (SAS 1996). Primarily, mixed model analysis of variance was used to calculate genetic variance components for calculation of heritability estimates and the degree of genotype-environmental interaction.

Three separate analysis were conducted in order to identify within location and across location differences among families. Two analysis were conducted specifically on each location and the third analyses combined the Tennessee and Georgia[2] data to evaluate differences in family performance between the two locations and the degree of genotype x environmental interaction. The relative position of each compartment (planting location of families within a bed) within replication was tested for differences.

Predicted genetic values were generated through best linear unbiased prediction (BLUP) procedures for all characteristics (Henderson 1984, White and Hodge 1989). Family and replication were considered random effects, and planting compartment within replication was considered a fixed effect. In each analysis, BLUP family means were calculated for each of the eleven families in each replication and for combined replications. Since the BLUP means are expressed as deviations around zero, the grand mean was added to each family so that all values are expressed as positive numbers and on an appropriate scale. In the BLUP

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[2] Data on file and provided by the USDA Forest Service, Institute for Tree Root Biology, Athens, Georgia.

statistical procedure, the general combining ability of each family is equal to the BLUP mean, but are reported here separately for clarity in reporting results. Individual tree and family heritability estimates and associated standard errors were calculated from the formulas given by Wright (1976)[3]. Pearson correlation coefficients were calculated to examine relationships between seedling characteristics.

In producing seedlings under Kormanik *et al.* (1989) specified nursery protocols, a wide variation in seedling sizes with a somewhat skewed distribution has been found within a single families (Kormanik *et al.* 1989). Using only means to identify superior families would not take into account the degree of variation and skewness in a family's seedlings. The proportion of seedlings (in percent) within a family in each replication and for combined replications was thereby examined by counting the number of seedlings above or below the BLUP family grand means.

Seedlings were then examined within families based on a simulated field grading criteria. Seedlings within each family which had six or more first-order lateral roots and a minimum seedling height (1 meter) were identified. The minimum number of six first-order lateral roots was chosen, since it was the mean number of first-order lateral roots of all seedlings grown at both locations. The minimum height of one meter was chosen based on observations that very tall seedlings are highly competitive in early successional stands. This procedure examined the location, family and the genotype-environmental interaction differences in the number of seedlings with higher than average number of first-order lateral roots and height.

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[3] Formulas located in the Appendix.

5. RESULTS

Early growing season results:

Tennessee location:

In early May, all seedlings were observed to have poor growth following germination. It was identified that the soil irrometers were inadvertently miscalibrated giving an incorrect high soil moisture levels that resulted in a water deficiency. Following the recalibration of the soil irrometers, the beds were then adequately irrigated throughout the remainder of the growing season.

The northern red oak seedlings responded to the increase in water levels and resumed growth. In contrast, the white oaks failed to resume growth following the increase in soil moisture. It was observed that the deficiency in soil water caused the majority of the white oak seedlings to set a terminal bud that failed to grow. Therefore, the white oak seedlings never attained sufficient size to warrant analysis.

Analyses of Tennessee seedlings:

General differences:

The northern red oak families grew to a sufficient size for grading, even though they were exposed to water deficiency in the early part of the growing season. A wide variation within and among families and between replications was found for the five seedling characteristics measured. Table 2.4 presents arithmetic mean, standard deviations, minimum and maximum values for first-order lateral roots, flush, root collar diameter, height, and VIGOR. Seedlings ranged from having 0 to 32 first-order lateral roots. The number of flushes from initial linear stem elongation within and between families, ranged from zero flushes up to five flushes. Seedlings varied from 7 centimeters to over 1 meter (161 centimeters) in height. Root collar diameters ranged from 2.20 millimeters to 14.60 millimeters. The calculated VIGOR values ranged from 0 to 4.16. Overall, the average seedling had 6.28 first-order lateral roots, 2.35 flushes, 50.86 cm in height, 6.96 mm root collar diameter and a VIGOR value of 1.00.

Replication differences:

In general, the seedlings in replication 1 were smaller than in replication 2. An analysis of the relative position of each compartment (planting location of families within a bed) within each replication found significant differences only in replication 1 for all

characteristics ($p \leq 0.0578$). Although seedlings in replication 2 on the east side of the bed appeared to grow larger than those on the west side (Table 2.5), there was no statistical significant differences

Correlation coefficients:

Correlation coefficients among the characteristics varied from moderate to strong (.48 - .92) for each individual replication (Table 2.6). When replications were combined, correlations among characteristics again varied from moderate to strong (.50-.93) (Table 2.6).

Variation in family means:

The BLUP means for the five characteristics differed among families within each replication (Table 2.7). In general, BLUP means were lower in replication 1 compared to replication 2.

The combined replication BLUP family means differed among the eleven families for the five characteristics (Table 2.8). The difference between the highest and lowest family value in first-order lateral roots, flush, height, root collar diameter and VIGOR was 2.40, 0.92, 22.17, 0.54, and 0.46, respectively. Overall, family 2459-4-14 had the highest VIGOR value (VIGOR = 1.40) and family 882-4-4 contained the lowest VIGOR value (VIGOR = 0.09).

In each replication, BLUP family means differed when compared to arithmetic means

for all the characteristics (Table 2.4 vs. Table 2.7). A comparison between the combined replication BLUP means (Table 2.8) to the BLUP means from individual replications (Table 2.7) found that individual replication BLUP means of some families can be higher or lower than combined replication BLUP means (Table 2.8). For example, the BLUP means of family 2459-4-14 for first-order lateral roots were 7.73 and 6.92 for replications 1 and 2, respectively, while the combined replication BLUP mean was 8.29 (Tables 2.7 and 2.8). For family 630-2-19, the first-order lateral roots' BLUP mean for replication 1 and 2 was 6.70 and 6.21, respectively, while the combined replication BLUP mean was 5.89 (Tables 2.7 and 2.8).

Seedling distribution analysis:

The distribution of seedlings in each family was examined by using the combined replication BLUP family mean number of first-order lateral roots. The number of seedlings above or below this mean was counted and was found to differ among families within replications (Table 2.9). The BLUP family means for the combined replications ranged from 5 to 8 (rounded BLUP mean) with family 882-4-4 having the lowest and family 2459-4-14 with the highest BLUP means for first-order lateral root number. Some families consistently had the same distribution of seedlings regardless of replication (families 526-3-3, 735-2-6, 565-2-29, 200-6-14-2, and 2459-4-14). In other families, the distribution of seedlings around the first-order lateral root mean fluctuated widely between replications (families 882-4-4, 902-4-2, 915-1-14).

The number of seedlings also differed among families when the combined family and replication BLUP mean of seven first-order lateral roots was used (Table 2.10). Family 882-4-4 was the lowest family overall, having only 6 and 37 percent of seedlings in replication 1 and 2 respectively, with seven or more first-order lateral roots. In contrast, three families (100-4-27, 540-2-10, 2459-4-14) produced approximately 50 percent or more seedlings above the BLUP mean of seven first-order lateral roots.

Analyses of Georgia seedlings:

General differences:

White oak seedlings from the Georgia location were not analyzed because the failure at the Tennessee location. prevented a comparison. In general, the northern red oak seedlings grew extremely well at the Georgia location. The northern red oak families grown in Georgia were relatively uniform in seedling performance between replications (Table 2.11). There was a wide variation of seedling characteristics within and among families as shown by the arithmetic calculations in Table 2.11. Overall, the seedlings had from 0 to 26 first-order lateral roots and flushed at least a single time, with some seedlings flushing up to nine times from initial linear stem elongation. Height varied widely, with some seedlings being only 22 centimeters in height, while the tallest individuals were over 2 meters tall (262 centimeters). Root collar diameters ranged from 2.90 millimeters to 19.20 millimeters. The calculated

VIGOR values ranged from 0 to 4.98. The overall average seedling had 4.86 first-order lateral roots, 3.86 flush, 126.71 cm in height, 9.16 mm root collar diameter, and a VIGOR value of 1.63.

Replication differences:

In general the replications at the Georgia location were very homogenous. However families did vary slightly between replications. The analysis of the relative position of each compartments (planting location of families within a bed) was only significant for height in replication 2 ($p = 0.0078$).

Correlation coefficients:

Pearson correlation coefficients were calculated between each of the seedling characteristic (Table 2.12). All characteristics were moderate to strongly correlated with each other (0.52 - 0.94) . Correlations among characteristics in either replication or combined replications were similar, with VIGOR generally having the highest correlations between the other characteristics.

Variation in family means:

In each replication, BLUP family means differed when compared to arithmetic means for all the characteristics (Table 2.11 and Table 2.13). BLUP family means for individual replications differed slightly among families between the two replications (Table 2.13).

The combined replication BLUP family means for the five characteristics were relatively uniform (Table 2.14). The difference in first-order lateral root number, flush, height, root collar diameter and VIGOR between the highest mean of a family and lowest was 1.72, 0.35, 17.66, 1.98, and 0.51, respectively. On a BLUP mean basis, family 2459-4-14 contained the most vigorous seedlings (VIGOR=1.86) and family 902-4-2 contained the lowest (VIGOR=1.35).

Comparing the combined replication BLUP family means (Table 2.13) with BLUP family means from individual replications (Table 2.14), shows that individual replication BLUP means of some families are higher or lower than the combined replication BLUP means. Overall, the combined replication BLUP family means for each characteristic were not consistently higher or lower than the individual replication means.

Seedling distribution analysis:

Using the combined replication BLUP mean number of first-order lateral roots for each family, the number of seedlings above or below this mean differed among families within replications (Table 2.15). The combined replication BLUP family means ranged from four

to six first-order lateral roots. A majority of families were relatively consistent between replications in the distribution of seedlings above or below the average number of first-order lateral roots. Only two families (100-4-27 and 915-1-14), fluctuated by more than 10 percent in the number of seedlings between replication with the BLUP family mean or higher number of first-order lateral roots.

The seedling distribution among families differed when compared to the combined family and replication BLUP mean of five first-order lateral roots (Table 2.16). In each replication, the majority of families produced less than 50 percent of the seedlings with five or more first order lateral roots. The differences between the highest family and lowest family in the percent number of seedlings with five or more first-order lateral roots for replication 1 and 2 was 18 and 23 percent, respectively. Family 902-4-4 was the poorest family overall, having only 34 percent of seedlings in either replication, with five or more first-order lateral roots. In contrast, four families (540-2-10, 915-1-14, 200-6-41-2, and 2459-4-14) produced 50 percent or more seedlings with five or more first-order lateral roots.

Combined Location Analyses:

General differences:

Overall, the Georgia seedlings had larger values than the Tennessee seedlings in all characteristics, except for first-order lateral root number (Tables 2.4 and 2.11). In comparing the average number of first-order lateral roots, the Tennessee seedlings had approximately 1

more first-order lateral roots than Georgia seedlings. The correlation coefficients ranged from weak to strongly (0.34 - 0.92) correlated (Table 2.17) among the five characteristics. Overall, VIGOR had the highest correlations among characteristics and first-order lateral root number had the lowest correlations.

The combined family BLUP means differed among locations and replications within location (Table 2.18). The combined family BLUP means for the Georgia location were higher than the Tennessee location for all characteristics, except for first-order lateral root number. The BLUP mean height was the largest differences between the Georgia (117.61 cm) and Tennessee location (56.51 cm) location. In examining differences among individual replications, the Georgia replications were not consistently higher than the Tennessee replications. For example, Tennessee BLUP height mean for replication 2 was 97.48, compared to the BLUP height mean of 79.23 for Georgia's replication 1. For first-order lateral root number, the BLUP mean for Georgia's replication 2 (6.20) was higher than the Tennessee replication 1 BLUP mean (5.86).

Replication differences:

The BLUP family means differed for each of the eleven families in all four replications across the two locations (Table 2.19). Although the arithmetic means of the Georgia seedlings were mostly larger than the Tennessee seedlings (Tables 2.4 and 2.11), the combined analysis BLUP family means for some Tennessee seedling characteristics were higher than those in Georgia (Table 2.19).

Variation in family means:

The combined replication BLUP family means for each characteristic differed by location among the eleven families (Table 2.20). The overall BLUP family mean across all replications and locations differed among families (Table 2.21). Across characteristics, a high BLUP mean for a given characteristic did not necessarily indicate a high mean for the other characteristics. On a BLUP mean basis, family 2459-4-14 produced the most vigorous seedlings (VIGOR = 1.46) and family 882-4-4 had the lowest VIGOR mean (1.24).

Seedling distribution analysis:

Using the combined replication and location BLUP mean of six first-order lateral roots, the number of seedlings above or below this mean differed among families and replications within locations (Tables 2.22 and 2.23). For the individual Tennessee families, the percentage of seedlings with six or more first-order lateral roots ranged from 10 to 58 percent in replication 1, 38 to 65 in replication 2, and 38 to 62 percent when replications were combined (Table 2.22). Examination of the proportions within families, found that some families fluctuated widely between replications, while others were consistent in the proportion of seedlings regardless of replication. Overall, 882-4-4, 630-2-19 and 916-1-14 were relatively poor in the production of seedlings with six or more first-order lateral roots. Families 100-4-27, and 2459-4-14 produced a relative high number of seedlings above the overall mean.

The families at the Georgia location were relatively uniform in producing seedlings with six or more first-order lateral roots (Table 2.23). Only families 915-1-14 and 2459-4-14 in replication 2 produced 50 percent or more seedlings with six or more first-order lateral roots. Most families produced 40 percent or more seedlings with six or more first-order lateral roots regardless of replication. Across both replications, family 2459-4-14 produced the most seedlings with six or more first-order lateral roots, and family 902-4-2 the least number of seedlings with six or more first order lateral roots.

The variation in the location BLUP means between Tennessee (seven) and Georgia (five) for first-order lateral root number and the combined location (six) caused the distribution of seedlings within family by location to vary around the mean (Table 2.24). Across families, the relatively low Georgia location BLUP mean of five first-order lateral roots caused most families to have 50 percent of the total number of seedlings to have five or more first-order lateral roots. In contrast, the higher BLUP mean for the Tennessee location (seven first-order lateral roots) and the combined locations (six first-order lateral roots) each caused a lower percent of seedlings, i.e., < 50%, for the eleven families to be distributed above the BLUP mean.

The location and combined location BLUP means for first-order lateral root number differed at the Tennessee (7) and Georgia location (5) with the combined location (6). Since the BLUP mean number of first-order lateral roots varied from five to seven, the distribution of seedlings around the individual and combined location BLUP means (families combined) also differed (Table 2.25). Using the overall combined location data as an example, the BLUP mean increased from five (Georgia location) to seven (Tennessee location) and the

percentage of seedlings having first-order lateral root numbers equal to the BLUP mean or greater decreased from 50 percent to 37 percent.

Field grading criteria:

The number of seedlings considered to be competitive under field conditions differed among families and locations, when a grading criteria of six or more first-order lateral roots, and height of 1 meter or greater was used (Table 2.26). Tennessee only produced 144 seedlings out of 2087 (seven percent), with six or more first-order lateral roots and 1 meter or greater in height. Among families, family 540-2-10 produced the most seedlings (26) and families 526-3-3 and 882-4-4 the least (4 each). Comparably, Georgia produced a higher number of competitive seedlings with 740 seedlings out of 1929 (38 percent) based on the field grading criteria. Among families, family 915-1-14 produced the most seedlings (86%) and family 735-2-6 the least (49%).

Heritability estimates:

Tennessee location:

Single tree and family heritability estimates differed between characteristics at the Tennessee location. Family heritability estimates varied between 0.501 and 0.747 calculated

for all characteristics with high standard errors (0.700 to 0.957) (Table 2.27). Single tree heritability estimates for all characteristics were comparably lower (0.068 to 0.429) with relatively low standard errors (0.032 to 0.099) (Table 2.28).

Georgia location:

Family heritability estimates from the Georgia location found that, all characteristics are highly heritable (0.644 to 0.889) with high standard errors (0.812 to 1.046) (Table 2.29). Single tree estimates were low for all characteristics (0.077 to 0.197) with low standard errors (0.030 to 0.065) (Table 2.30).

Combined locations:

Family heritabilities based on the combined locations ranged from low to high (0.149 to 0.813) with a wide variation in standard errors (0.356 to 1.537) (Table 2.31). First-order lateral root number had the lowest heritability estimate ($h^2 = 0.149$, s.e. $\pm$ 0.356) compared to the other characteristics. Single tree heritability estimates were considerably lower compared to the family estimates (0.014 to 0.0209) with low standard errors (0.013 to 0.101) (Table 2.32). First-order lateral roots had the lowest heritability estimate ($h^2 = 0.014$, s.e. $\pm$ 0.013) and flush had the highest estimate ($h^2 = 0.209$, s.e. $\pm$ 0.101).

General combining ability:

Tennessee location:

The general combining ability of individual families differed between the two replications across characteristics (Table 2.33). Neither replication 1 or 2 had all families with either positive or negative general combining ability values. When the replications were combined (Table 2.34), the general combining ability estimates of most families were relatively consistent i.e., all negative or positive, in their values across characteristics compared to other familes which varied across characteristics.

Georgia location:

The general combining ability estimates for individual families within replication also varied between replications (Table 2.35). As with the Tennessee location, neither replication had relatively the same general combining ability values i.e., all negative or positive, for the eleven families. When the replications were combined (Table 2.36), some families were consistently (all positive or negative) in their values across characteristics (e.g. families 882-4-4 and 565-2-29) compared to others which varied across characteristics (e.g.. families 735-2-6 and 630-2-19).

Combined locations:

Using the combined location data, the general combining ability estimates for each characteristic by location and replication are given in Tables 2.37 - 2.41. Some general combining ability values for different characteristics were relative consistent for some families between locations and replications, while other general combing abilities varied. Overall, most families varied between replications and locations in the general combining ability for a given characteristic. In the combined general combining ability estimates across replications and locations, some families were consistent in the estimates, i.e., all negative or positive, while other families varied across the characteristics (Table 2.42).

