# INTERACTIONS AMONG SILVICULTURAL INTENSITY, GENOTYPE, AND ENVIRONMENT AND THEIR EFFECTS ON THE GROWTH AND MORTALITY OF LOBLOLLY PINE AND SLASH PINE FAMILIES

A Thesis

by

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# ABSTRACT

Managed pine forests are central to the economic vitality of the southeastern US. Over the past fifty years, the productivity of managed pine forests of this region have increased significantly with the development of new silvicultural technologies and the use of improved tree genetic material. Of the pine species present in the southeastern US, loblolly pine has arguably been the most intensively studied and widely planted by forest managers.

Efficient operational deployment of improved genetic materials requires an understanding of how possible site conditions and silvicultural treatment may interact to affect maximum yield. There are a wide range of site conditions in the south as the result of regional climate gradients, soil type and soil drainage patterns. On the western edge of loblolly pine's natural extent, Texas has a drier climate than areas to the east, and in Louisiana, there are also poorly drained Ultisols that are found in areas with little relief and are prone to flooding. However, on the basis of 10-year forest inventory data of pure-family plots from three different sites and under two levels of cultural regime intensity, my study found that superior genotype, Lob 5 from South Carolina, still showed best performance in the Western Gulf area, and high intensive treatment could improve stand growth and resistance to wind damage significantly. Further, my study compared the stand production and dynamics between pure- and mixed-family plots. I found that Lob 5 and Lob 4 showed the growth traits of competitive ideotype, and low intensive treatment increased the deployment effect significantly for competitive ideotype. Finally, my study examined leaf area index (LAI) and foliar nitrogen concentration (foliar N). The result showed that fast growing genotype had lower LAI and foliar N than slow growing one. It indicated that fast growing genotype had high resource use efficiency and nutrient requirement.

This research provided critical information to guide industrial forest management in the WG (Western Gulf) area. First, introduced superior genotype continued to show good performance in this area. Second, combination of good genotype and high intensive treatment would increase plantation production significantly. Third, identification of ideotype would increase the accuracy of growth potential estimation in progeny test.

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# NOMENCLATURE

| | |
|---|---|
| LAI | leaf area index |
| N | nitrogen |
| FN | foliar nitrogen concentration |
| FBRC | forest biology research cooperative |
| PPINES | pine productivity interactions on experimental sites |
| WG | western gulf |
| EG | eastern gulf |
| BGL | Bogalusa |
| DR | DeRidder |
| KB | Kirbyville |
| LI | low intensity |
| HI | high intensity |
| Lob | loblolly pine |
| BAHA | basal area per hectare |
| VOLHA | stem volume per hectare |
| DBH | diameter at breast height |
| ANOVA | analysis of variance |
| G | genotype |
| E | environment |

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# CHAPTER I

# INTRODUCTION, LITERATURE REVIEW AND HYPOTHESES

## I.1 Importance of Southern Loblolly Pine Plantations

Southern pine forests are central to the economic vitality of the nation: the forest products industry is responsible for 5.5% of the jobs and 7.5% of total industrial output in the southeastern United States (Wear and Greis, 2002). This area also produces more industrial timber than any other country in the world, and comprises almost one-half of the world's industrial forest plantations (Prestemon and Abt, 2002). Timber market models forecast that timber production in the United States will increase by about a third between 1995 and 2040. Nearly all of this growth will come from the South, where production is forecast to increase 56% for soft-woods and 47% for hardwoods (Wear and Greis, 2002).

Loblolly pine is by far the most important forest tree species in the South, with over 1 billion seedlings planted annually by the forest industry and non-industrial private forest landowners (McKeand *et al.*, 2003b). In the pine forest land area of the South, about half is under some level of forest management, and is primarily planted to loblolly pine (Smith *et al.*, 2009).

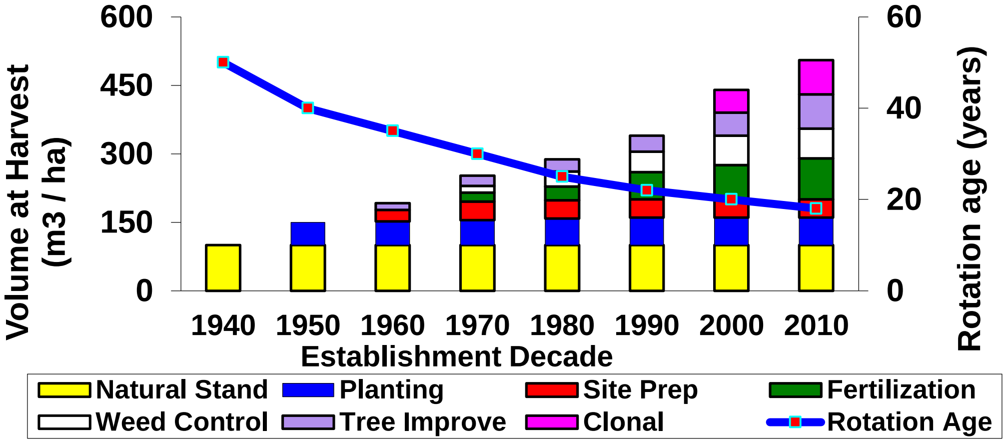
## I.2 Combined Effects of Silvicultural Treatments and Genetic Improvement