6. DISCUSSION

Tennessee location:

White oak:

The miscalibration of the soil irrometers that caused the Tennessee nursery beds to be water deficient had a profound impact on the white oak study. The white oak acorns germinated adequately and set a terminal bud at approximately the same time the water deficiency occurred. Following increased soil moisture levels, the white oak seedlings generally remained dormant and did not resume growth for the remainder of the growing season. Studies on the effects of water stress have been shown to influence growth in many plant species (Levitt 1980). Water stress can cause decreased cell growth that reduces leaf elongation, decreased ion uptake which leads to nutrient deficiency and have indirect effects on photosynthesis and respiration through stomatal closure (Levitt 1980). The white oak seedlings were not observed to be nutrient deficient, however, the leaves on many seedlings were smaller than normal nursery grown seedlings.

The results of the water stress indicated that white oak requires a yet undefined level of soil moisture early in the growing season to continue growth throughout the entire season. The replication of white oak seedlings grown in Georgia, which did not have water deficiency, grew extremely well with some seedlings reaching greater than 1 meter in height. Although the miscalibration of the soil irrometers precluded genetic analyses of variation in seedling

characteristics, it did identify a critical period for water utilization within the early growing season. The growth of the Georgia grown seedlings infers that the maintenance of soil moisture at a minimum of 50 centibars is needed for adequate white oak seedling growth in nursery beds.

White oak is rated as intolerant to drought and has slow juvenile growth rate (Smith 1993). The occurrence of the interaction between water deficiency and early growing season development in white oak, identifies a critical factor for successful seedling-based regeneration of white oak. A sensitivity to low soil moisture levels in the early growing season could explain some of the past failures with natural and artificial regeneration of white oak. While the white oak seedlings in this study did not die, the lack of significant growth would have placed the seedlings at a competitive disadvantage in field conditions. Natural and artificial regenerations studies have shown that white oak seedlings which become overtopped by faster growing species become suppressed and fail to regenerate successfully (Smith 1993).

To date, research has not been conducted to determine the interaction of soil moisture levels and growth of white oak seedlings, or the response of different white oak genetic families to water deficiency. White oak is naturally found on a dichotomy of sites ranging from mesic to relatively xeric. Natural selection may have occurred in these different conditions, resulting in the presence of genetic variation along edaphic gradients in natural populations. Confirmation followed by characterization of this putative variability in the white oak populations would lead to the correct matching of seed sources to sites or identify families which can tolerate a range in edaphic conditions. If this variability is present in white

oak, mismatching ecotypes with sites, e.g., planting mesic ecotypes on xeric sites, may explain some of the many failures of white oak artificial regeneration.

The failure of white oak seedlings to resume growth following early growing season water stress, was not as pronounced in the northern red oak families. The seedlings from the two species were at the approximately same stage in development and under comparable fertility and irrigation treatments. In contrast to the white oak seedlings, the northern red oak seedlings responded and continued growth and development following increased soil moisture levels. This difference in drought tolerance between the two species is significant, as it further distinguishes the biology of each species and reemphasizes the importance on understanding a species' silvics and applying that understanding through forest management activities.

Individual location analyses:

General differences:

The northern red oak seedlings grew to sufficient size for grading at the Georgia location and the Tennessee location following the increase in soil moisture levels. Overall, the Georgia northern red oak seedlings grew extremely well in comparison to the Tennessee trees. For all seedling characteristics, the range of seedling sizes within a family are similar to those previously described by Kormanik *et al.* (1993). Even though the Tennessee location had smaller seedlings, the range of seedling sizes were similar to what is expected under the Kormanik nursery protocols.

In examining individual characteristics, variation between locations was found. For example, height was found to have a dramatic differences between locations, with some Georgia seedlings reaching well over 2 meter in height. In comparing first-order lateral root number means between each locations, it was found that the Tennessee location produced more first-order lateral roots than Georgia. This was contrary to expectations, as the poorer growth at Tennessee was expected to have resulted in the production of fewer first-order lateral roots. Bias between the two individuals identifying first-order lateral roots at each respective location is a possible reason more first-order lateral roots at the Tennessee location were identified. The identification bias only the affected mean value of first-order lateral root numbers and did not effect family rankings since they were similar at each location.

The miscalibration of the soil irrometers underscored the importance of keeping growing conditions near optimal under the Kormanik nursery protocols or seedling growth and performance will be impacted. Tennessee seedlings may have never equaled the Georgia in growth and development because of environmental differences such as the longer growing season in Georgia. However, the wide discrepancies in growth and development between seedlings at the two locations was of such magnitude that other factors, such as water deficiency, probably affected the Tennessee seedlings.

Replication differences:

At either location, variation in family performance among the seedling characteristics, did occur between replications. However, the Georgia grown families varied considerably

less than the Tennessee grown families. This uniformity of family performance between replications at the Georgia location reflects the homogeneity of the Georgia nursery beds. The raised beds have been in production for a number of years, and the soil fertility baseline is near optimal.

Variation in family performance for the Tennessee families was found between the two replications and could be due to several factors. Variation in the proportion of soil components between each replication could have occurred, since the bed soil was mixed in small batches. In addition, the commercially purchased hardwood mulch could have contained bark from black walnut (*Juglans nigra* L.) which could have caused an allopathic effect on seedling growth. As the soil was mixed in small batches, different proportions of black walnut bark could have caused seedling growth differences within a single bed and between beds. Soil fertility levels were closely monitored throughout the growing season and is not considered to have affected seedling performance (Kormanik, P.P. 1996. USDA Forest Service, Athens GA. Personnel Communication to M.A. Remaley).

The application of additional liquid fertilizer to compensate for the delayed growth, caused an unintended bias in the growth of the seedlings in replication 2. Although a compartment effect was not statistically significant in that replication, it was observed that families were larger on the east end of the bed when compared to the west end. Seedling height appeared to exhibited the greatest impact of the fertilizer bias. The test for significance of the compartment effect, however, may not be fully reliable since family effects were confounded with compartment. The unintended bias does identify how changes in fertility regimes can affect seedling performance. Although the liquid fertilizer was only applied a few

times, dramatic effects were found. In field planting of oak seedlings, minor changes in site productivity and between sites could also have similar effects and could contribute to the overall success or failure of plantings.

The Tennessee replication differences indicated that particular families, are sensitive to environmental change (genotype x environmental interaction), while other families are relatively insensitive. If this differential genotype x environmental interaction among families is also found in field tests, it could influence future selection of genetic families for seed orchards or refinement of present orchards. Development of seed orchards for specific environments would be possible using site specific families. Alternatively, orchards could be constructed with families relatively insensitive to environmental change, which would subsequently produce progeny that could be planted on a wide range of sites.

Correlation coefficients:

The correlation coefficients among the different characteristics were similar at both locations. In general, the moderate to strong positive correlations between all characteristics indicated that as one seedling characteristics increased in size or number, other characteristic correspondingly increased. This may be important for selecting for quality seedlings in nursery grading operations. For example, counting the number of first-order lateral roots would be very time consuming and cost prohibitive in nursery operations, where many thousands of seedlings must be processed daily. The correlation coefficients indicate that selecting seedlings with a minimum height or root collar diameter would indirectly select

seedlings with high numbers of first-order lateral roots. These relationships among seedling characteristics, therefore, would increase the feasibility of operationally selecting high quality seedlings.

Variation in family means:

The combined replication BLUP means at each location varied among the eleven families indicating that selection of superior families is possible based on family means. Although the variation at the Tennessee location was greater, selection of superior families also was possible at the Georgia location. Furthermore, the relatively large difference in BLUP means among families after a single growing season indicated that nursery-based screening of families is possible.

In traditional tree improvement activities, families are greenhouse or nursery propagated, field planted, and evaluated after a number of years. After appropriate evaluation, genetically superior families and/or trees are selected. While the genetic superiority in the nursery cannot be extrapolated to the field without further studies, the wide variation in family means in the nursery beds offers the opportunity for rapid identification of families that have a greater probability of competing in regeneration plantings. By removing inferior families in the nursery, costs associated with progeny testing can be reduced, as these families would have a higher probability of being overtopped in the field and suppressed. Progeny tests could be smaller in size, since fewer families would be planted. This would significantly reduce establishment and maintenance costs. Alternatively, progeny test size

would not necessarily be reduced if a larger number of families are planted with the anticipation of culling a portion of the inferior families. Therefore, the progeny tests would evaluate more families that have the potential for competing with other vegetation.

Distribution analysis:

The seedling distribution analysis for each location revealed that the proportion of quality seedlings, e.g., seedlings that have adequate numbers of first-order lateral roots, varies among families. Furthermore, the proportion of quality seedlings within a family was found to vary between replications and locations. The distribution analysis indicates that families cannot be selected based solely on family means. Past research has shown that the families are not normally distributed, i.e., a higher proportion of seedlings are below the mean than above the mean. Furthermore, some families in this study were found to exhibit a more non-symmetrical distribution than other families. This indicated that individual families should be screened for the proportion of quality seedlings.

The results of the distribution analysis indicated that a selection system for families will need to be based on a combination of BLUP family means and the proportion of quality seedlings a family can produce. For nursery managers who desire to produce many seedlings with certain characteristics, e.g., seedlings with six or more first-order lateral roots, families that produce a relatively low percentage of high quality seedlings will need to be identified and culled from the nursery supply. Correspondingly, acorns of families that produce a high proportion of quality seedlings with a minimum number of first-order lateral roots would be

sown in greater numbers.

These results emphasize the importance of oak seed orchards in suppling nurseries with quality seed. Currently most nurseries rely on seed collected from wild or urban trees, which is often bulked by species to meet nursery production demands. With this type of system, identification of seed sources that produce high or poor quality seedlings can be very difficult. In oak seed orchards, families can be screened for many attributes including the ability to produce high quality seedlings. Trees producing inferior progeny can be culled from the orchard. Once quality mother trees have been properly identified, nursery managers can determine how many seeds to plant from certain seed sources to meet anticipated seedling demands.

Combined analysis:

Comparisons between locations:

The combined location analysis results paralleled the results of the individual location analyses. As with the individual location analyses, the combined location BLUP means varied among families. Furthermore, the combined location analysis mirrored the individual location analyses in that a significant location effect (genotype x environmental interaction) was present causing families to vary in their relative performance. The results again indicated that adequate variation between BLUP family means is present making family selections possible irrespective of location effects.

Seedling distribution analysis:

The seedling distribution analysis of the number of seedlings with a specified number on first-order lateral roots identified important biological/operational factors in grading seedlings for quality. The combined location distribution analysis found that the proportion of seedlings within a family will vary. Examining families for the proportion of seedlings with six or more first-order lateral roots across locations revealed variation among families in producing high or low numbers of quality seedlings. As with the individual location analyses, the results indicate that each family will need to be evaluated for ability to produce a high proportion of quality seedlings under nursery conditions.

Since the individual location BLUP means in the combined seedling distribution analysis varied, the number of seedlings with the location mean or higher first-order lateral roots varied. For example, using either of the location means [Tennessee (seven), Georgia (five)] or the combined location mean (6) between 43 and 50 percent of the seedlings had the BLUP mean or higher number of first-order lateral roots. As discussed in the individual location analyses, bias may be partially responsible for the differences in the location means as well as differences in growing conditions.

For researchers and nursery managers, bias in counting the number of first-order lateral roots or environmental effects on seedling growth and development needs to be recognized. Once a nursery based grading system is developed, choosing the appropriate number of first-order lateral roots will most likely be based on a calculated mean. If for example, as the BLUP mean or arithmetic mean varies between analyses and/or nurseries or

nursery beds, the proportion of quality seedlings will vary correspondingly. Thus, standardization of nursery protocols will be needed in order to grow seedlings to sufficient sizes and enable the proper comparison of seedling characteristics.

Field grading criteria:

Under a simulated field grading criteria, based on height and number of first-order lateral roots, i.e., height > 1 meter and 6 or more first-order lateral roots, significant differences between locations were found. For example, Tennessee produced only 7 percent of high quality seedlings compared to 38 percent at the Georgia location. This indicates that if seedlings fail to grow adequately during the growing season, the number of "quality" seedlings will be less than projected.

For nursery managers, the Georgia location results indicate that acorn collections (adjusted for germination rates) should be sufficient to anticipate a 60% cull rate in terms of suppling seedlings to relatively good unmanaged sites. Furthermore, the Tennessee results indicated that nurseries must maintain adequate growing conditions for the production of a high quality seedlings.

Evaluation of VIGOR:

Currently for research studies, seedlings are visually selected across multiple characteristics and graded as quality seedlings. Often these seedlings have approximately six or more first-order lateral roots, adequate height (> 1 meter), and a sufficient stem size, i.e., thickness (Kormanik, P.P. 1997. USDA Forest Service Athens, Georgia Personnel Communication to M.A. Remaley). To date, these seedlings are subjectively graded and cannot be quantitatively expressed. In recognition of this, a multiple seedling characteristic, i.e. VIGOR, was calculated to mathematically express seedlings qualities across the characteristics of greatest importance, i.e., height, root collar diameter, and first-order lateral root number.

The results of the individual location analysis and the combined location analysis indicated that the family BLUP means for VIGOR vary similar to the other characteristics. Similar to what was found with the individual characteristics, this indicates that selection of families is possible based on the VIGOR variable.

The current limitations of the calculated VIGOR variable is due to the lack of validation through field testing. However, it has been found that seedlings that have a high VIGOR value, outperform smaller seedlings in field tests (Kormanik, P. P. 1997. USDA Forest Service Athens, Georgia. Personnel communication to M.A. Remaley). Often seedling characteristics, e.g., tap root, undoubtably have an affect on seedling growth. These characteristics need to be examined related to seedling quality. Such characteristics included tap root volume, tap root shape, and number of flushes from initial linear leaf elongation.

These characteristics should be quantitatively assessed and evaluated and eventually incorporated in a derivation of the present VIGOR formula.

Heritability estimates and general combining abilities:

Family heritability estimate were higher than the single tree estimates at the individual and combined locations, which is similar to other forest tree species (Zobel and Talbert 1984). The heritability estimates indicate the relative level of the estimates remained constant with variation in family performances within and between locations. Location effects and genotype x environmental interaction are not of sufficient magnitude to diminish these relatively high heritability estimates.

The importance of the heritability estimates is in the developing of a selection system for families. Selection of superior individual trees within superior families would achieve a substantial genetic gain. Furthermore, the combination of high heritability estimates for the studied characteristics coupled with the nursery screening of family performance could translate to faster and more substantial gains.

Variation in the general combing ability estimates from the individual location analyses and combined analysis was found. This indicates that variation among a family's ability to produce above or below average progeny exists in the natural population. For future second generation oak seed orchards, genetic family general combining ability will need to be evaluated in addition to traditional evaluation of family performance and selection. Thus trees with high general combining ability have the propensity to produce progeny with the

trait of interest.

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APPENDIX

Table 2.1 Weight of 100 acorns for northern red oak and white oak genetic families used for the Tennessee and Georgia studies.

Northern red oak		White oak	
Family	Weight of 100 acorns (grams)	Family	Weight of 100 acorns (grams)
100-4-27	502	SAWO-3	265
200-6-14-2	330	SAWO-7	272
526-3-3	375	SAWO-12	286
540-2-10	414	SAWO-14	413
565-2-29	427	SAWO-28	216
630-2-19	653	KYWO-11	228
735-2-6	404	KYWO-31	274
850-2-23	723	NAWO-1	273
882-4-4	480	NAWO-23	408
902-4-2	538	NAWO-24	381
915-1-14	461	NAWO-28	329
2459-4-14	560	NAWO-29	231

Table 2.2 Amounts of fertilizer used to adjust soil levels to comparable levels of fertility at the Tennessee location. Beds 1 and 2 were planted with northern red oak. Beds 3 and 4 were planted with white oak.

Date	Bed	Fertilizer/ Active Ingredient	Amount per bed	Lbs. per acre of product
8-31-1994	1,2,3,4	K-Mag	500 grams	200
9-6-1994	1,2,3,4	Solubar[1]	12 grams	5
11-17-1994	1	Triple superphosphate (0-46-0)	1441 grams	576
11-17-1994	1	K-Mag	626 grams	250
11-17-1994	2	Triple superphosphate (0-46-0)	2181 grams	872
11-17-1994	2	K-Mag	351 grams	140
11-17-1994	3	Triple superphosphate (0-46-0)	1003 grams	401
11-17-1994	3	K-Mag	502 grams	201
11-17-1994	4	Triple superphosphate (0-46-0)	1378 grams	551
11-17-1994	4	K-Mag	652 grams	261
7-15-1995	1	K-Mag	625 grams	250
7-15-1995	2	K-Mag	650 grams	260
7-15-1995	3	K-Mag	500 grams	200
7-15-1995	4	K-Mag	650 grams	260

[1] Solubar is a registered trademark of U.S. Borax and Chemical Corporation.

Table 2.3 Fertilizer amounts applied to the raised nursery bed during the 1994 growing season at the Tennessee location. Beds 1 and 2 were planted with northern red oak. Beds 3 and 4 were planted with white oak.

DATE	BED	AMENDMENT	Amount per bed	Lbs. per acre of product
4-28-1995	1,2,3,4	Ammonium nitrate	188 grams	79
5-3-1995	1,2,3,4	Ammonium nitrate	188 grams	79
5-15-1995	1,2,3,4	Ammonium sulfate	628 grams	251
5-26-1995	1,2,3,4	Ammonium sulfate	628 grams	251
6-2-1995	1,2,3,4	Ammonium nitrate	396 grams	158
6-9-1995	1,2,3,4	20-20-20	60 grams	24
6-13-1995	1,2,3,4	Ammonium nitrate	396 grams	158
6-13-1995	1,2,3,4	20-20-20	60 grams	24
6-25-1995	1,2,3,4	Ammonium nitrate	396 grams	158
7-05-1995	1,2,3,4	Ammonium nitrate	396 grams	158
7-06-1995	1,2,3,4	20-20-20	60 grams	24
7-15-1995	1,2,3,4	Ammonium nitrate	396 grams	158
7-26-1995	1,2,3,4	Ammonium nitrate	396 grams	158
7-31-1995	1,2,3,4	20-20-20	60 grams	24
8-04-1995	1,2,3,4	Ammonium nitrate	396 grams	158
8-15-1995	1,2,3,4	20-20-20	60 grams	24
8-25-1995	1,2,3,4	Ammonium nitrate	396 grams	158
9-01-1995	1,2,3,4	Ammonium nitrate	396 grams	158

Table 2.4. Replication, family, characteristic, number of seedlings, mean, standard deviation, minimum and maximum for the seedling characteristics measured from the Tennessee data.