### I.2.1 Literature Review

Over the past 50 years, the extent of southern pine plantations has increased from $8.1\times10^5$ to $1.3\times10^7$ $ha^2$, and the production per hectare has increased from 6.2 $m^3ha^{-1}yr^{-1}$

to 27.6 $m^3ha^{-1}yr^{-1}$ (Fox *et al.*, 2007). These productivity gains are attributable to the adoption of intensive silvicultural practices, such as site preparation, fertilization, weed and pest control, and breeding of elite genotypes (Fox *et al.*, 2007; Aspinwall *et al.*, 2011; Figure 1-1). Research has demonstrated the significant influence that these management practices can have on loblolly pine productivity. For example, results of seven long-term experiments from five southern states showed that loblolly pine growth responses to intensive cultural regimes ranged from a 2- to 3.5-fold increase at age 15 years over controls (Jokela *et al.*, 2004). Estimated gains in volume production for plantations with genetically improved stock that are being established in the current era range from 10% to 30% over unimproved planting stock (McKeand *et al.*, 2003b). There are three deployment strategies utilized to produce planting stock for southern plantations which are listed in increasing order of genetic gain, including open-pollinated forestry, full-sib family forestry and clonal forestry (McKeand *et al.*, 2003b).

Figure 1-1: Estimated total yield and contributions of individual silvicultural practices to productivity of pine plantations in the southern United States from 1940 to 2000. (Redrawn by E. Jokela from Fox et al. 2007)



Obtaining optimum plantation production requires the use of integrated systems that couple intensive management of both site and genetic resources. Managed pine forests generally undergo a combination of management practices over stand history, including soil mounding (bedding), the planting of genetically improved pine seedlings, levels of competition or 'weed' control, and fertilization (Jokela *et al.*, 2010). One study estimated that if the best genetic material is planted with the best silvicultural inputs, mean annual increments of 20.7 $m^3ha^{-1}yr^{-1}$ can be routinely obtained (Allen, 2008). Therefore, interactions among the forest plantation management options, for example, genetic improvement and silvicultural treatments, need to be understood and taken into account (Allen *et al.*, 2005). However, research is rare that quantifies the combined effects of cultural regimes and genetic improvement on the production of a first-generation full-sib loblolly pine family (Roth et al. 2007). To examine the interaction between genetics and silviculture, a series of field research installations were established by University of Florida's Forest Biology Research Cooperative across the Gulf Coastal Plain. These installations had plots of single families of loblolly pine and in some cases slash pine (*Pinus elliottii Engelm.*), mixed plots of loblolly pine families, and were maintained at two levels of silvicultural intensity (High and Low). The results from these research sites have been reported in recent years, with studies focused on either the Eastern Gulf Coastal Plain (Chmura *et al.*, 2007; Roth *et al.*, 2007; Staudhammer *et al.*, 2009), or early stages of growth (<3 years) for the Western Gulf Coastal Plain (Chmura *et al.*, 2007). For example, in a seven-year-old loblolly pine plantation of the Eastern Gulf Coastal Plain, significant interactions of family and silvicultural treatment for stem volume were found at stand ages of five- and seven-years (Roth *et al.*, 2007; Staudhammer *et al.*, 2009), and in a two-year-old loblolly pine plantation of the Western Gulf Coastal Plain, the effect of combined fertilization and weed control increased volume index by 58% compared to the control (Chmura *et al.*, 2007), However, the Chmura et al (2007) results are limited to the early growth period (age 3 years), and since this time multiple hurricanes and a drought have hit the study area.

In this study, I examined the combined effects of fertilization and genotype on stand growth after a 10-year growing period for sites in the Western Gulf Coastal Plain. My research tested the following hypotheses.

### I.2.2 Hypothesis

H1: If a genotype can show better growth performance under low silvicultural practices, then it will show better growth response to the high silvicultural intensity.

## I.3 Genotype × Environment Interactions

### I.3.1 Literature Review

In trying to maximize plantation productivity, foresters often introduce elite loblolly pine families into areas with different climatic and edaphic conditions than found in their original provenance. With this process, the underlying question is if the elite families will continue to show good growth performance in the new environment and how the cultural treatments will interact with genotype and environment to affect the growth performance. Therefore, site- and genotype- specific management regimes could then be developed to insure that intensive management is practiced effectively and sustainably across the region (Fox, 2000). However, only limited information is available on G × E interactions for southern pine species using family block experiments among different intensities of silvicultural treatments (McCrady and Jokela, 1998; Roth *et al.*, 2007).

The G × E interaction may be manifested as rank changes among genotypes when grown under different environments/cultural conditions, or as "scale effects" in which the absolute differences among genotypes change with environment (Roth *et al.*, 2007). Past studies of different genotypes and locations showed that very few genetic × environmental (G × E) interactions had been found for first- and second-generation open pollinated families under traditional silvicultural systems (McKeand *et al.*, 1997; McKeand *et al.*, 1999; Martin and Shiver, 2002; McKeand *et al.*, 2003a; McKeand *et al.*, 2006). For example, by comparing 12-year improved and unimproved loblolly pine genotypes from 31 sites in the Coastal Plain and Piedmont area, researchers did not find any G × E interactions (Martin and Shiver, 2002). For a more recent example, after two-year growing periods in my research sites, there were no rank change of volume index in the four loblolly pine genotypes across silvicultural intensity (Chmura *et al.*, 2007). The likelihood of G × E interactions may increase with intensified genetic selection (Bridgwater *et al.*, 2005), and increased silvicultural intensity (McKeand *et al.*, 2006). For example, in two sites separately located in Florida and Georgia, for five-year-old full-sib loblolly stands under combined silvicultural management, researchers found that there was significant interaction between genotype and location ($p<0.028$) for basal area and standing stem volume (Roth *et al.*, 2007). In the same forest stands after another two-year growing period, a more significant interaction of location, deployment and genotype ($p<0.0001$) was found (Staudhammer *et al.*, 2009).