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
526-3-3	FOLR	94	95	5.37	6.32	4.78	5.98	0	0	22.00	29.00
	FLUSH	94	95	1.97	2.32	0.89	1.14	0	0	4.00	5.00
	HT	94	95	40.20	45.93	23.21	26.13	11.00	8.00	101.00	115.00
	RCD	94	95	6.96	7.28	1.88	2.29	3.10	3.30	11.70	12.90
	VIGOR	94	95	0.81	1.00	0.86	0.99	0	0	3.35	3.98
735-2-6	FOLR	61	89	4.70	5.97	3.80	4.86	0	0	16.00	19.00
	FLUSH	61	89	2.31	2.89	0.99	0.99	0	1.00	4.00	5.00
	HT	61	89	37.25	59.71	19.65	27.22	11.00	15.00	93.00	137.00
	RCD	61	89	6.75	6.56	1.55	2.11	3.20	2.90	10.40	12.40
	VIGOR	61	89	0.68	1.00	0.65	0.94	0	0	2.45	3.32
902-4-2	FOLR	100	100	5.64	8.53	4.76	6.79	0	0	21.00	32.00
	FLUSH	100	100	2.10	2.81	1.22	1.01	0	0	4.00	5.00
	HT	100	100	40.65	62.42	22.70	31.05	11.00	13.00	100.00	145.00
	RCD	100	100	6.18	7.55	1.85	2.59	3.20	2.80	11.00	14.50
	VIGOR	100	100	0.74	1.41	0.80	1.16	0	0	3.08	4.16

Table 2.4. (continued)

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
100-4-27	FOLR	100	100	7.11	8.04	4.85	5.12	0	0	23.00	24.00
	FLUSH	100	100	2.18	2.86	1.25	1.00	0	0	4.00	4.00
	HT	100	100	43.38	71.40	24.64	32.93	9.00	9.00	104.00	141.00
	RCD	100	100	6.52	7.40	2.17	2.48	2.90	2.20	12.50	12.40
	VIGOR	100	100	0.93	1.44	0.83	1.02	0	0	3.60	3.45
565-2-29	FOLR	100	100	6.41	6.56	4.38	5.52	0	0	18.00	24.00
	FLUSH	100	100	1.81	2.72	0.95	1.02	0	1.00	4.00	5.00
	HT	100	100	31.83	56.17	20.07	29.84	8.00	11.00	89.00	142.00
	RCD	100	100	6.09	7.53	1.90	2.31	3.00	2.20	11.40	13.50
	VIGOR	100	100	0.69	1.16	0.71	1.03	0	0	2.91	3.92
630-2-19	FOLR	99	98	4.84	5.15	4.28	4.64	0	0	19.00	18.00
	FLUSH	99	98	2.13	2.53	0.90	1.09	0	0	4.00	4.00
	HT	99	98	43.58	69.83	26.88	34.91	7.40	9.00	124.00	161.00
	RCD	99	98	7.15	8.22	2.16	2.70	3.30	3.50	13.00	14.60
	VIGOR	99	98	0.83	1.27	0.90	1.14	0	0	3.71	4.14

Table 2.4. (continued)

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
915-1-14	FOLR	100	100	3.61	6.91	3.45	5.73	0	0	14.00	24.00
	FLUSH	100	100	1.25	2.58	1.18	1.12	0	0	4.00	4.00
	HT	100	100	26.03	63.60	15.52	30.54	7.00	13.00	77.00	127.00
	RCD	100	100	5.43	7.47	1.37	1.99	2.70	3.60	8.80	12.00
	VIGOR	100	100	0.34	1.24	0.45	1.03	0	0	2.05	3.42
200-6-14-2	FOLR	97	93	6.52	6.94	5.85	6.46	0	0	21.00	26.00
	FLUSH	97	93	1.72	2.12	0.99	0.94	0	0	4.00	4.00
	HT	97	93	31.23	44.91	23.23	27.16	7.00	13.00	127.00	142.00
	RCD	97	93	5.89	6.93	2.06	2.21	2.50	3.30	11.00	12.80
	VIGOR	97	93	0.69	0.98	0.86	1.03	0	0	3.50	3.53
2459-4-14	FOLR	90	93	7.86	8.48	5.96	6.51	0	0	23.00	24.00
	FLUSH	90	93	2.42	2.68	1.06	0.82	0	0	4.00	4.00
	HT	90	93	55.99	68.04	28.51	25.40	11.00	7.00	119.00	125.00
	RCD	90	93	7.22	7.75	2.22	2.00	2.90	3.80	12.00	12.10
	VIGOR	90	93	1.24	1.44	1.03	1.05	0	0	3.49	3.71

Table 2.4. (continued)

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
540-2-10	FOLR	100	100	7.83	6.55	6.35	5.03	0	0	26.00	22.00
	FLUSH	100	100	2.90	3.36	1.05	0.85	0	0	5.00	5.00
	HT	100	100	60.99	76.48	27.97	28.18	10.00	15.00	131.00	139.00
	RCD	100	100	7.18	7.89	2.10	1.98	2.80	2.70	12.10	12.60
	VIGOR	100	100	1.27	1.37	1.04	0.99	0	0	3.83	3.53
882-4-4	FOLR	90	88	2.08	6.01	2.57	5.35	0	0	15.00	25.00
	FLUSH	90	88	1.50	2.53	0.99	0.98	0	0	4.00	5.00
	HT	90	88	29.73	53.55	15.59	25.69	13.00	11.00	99.00	121.00
	RCD	90	88	5.94	7.23	1.58	2.01	3.70	3.20	12.90	13.80
	VIGOR	90	88	0.31	1.02	0.50	0.97	0	0	3.25	3.75

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.5. Arithmetic means for family characteristics in replication 2 by planting order from east to west at the Tennessee location.

Compartment	Family	FOLR[1]	HT[1]	RCD[1]	FLUSH[1]	VIGOR[1]
1	902-4-2	8.53	62.42	7.55	2.81	1.41
2	540-2-10	6.55	76.48	7.89	3.36	1.37
3	2459-4-14	8.48	68.04	7.75	2.68	1.44
4	915-1-14	6.91	63.60	7.47	2.58	1.25
5	735-2-6	5.97	59.71	6.56	2.89	1.00
6	630-2-19	5.15	69.83	8.22	2.53	1.27
7	100-4-27	8.04	71.40	7.40	2.86	1.44
8	526-3-3	6.32	45.93	7.28	2.32	1.00
9	882-4-4	6.01	53.55	7.23	2.53	1.02
10	565-2-29	6.56	56.17	7.53	2.72	1.16
11	200-6-14-2	6.94	44.91	6.93	2.12	0.98

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.6. Correlation coefficients for seedlings grown in replication 1 and 2 and combined replications at the Tennessee location. All correlations were significant at p = .001.

	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
Replication 1				
FOLR[1]	0.51	0.75	0.78	0.92
FLUSH		0.78	0.54	0.62
HEIGHT			0.81	0.91
RCD				0.91
Replication 2				
FOLR	0.48	0.71	0.79	0.92
FLUSH		0.78	0.59	0.60
HEIGHT			0.84	0.88
RCD				0.92
Combined				
FOLR	0.50	0.71	0.78	0.92
FLUSH		0.7*	0.54	0.63
HEIGHT			0.83	0.89
RCD				0.92

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.7. BLUP mean estimates and standard errors for seedling characteristics of different families grown in Tennessee by replication.

	FOLR[1]		FLUSH[1]		HEIGHT[1]		RCD[1]		VIGOR[1]	
Family (replication)	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error
526-3-3 (1)	6.28	0.72	2.32	0.21	52.45	5.80	7.07	0.33	1.02	0.14
526-3-3 (2)	6.85	0.70	2.36	0.20	51.25	5.67	7.02	0.32	1.06	0.14
735-2-6 (1)	6.88	0.75	2.58	0.22	57.96	6.10	7.55	0.36	1.18	0.15
735-2-6 (2)	6.42	0.71	2.43	0.21	54.26	5.76	6.52	0.31	1.00	0.14
882-4-4 (1)	5.36	0.71	2.23	0.20	53.41	5.67	6.81	0.32	0.94	0.14
882-4-4 (2)	7.20	0.72	2.46	0.21	53.19	5.78	7.02	0.33	1.10	0.14
902-4-2 (1)	6.55	0.72	2.40	0.21	56.06	5.90	6.91	0.33	1.05	0.14
902-4-2 (2)	7.54	0.73	2.56	0.21	57.39	5.93	7.40	0.33	1.25	0.14
100-4-27 (1)	7.25	0.69	2.43	0.20	53.69	5.52	7.10	0.31	1.12	0.13
100-4-27 (2)	6.99	0.69	2.49	0.20	60.74	5.51	7.11	0.31	1.19	0.13
540-2-10 (1)	7.52	0.67	2.45	0.19	54.34	5.31	7.13	0.30	1.17	0.13
540-2-10 (2)	6.31	0.67	2.71	0.19	63.60	5.30	7.54	0.30	1.17	0.13
565-2-29 (1)	7.05	0.70	2.24	0.20	49.44	5.70	6.66	0.31	1.01	0.14
565-2-29 (2)	6.55	0.73	2.51	0.21	56.20	5.98	7.27	0.34	1.11	0.14

Table 2.7. (continued)

	FOLR[1]		FLUSH[1]		HEIGHT[1]		RCD[1]		VIGOR[1]	
Family (replication)	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error
630-2-19 (1)	6.70	0.68	2.45	0.19	51.85	5.42	7.28	0.30	1.07	0.13
630-2-19 (2)	6.21	0.68	2.37	0.19	61.41	5.42	7.62	0.30	1.15	0.13
915-1-14 (1)	5.47	0.67	1.87	0.19	41.11	5.34	6.09	0.30	0.76	0.13
915-1-14 (2)	7.49	0.67	2.76	0.19	65.56	5.33	7.43	0.30	1.31	0.13
200-6-14-2 (1)	7.16	0.71	2.45	0.20	55.21	5.72	6.73	0.31	1.11	0.14
200-6-14-2 (2)	6.63	0.75	2.16	0.22	48.31	6.10	6.78	0.36	0.99	0.15
2459-4-14 (1)	7.73	0.73	2.66	0.21	64.52	5.97	7.65	0.34	1.34	0.14
2459-4-14 (2)	6.92	0.72	2.33	0.21	54.29	5.80	7.30	0.32	1.11	0.14

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.8. BLUP mean estimates and standard errors for the combined replications of seedling characteristics of different families grown in Tennessee.

	FOLR[1]		FLUSH[1]		HEIGHT[1]		RCD[1]		VIGOR[1]	
Family	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error
526-3-3	6.20	0.69	2.14	0.21	45.33	5.71	7.06	0.25	0.96	0.13
735-2-6	6.43	0.70	2.71	0.21	57.68	5.72	7.05	0.25	1.07	0.13
882-4-4	5.41	0.70	2.17	0.21	49.53	5.77	6.95	0.25	0.90	0.13
902-4-2	7.51	0.69	2.62	0.21	59.45	5.67	7.14	0.25	1.22	0.13
100-4-27	7.73	0.68	2.56	0.20	60.88	5.61	7.10	0.25	1.24	0.13
540-2-10	7.16	0.72	2.96	0.22	65.97	6.00	7.28	0.25	1.27	0.14
565-2-29	6.84	0.69	2.27	0.21	48.15	5.67	6.97	0.25	1.01	0.13
630-2-19	5.89	0.68	2.39	0.20	59.19	5.60	7.36	0.25	1.13	0.13
915-1-14	5.96	0.69	2.07	0.21	49.64	5.70	6.86	0.25	0.94	0.13
200-6-14-2	7.10	0.70	2.04	0.21	45.07	5.78	6.84	0.25	0.97	0.13
2459-4-14	8.29	0.69	2.68	0.21	67.24	5.65	7.38	0.25	1.40	0.13

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.9. Percentage of seedlings by family within and across replications with a first-order lateral root number equal to or greater than the combined replication first-order lateral mean for each respective family.

Family (BLUP mean)	Replication 1	Replication 2
526-3-3 (6)	43	47
735-2-6 (6)	40	45
882-4-4 (5)	16	50
902-4-2 (8)	29	53
100-4-27 (8)	40	51
540-2-10 (7)	56	46
565-2-29 (7)	49	41
630-2-19 (6)	31	46
915-1-14 (6)	33	56
200-6-14-2 (7)	37	43
2459-4-14 (8)	46	48

Table 2.10. Percentage of seedlings by family within and across replications with 7 or more first-order lateral roots.

Family	Replication 1	Replication 2	Combined
526-3-3	36	42	39
735-2-6	38	39	38
882-4-4	06	37	21
902-4-2	37	59	38
100-4-27	50	57	53
540-2-10	56	46	51
565-2-29	49	41	45
630-2-19	36	39	32
915-1-14	18	49	33
200-6-14-2	37	43	40
2459-4-14	52	54	53

Table 2.11. Replication, family, characteristic, number of seedlings, mean, standard deviation, minimum and maximum for the seedling characteristics measured from the Georgia data.

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
526-3-3	FOLR	78	84	4.76	5.08	4.64	4.59	0	0	16.00	19.00
	FLUSH	78	84	3.40	3.86	0.93	0.97	1.00	2.00	5.00	6.00
	HEIGHT	78	84	110.29	117.05	46.72	43.09	38.00	33.00	217.00	243.00
	RCD	78	84	8.97	9.17	3.16	2.66	3.30	4.00	15.70	14.70
	VIGOR	78	84	1.56	1.65	1.35	1.28	0	0	4.36	4.32
735-2-6	FOLR	75	81	4.23	3.80	3.95	3.58	0	0	16.00	14.00
	FLUSH	75	81	4.07	4.26	0.88	0.88	2.00	2.00	5.00	5.00
	HEIGHT	75	81	107.23	126.00	37.07	43.65	28.00	36.00	177.00	211.00
	RCD	75	81	8.97	9.23	2.64	2.55	3.40	4.50	17.60	14.50
	VIGOR	75	81	1.42	1.48	1.16	1.24	0	0	4.49	3.76
902-4-2	FOLR	92	91	3.66	3.48	3.93	3.94	0	0	15.00	15.00
	FLUSH	92	91	4.08	3.69	0.97	1.08	2.00	2.00	6.00	6.00
	HEIGHT	92	91	124.63	122.68	38.40	46.97	46.00	48.00	206.00	223.00
	RCD	92	91	8.37	8.47	2.57	2.80	3.60	4.10	14.50	15.20
	VIGOR	92	91	1.31	1.29	1.23	1.32	0	0	4.15	4.00

Table 2.11. (continued)

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
100-4-27	FOLR	88	89	4.57	3.78	4.33	4.14	0	0	19.00	16.00
	FLUSH	88	89	4.10	4.17	1.08	0.98	2.00	2.00	6.00	6.00
	HEIGHT	88	89	140.73	140.91	53.41	50.10	33.00	42.00	246.00	242.00
	RCD	88	89	9.24	9.41	2.80	3.12	2.90	4.00	15.50	17.90
	VIGOR	88	89	1.70	1.53	1.40	1.45	0	0	4.54	4.81
565-2-29	FOLR	84	86	5.35	4.95	4.65	5.54	0	0	17.00	24.00
	FLUSH	84	86	4.06	3.97	1.02	1.10	2.00	2.00	7.00	9.00
	HEIGHT	84	86	140.20	127.38	49.53	47.70	27.00	18.00	260.00	248.00
	RCD	84	86	10.01	9.67	2.92	2.89	3.50	3.20	19.20	17.30
	VIGOR	84	86	1.90	1.64	1.45	1.48	0	0	4.98	4.66
630-2-19	FOLR	95	83	4.24	5.11	4.75	4.81	0	0	25.00	16.00
	FLUSH	95	83	3.49	3.76	0.93	0.97	2.00	2.00	5.00	5.00
	HEIGHT	95	83	124.04	139.72	43.74	48.66	46.00	43.00	216.00	238.00
	RCD	95	83	8.77	9.23	3.05	2.98	2.90	2.90	17.10	15.40
	VIGOR	95	83	1.49	1.76	1.34	1.42	0	0	4.86	4.31

Table 2.11. (continued)

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
915-1-14	FOLR	106	80	5.49	7.69	5.52	6.89	0	0	22.00	26.00
	FLUSH	106	80	3.78	3.69	1.17	0.89	1.00	2.00	7.00	5.00
	HEIGHT	106	80	118.84	133.00	52.14	44.33	22.00	44.00	233.00	225.00
	RCD	106	80	9.46	10.33	3.01	3.34	3.90	4.20	16.40	18.70
	VIGOR	106	80	1.71	2.20	1.48	1.54	0	0	4.57	4.72
200-6-14-2	FOLR	96	79	4.67	5.49	4.99	4.98	0	0	20.00	19.00
	FLUSH	96	79	3.50	3.70	0.96	0.92	2.00	2.00	5.00	6.00
	HEIGHT	96	79	117.17	124.61	45.31	44.90	41.00	43.00	213.00	232.00
	RCD	96	79	8.53	8.66	2.90	2.90	3.00	3.90	14.50	15.90
	VIGOR	96	79	1.48	1.67	1.38	1.36	0	0	4.34	4.55
2459-4-14	FOLR	81	91	5.53	6.20	4.55	5.65	0	0	18.00	20.00
	FLUSH	81	91	3.79	3.86	0.82	0.98	2.00	2.00	6.00	6.00
	HEIGHT	81	91	124.16	125.07	43.18	52.43	41.00	22.00	219.00	253.00
	RCD	81	91	11.03	10.03	3.30	3.31	5.30	3.40	16.90	18.90
	VIGOR	81	91	2.02	1.95	1.42	1.54	0	0	4.55	4.62

Table 2.11. (continued)

Family	Characteristic[1]	Number of seedlings		Mean		Standard deviation		minimum		maximum	
		1	2	1	2	1	2	1	2	1	2
882-4-4	FOLR	93	96	4.01	3.95	4.08	4.51	0	0	18.00	19.00
	FLUSH	93	96	3.65	3.83	0.99	0.85	2.00	2.00	5.00	6.00
	HEIGHT	93	96	118.80	133.46	41.64	42.02	47.00	53.00	219.00	243.00
	RCD	93	96	8.49	9.06	2.65	2.50	3.90	4.40	14.50	16.40
	VIGOR	93	96	1.38	1.42	1.25	1.34	0	0	4.43	4.59
540-2-10	FOLR	93	88	5.52	5.61	5.13	5.45	0	0	20.00	23.00
	FLUSH	93	88	3.87	4.31	1.04	1.02	2.00	2.00	5.00	6.00
	HEIGHT	93	88	124.85	145.85	46.88	47.94	40.00	48.00	219.00	262.00
	RCD	93	88	8.14	8.70	2.73	2.89	3.70	3.90	15.60	15.80
	VIGOR	93	88	1.61	1.77	1.33	1.42	0	0	4.53	5.02

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.12. Correlation coefficients for seedlings grown in replication 1 and 2 and combined replications at the Georgia location.
All correlations were significant at p = .001.