In this study, I will determine if there are any rank changes throughout a ten-year growing period for Western Gulf study sites. I will compare ten-year stand growth of six full-sib loblolly pine genotypes, with two intensity levels of silvicultural treatments in three different research sites. Through the comparison of stand growth in the three sites, the following hypotheses will be tested.

### I.3.2 Hypothesis

H1: There will be G × E interactions for the stand growth performances across the three sites.

H2: The high silvicultural treatments will intensify the G × E interaction.

## I.4 Intergenotypic Competitive Interactions and Identification of Ideotype

### I.4.1 Literature Review

In a review of the agronomic literature, Newton et al. (2009) reported that many studies have found a significant effect of intergenotypic competition on agronomic crop yield. However, in forestry only a few studies have analyzed the effect of intergenotypic competition for tree species generally (Perry, 1985; Knowe *et al.*, 1994; Foster *et al.*, 1998; Staudhammer *et al.*, 2009), or specifically on loblolly pine (Staudhammer *et al.*, 2009). A deeper understanding of inter-genotypic competition is important because it can reduce the biases in the progeny tests of tree breeding programs (Pavan *et al.*, 2011), and the mixing of crop varieties with complementary interactions can lead to enhanced yield and pest resistance (Adams *et al.*, 1973; Staudhammer *et al.*, 2009).

In studies conducted by tree breeding programs, there are two factors which may limit the accuracy of the progeny test. First, a single-tree plot is the most common method used in family-level genetic selection programs. Though it is an efficient mixed layout for testing a large number of families, the breeders can only estimate the performance of genetic material in the operational plantings. They may not be able to correctly predict the growth performance in the future deployment environment where there may be new competitive conditions, like growing in pure family blocks, growing with different neighboring trees, or growing under different cultural treatments.

Second, in progeny tests, selection criteria are based on juvenile tree growth in mixed plots. Evaluating growth with different types of competition can be facilitated by using the ideotype concept. The concept of ideotype is a biological model of a plant that explicitly describes the phenotypic characteristics of high-productivity plants (Donald, 1968; Martin *et al.*, 2001; Dickmann *et al.*, 2010). There are two main categories of ideotypes (Donald and Hamblin, 1976; Cannell, 1978). One is crop ideotype which can efficiently exploit locally available resources, and would not compete strongly with neighboring trees. Thus, the crop ideotype will produce the greatest yield per area (Cannell, 1978). The second category is competitive ideotype, which could rapidly exploit site resources by aggressively expanding its crown and root system. This ideotype would have the greatest individual tree growth. Therefore, with the different growth strategies, the competitive ideotype could result in superior phenotypes when growing with the crop ideotype or when inter-tree competition is low, with the result being that the yield of a crop ideotype in a pure stand would be negatively correlated with their yield in a mixture of families (Martin *et al.*, 2001). Comparing the growth performance of individual genotypes between pure and mixed plots in long-term block-plot trials will effectively solve the two problems listed above (Staudhammer *et al.*, 2009; Gould *et al.*, 2011). For example, a series of replicated experimental trials of loblolly and slash pine were installed in four sites of the Eastern Gulf area, with controlled genotype, planting density, and silvicultural intensity. Results showed significant intergenotypic competitive interactions for stand growth (Roth *et al.*, 2007). Meanwhile, the growth comparison between pure and mixed plots led to the identification of crop and competitive ideotypes (Staudhammer *et al.*, 2009). In the Western Gulf study, the identified competitive ideotype from the Eastern Gulf was also planted at all three sites.

In Texas and Louisiana, there are different edaphic and climatic conditions compared with the Eastern Gulf area. The effects of silviculture treatments and deployment on loblolly pine genotype performance remain poorly understood and there is also little information about the loblolly pine ideotype identification in long-term block-plot plantings. In this study, I tried to give answers to the above questions by testing the following hypotheses.

### I.4.2. Hypothesis

H1: Genotype performances will differ between pure and mixed plots because different ideotypes exist among families.

H2: The competitive ideotype from the Eastern Gulf studies will be the competitive ideotype in the Western Gulf.

H3: Silvicultural treatment will amplify the growth differences of genotypes in mixed plots because of greater resource acquisition by competitive ideotypes.

## I.5 Leaf Area and Foliar Nitrogen Difference between Crop and Competitive Ideotypes of Loblolly Pine Genotypes

### I.5.1 Literature Review

Forest stand growth is determined by the amount of solar radiation intercepted, the photosynthetic efficiency of the canopy, the consumption of fixed carbon in respiration, and the allocation of fixed carbon to stemwood (Vose and Allen, 1988). Previous studies have found that genotypes within loblolly pine differ in growth and biomass accumulation (McCrady and Jokela, 1998; Roberts, 2002; McKeand *et al.*, 2006;

Chmura *et al.*, 2007; Roth *et al.*, 2007). However, very few studies have tried to explain why these differences occur. Moreover, according to seven long-term experiments in the South, most loblolly pine plantations achieve just one fourth to half of total standing stem biomass before canopy closure (Jokela *et al.*, 2004). Therefore, after canopy closure, analysis of effects of morphological and physiological properties on stand growth can reveal whether designation of crop and competitive ideotypes is valuable. This analysis also increases understanding of the factors that contribute to forest productivity, and then forest management can be improved by better focusing silvicultural activities towards maximizing the most important factors (Will *et al.*, 2005).

Many studies have found loblolly pine stand growth was correlated with light interception at the stand-level (Cannell, 1989; Dalla-Tea and Jokela, 1991; McCrady and Jokela, 1998; Will *et al.*, 2005; Chmura and Tjoelker, 2008). Some leaf traits and crown structure properties can influence tree light interception. Of these factors, total leaf area is one of the most important properties for light interception (Wang and Jarvis, 1990). In a 25-yr-old loblolly pine forest of southern North Carolina, one study observed a strong positive linear relationship between light interception and leaf area index (LAI) (Campoe *et al.*, 2013). Another study also found that the loblolly pine stemwood growth was positively and linearly related to LAI across treatments and stands (Albaugh *et al.*, 1998). Leaf area also affects canopy transpiration, respiration, and photosynthesis efficiency (Clinton *et al.*, 2011; Gspaltl *et al.*, 2013).

Many previous studies have used LAI to explain differences between silvicultural methods and intensities on southern pine growth. One study of a 6-yr-old loblolly and slash pine forest found that significant species differences in aboveground biomass production were principally due to the difference of LAI (Dalla-Tea and Jokela, 1991). Another study found that LAI explained >95% of the total variation in stemwood biomass production among all silvicultural treatments (Jokela and Martin, 2000). There are very few studies about LAI difference in full-sib genotypes of southern loblolly pine. In 4-year-old half-sib loblolly pine stands, there were significant genotype variations in LAI and light interception, and these differences were associated with contrasting genotype performance (McCrady and Jokela, 1998; McGarvey *et al.*, 2004). However, the previous study on 3-year-old loblolly pine stands in the Western Gulf area, found no significant differences between superior and average loblolly families on specific leaf area and leaf area density in most sites (Chmura *et al.*, 2007). Therefore, there is a need to examine the LAI difference again when the crowns are closed at seven or eight years old. Moreover, in some long-term studies, the relationship between stemwood biomass increment and LAI was strong at LAI <3.0, but was considerably more variable at higher LAIs (Jokela et al., 2004). Thus, this situation should be considered when comparing the LAI after crown closure.

Nitrogen (N) is the nutrient that most commonly limits growth of southern pine (Fox *et al.*, 2007). Foliar N can reflect many aspects of plant growth. First, it can be an effective index of plant nutrient limitation because it correlates with increased growth response to the addition of a limiting nutrient. Second, studies with southern loblolly pine have consistently found that foliar N levels were positively associated with foliage biomass production, annual height growth, and chlorophyll concentrations (Zhang *et al.*, 1997; Xiao *et al.*, 2003; Chmura and Tjoelker, 2008). Foliar N was also important in determining foliage development and tree growth in subsequent years since approximately 75% of the N contained in leaves is re-translocated and used for new foliage growth (Zhang and Allen, 1996).

However, studies about the variation in foliar N response to fertilization between full-sib genotypes of southern loblolly pine are very limited, and the results are variable. In half-sib genotypes of 3-yr-old slash pine, and 4- and 5-yr-old loblolly pine, researchers found that improved and unimproved genotypes had different foliar nutrient concentrations and growth performance response to intensive management (Xiao *et al.*, 2003; McGarvey *et al.*, 2004). But another study of four half-sib genotypes of loblolly pine seedlings found no foliar N difference between the examined genotypes (Samuelson, 2000). The mixed results of these two studies may result from the differences in tree ages and improved degree of the tree genotype. Moreover, some studies found that the significance of genotype effect on foliar N also depended on the units of foliar N expression. For example, in my research sites when the forest stands were 5-years-old, researchers found that the genotype effect was much more significant for a mass-based foliar N concentration than area-based foliar N (Chmura and Tjoelker, 2008). In addition, the measurement timing following fertilization may also be important to detect the foliar N difference. One study found that the rise and subsequent return of foliar N to non-fertilized levels following fertilization occurred within a time frame of just over 100 days (Gough *et al.*, 2004).

In my study, considering the LAI changes with stand development, the different expression of foliar N concentration, and measurement timing, I compared the LAI and foliar N differences between crop and competitive ideotypes. From this comparison, the genotype effect on LAI and foliar N, and effect of LAI and foliar N on stand growth was examined in a11-yr-old full-sib loblolly pine. Furthermore, I also tested the impact of silvicultural intensity on these tree and forest attributes.

### I.5.2 Hypothesis

H1: The competitive ideotypes will have a greater stand LAI and foliar N concentration.

H2: High silvicultural intensity will increase the differences in LAI and foliar N concentration because the competition ideotype will require more resources

H3: LAI and foliar N will be positively correlated with stand growth because these are indication of photosynthetic capture.

# CHAPTER II

# WESTERN GULF PINE PRODUCTIVITY INTERACTIONS: FAMILY, ENVIRONMENT AND SILVICULTURE EFFECTS ON GROWTH AND STAND DYNAMICS THROUGH AGE 10 YEARS OF LOBLOLLY AND SLASH PINE FORESTS

## II.1. Introduction

Forest scientists in the southeastern United States have improved pine yields through a series of technological advances. Forest growth has been dramatically increased through silvicultural practices that include site preparation, fertilization, and weed control. Incorporating improved tree genetic material into forest operations has also increased forest production, often while enhancing tree resistance to pests and disease, and improving wood characteristics. Research has demonstrated the significant influence that these management practices can have on loblolly pine (*Pinus taeda L.*) productivity. For example, results of seven long-term experiments from five southern states showed that loblolly pine plantation growth responses to intensive cultural regimes ranged from a 2- to 3.5-fold increase over controls (Jokela *et al.*, 2004). Estimated gains in volume production for plantations with genetically improved stock that were established in the current era ranged from 10% to 30% over unimproved planting stock (McKeand *et al.*, 2003b).