	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
Replication 1				
FOLR[1]	0.59	0.77	0.81	0.94
FLUSH		0.81	0.64	0.68
HEIGHT			0.85	0.88
RCD				0.92
Replication 2				
FOLR	0.52	0.73	0.81	0.94
FLUSH		0.81	0.62	0.63
HEIGHT			0.84	0.85
RCD				0.92
Combined				
FOLR[1]	0.55	0.75	0.81	0.94
FLUSH		0.81	0.63	0.66
HEIGHT			0.85	0.87
RCD				0.92

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.13. BLUP mean estimates and standard errors for family and seedling characteristics for Georgia by replication.

	FOLR[1]		FLUSH[1]		HEIGHT[1]		RCD[1]		VIGOR[1]	
Family (replication)	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error
526-3-3 (1)	5.14	0.31	3.65	0.11	117.65	4.19	8.91	0.11	1.59	0.06
526-3-3 (2)	5.20	0.31	3.86	0.11	117.69	4.18	8.92	0.11	1.60	0.06
735-2-6 (1)	5.13	0.31	3.85	0.12	116.33	4.24	8.92	0.11	1.59	0.06
735-2-6 (2)	5.06	0.31	3.91	0.11	121.12	4.16	8.92	0.11	1.60	0.06
882-4-4 (1)	5.10	0.31	3.76	0.11	118.63	4.13	8.90	0.11	1.59	0.06
882-4-4 (2)	5.10	0.31	3.79	0.11	121.31	4.16	8.93	0.11	1.59	0.06
902-4-2 (1)	5.08	0.31	4.00	0.11	123.05	4.18	8.92	0.11	1.59	0.06
902-4-2 (2)	5.07	0.32	3.61	0.12	114.99	4.32	8.89	0.11	1.58	0.06
100-4-27 (1)	5.29	0.31	3.88	0.12	123.45	4.21	8.91	0.11	1.61	0.06
100-4-27 (2)	4.95	0.31	3.87	0.11	122.35	4.16	8.93	0.11	1.59	0.06
540-2-10 (1)	5.16	0.31	3.77	0.12	119.63	4.21	8.90	0.11	1.59	0.06
540-2-10 (2)	5.27	0.32	3.94	0.12	123.38	4.29	8.92	0.11	1.61	0.06
565-2-29 (1)	5.31	0.32	3.90	0.12	124.70	4.28	8.94	0.11	1.62	0.06
565-2-29 (2)	5.07	0.32	3.80	0.12	118.91	4.22	8.92	0.11	1.59	0.06

Table 2.13. (continued)

Family (replication)	FOLR[1] BLUP Mean	FOLR[1] Standard error	FLUSH[1] BLUP Mean	FLUSH[1] Standard error	HEIGHT[1] BLUP Mean	HEIGHT[1] Standard error	RCD[1] BLUP Mean	RCD[1] Standard error	VIGOR[1] BLUP Mean	VIGOR[1] Standard error
630-2-19 (1)	4.99	0.31	3.71	0.11	119.93	4.16	8.91	0.11	1.58	0.06
630-2-19 (2)	5.31	0.31	3.78	0.12	121.95	4.24	8.92	0.11	1.62	0.06
915-1-14 (1)	4.99	0.31	3.83	0.11	116.54	4.09	8.87	0.10	1.58	0.06
915-1-14 (2)	5.56	0.31	3.75	0.11	124.92	4.21	8.99	0.11	1.64	0.06
200-6-14-2 (1)	5.10	0.31	3.71	0.11	117.76	4.17	8.90	0.11	1.58	0.06
200-6-14-2 (2)	5.26	0.31	3.79	0.11	120.91	4.18	8.92	0.11	1.61	0.06
2459-4-14 (1)	5.22	0.32	3.80	0.12	119.17	4.36	8.97	0.11	1.62	0.06
2459-4-14 (2)	5.26	0.32	3.82	0.12	121.25	4.26	8.90	0.11	1.61	0.06

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.14. BLUP mean estimates and standard errors for the combined replications of seedling characteristics of different families grown in Georgia.

	FOLR[1]		FLUSH[1]		HEIGHT		RCD[1]		VIGOR[1]	
Family	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error
526-3-3	5.25	0.44	3.66	0.11	111.53	4.30	8.80	0.29	1.58	0.11
735-2-6	4.42	0.45	4.00	0.11	115.08	4.40	8.94	0.30	1.48	0.11
882-4-4	4.48	0.43	3.72	0.11	119.28	4.22	8.55	0.29	1.43	0.10
902-4-2	4.24	0.44	3.80	0.11	116.10	4.31	8.15	0.29	1.35	0.11
100-4-27	4.68	0.43	3.99	0.11	129.19	4.26	9.04	0.29	1.59	0.11
540-2-10	5.69	0.43	3.93	0.11	124.47	4.27	8.22	0.29	1.64	0.11
565-2-29	5.42	0.44	3.92	0.11	125.49	4.29	9.52	0.29	1.70	0.11
630-2-19	4.99	0.43	3.64	0.11	122.57	4.26	8.74	0.29	1.59	0.11
915-1-14	6.34	0.44	3.76	0.11	121.86	4.31	9.62	0.29	1.83	0.11
200-6-14-2	5.33	0.43	3.65	0.11	117.15	4.26	8.41	0.29	1.56	0.11
2459-4-14	5.96	0.44	3.81	0.11	120.09	4.30	10.13	0.29	1.86	0.11

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.15. Percentage of seedlings by family within and across replications with the family BLUP mean or greater number of first-order lateral roots from the Georgia location.

Family (BLUP mean)	Replication 1	Replication 2	Combined
526-3-3 (5)	45	46	46
735-2-6 (4)	49	46	47
882-4-4 (4)	45	41	33
902-4-2 (4)	36	38	37
100-4-27 (5)	49	39	44
540-2-10 (6)	47	46	46
565-2-29 (5)	51	42	46
630-2-19 (5)	39	46	42
915-1-14 (6)	42	54	47
200-6-14-2 (5)	48	55	50
2459-4-14 (6)	43	52	48

Table 2.16. Percentage of seedlings by family within and across replications with five or more first-order lateral roots from the Georgia location.

Family	Replication 1	Replication 2	Combined
526-3-3	45	46	46
735-2-6	39	35	37
882-4-4	39	35	37
902-4-2	34	34	34
100-4-27	49	39	44
540-2-10	52	53	52
565-2-29	51	42	46
630-2-19	39	46	42
915-1-14	47	59	52
200-6-14-2	48	55	50
2459-4-14	49	57	53

Table 2.17. Correlation coefficients for seedlings characteristics from the combined location analysis. All correlations were significant at p = .001.

	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
FOLR[1]	0.34	0.41	0.66	0.83
FLUSH		0.85	0.67	0.64
HEIGHT			0.83	0.78
RCD				0.92

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.18. Overall BLUP mean estimates and standard errors by location and location by replication for seedling characteristics from the combined location analysis.

	FOLR[1]		FLUSH[1]		HEIGHT[1]		RCD[1]		VIGOR[1]	
Location (replication)	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error	BLUP Mean	Standard error
Georgia (1 and 2)	5.51	0.70	3.75	0.69	117.61	32.77	8.62	0.93	1.46	0.22
Tennessee (1 and 2)	6.40	0.70	2.51	0.69	56.51	32.77	7.30	0.93	1.22	0.22
Georgia (1)	5.40	0.61	3.05	0.31	79.23	12.23	7.36	0.74	1.20	0.25
Georgia (2)	6.20	0.60	3.34	0.31	99.16	12.23	9.15	0.74	1.76	0.25
Tennessee (1)	5.86	0.59	2.72	0.31	72.37	12.07	7.15	0.73	0.97	0.25
Tennessee (2)	6.37	0.58	3.42	0.31	97.48	12.06	8.18	0.73	1.44	0.25

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.19. BLUP mean estimates for family by replication for the seedling characteristics from combined location analysis.

Family (replication, location)	FOLR[1] BLUP MEAN	FLUSH[1] BLUP Mean	HEIGHT[1] BLUP Mean	RCD[1] BLUP Mean	VIGOR[1] BLUP Mean
526-3-3 (1^{TN})	5.69	3.18	90.82	8.17	1.36
526-3-3 (2^{TN})	5.95	3.03	83.62	7.83	1.28
526-3-3 (1^{GA})	5.90	2.95	84.56	7.85	1.32
526-3-3 (2^{GA})	6.06	3.24	85.21	8.00	1.36
735-2-6 (1^{TN})	5.98	3.18	87.33	8.16	1.35
735-2-6 (2^{TN})	5.71	3.09	86.95	7.58	1.27
735-2-6 (1^{GA})	5.92	3.23	86.34	8.26	1.39
735-2-6 (2^{GA})	5.61	3.20	86.39	7.85	1.29
882-4-4 (1^{TN})	4.71	2.85	83.54	7.79	1.22
882-4-4 (2^{TN})	6.37	3.22	87.06	8.00	1.36
882-4-4 (1^{GA})	5.79	3.15	87.26	7.87	1.33
882-4-4 (2^{GA})	5.82	3.20	89.30	8.03	1.32
902-4-2 (1^{TN})	5.75	3.16	88.55	7.85	1.33
902-4-2 (2^{TN})	6.66	3.12	85.66	8.05	1.39
902-4-2 (1^{GA})	5.62	3.32	90.10	7.80	1.28
902-4-2 (2^{GA})	5.80	2.95	83.26	7.94	1.31

Table 2.19. (continued).

Family (replication, location)	FOLR[1] BLUP Mean	FLUSH[1] BLUP Mean	HEIGHT[1] BLUP Mean	RCD[1] BLUP Mean	VIGOR[1] BLUP Mean
100-4-27 (1^{TN})	6.40	3.12	84.88	7.98	1.37
100-4-27 (2^{TN})	6.18	3.16	89.54	7.95	1.40
100-4-27 (1^{GA})	6.12	3.18	89.03	7.83	1.34
100-4-27 (2^{GA})	5.40	3.19	88.30	8.04	1.28
540-2-10 (1^{TN})	6.76	3.45	91.51	8.17	1.47
540-2-10 (2^{TN})	5.45	3.27	86.51	8.00	1.30
540-2-10 (1^{GA})	5.97	2.93	86.08	7.83	1.35
540-2-10 (2^{GA})	6.28	3.16	89.42	7.93	1.38
565-2-29 (1^{TN})	6.26	2.92	82.96	7.77	1.30
565-2-29 (2^{TN})	5.75	3.24	88.11	8.08	1.36
565-2-29 (1^{GA})	6.27	3.25	91.92	8.05	1.40
565-2-29 (2^{GA})	5.66	3.13	84.99	7.97	1.29
630-2-19 (1^{TN})	5.94	3.27	85.72	8.07	1.34
630-2-19 (2^{TN})	5.44	3.09	88.99	8.13	1.34
630-2-19 (1^{GA})	5.60	3.01	87.39	7.93	1.31
630-2-19 (2^{GA})	6.31	3.11	88.73	8.00	1.40

Table 2.19. (continued).

Family (replication, location)	FOLR[1] BLUP Mean	FLUSH[1] BLUP Mean	HEIGHT[1] BLUP Mean	RCD[1] BLUP Mean	VIGOR[1] BLUP Mean
915-1-14 (1^{TN})	4.90	2.69	80.82	7.52	1.17
915-1-14 (2^{TN})	6.50	3.23	90.15	8.13	1.39
915-1-14 (1^{GA})	5.82	3.31	85.74	8.03	1.35
915-1-14 (2^{GA})	6.70	3.11	90.01	8.15	1.45
200-6-14-2 (1^{TN})	6.31	3.10	86.35	7.85	1.34
200-6-14-2 (2^{TN})	5.85	3.01	85.33	7.93	1.31
200-6-14-2 (1^{GA})	5.83	3.07	85.40	7.78	1.29
200-6-14-2 (2^{GA})	6.07	3.16	87.85	7.85	1.35
2459-4-14 (1^{TN})	6.73	3.43	94.04	8.15	1.47
2459-4-14 (2^{TN})	6.10	3.05	86.55	7.90	1.32
2459-4-14 (1^{GA})	6.09	3.03	83.24	8.29	1.31
2459-4-14 (2^{GA})	6.06	3.04	85.14	7.90	1.34

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.20. BLUP mean estimates for family by location for the seedling characteristics from the combined location analysis.

Family (location)	FOLR[1] BLUP Mean	FLUSH[1] BLUP Mean	HEIGHT[1] BLUP Mean	RCD[1] BLUP Mean	VIGOR[1] BLUP Mean
526-3-3 (Georgia)	6.02	3.13	84.79	7.89	1.34
526-3-3 (Tennessee)	5.58	3.13	87.23	8.05	1.31
735-2-6 (Georgia)	5.42	3.14	86.33	8.15	1.34
735-2-6 (Tennessee)	5.65	3.13	87.15	7.77	1.30
882-4-4 (Georgia)	5.55	3.13	88.34	7.93	1.32
882-4-4 (Tennessee)	4.80	3.12	85.22	7.82	1.26
902-4-2 (Georgia)	5.28	3.13	86.66	7.78	1.26
902-4-2 (Tennessee)	6.63	3.13	87.11	7.95	1.38
100-4-27 (Georgia)	5.42	3.14	88.74	7.91	1.29
100-4-27 (Tennessee)	6.87	3.13	87.21	7.97	1.42
540-2-10 (Georgia)	6.42	3.12	87.78	7.79	1.38
540-2-10 (Tennessee)	6.36	3.15	89.10	8.22	1.41

Table 2.20. (continued)

Family (location)	FOLR[1] BLUP Mean	FLUSH[1] BLUP Mean	HEIGHT[1] BLUP Mean	RCD[1] BLUP Mean	VIGOR[1] BLUP Mean
565-2-29 (Georgia)	5.99	3.14	88.52	8.06	1.35
565-2-29 (Tennessee)	6.09	3.13	85.47	7.88	1.32
630-2-19 (Georgia)	5.95	3.13	88.11	7.97	1.37
630-2-19 (Tennessee)	5.23	3.13	87.37	8.26	1.34
915-1-14 (Georgia)	6.79	3.14	87.91	8.22	1.44
915-1-14 (Tennessee)	5.25	3.12	85.41	7.68	1.23
200-6-14-2 (Georgia)	5.95	3.13	86.60	7.66	1.31
200-6-14-2 (Tennessee)	6.30	3.13	85.78	7.82	1.31
2459-4-14 (Georgia)	6.28	3.12	84.06	8.24	1.37
2459-4-14 (Tennessee)	7.22	3.14	90.45	8.10	1.44

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.21. BLUP mean estimates for family by seedling characteristics from the combined location analysis.

Family	FOLR[1]	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
526-3-3	5.91	2.95	79.19	7.97	1.31
735-2-6	5.84	3.38	84.66	7.96	1.29
882-4-4	5.75	2.98	84.95	7.86	1.24
902-4-2	5.96	3.18	85.75	7.85	1.30
100-4-27	6.01	3.30	93.92	7.94	1.37
540-2-10	6.07	3.54	97.37	7.90	1.45
565-2-29	5.98	3.15	86.56	7.94	1.33
630-2-19	5.86	3.04	92.13	7.79	1.37
915-1-14	5.97	2.88	84.09	7.95	1.34
200-6-14-2	6.00	2.87	80.57	7.71	1.28
2459-4-14	6.17	3.16	88.48	7.72	1.46

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.22. Percentage of seedlings by family within replications at the Tennessee location with equal to or greater than six first-order lateral roots.

Family	Replication 1	Replication 2
526-3-3	43	47
735-2-6	40	45
882-4-4	10	45
902-4-2	63	60
100-4-27	60	65
540-2-10	57	52
565-2-29	56	38
630-2-19	31	46
915-1-14	33	56
200-6-14-2	46	46
2459-4-14	58	57

Table 2.23. Percentage of seedlings by family within replications at the Georgia location with equal to or greater than six first-order lateral roots.

Family	Replication 1	Replication 2
526-3-3	38	43
735-2-6	32	31
882-4-4	32	28
902-4-2	32	26
100-4-27	40	34
540-2-10	47	46
565-2-29	46	37
630-2-19	33	42
915-1-14	42	54
200-6-14-2	42	43
2459-4-14	43	52

Table 2.24. Percentage of seedlings with the BLUP mean or more first-order lateral roots by location and combined locations.

	Tennessee (7)	Georgia (5)	Combined locations (6)
Tennessee	41	54	47
Georgia	37	49	39
Combined locations	37	50	43

Table 2.25. Percentage of seedlings within families with the BLUP mean or more first-order lateral roots by location and combined locations.

Family	Tennessee FOLR (7)	Georgia FOLR (5)	Combined FOLR (6)
526-3-3	36	47	43
735-2-6	29	43	37
882-4-4	23	35	29
902-4-2	34	47	41
100-4-27	42	57	50
540-2-10	39	55	50
565-2-29	41	56	47
630-2-19	33	46	38
915-1-14	38	50	43
200-6-14-2	37	53	44
2459-4-14	47	60	53

Table 2.26. Number of seedlings by family with 6 or more first-order lateral roots and 1 meter or greater in height by location and combined locations.

Family	Tennessee	Georgia	Combined
526-3-3	4	63	67
735-2-6	6	49	55
882-4-4	4	55	59
902-4-2	17	53	70
100-4-27	22	65	87
540-2-10	26	83	109
565-2-29	7	70	77
630-2-19	23	66	89
915-1-14	13	86	99
200-6-14-2	7	72	79
2459-4-14	15	78	93
Total	144	740	884

Table 2.27. Family heritability estimates and associated standard errors for seedling characteristics grown at the Tennessee location.

Characteristic	h^2	standard error
First-order lateral roots	0.672	0.885
Root collar diameter	0.501	0.700
Flush	0.747	0.957
Height	0.722	0.934
VIGOR	0.649	0.861

[1]VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.28. Single tree heritability estimates and associated standard errors for seedling characteristics grown at the Tennessee location.

Characteristic	h^2	standard error
First-order lateral roots	0.160	0.058
Root collar diameter	0.068	0.032
Flush	0.412	0.098
Height	0.429	0.099
VIGOR	0.169	0.061

[1]VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.29 Family heritability estimates and associated standard errors for seedling characteristics grown at the Georgia location.

Characteristic	h^2	standard error
First-order lateral roots	0.759	0.934
Root collar diameter	0.889	1.046
Flush	0.644	0.825
Height	0.631	0.812
VIGOR	0.725	0.903

[1]VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.30. Single tree heritability estimates and standard errors for seedling characteristics grown at the Georgia location.

Characteristic	h^2	standard error
First-order lateral roots	0.101	0.041
Root collar diameter	0.197	0.065
Flush	0.114	0.045
Height	0.077	0.034
VIGOR	0.062	0.030

[1]VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.31. Family heritability estimates and standard errors for seedling characteristics for the combined location analysis.

Characteristic	h^2	standard error
First-order lateral roots	0.149	0.356
Root collar diameter	0.304	0.678
Flush	0.813	1.537
Height	0.749	1.445
VIGOR	0.214	0.495

[1]VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.32. Single tree heritability estimates and standard errors for seedling characteristics for the combined location analysis.

Characteristic	h^2	standard error
First-order lateral roots	0.014	0.013
Root collar diameter	0.020	0.017
Flush	0.209	0.101
Height	0.116	0.065
VIGOR	0.028	0.021

[1]VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.33. General combining ability estimates of families grown in Tennessee by replication.

	FOLR[1]		FLUSH[1]		HEIGHT		RCD[1]		VIGOR[1]	
Replication	1	2	1	2	1	2	1	2	1	2
Family										
526-3-3	-0.496	0.075	-0.104	-0.063	-2.832	-4.032	-0.019	-0.071	-0.077	-0.042
735-2-6	0.104	-0.352	0.158	0.016	2.674	-1.024	0.046	-0.568	0.080	-0.104
882-4-4	-1.413	0.422	-0.193	0.044	-1.876	-2.092	-0.283	-0.086	-0.163	-0.003
902-4-2	-0.228	0.766	-0.021	0.140	0.772	2.102	-0.184	0.311	-0.047	0.145
100-4-27	0.480	0.218	0.014	0.070	-1.598	5.458	0.009	0.023	0.023	0.092
540-2-10	0.745	-0.465	0.030	0.292	-0.944	8.317	0.044	0.045	0.072	0.067
565-2-29	0.273	-0.229	-0.184	0.094	-5.841	0.917	-0.429	0.118	-0.087	0.012
630-2-19	-0.080	-0.565	0.031	-0.046	-3.431	6.125	0.194	0.526	-0.033	0.055
915-1-14	-1.303	0.711	-0.546	0.339	-14.176	10.280	-0.969	0.379	-0.344	0.021
200-6-14-2	0.386	-0.147	0.029	-0.257	-0.76	-6.970	-0.360	-0.308	0.009	-0.113
2459-4-14	0.958	0.141	0.246	-0.088	9.237	-0.989	0.551	0.210	0.242	0.005

[1]FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.34. General combining ability estimates of families grown in Tennessee across replications.

Family	FOLR[1]	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
526-3-3	-0.580	-0.283	-9.950	-0.034	-0.143
735-2-6	-0.341	0.293	2.391	-0.040	-0.028
882-4-4	-1.364	-0.251	-5.752	-0.141	-0.199
902-4-2	0.740	0.200	4.166	0.049	0.118
100-4-27	0.960	0.141	5.596	0.013	0.138
540-2-10	0.385	0.545	10.686	0.188	0.168
565-2-29	0.601	-0.152	-7.138	-0.119	-0.090
630-2-19	-0.887	-0.025	3.905	0.275	0.026
915-1-14	-0.814	-0.350	-5.647	-0.225	-0.162
200-6-14-2	0.328	-0.384	-10.213	-0.255	-0.125
2459-4-14	1.512	0.265	11.956	0.291	0.298

[1]FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.35. General combining ability estimates of families grown in Georgia by replication.

	FOLR[1]		FLUSH[1]		HEIGHT[1]		RCD[1]		VIGOR[1]	
Replication	1	2	1	2	1	2	1	2	1	2
Family										
526-3-3	-0.021	0.037	-0.162	0.052	-2.603	-2.563	-0.007	0.003	-0.005	0.004
735-2-6	-0.038	-0.106	0.041	0.100	-3.929	0.865	0.001	-0.001	-0.007	-0.004
882-4-4	-0.067	-0.065	-0.049	-0.016	-1.627	1.051	-0.024	0.014	-0.010	-0.008
902-4-2	-0.084	-0.095	0.189	-0.196	2.799	-5.263	0.005	-0.025	-0.008	-0.017
100-4-27	0.124	-0.217	0.075	0.060	3.197	2.096	-0.010	0.014	0.011	-0.012
540-2-10	-0.004	0.105	-0.042	0.034	-0.626	3.123	0.019	-0.001	-0.005	0.009
565-2-29	0.147	-0.097	0.091	-0.007	4.444	-1.345	0.017	-0.001	0.021	-0.011
630-2-19	-0.176	0.143	-0.098	-0.023	-0.330	1.699	-0.010	0.005	-0.016	0.015
915-1-14	-0.170	0.398	0.020	-0.056	-3.715	4.663	-0.048	0.067	-0.022	0.045
200-6-14-2	-0.063	0.094	-0.100	-0.014	-2.497	0.656	-0.018	0.005	-0.015	0.011
2459-4-14	0.055	0.099	-0.009	0.010	-1.090	0.995	0.055	-0.022	0.015	0.011

[1] FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.36. General combining ability estimates of families grown in Georgia across replications.

Family	FOLR[1]	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
526-3-3	0.083	-0.151	-8.721	-0.124	-0.019
735-2-6	-0.747	0.194	-5.173	0.017	-0.118
882-4-4	-0.684	-0.088	-0.972	-0.369	-0.172
902-4-2	-0.924	-0.010	-4.161	-0.769	-0.251
100-4-27	-0.481	0.185	8.936	0.008	-0.012
540-2-10	0.521	0.126	4.216	-0.703	0.039
565-2-29	0.258	0.116	5.231	0.604	0.105
630-2-19	-0.170	-0.167	2.311	-0.183	-0.012
915-1-14	1.179	-0.050	1.602	0.703	0.228
200-6-14-2	0.163	-0.157	-3.107	-0.504	-0.044
2459-4-14	0.800	0.001	-0.162	1.210	0.258

[1]FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Table 2.37. General combining ability estimates of families for first-order lateral roots by location and replication within location.

	Tennessee		Georgia	
Replication	1	2	1	2
Family				
526-3-3	-0.268	-0.006	-0.059	0.105
735-2-6	-0.025	-0.247	-0.038	-0.350
882-4-4	-1.248	0.410	-0.162	-0.135
902-4-2	-0.209	0.699	-0.337	-0.155
100-4-27	0.442	0.219	0.164	-0.557
540-2-10	0.804	-0.510	0.017	0.322
565-2-29	0.306	-0.209	0.316	-0.292
630-2-19	-0.016	-0.515	-0.356	0.352
915-1-14	-1.060	0.546	-0.137	0.742
200-6-14-2	0.354	-0.105	-0.123	0.118
2459-4-14	0.772	0.145	0.138	0.099

Table 2.38. General combining ability estimates of families for root collar diameter by location and replication within location.

	Tennessee		Georgia	
Replication	1	2	1	2
Family				
526-3-3	0.211	-0.129	-0.112	0.041
735-2-6	0.202	-0.383	0.297	-0.111
882-4-4	-0.169	0.036	-0.094	0.066
902-4-2	-0.106	0.094	-0.157	-0.016
100-4-27	0.025	-0.012	-0.129	0.077
540-2-10	0.213	0.040	-0.126	-0.034
565-2-29	-0.190	0.118	0.091	0.010
630-2-19	0.110	0.173	-0.027	0.037
915-1-14	-0.436	0.166	0.065	0.187
200-6-14-2	-0.112	-0.026	-0.179	-0.112
2459-4-14	0.194	-0.060	0.329	-0.059

Table 2.39. General combining ability estimates of families for height by location and replication within location.

	Tennessee		Georgia	
Replication	1	2	1	2
Family				
526-3-3	3.762	-3.437	-2.497	-1.847
735-2-6	0.272	-0.108	-0.716	-0.675
882-4-4	-3.522	0.003	0.201	2.243
902-4-2	1.490	-1.402	3.041	-3.801
100-4-27	-2.183	2.477	1.970	1.240
540-2-10	4.450	-0.555	-0.985	2.355
565-2-29	-4.097	1.049	4.859	-2.066
630-2-19	-1.339	1.928	0.327	1.671
915-1-14	-6.237	3.091	-1.322	2.949
200-6-14-2	-0.711	-1.730	-1.661	0.788
2459-4-14	6.980	-0.511	-3.821	-1.922

Table 2.40. General combining ability estimates of families for flush by location and replication within location.

	Tennessee		Georgia	
Replication	1	2	1	2
Family				
526-3-3	0.050	-0.101	-0.183	0.107
735-2-6	0.050	-0.042	0.095	0.071
882-4-4	-0.281	0.085	0.022	0.069
902-4-2	0.034	-0.015	0.191	-0.176
100-4-27	-0.016	0.030	0.049	0.057
540-2-10	0.317	0.142	-0.199	0.024
565-2-29	-0.210	0.111	0.005	0.001
630-2-19	0.136	-0.046	-0.124	-0.026
915-1-14	-0.439	0.102	0.180	-0.017
200-6-14-2	-0.034	-0.119	-0.060	0.027
2459-4-14	0.297	-0.080	-0.105	-0.088

Table 2.41. General combining ability estimates of families by location and replication for VIGOR[1] by location and replication within location.

	Tennessee		Georgia	
Replication	1	2	1	2
Family				
526-3-3	0.018	-0.056	-0.021	0.024
735-2-6	0.014	-0.065	0.050	-0.054
882-4-4	-0.120	0.024	-0.007	-0.019
902-4-2	-0.007	0.053	-0.060	-0.033
100-4-27	0.026	0.064	0.002	-0.062
540-2-10	0.126	-0.045	0.009	0.042
565-2-29	-0.042	0.024	0.061	-0.053
630-2-19	0.001	0.005	-0.026	0.061
915-1-14	-0.175	0.051	0.006	0.113
200-6-14-2	-0.003	-0.026	-0.053	0.014
2459-4-14	0.131	-0.020	0.028	0.002

[1]VIGOR = [log(root collar diameter[2] x height x first-order lateral roots / 10,000) +1)].

Table 2.42. General combining ability estimates of families across locations and replications.

Family	FOLR[1]	FLUSH[1]	HEIGHT[1]	RCD[1]	VIGOR[1]
526-3-3	-0.042	-0.181	-7.870	0.007	-0.030
735-2-6	-0.112	0.249	-2.403	0.003	-0.048
882-4-4	-0.208	-0.151	-2.107	-0.095	-0.104
902-4-2	0.001	0.048	-1.313	-0.109	-0.040
100-4-27	0.049	0.172	6.863	-0.024	0.025
540-2-10	0.116	0.406	10.310	0.055	0.112
565-2-29	0.022	0.024	-0.501	0.017	-0.008
630-2-19	-0.098	-0.086	5.065	0.172	0.034
915-1-14	0.016	-0.249	-2.975	-0.011	-0004
200-6-14-2	0.045	-0.265	-6.491	-0.253	-0.058
2459-4-14	0.211	0.034	1.422	0.238	0.120

[1]FOLR= number of first-order lateral roots, FLUSH = number of flushes, HEIGHT = Total height in centimeters, RCD = root collar diameter in millimeters, VIGOR = [log(root collar diameter^2 x height x first-order lateral roots / 10,000) +1)].

Heritability estimates (derived from Wright 1976)

Single tree heritability formula for a single location:

$$\frac{4V_f}{V_e + V_{fr} + V_f}$$

Single tree heritability formula for two locations:

$$\frac{4V_f}{V_e + V_{fr} + V_{fl} + V_f}$$

Family heritability formula for a single location:

$$\frac{V_f}{V_e/NRL + V_{fr}/RS + V_{fl}/L + V_f}$$

Family heritability formula for two locations:

$$\frac{V_f}{V_e/NRL + V_{fr}/RS + V_{fl}/L + V_f}$$

V_f =variance due to family
V_{fr} =variance due to family x replication
V_{fl} =variance due to family x location
V_e =variance due to family within plots
N =harmonic mean number of trees per plot
R=number of replications per location
L=number of locations

Standard deviations of heritability estimates (derived from Wright 1976):

Standard deviation formula for single tree heritability:

$$\frac{(1 - h^2/4)[1 + (NRL)h^2/4]}{NRS[(F-1)/2]^{1/2}}$$

Standard deviation formula for family heritability:

$$\frac{(1 - t)(1 + NRL\,t)}{[(NRL)(F-1)/2]^{1/2}}$$

V_f =variance due to family
V_{fr} =variance due to family x replication
V_{fl} =variance due to family x location
V_e =variance due to family within plots
N=harmonic mean number of trees per plot
R=number of replications per location
L =number of locations
F=number of families
t=intraclass correlation, which equals one-fourth of the single tree heritability

PART 3:

Polyembryony occurrence and variation between genetic families in northern red oak *(Quercus rubra* L.).

1. ABSTRACT

Polyembryonic acorns in northern red oak (*Quercus rubra* L.) have been previously noted, but published reports have not indicated the frequency of occurrence within and among genetic families. Seed sources from Overton County, Tennessee, planted in a northern red oak seedling seed orchard, have been identified as producing multi-seeded acorns. In 1995, germination tests and acorn dissection studies were conducted to determine the frequency and distribution of polyembryony within and among selected genetic families. Six half-siblings from Overton County, Tennessee, were found to produce polyembryonic acorns with a maximum of four embryos per acorn, while the five other genetic families produced only single seeded acorns. These results indicate an inheritance pattern of polyembryony between Overton County seed sources and their progeny. Evaluation of acorn size and polyembryony indicated that as the size of the acorn increased, polyembryonic acorns increased in frequency. Polyembryonic acorns are undesirable in nursery operations as they can alter seedbed densities, thereby affecting optimum conditions for seedling development. Seed orchard and nursery managers should evaluate seed sources for occurrence of multiple embryos and then eliminate polyembryonic sources from future seed collections.

2. INTRODUCTION

In the genus *Quercus*, the pistillate flowers have a 3-locular and 6-ovuled ovary that can potentially develop six embryos per seed (Ferald 1950). Usually only a single ovule develops into a single acorn, due to either a lack of pollination or abortion of the remaining ovules (Wood 1866, Mogensen 1975, Cecich, R. 1997. USDA Forest Service Columbia, MO. Personnel Communication to M.A. Remaley). Stevens and Matthew (1989) reviewed studies on polyembryonic acorns and found that 10 species of *Quercus* were known to produce multi-seeded acorns. In North American oaks, polyembryonic acorns have been reported in northern red oak (*Quercus rubra* L.) (Hosner 1959), southern red oak (*Q. falcata* Michx.) (Buchholz 1941), cherrybark oak (*Q. falcata* var. *padodifolia* Ell.) (Hosner 1959), shumard oak (*Q. shumardii* Buckl.) (Hosner 1959), black oak (*Q. velutina* Lam.) (Coker 1904, Hosner 1959), pin oak (*Q. palustris* Muenchh.), bur oak (*Q. macrocarpa* Michx.) (Garrison and Augspurger 1983), chestnut oak (*Q. prinus* L.) (Coker 1904, Smith 1914) and white oak (*Q. alba* L.) (Smith 1914, Harvey 1917).

Polyembryony can have a profound effect on growing oak species in nurseries. In nursery seedling production, acorns are sown to achieve a uniform bed density that allows for optimum development of the seedlings (Olson 1974). The sowing density is based on the premise that a single acorn will produce a single seedling. The occurrence of polyembryonic acorns can disrupt optimum bed densities and impact the growth of adjacent seedlings. Correspondingly, the identification of trees that produce polyembryonic seeds is desirable, so that their progeny are not included in seed collections.

In 1994, progeny from an open-pollinated family in a northern red oak seedling seed orchard were observed to contain 67 percent multi-seeded acorns (Remaley, unpublished data). The occurrence and frequency of polyembryonic acorns in northern red oak genetic families has not been previously reported. A study was conducted to identify the occurrence and distribution of polyembryonic acorns within half-sib families. In addition, the relationships between acorn size and the occurrence of polyembryony was investigated.

3. MATERIALS AND METHODS

Two separate procedures, a greenhouse germination test and acorn dissections, were conducted to determine the number of embryos per acorn and to examine relationships between acorn size and number of embryos per acorn. Acorns were collected for study in 1995 from a northern red oak seedling seed orchard located on the Watuaga Ranger District of the Cherokee National Forest near Elizabethton, Tennessee. The orchard is a converted Tennessee Valley Authority progeny test established in 1973 (LaFarge and Lewis 1987).

Eleven trees from eight different seed sources were selected to provide acorns for the study (Table 3.1)[1]. Trees 850-2-23, 850-3-15, 850-4-20, and 850-5-2 were selected because they are half-siblings from one tree (850) from Overton County, Tennessee, and multiple seedlings per acorn had been previously observed in the progeny from tree 850-2-23. Tree 856-6-19 was selected as it also originated from Overton County, Tennessee. Tree 550-8-11 was selected because it produces the largest acorns in the orchard. The remaining 5 mother trees were selected at random for comparison.