Obtaining optimum plantation production requires the use of integrated systems that couple intensive management of both site and genetic resources. Managed pine forests generally undergo a combination of management practices over stand history, including soil mounding (bedding), the planting of genetically improved pine seedlings, levels of competition or 'weed' control, and fertilization (Jokela *et al.*, 2010). The combined use of tree genetics and intensive silviculture throughout the region has increased forest productivity by 3-4x above less intensive practices (Fox *et al.*, 2007). One study also estimated that if the best genetic material is planted with the best silvicultural inputs, mean annual increments of 21 $m^3ha^{-1}yr^{-1}$ can be routinely obtained (Allen, 2008). Therefore, interactions among the forest plantation management options, for example, genetic improvement and silvicultural treatments, need to be understood and taken into account (Allen *et al.*, 2005). However, research is rare that quantifies the combined effects of cultural regimes and genetic improvement on the production of a first-generation full-sib loblolly pine family (Roth *et al.*, 2007).

In addition to silvicultural practices and genetic resources, obtaining optimum plantation production by an integrated system also requires consideration of local environmental characters, such as temperature, precipitation, soil, edaphic characteristics, extreme weather and disease. The Western Gulf (WG) Region of the southeastern United States includes five states, Texas, Louisiana, Mississippi, Arkansas and Oklahoma, where there is significant variation in weather and soil characteristics, and as a result, site productivity. State and federal agencies and private industry within the WG Region are planting genetically improved seedlings on diverse sites across large geographical regions (Yeiser *et al.*, 2001). Therefore, there is a need to examine genotype by environment (G× E) interactions for superior families of loblolly pine.

The G × E interaction may be manifested as rank changes among families when grown under different environments/cultural conditions, or as “scale effects” in which the absolute differences among families change with environment (Roth *et al.*, 2007). Past studies of different genotypes and locations showed very few G × E interactions for first- and second-generation open pollinated families grown under traditional silvicultural systems (McKeand *et al.*, 1997; McKeand *et al.*, 1999; Martin and Shiver, 2002; McKeand *et al.*, 2003a; McKeand *et al.*, 2006). However, The likelihood of G × E interaction may increase with intensified genetic selection where the selection of both parents is controlled (Bridgwater *et al.*, 2005) and increased silvicultural intensity (McKeand *et al.*, 2006). For example, in two sites separately located in Florida and Georgia, researchers found significant interaction between genotype and location for basal area and standing stem volume for five-year-old full-sib loblolly stands under combined silvicultural management (Roth *et al.*, 2007). After another two years, a significant interaction of location, deployment and genotype was found in the same forest stands (Staudhammer *et al.*, 2009).

The interactions between silvicultural treatments, regional and family level deployment have been extensively studied by industry-university research cooperatives. This study was supported by the FBRC (Forest Biology Research Cooperative) which was led by University of Florida. The research sites were part of the PPINES (Pine Productivity Interactions on Experimental Sites) field experiments under the management of FBRC. The PPINES had two series of experiments. In the Eastern Gulf (EG) PPINES series (est. winter of 1999-2000), factorial full-sib family blocks with spacing and cultural treatments were located in five locations in Florida and Georgia.

Three PPINES sites were also established in the Western Gulf (WG) states of Louisiana and Texas (WG-PPINES). Similar to EG-PPINES, the WG-PPINES installations included family blocks and culture treatments, but one spacing treatment. The genetic material for the WG-PPINES study mostly originated in the WG area, but one family overlapped with the EG-PPINES material. The WG-PPINES sites have been hit by a number of hurricanes and a drought. During the last 10 years, five hurricanes (Rita, Katrina (2005); Humberto (2007); Ike, Gustav (2008)) have either passed directly over or had a substantial precipitation or wind effect on the research areas. In the summer of 2011, the Texas site was under extreme drought conditions for the better part of a year. Although these climatic events do make cross-site comparisons difficult, they reflect the reality of growing trees in the region and may have different effects on families of loblolly pine and slash pine.

This study included analysis of the effects of genotype, silvicultural treatment and their interaction on different ages through 10-year stand stem volume, basal area, DBH per tree, and cumulative mortality. The other objectives of this study were to investigate and quantify the interaction of genotype and environment in full-sib families of loblolly pine in the WG area. The following hypothesis were tested:

H1: If a genotype can show better growth performance under low silvicultural practices, then it will show better growth response to the high silvicultural intensity.

H2: There will be G × E interactions for the stand growth performances.

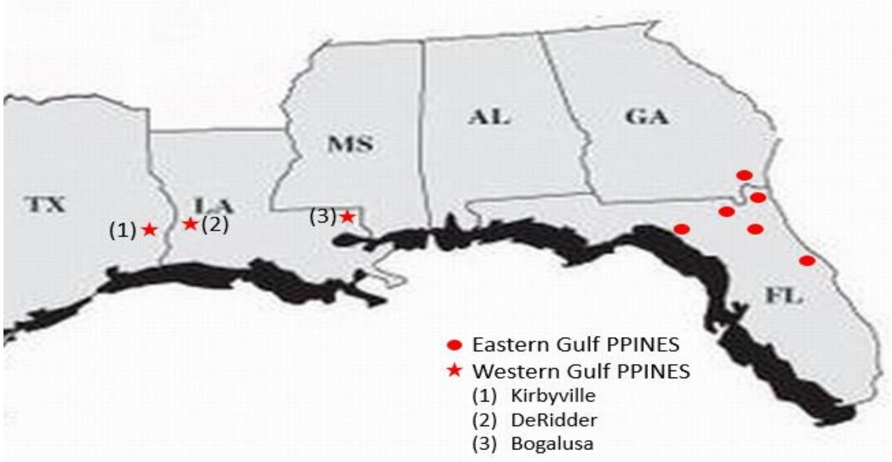
H3: The high silvicultural treatments will intensify the G × E interaction.