Acorns were collected from the orchard periodically throughout the fall and were subjected to a floatation test (Olson 1974), and the floating acorns were discarded. All sinking acorns were then bulked by mother tree, placed in plastic bags and put in a cold room at 2°- 5° C for several months. The acorns from each tree were randomly divided into two groups for the acorn dissection and acorn germination studies (Table 3.1). The number of acorns used for the germination study and acorn dissection was variable due to low acorn

[1] All tables are located in the Appendix.

numbers in some families.

In only two tree collections (850-2-23, 856-6-19) were there adequate acorn numbers to allow segregation into size classes for dissection and germination. Acorns were sized based on the smallest cross-sectional dimension. The size classes were: 1 inch (2.54 cm), 13/16 inch (2.06 cm), 3/4 inch (1.91 cm), 5/8 inch (1.59 cm), and less than 5/8 of an inch (<1.59 cm). In the remaining nine individual tree seedlots, different sizes of acorns were present, but in an inadequate number for segregation into size classes.

For the germination test, acorns were germinated under greenhouse conditions in contrast to a standard germination test as described by Bonner and Vozzo (1987) for two reasons. The acorns had been collected for over a two month period and acorns had varying lengths of stratification with unknown losses in acorn quality. Additionally, the standard "cut and peel" method may not allow the full development of seedlings, and the resulting damage could have an effect on smaller embryos of multi-seeded acorns (Bonner and Vozzo 1987).

Acorns were planted in mid-January in Root trainer™ cells containing 45 cubic inches of soil media, with one acorn per cell planted approximately 2 centimeters below the soil surface. Following planting, the seed trays were placed in a heated greenhouse (16° - 20° C) to facilitate germination. After 30 days, each germinated acorn was evaluated for number of seedlings produced. Acorns that failed to germinate were not included in the analysis.

The numbers of embryos per acorn also were ascertained by dissection. Acorn dissections were conducted by Dr. Bob Cecich, North Central Forest Experimentation, USDA Forest Service, Columbia, MO. Each acorn was dissected by removing the cotyledons from the pericarp, followed by a cut along the transverse axis of the entire tissue complex at the

midpoint of the longitudinal axis. The number of embryonic axes were then counted. Acorns with extensive insect or fungal damage were not included in the analysis.

4. STATISTICAL ANALYSES

For the germination test and dissection data, the frequencies of polyembryonic acorns across families were compared using chi-square analysis. The data were analyzed using the SAS General Linear Model (GLM) procedure (SAS Institute 1996) to examine family differences in number of embryos per acorn. For the size class analysis, data for trees 850-2-23 and 856-6-19 were analyzed by tree and then combined to test for differences in polyembryony among size classes.

5. RESULTS

Germination Test:

The germination test revealed large differences among genetic families for the frequency of polyembryony (X^2= 132, 30 d.f., p=0.001). Only the families originating from Overton County, Tennessee, were polyembryonic (Table 3.2). In the germination test, the maximum number of seedlings per acorn was four. Overall, 77, 19, 3.3, and 1 percent of the acorns planted produced 1, 2, 3, and 4 seedlings per acorn, respectively. The number of embryos per acorn was different (p=0.0001) among families. Families 526-3-3, 323-7-26, 550-8-11, 902-4-2, 915-1-14, 6431-2-23 produced only single seedling acorns.

Families originating from Overton County, Tennessee, ranged from 1 to 4 seedlings per acorn with mean number of embryos per acorn between 1.09 and 1.68 (Table 3.3). Families 850-2-23 and 856-6-19 accounted for 78.8, 100, and 100 percent of the 2, 3, and 4 seedlings per acorn, respectively. The remaining Overton County, Tennessee, families produced only one or two seedlings per germinated acorn.

For the sized seedlots of families 850-2-23 and 856-6-19, the number of seedlings per acorn was significantly different among size classes (Table 3.2) (X^2= 116, 12 d.f., p=0.01). In general, the frequency of multiple seedlings per acorn increased as the size of the acorn increased. For the pooled data, the mean number of embryo per size class is given in Table 3.4. The mean number of embryos per acorn increased from 1.18 in the <5/8" size class to 2.62 in the 1" size class (Table 3.5).

Acorns from family 850-2-23 produced 86, 74, 54, 28, and 22 percent multiple seedlings in the 1", 13/16", 3/4", 5/8", and <5/8" size classes, respectively (Table 3.2). Family 856-6-19 had 44, 19, 4 and 0 percent multiple seedlings in the 13/16", 3/4", 5/8", and <5/8" size classes, respectively. In contrast, the large acorns from family 550-8-11 did not produce any multiple seedling acorns.

Acorn dissections:

The number of embryos per acorn differed between genetic families (X^2= 143, 18 d.f., p=0.001). Acorn dissections detected a maximum of three embryos per acorn (Table 3.5). The frequency and total number of embryos detected by dissection was less than the germination test. The mean number of embryos per acorn varied from 1.06 to 1.84 (Table 3.6). Only families 850-2-23, 850-3-15, 850-5-2, and 856-6-19 were found to have acorns with multiple embryos. For these four families, eighty-two percent of the acorns had a single embryo, 15 percent had two embryos, and 2 percent had three embryos per acorn. Family 850-2-23 exhibited the greatest amount of polyembryony, accounting for 78 percent of the two embryo acorns and 100 percent of the three embryo acorns. Within family 850-2-23, 26 percent of the acorns had single embryos, 64 percent had 2 embryos and 10 had percent with 3 embryo acorns.

Acorn dissections by size class revealed that as acorn size increased, the frequency of multiple embryo acorns generally increased (Table 3.5). Within the seedlots from family 850-2-23 and 856-6-16, there were significant differences between size classes (p=0.0001 and

p=0.0007 respectively). The mean number of embryos per acorn from family 850-2-23 and 856-6-19 increased from the <5/8" size class to the 1" size class (Table 3.7). All of the 1" sized acorns from family 850-2-23 contained multiple embryos, as compared to no multiple embryo acorns in the less than 5/8" size class. Acorns from family 856-6-19 primarily contained single embryo acorns. No multiple embryo acorns were found in the smallest size class (< 5/8"), while 52 percent of the acorns in the 13/16" size class were multiple embryos.

6. DISCUSSION

Only families 850 and 856 that originated in Overton County, Tennessee, produced multi-seedling acorns. Tennessee Valley Authority records do not indicate exact tree locations, but it is possible that the trees originated in the same stand and are related. No acorns had five or the maximum of six seedlings per acorn, which is biologically possible. This does not preclude, however, the possibility that all six ovules were pollinated, fertilized and yet failed to fully develop.

The acorn germination tests revealed more multiple seeded acorns compared to the acorn dissection data. Various reasons could account for this discrepancy including: differences in sample sizes between the germination test and dissections, some embryos were too small to be identified through dissection, or one or both samples were not representative of the population.

The results of the size class evaluation generally indicated that as the acorn size increases there was an increase in the occurrence of multiple seedlings increased. However, this is only apparent in families where polyembryony is present. The largest acorns in the orchard were produced by tree 550-8-11, yet showed no evidence of producing polyembryonic acorns.

The relationship between acorn size and multiple seedling occurrence may be related to the position of the female flower on the tree and/or pollination biology. In small acorns, the physical amount of space may preclude the full development of more than one embryo. All six ovules could have been successfully pollinated and fertilized, yet the location of the

female flower in the crown of the tree did not allow adequate resources to be allocated for the embryos to fully develop. It has been observed that smaller acorns come from the smaller lateral branches in the crown's interior, which presumably receive less resources during acorn development than main branches. Another possibility is that successful pollination of the six ovules may not have occurred in the interior of the crown, hence only a single seed develops. Studies of the pollination of pistillate flowers from the outside of the crown in forest grown trees have not identified a lack of pollination for fertilization (Cecich, R. 1997. USDA Forest Service Columbia, MO. Personnel Communication to M.A. Remaley). However, studies on pollen flow within the crowns of orchard grown trees have not been conducted and are needed to help resolve this issue.

To date, there are no published reports on the inheritance of polyembryony in *Quercus*. Tennessee Valley Authority records contained information about the ratios of acorn/seedling production in conjunction with the nursery phase of the 1973 progeny tests (Table 3.8)[2]. Fifteen of the 291 seed sources produced more seedlings than acorns planted. These seed sources included 850 from Overton County, Tennessee, suggesting a pattern of inheritance for polyembryony. However, the records indicated that seed source 856 did not produce more seedlings than acorns planted. It could be possible that seed source 856 did produce multi-seedling acorns, but had relatively poor germination overall. The Tennessee Valley Authority records furthermore were not adjusted for ungerminated acorns, so the data from seedlots with lower numbers of seedlings than acorns planted could be misleading.

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[2] Data on file at the University of Tennessee, Department of Forestry Wildlife and Fisheries.

Additional study of polyembryony in *Quercus* using controlled pollinations could lead to further understanding of the reproductive biology and inheritance of this phenomenon.

These results indicate that seed orchard and nursery managers should screen for tree or seed sources that produce polyembryonic acorns. While polyembryony is not common, it is undesirable to use seed sources that have a high percent of multiple seeded acorns, as projected nursery bed densities would be altered. In seed orchards, polyembryonic trees should be removed to prevent possible inheritance of the characteristic through seed and pollen contamination of other seedlots.

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APPENDIX

Table 3.1. Genetic family, parent tree number, parent origin, seedlot type and number of acorns used in the germination and dissection analysis for polyembryony.

Genetic Family	TVA Parent Number	Parent Origin (County, State)	Seed lot Type	Germination	Dissection
323-7-26	323	Trigg, KY	Bulk	26	10
526-3-3	526	Morgan, TN	Bulk	27	51
550-8-11	550	Cambell, TN	Bulk	27	0
850-2-23	850	Overton, TN	Sized	120	90
850-3-15	850	Overton, TN	Bulk	34	38
850-4-20	850	Overton, TN	Bulk	11	27
850-5-2	850	Overton, TN	Bulk	13	18
856-6-19	856	Overton, TN	Sized	87	87
902-4-2	902	Henderson, TN	Bulk	27	10
915-1-14	915	Henderson, TN	Bulk	27	10
6431-2-23	6431	Williamson, ILL	Bulk	26	10

Table 3.2. Genetic family, seed lot type, number of acorns and resulting number of polyembryonic acorns from the germination test.

Family	Seed Lot type	Number of Acorns Germinated	1 seedling acorns	2 seedling acorns	3 seedling acorns	4 seedling acorns
323-7-26	Bulk	26	26	0	0	0
526-3-3	Bulk	27	27	0	0	0
550-8-11	Bulk	27	27	0	0	0
850-2-23	1"	21	3	5	10	3
850-2-23	13/16"	27	7	17	3	0
850-2-23	3/4"	24	11	13	0	0
850-2-23	5/8"	25	18	4	1	0
850-2-23	<5/8"	23	18	4	1	0
850-3-15	Bulk	34	19	15	0	0
850-4-20	Bulk	11	10	1	0	0
850-5-2	Bulk	13	12	1	0	0

Table 3.2 (continued).

Family	Seed Lot type	Number of Acorns Germinated	1 seedling acorns	2 seedling acorns	3 seedling acorns	4 seedling acorns
856-6-19	13/16"	27	15	11	1	0
856-6-19	3/4"	26	21	5	0	0
856-6-19	5/8"	24	23	1	0	0
856-6-19	<5/8"	10	10	0	0	0
902-4-2	Bulk	27	27	0	0	0
915-1-14	Bulk	27	27	0	0	0
6431-2-23	Bulk	26	26	0	0	0

Table 3.3. Mean number of seedlings and standard deviation for genetic families that produced multiple seedlings in the germination test.

Family	Number of acorns planted	Mean number of seedlings	Standard Deviation
850-4-2	11	1.09	0.30
850-5-2	13	1.08	0.28
850-2-23	119	1.68	0.77
850-3-15	34	1.44	0.50
856-6-19	87	1.21	0.44

Table 3.4. Pooled data from Families 850-2-23 and 856-6-19 for the number of embryos per size class from the germination test.

Size class	Number of acorns	Mean	Standard Deviation
1"[3]	21	2.62	0.92
13/16"	54	1.67	0.61
3/4"	50	1.36	0.48
5/8"	49	1.16	0.37
<5/8"	33	1.18	0.46

[3] All acorns in the 1 inch size class came from Family 850-2-23.

Table 3.5. Number of embryos per acorn as detected by acorn dissections.

Family	Seed Lot type	Number of Acorns Dissected	1 embryo acorns	2 embryo acorns	3 embryo acorns
323-7-26	Bulk	10	10	0	0
526-3-3	Bulk	51	51	0	0
850-2-23	1	10	0	6	4
850-2-23	13/16"	20	12	8	0
850-2-23	3/4"	20	8	11	1
850-2-23	5/8"	20	15	5	0
850-2-23	<5/8"	20	15	5	0
850-3-15	Bulk	38	33	5	0
850-4-20	Bulk	27	27	0	0
850-5-2	Bulk	18	17	1	0
856-6-19	13/16"	27	15	11	1
856-6-19	3/4"	26	21	5	0
856-6-19	5/8"	24	23	1	0
856-6-19	<5/8"	10	10	0	0
902-4-2	Bulk	10	10	0	0
915-1-14	Bulk	10	10	0	0
6431-2-23	Bulk	10	10	0	0

Table 3.6. Mean number of embryos and standard deviation for genetic families which produced multiple embryos, as detected by acorn dissections.

Family	Number of acorns dissected	Mean number of seedlings	Standard Deviation
850-5-2	18	1.06	0.24
850-2-23	90	1.84	0.58
850-3-15	38	1.13	0.34
856-6-19	87	1.07	0.27

Table 3.7. Pooled data from families 850-2-23 and 856-6-19 for the number of seedlings per size class, as detected by acorn dissections.

Size class	Number of acorns dissected	Mean number of seedlings	Standard Deviation
1"[4]	10	2.40	0.52
13/16"	47	1.45	0.54
3/4"	46	1.39	0.54
5/8"	44	1.14	0.35
<5/8"	30	1.17	0.38

[4] All acorns in the 1 inch size class are from Family 850-2-23.

Table 3.8. Origin of TVA parent trees that produced more seedlings than acorns planted.

Parent Number	General Location County, State	Number of seed planted	Number of seedlings	Difference
407	Pickett, TN	221	240	19
501	Union, TN	234	240	6
510	Anderson, TN	300	318	18
519	Union, TN	280	288	8
520	Cambell, TN	348	436	88
524	Morgan, TN	250	282	32
530	Morgan, TN	80	96	16
571	Grundy, TN	260	276	16
572	Grundy, TN	280	318	38
617	Monroe, TN	353	372	19
850	Overton, TN	452	544	92
895	Washington, VA	217	220	3
2411	Buncombe, NC	315	318	3
2414	Buncombe, NC	100	208	108
2427	Henderson, NC	300	318	18

PART 4:

Relationship between acorn moisture content and time of collection after natural seed fall in northern red oak (*Quercus rubra* L.).

1. ABSTRACT

A two year study was conducted on the relationship between acorn moisture content and the number of days following natural seed fall in northern red oak (*Quercus rubra* L.). The effects of ambient weather conditions, shading, and time of collection after natural seedfall on acorn moisture content were evaluated. Acorns from open-pollinated genetic families from a seedling seed orchard were exposed to five levels of shading from full sunlight to 100 percent shade for a thirty day period. Results indicated that acorn moisture content failed to desiccate below 25 to 30 percent, the threshold of embryo mortality, for the range of environmental conditions encountered. In seed orchards or natural stands, other factors such as predation should be of greater concern than acorn desiccation in the timing of acorn collections.

2. INTRODUCTION

Oak species are propagated for reforestation in commercial nurseries by acorns. Seed collectors meet nursery demands by collecting acorns throughout the fall season during the period when they mature and drop. The care of collected acorns should be based upon the biological characteristics of the seed. Acorns are classified as "temperate recalcitrant" seeds, and collection procedures should focus on the preservation of the living embryo (Bonner and Vozzo 1987). Moisture content is a critical factor for acorn viability. Desiccation below approximately 25 to 35 percent total moisture content can cause acorn embryo mortality (Bonner 1993).

Studies on acorn moisture content have primarily focused in two areas: the changes in moisture content related to acorn maturation (Bonner 1974, 1976) and changes in moisture content following collection and in storing acorns (Bonner and Vozzo 1987). Water loss has been found to occur through the cutinized exodermal layer, in addition to the vascular bundles in the cup scar (Korstian 1927, Bonner 1968). Korstian (1927) studied the loss of acorn moisture content following acorn drop. He found that moisture content will decrease from 65 percent to 15 percent following 180 hours of continued drying on a laboratory bench.

Acorns usually mature and fall from the tree from August to December (Olson 1974). This is a critical time period for seed collectors, who are concerned with locating seed bearing trees and collecting enough seed to meet demands before predation by animals. In addition to acorns produced in natural stands and urban trees, oak seed orchards are now beginning to bear acorns, using nets to catch mature acorns and to facilitate collection (Schlarbaum *et*

al. 1993, Byram and Lowe 1996). Acorns are collected off the nets based on the amount of acorn drop, concerns about acorn desiccation, predation pressure, and labor availability. In a northern red oak (*Quercus rubra* L.) seedling seed orchard located near Elizabethton, Tennessee, acorns are usually collected between two to seven day intervals from individual trees by two to four persons from mid-September to mid-November (Proffitt, C.K. 1997 USDA Forest Service Elizabethton, TN. Personal communication to M.A. Remaley).

For seed collectors and oak seed orchard managers, there is a deficiency in knowledge of the critical factors affecting acorn moisture content after maturation and drop currently exists. A study was conducted in order to determine the maximum length of time acorns can be left in simulated seed orchard conditions before desiccating below 25 percent moisture content.

3. MATERIALS AND METHODS

A two year, replicated experiment was designed to determine environmental effects on acorn moisture content. In 1994 and 1995, ten heavy-bearing trees from a northern red oak seedling seed orchard (Table 4.1)[1] were selected to provide acorns for the experiment. The orchard is a converted Tennessee Valley Authority progeny test established in 1973 from seed sources throughout the Tennessee Valley Region (LaFarge and Lewis 1987).

In early September of both years, each tree had orchard netting placed underneath the crown. The trees were monitored for a simultaneous large drop of sound acorns within a 24 hour period. It was desired to collect all acorns for the experiment from all trees on the same day to decrease possible variation in moisture content and decrease the effects of different maturation rates. A large number of acorns per tree (450) were needed to complete a sampling scheme of 30 acorns for 15 two day intervals after initial collection from the tree. The nets of each tree were cleaned daily of acorns to ensure that the collections would come from a single day of drop.

When the trees had dropped a critical number of acorns, the acorns were collected from the nets and placed in water to separate sound, sinking acorns from floating, insect parasitized acorns (Olson 1974). The sinking acorns were then bagged, maintaining tree origin. A range of acorn sizes were observed to occur in each seedlot, but inadequate numbers prohibited sizing the seedlot for uniformity in size. In 1994, collection from four trees were delayed by four days because acorn drop was insufficient for the experiment.

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[1]All tables are located in Appendix.

Acorn collection occurred on October 19, 1994 and October 23, 1994 for six and four of ten trees respectively. In 1995, all ten trees were collected on October 22. Only three trees (Table 2.1) were used in both 1994 and 1995 because of variable acorn production between the two years.

The experiment was conducted on the University of Tennessee's, Plant Sciences Farm, located near Knoxville, Tennessee. To simulate difference shading regimes that acorns would experience under tree crowns, acorns were placed under varying shaded treatments. Furthermore, it is standard practice to place orchard netting under the crowns of trees on top of the existing orchard sod to facilitate collection. In recognition of these facts, the experiment consisted of placing orchard netting in full sun over a dense grass sod. For each of the two replications, 3 wooden frames (9.1 meters in length by 1.5 meters in width by 20 centimeters in height), covered with standard poultry netting (2.5 centimeters holes) to protect against predation, were placed 1.5 meters apart on the orchard netting. Each replication contained four shade treatments and a full sunlight treatment that were randomly assigned to five 1.5 meter by 1.5 meter plots. Thirty, 50, and 78 percent greenhouse shade cloth were fastened over three plots respectively. The fourth shade plot received total shade by covering with .635 cm plywood and the fifth plot received no shade. Acorns from each individual trees collection was then randomly assigned to a treatment plot within a replication.

At two day intervals, a random sample of thirty acorns was removed from each treatment plot at approximately 8:00 am to determine acorn moisture content. The sample from each treatment plot then was subjected to a floatation test, rapidly removed from water and towel dried. From the thirty acorns, five sinking acorns were randomly sampled for

moisture content determination and weighted. The five acorns were dissected into pieces and oven dried at 105°C in a forced draft oven for 24 hours. Moisture content was then calculated as a percent of fresh weight (Bonner and Vozzo 1987). From the moisture content data from each treatment plot, the change in moisture content was calculated between adjacent sample dates to examine moisture content fluctuations in acorns relative to weather parameters.

During the experiment, maximum and minimum temperature, and precipitation was measured at the weather station located at the Plant Sciences Farm. From this data, maximum temperature, minimum temperature, and precipitation were calculated for each two day sample period. Relative humidity was not analyzed, as the weather station was not equipped to measure relative humidity. In addition, there were significant differences in topography and distance between the nearest weather station that records relative humidity and the location of the experiment. Relative humidity ranged from 30 to 100 percent in both years of study as reported by the National Weather Service for Knoxville, Tennessee.

4. STATISTICAL ANALYSIS

Moisture content and interval change in moisture content were analyzed for each year and combined years using the General Linear Model (GLM) procedure (SAS Institute 1996). Separate analyses were used to examine the effect of the number of days from acorn collection and weather variables on moisture content, as they were found to be linearly dependent. Pearson correlation coefficients were calculated to determine relationships among variables within and across years.

5. RESULTS

In 1994 and 1995, acorn moisture content failed to fall below the threshold of 25 percent moisture content for acorn embryo viability, regardless of treatment (Figures 4.1 - 4.4)[2]. Maximum and minimum temperatures did not appear to cause significant changes in acorn moisture content (Figures 4.5 and 4.6). Correlation coefficients calculated within or across years by treatment indicated relatively weak associations (r = -.30 to + .30) among moisture content, change in moisture content and environmental variables (Tables 4.7 - 4.9).

Weather variables affected moisture content differently in each year [R^2=0.377 (1994), R^2=0.76 (1995)]. Precipitation [p=0.0001 (1994), p=0.0001 (1995)], minimum temperature [1994 p=0.046 (1994), p=0.0136 (1995)] and maximum temperature [p=0.0024 (1994), p=0.1650 (1995)] significantly affected moisture content, except for maximum temperature in 1995. The shading treatments [p=0.0001 (1994), p=0.0001 (1995)] was also found to effect moisture content in both years.

The duration of exposure from initial acorn collection affected moisture content moderately within year [R^2=0.695 (1994), R^2=0.807 (1995)]. In both years, sample day affected acorn moisture content (1994 and 1995 p=0.0001) as did shading treatment [p=0.0001 (1994), p=0.0001 (1995)].

For the change of moisture content between each sample interval, weather variables were found to slightly influence moisture content between sample intervals [R^2=0.208 (1994), R^2=0.302 (1995)]. In both years, only precipitation related to a change in moisture content

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[2] All figures are located in Appendix.

(1994 and 1995 p=0.0001) was found to influence the change in moisture content and treatment, maximum and minimum temperature all were non-significant ($p \geq 0.393$). The duration of exposure explained slightly more change in moisture content than the weather variables [R^2=0.337 (1994), R^2=0.379 (1995)]. Within each year, the experimental duration was significant (1994 and 1995 p=0.0001) and treatment, maximum and minimum temperature all had a non-significant effect ($p \geq 0.553$).

In the combined analysis, weather variables and duration of exposure did have a large effect on moisture content variability (R^2=0.867). Year, treatment, maximum temperature, precipitation, day of sample, and treatment day interaction were all significant ($p < 0.003$). Minimum temperature was non-significant (p=0.212). Comparably, the effects of weather and experimental duration did not greatly effect the change in moisture content between sample intervals (R^2=0.473). Year, treatment, maximum temperature, day of sample, and treatment day interaction were all non-significant ($p > 0.279$). Precipitation and minimum temperature, however, did have a significant (p=0.001, p=0.107 respectively) effect on the change in moisture content.

6. DISCUSSION

The results of this experiment found that acorns never desiccated to below the threshold of embryo viability in either year of study. Therefore, the objective of the experiment to determine the maximum length of time acorns can be left in simulated seed orchard conditions before desiccating below 25 percent moisture content was not determined. This is in direct contrast to work by Korstian (1927) and what is commonly believed to occur in orchards or natural stands. Under the weather conditions experienced in the both years, acorn collections could have been delayed for as much as thirty days after drop.

The correlation coefficients provide evidence of the negligible effects of the weather and treatments. The correlation coefficients did not follow an anticipated relationship among maximum temperature, shading, and moisture content, e.g., higher temperatures and decreasing amounts of shading should result in more desiccation. For example, the 1994 correlations between maximum two day temperature and moisture content for 0%, 30%, 50%, 78% and 100% are -.23, .01, -.07, - .01, and -.43, respectively. This indicated a variable effect of maximum temperature and shading on acorn moisture content.

Moisture content was significantly affected by weather variables, duration of experiment, and treatment. However, this is of relatively little importance since acorns did not desiccate to levels of embryo mortality. Over the duration of the experiment there were minor changes in moisture content. If the acorns initially had a lower moisture content, the effects could have been more profound. In other weather regimes, hotter or cooler climates or other species of oak acorns, acorn moisture contents may be more sensitive to these factors

and embryo mortality could occur.

These results indicated that acorn desiccation did not occur over a thirty day period and thereby may not be a critical concern in seed orchards with similar weather regimes. Embryo viability, as indicated from acorn moisture content, was retained for thirty days after initial drop from the tree. Correspondingly, collection of acorns should be scheduled around labor availability and predation pressures and not concerns of acorn desiccation. For collections from naturally occurring trees under similar environmental conditions, the results indicate that acorn collection under similar weather conditions probably can be delayed until after acorn drop is complete without experiencing excessive desiccation.

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APPENDIX

Table 4.1. Seed sources from the Watuaga northern red oak seed orchard used for the acorn quality study.

Family	Year of study	% shade	Mother Tree source County, State
330-8-2	1995	30	Trigg, KY.
405-4-5	1994	0	Pickett, TN.
513-5-23	1995	50	Cambell, TN.
528-2-16	1994,1995	50,78	Morgan, TN.
557-1-6	1994	30	Morgan, TN.
558-1-22	1994	0	Cambell, TN.
577-1-19	1994	78	Claiborne, TN.
580-1-1	1994	100	Claiborne, TN.
595-6-19	1995	0	Van Buren, TN.
601-2-2	1994	78	Buncombe, NC.
600-2-8	1995	100	Buncombe, NC.
701-5-11-2	1995	30	Anderson, TN.
905-9-22	1995	78	Henderson, TN.
911-6-17	1995	100	Henderson, TN.
914-1-24	1994,1995	50,0	Henderson, TN.
1164-2-10	1994,1995	30,50	Monroe, TN.
2451-1-15	1994	100	Anderson, TN.

Table 4.2 Pearson correlation coefficients among moisture content and weather variables for the 1994 study.

	Maximum temperature	Minimum temperature	Precipitation
Moisture content	-0.092	0.224***	0.341****
Maximum temperature		0.304****	0.239***
Minimum temperature			0.460****

Table 4.3. Pearson correlation coefficients among moisture content and weather variables for the 1995 study.

	Maximum temperature	Minimum temperature	Precipitation
Moisture content	-0.143***	-0.077	0.211***
Maximum temperature		0.680****	0.168**
Minimum temperature			0.474****

* P= .10, ** P= .05, *** P= .01, **** P=.001

Table 4.4. Pearson correlation coefficients for moisture content among shade and weather variables by year and treatment.

Year	Treatment (% shade)	Maximum temperature	Minimum temperature	Precipitation
1994	0	-0.150	-0.164	0.330 *
1994	30	0.021	0.490 ***	0.471 ***
1994	50	-0.052	0.625 ****	0.551 ****
1994	78	0.010	0.335 *	0.441 **
1994	100	-0.344 *	-0.343*	0.052
1995	0	-0.258	-0.106	0.450 **
1995	30	-0.456 **	-0.406**	0.311*
1995	50	-0.331*	-0.176	0.322*
1995	78	-0.184	-0.026	0.346
1995	100	0.429 **	0.231	0.039

* P= .10, ** P= .05, *** P= .01, **** P=.001

Table 4.5. Pearson correlation coefficients among moisture content and study variables across years.

	Maximum temperature	Minimum temperature	Precipitation
Moisture content	-0.398****	-0.208****	0.369****
Maximum temperature		0.662****	-0.082
Minimum temperature			0.222****

Table 4.6. 1994 Pearson correlation coefficients for interval change in moisture content among study variables across years.

	Maximum temperature	Minimum temperature	Precipitation
Change in moisture content	0.175**	0.005***	0.431****
Maximum temperature		0.034****	0.239***
Minimum temperature			0.459****

* P= .10, ** P= .05, *** P= .01, **** P=.001

Table 4.7. 1995 Pearson correlation coefficients for interval change in moisture content among study variables across years.

	Maximum temperature	Minimum temperature	Precipitation
Change in moisture content	0.110	0.321****	0.543****
Maximum temperature		0.680****	0.167**
Minimum temperature			0.474****

* P= .10, ** P= .05, *** P= .01, **** P=.001

Table 4.8. Pearson correlation coefficients for interval change in moisture content among study variables by year and treatment.

YEAR	TREATMENT	Maximum temperature	Minimum temperature	Precipitation
1994	0	0.332	0.348	0.577***
1994	30	0.220	0.343*	0.415**
1994	50	0.221	0.392**	0.616****
1994	78	0.180	0.022	0.369**
1994	100	-0.236	0.007	0.184
1995	0	0.171	0.332*	0.642****
1995	30	0.110	0.429**	0.705****
1995	50	0.193	0.467**	0.564***
1995	78	0.023	0.334	0.616****
1995	100	0.124	0.058	0.227

* P= .10, ** P= .05, *** P= .01, **** P=.001

Table 4.9. Change in moisture content correlations across years for study variables.

	Maximum temperature	Minimum temperature	Precipitation
Change in moisture content	0.067	0.240****	0.482****
Maximum temperature		0.662****	-0.082
Minimum temperature			0.222****

* P= .10, ** P= .05, *** P= .01, **** P=.001

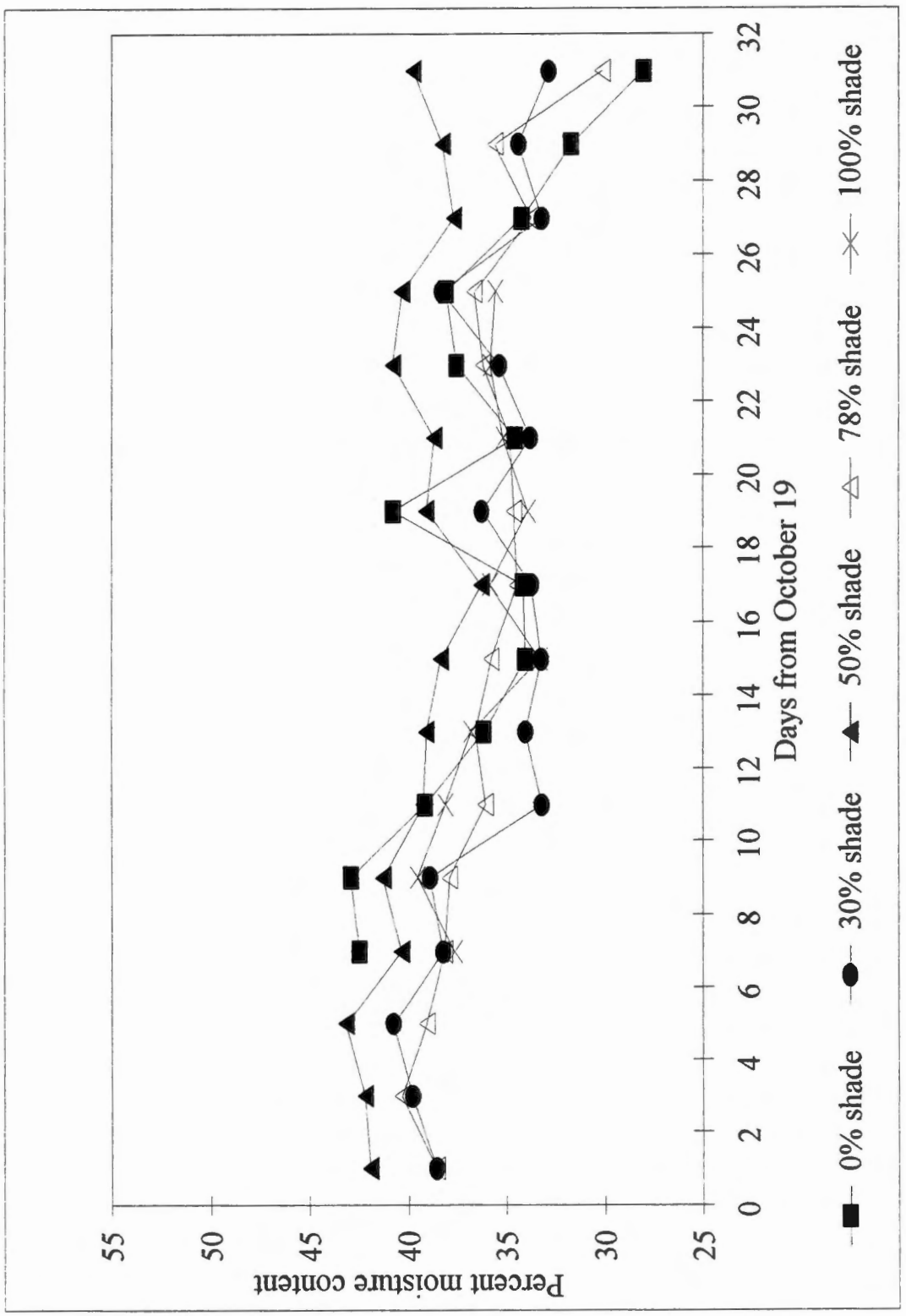
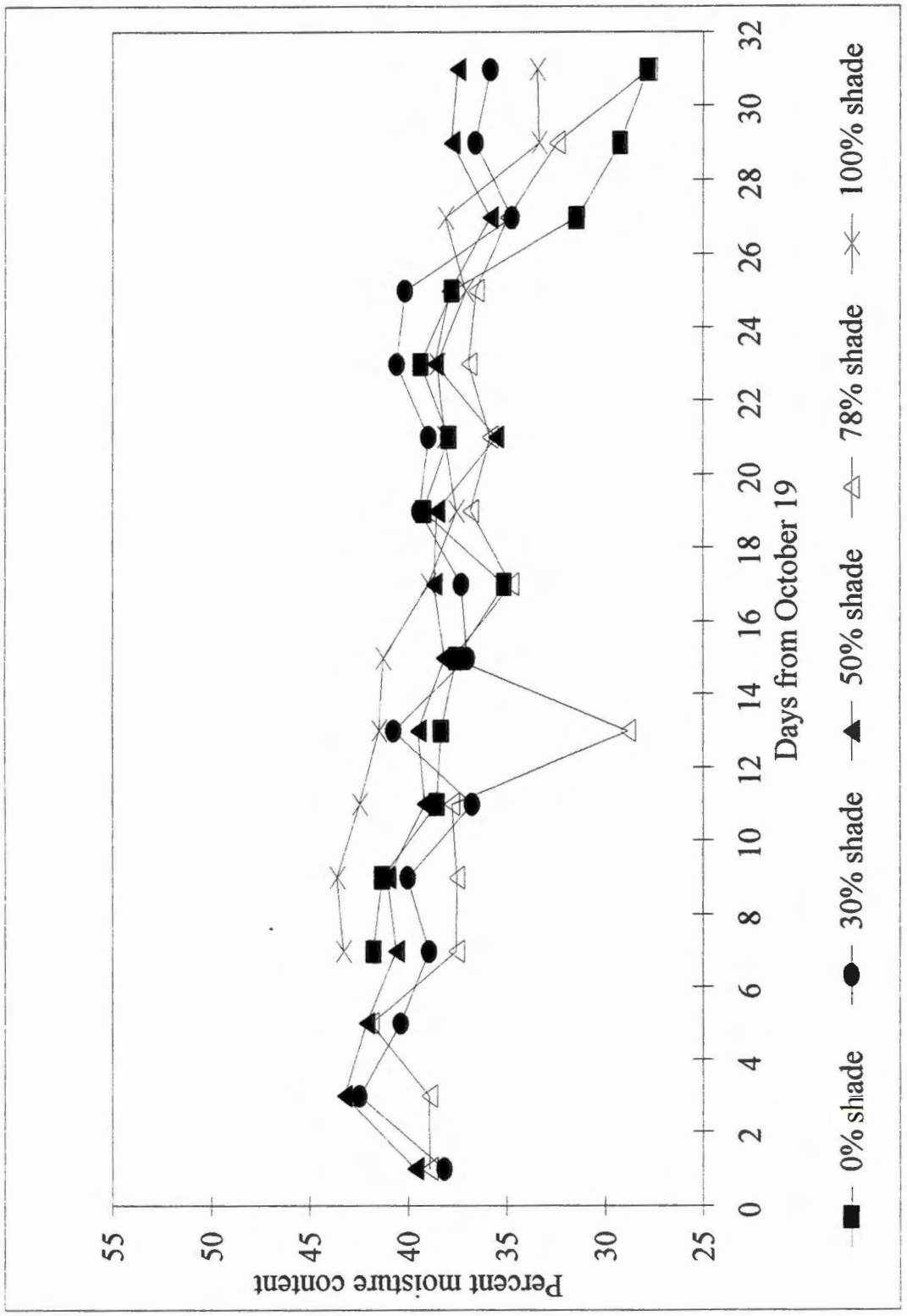


Figure 4.1. 1994 replication 1 moisture content by day and treatment.