## II.2 Methods

### II.2.1 Experimental Description

The western series of the PPINES locations were established in eastern Texas and Louisiana on three sites: Kirbyville, Texas (30º 35' N, 93º 59' W); DeRidder, Louisiana (30º 51' N, 93º 21' W); and Bogalusa, Louisiana (30º 52' N, 89º 51' W). The Bogalusa site is located in the Eastern Gulf (EG) Coastal Plain area and two other sites are located in the Western Gulf (WG) Coastal Plain, but together are hereafter referred to as Western Gulf (WG) Coastal Plain sites (Figure 2-1).

Figure 2-1: The distribution of PPINES sites.



Hot and humid summers and mild winters characterize the climate of this region, with some variation across sites in precipitation but little in difference in temperature (Table 2-1). Edaphic characteristics differ among sites, particularly in their soil drainage classification and texture in the surface and subsurface layers. The Kirbyville site is a moderately well drained site, DeRidder is a somewhat poorly drained site and Bogalusa is a poorly drained site. Both DeRidder and Bogalusa have a silt loam surface and sub-surface soil texture, while Kirbyville has a fine sandy loam surface soil and sandy clay loam sub-surface soil (Chmura *et al.*, 2007).

Table 2-1: Mean values for the study period (2002-2012) of climatic data[a] for each of three experimental sites in the Western Gulf Coastal Plain area.

| Site | Average Temperature (℃) | Annual Precipitation (cm) |
|---|---|---|
| Bogalusa, LA | 19.2 | 1506[b] |
| DeRidder, LA | 19.8 | 1563 |
| Kirbyville, TX[c] | 19.8 | 1365 |

[a] From the nearest recording station, NOAA, National Oceanic and Atmospheric Administration

[b] Data from 2002 to 2006

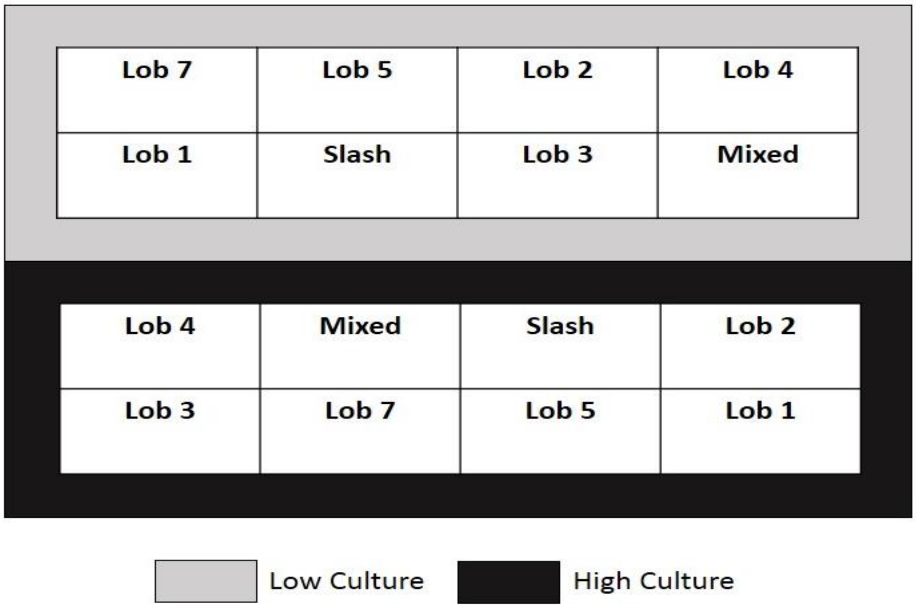
[c] Town Bluff Dam, Texas

### II.2.2 Experimental Design

At each research site, the experiment was a $2 \times 8$ $(\text{silviculture} \times \text{genetic entry})$ factorial and the experiment was planted by using a randomized complete block, split-plot design. In each site, there were five complete and replicated blocks which included two different silvicultural intensities for the whole plot (Figure 2-2). The two contrasting silvicultural treatments-low intensity (LI) versus high intensity (HI) were assigned as a whole-plot factor. Within each of these whole-plot treatments, there are eight sub-plots representing the genetic entries. Seven of the sub-plots were pure-planted with a single family, with one plot established with a proportional mixture of randomly planted all seven loblolly pine and the slash pine (*Pinus elliotii Englem.*) families. These mixed plots are discussed in chapter III.

In this research, genetic entries are alpha numerically coded using the prefix letter “Lob” for loblolly pine. The seven genetic entries consisted of five elite full-sib families of loblolly pine, one poorer growing loblolly pine family and one elite family of slash pine. Lob 1, 2, and 3 are the three top loblolly pine families that originated from southeastern Texas, Lob 4 is an elite family from Livingston Parish, LA, Lob 5 is from the Atlantic Coastal Plain area (superior loblolly) and Lob 7 is the poor grower from Texas. Families selected in these trials were chosen based on their aboveground growth performance from long-term genetic progeny tests.

Figure 2-2: Schematic diagram of experimental layout for one block at one site.



| | | | |
|---|---|---|---|
| **Lob 7** | **Lob 5** | **Lob 2** | **Lob 4** |
| **Lob 1** | **Slash** | **Lob 3** | **Mixed** |

| | | | |
|---|---|---|---|
| **Lob 4** | **Mixed** | **Slash** | **Lob 2** |
| **Lob 3** | **Lob 7** | **Lob 5** | **Lob 1** |

### II.2.3 Treatment Description

The experimental sites were established between November 2001 and January 2002. At establishment, all plots received initial site preparation of single pass bedding, and were sprayed with Arsenal® (imazapyr) and Garlon™ (triclopyr) to control the herbaceous and woody vegetation. Establishment fertilization was at the level of 280.5 kg $ha^{-1}$ of diammonium phosphate (51 kg $ha^{-1}$ N and 56 kg $ha^{-1}$ P) at the time of planting for all sites and both silvicultural treatments. The objective of this site preparation was to provide a suitable environment for optimum growth while minimizing the variation within individual study sites.

LI and HI treatments differed at the beginning of second growing season when LI did not receive any fertilization or weed control, while the HI received competing vegetation control until canopy closure. In addition, fertilizer additions continued in HI, with rates determined for each site based on yearly analyses of foliar nutrient concentrations. Foliar analyses were used to guide fertilization based on the critical foliage nutrient concentrations given in Gregoire and Fisher (2004). The total amounts of nutrients applied throughout the three growing seasons (from 2002 to 2005) in the HI treatment at each site are presented in Table 2-2.

Table 2-2: Cumulative fertilizer elemental application (kg ha$^{-1}$) up to age 3 for the HI treatments[a]

| Site | N | P | K | Ca | Mg | S | B | Zn | Mn | Fe | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Bogalusa, LA** | 280 | 101 | 90 | 0 | 45 | 90 | 1 | 0 | 0 | 0 | 0 |
| **DeRidder, LA** | 302 | 123 | 66 | 33 | 27 | 61 | 0.5 | 0 | 0 | 0 | 3 |
| **Kirbyville, TX** | 254 | 157 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

[a] LI treatment all totally received 51 kg ha$^{-1}$ N and 56 kg ha$^{-1}$ P at the time of planting only.

Seedlings were raised in 66 ml Ray Leach "Cone-tainer"™ cells (Stuewe & Sons, Inc. Corvallis, Oregon, USA) in 2001. Only one planting density of 1223 trees·ha$^{-1}$ (2.4×3.3 m) was used in the western series of the PPINES locations (Chmura *et al.*, 2009). There were 72 trees (8 beds × 9 trees) in each individual sub-plot, with the inner 42 trees designed as the measurement plot. Cultural treatment main-plots were separated by eight rows of buffer trees within a block.

### II.2.4 Forest Inventory Data

Growth analysis was based on the stand inventory data-tree height and diameter at 1.3 m (DBH). These data were collected for all families in the experiment at the end of the annual growing period (December-March).

① Bogalusa, tree height was measured on every tree at ages 1, 2 and 3 years and on a random 20% subset of trees at age 4 and 10 years. DBH was measured on every tree at ages 2, 3, 4 and 10 years.

② DeRidder, tree height was measured on every tree at ages 1, 2 and 3 years and on a random 20% subset of trees at age 6 and 10 years. DBH was measured on every tree at ages 2, 3, 6 and 10 years.

③ Kirbyville, tree height was measured on every tree at ages 1 and 2 years and on a random 20% subset of trees at age 3 4 and 10 years. DBH was measured on every tree at ages 2, 3, 4 and 10 years.

Mortality and damage were assessed on each tree during each inventory. Because of the low appearance of other types of damage, each tree was scored just for the presence or absence of damage from tropical storms.

Response variables of interest included individual tree level, such as height per tree and DBH per tree, as well as measures of stand occupation, such as basal area per hectare (BAHA; $m^2\ ha^{-1}$), stem volume per hectare (VOLHA; $m^3\ ha^{-1}$), cumulative mortality (CM; %), and disease and damage (%). The relevant variables were calculated using the following equations:

[1] $\text{Basal Area} = 0.00007854 \times \text{DBH}^2$

[2] $\text{Stem Volume} = (0.00395569\times(\text{DBH}^{1.8945})) \times (\text{tree height}^{0.9288}) \times 0.000056$

(Clutter et al. 1984)

Basal area and volume were first calculated on a tree-level basis. Then the family-level estimates of basal area and volume were scaled to per acre and per tree basis to obtain estimates of BAHA, VOLHA, tree height, and DBH. Tree mortality was calculated at the stand level by family and was assessed as the proportion of dead trees in the subplot. Damage was the proportion of trees in a subplot which were affected by tropical storms. For the stand-level variables of mortality and damage presence, observations were weighted by the initial number of trees of a specific family in each plot.

### II.2.5 Statistical Analysis

The change in a response variable was modeled as a function of interactions among location, block, family, and silvicultural intensity. To test for differences in tree-level and stand-level attributes among treatment, separate analyses were performed for the two-level attributes.