4.2. 1994 replication 2 moisture content by day and treatment.

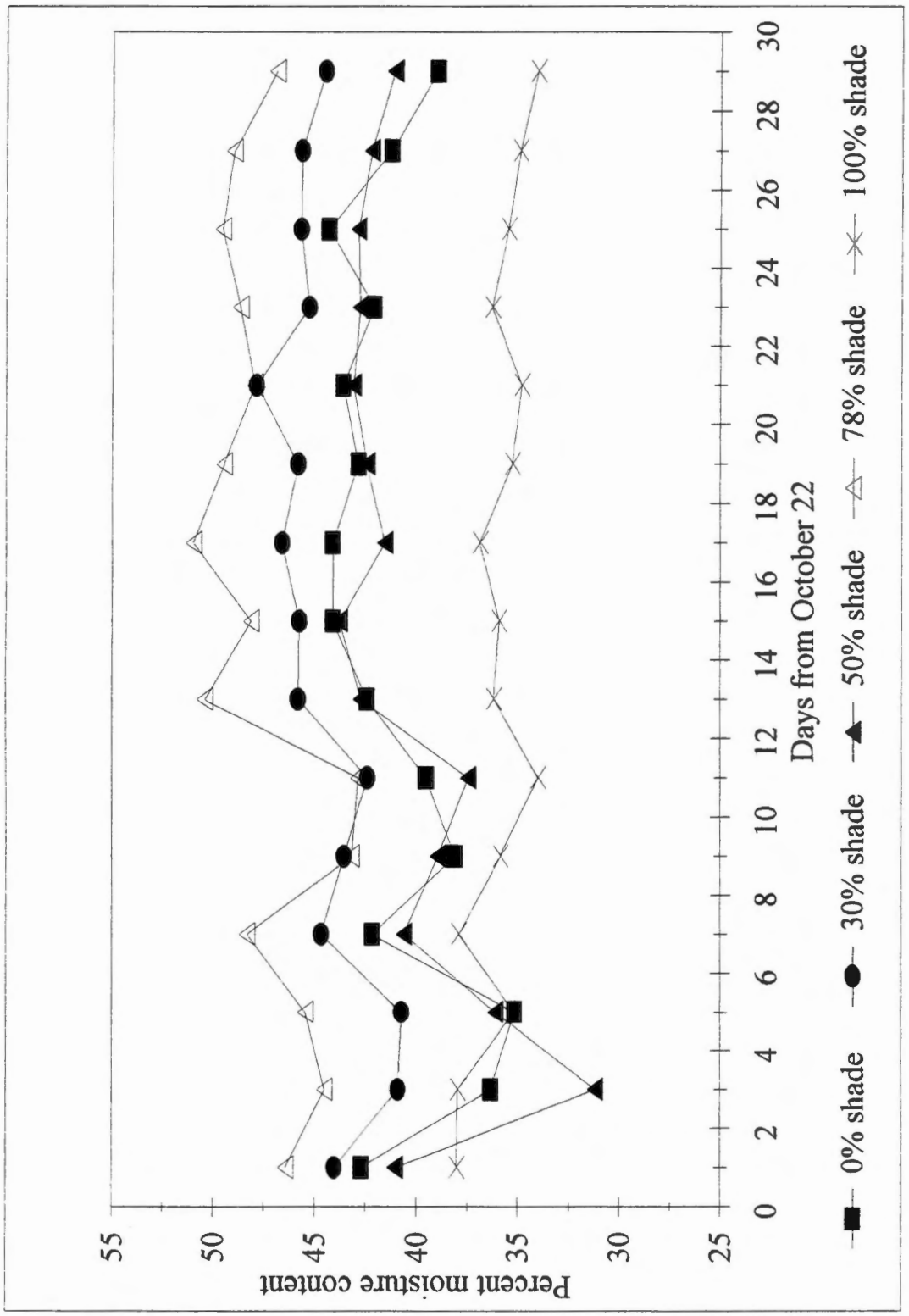


Figure 4.3. 1995 replication 1 moisture content by day and treatment.

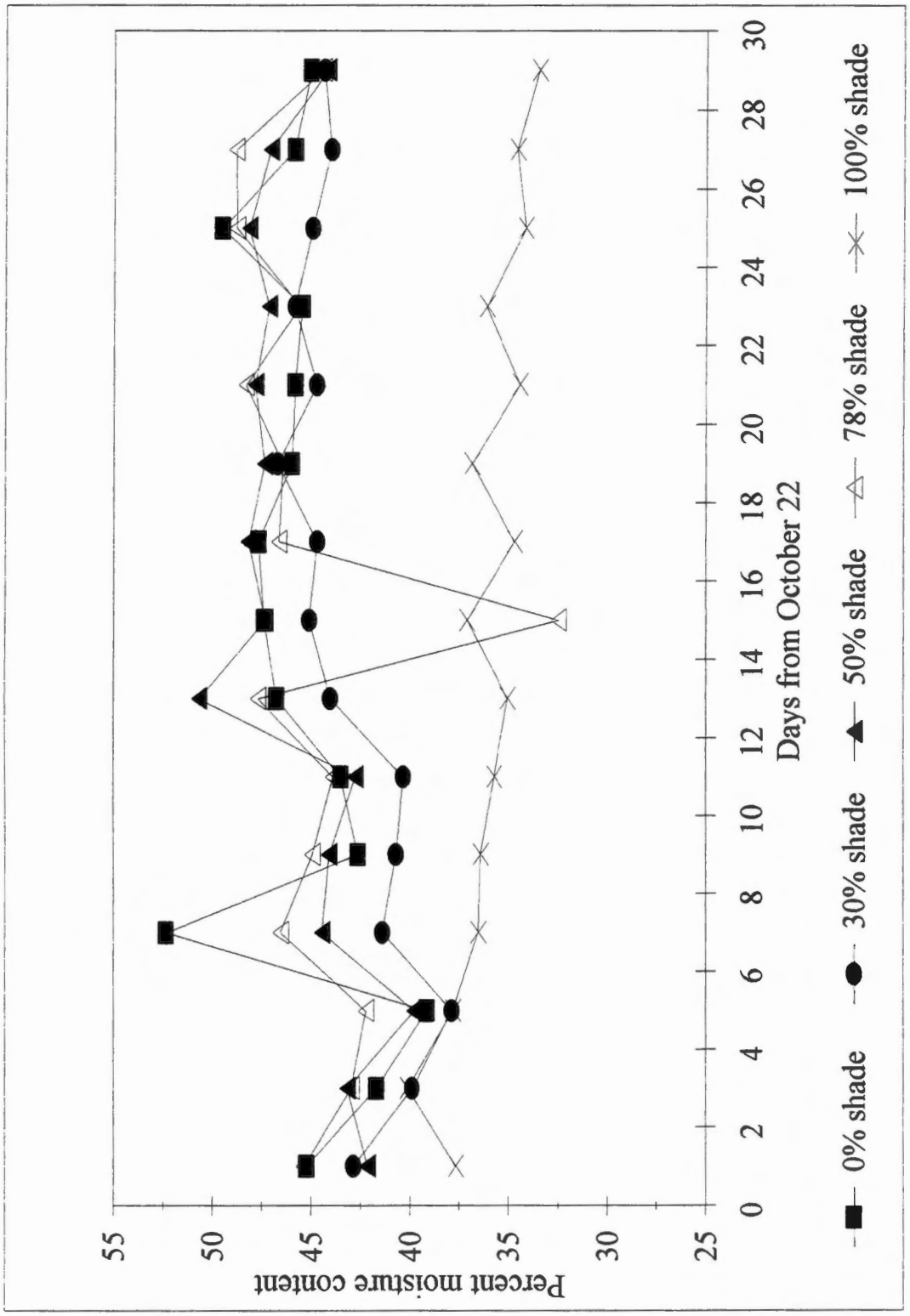


Figure 4.4. 1995 replication 2 moisture content by day and treatment.

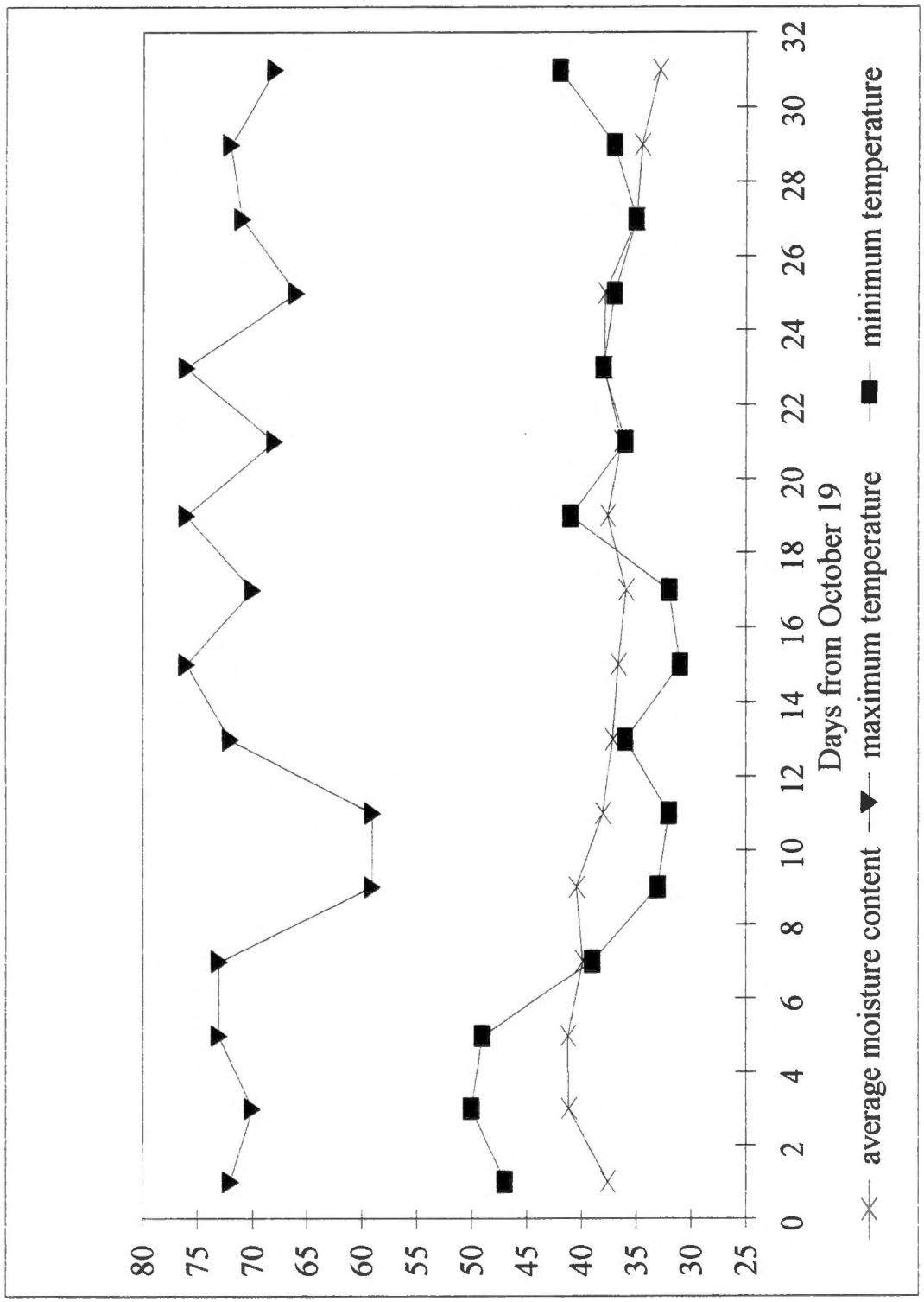


Figure 4.5. 1994 average moisture content in percent and temperature data in degrees Fahrenheit.

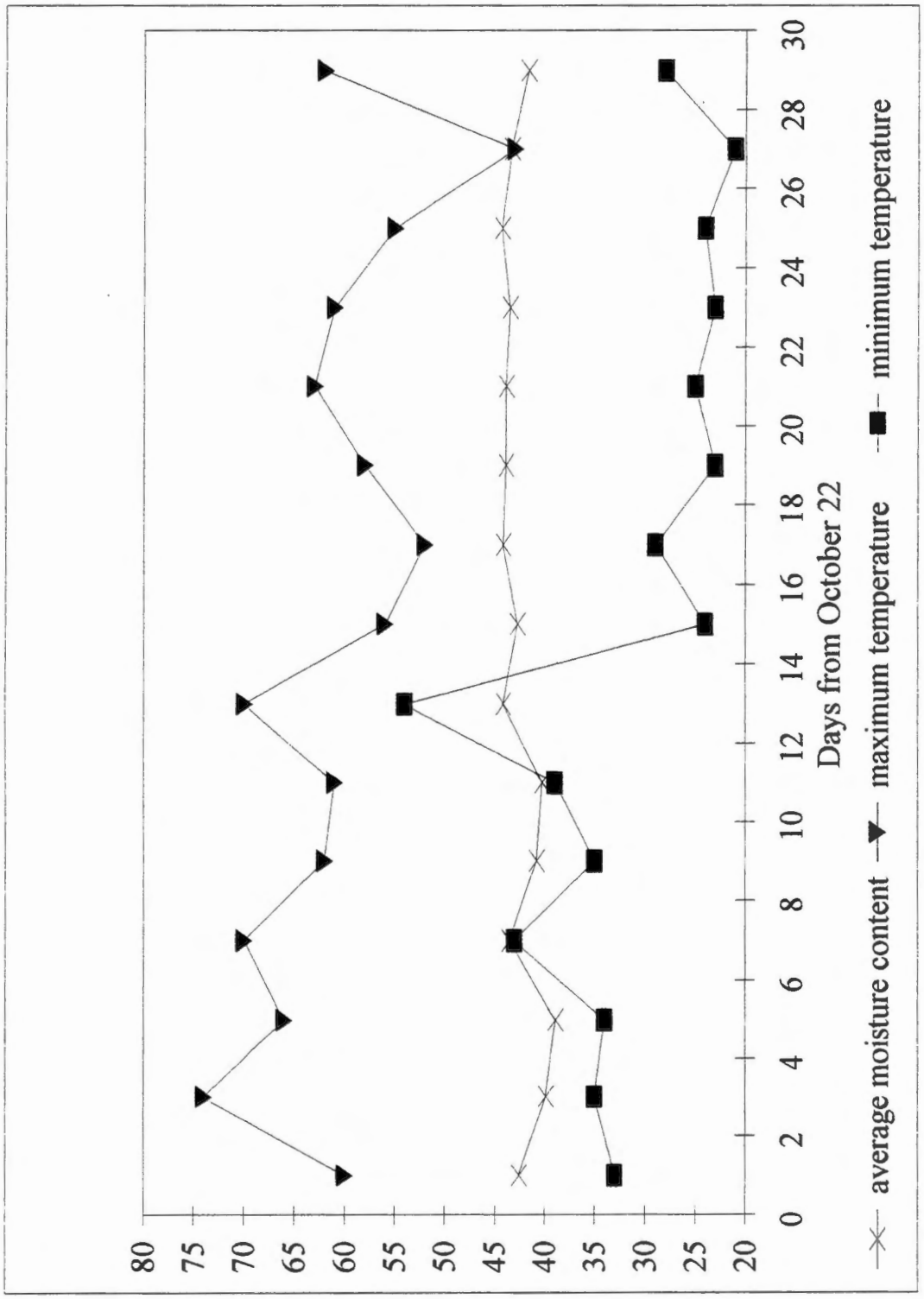


Figure 4.6. 1995 average moisture content in percent and temperature data in degrees Fahrenheit.

Vita

Mark Alexander Remaley was born in Mountain View, California, September 11, 1970. After moving around the country through childhood, Mark graduated from High School in Germantown Tennessee in 1988. Mark attended the University of Tennessee for his undergraduate work in 1988 in the school of Business Administration. In 1992, he transferred to the Department of Forestry Wildlife and Fisheries and was awarded a degree in Forest Resource Management in 1994. In 1994, Mark received an assistantship in the Department of Forestry Wildlife and Fisheries for graduate work leading to a Masters of Science degree. In January 1998, Mark accepted a position with International Paper Company in Wilmington North Carolina as associate forester in Cape Fear Logging and Fiber Supply division. In July 1998, Mark was promoted to Procurement Analysist and transferred to the Riegelwood Paper Mill. Mark married Laurin Gendreau in 1997, and they currently reside in Wilmington, North Carolina.