① Combined Effect of Genotype and Silvicultural Intensity

To test the combined effect on the tree-level attributes DBH, tree height, BAHA and VOLHA, separate analyses of variance (ANOVA) were performed for each site. The basic model was:

[3] $Y_{iklr} = \mu + G_k + C_l + b_i + GC_{kl} + bG_{ik} + bC_{il} + bGC_{ikl} + \varepsilon_{(ikl)r}$

where $Y_{iklr}$ is the response variable (DBH, tree height, BAHA or VOLHA) of the rth tree in the ith block, kth genotype and lth silvicultural intensity (i=1, 2, 3, 4, 5; k=1, 2, 3, 4, 5, 7; l=1, 2), $\mu$ is the overall mean; $G_k$ is the fixed effect of kth genotype; $C_l$ is the fixed effect of lth silvicultural intensity; $b_i$ is the random effect of ith block; $GC_{kl}$ is the interaction effect of kth genotype and lth silvicultural intensity; $bG_{ik}$ is the random effect of kth genotype in the ith block; $bC_{il}$ is the random effect of lth culture in the ith block; $bGC_{ikl}$ is the random effect of the kth genotype and lth silvicultural intensity in the ith block; $\varepsilon_{(ikl)r}$ is the random error of the rth tree in ith block, kth genotype, lth silvicultural intensity.

To test the combined effect on the stand-level attributes of annual mortality, cumulative mortality, disease and damage occurrence, separate ANOVAs were performed for each site. The basic model was:

[4] $Y_{ikl} = \mu + G_k + C_l + b_i + GC_{kl} + bG_{ik} + bC_{il} + bGC_{ikl} + \varepsilon'_{(kl)i}$

where $Y_{ikl}$ is the stand level variable proportion of death disease or damage of the trees in the ith block, kth genotype, lth silvicultural intensity; $\varepsilon'_{(ikl)i}$ is the random error of the ith block in kth genotype and lth silvicultural intensity; and all other variables are as previously defined.

② Interaction of Genotype by Environment

To test the interaction effect on the tree-level attributes DBH, tree height, BAHA and VOLHA, separate ANOVAs were performed for three sites using the same model. The basic model was:

[5] $Y_{ijkl} = \mu + L_j + G_k + C_l + b(L)_{ij} + LG_{jk} + LC_{jl} + GC_{kl} + b(L)G_{ijk} + b(L)C_{ijl} +$

$LGC_{jkl} + b(L)LG_{ijk} + b(L)LC_{ijl} + b(L)GC_{ijkl} + b(L)LGC_{ijkl} + \varepsilon''_{(ijkl)r}$

where $Y_{ijkl}$ is the response variable (DBH, tree height, BAHA or VOLHA) of the rth tree in the ith block, jth location, kth genotype and lth silvicultural intensity (j=1, 2, 3); $L_j$ is the fixed effect of location; $b(L)_{ij}$ is the random effect of the ith block nested within the jth location; $LG_{jk}$ is the interaction effect of jth location and kth genotype; $LC_{jl}$ is the interaction effect of jth location and lth silvicultural intensity; $LGC_{jkl}$ the interaction effect of jth location, kth genotype and lth silvicultural intensity; $\varepsilon''_{(ijkl)r}$ is the random error of the rth tree in the ith block in the jth location, kth genotype and lth silvicultural intensity and all other variables are as previously defined.

To test the interaction effect on the stand-level attributes annual mortality, cumulative mortality, disease and damage occurrence, separate ANOVAs were performed for three sites using the same model. The basic model was:

$$[6] Y_{ijkl} = \mu + L_j + G_k + C_l + b(L)_{ij} + LG_{jk} + LC_{jl} + GC_{kl} + b(L)G_{ijk} + b(L)C_{ijl} + LGC_{jkl} + b(L)LG_{ijk} + b(L)LC_{ijl} + b(L)GC_{ijkl} + b(L)LGC_{ijkl} + \varepsilon'''_{(jkl)i}$$

where $Y_{ijkl}$ is the stand level variable proportion of death disease or damage of the trees in the ith block, jth location, kth genotype, lth silvicultural intensity; $\varepsilon'''_{(ikl)i}$ is the random error of the ith block in jth location, kth genotype and lth silvicultural intensity; and all other variables are as previously defined.

Analyses were conducted in mixed-models framework using the SAS procedures MIXED and GLIMMIX (Littel *et al.*, 2006). First, at the sub-plot level, if the tree mortality was more than 50%, this plot was excluded from stand growth analysis, but was still included in mortality analysis. After this step, about five sub-plots were deleted every year at each site. There were still thirty five sub-plots left and three sub-plots per treatment combination meeting the analysis requirement. Second, at the individual tree level, the studentized residuals and Cook's D influence of the response variable data were calculated to find outliers. These outliers were then deleted to increase the least squares coefficients. Third, the data were tested for normality using the Kolmogorov-Smirnov test in the SAS UNIVARIATE procedure. If the data were not significantly different from normal distribution (P>0.05), they was analyzed with the MIXED procedure. If data did not fit the normal distribution, a log transformation was used on the data to result in approximately normal data. Then, the GLIMMIX procedure was used to analyze the data. Moreover, in the data of stand growth at 4, 6 and 10 years old, only about 20% of tree heights was collected. The PROC NLIN procedure was used to predict the height value from DBH, family and silvicultural intensity.

To test the assumptions of proper model specification and homogeneous variation necessary for analysis of variance, probability plots of residuals versus predicted values was conducted, and then Bartlett's test method in PROC GLM was used to make the equal variance test. Where models showed significant effects ($P < 0.05$), least squares means were generated between levels of the factors of interest.

## II.3 Results

Statistical analyses conducted on the inventory data at different ages and sites revealed numerous examples of significant main effects (culture, family, location) and interactions (culture × family, family × location (G × E), culture × family × location) for DBH, height, basal area, stand volume, mortality and damage for both loblolly and slash pine (Table 2-3 Table 2-4). The analyses also indicated how the main effects and interactions changed with stand development. Overall, the top performing loblolly pine family at all three sites was lob 5, a superior family introduced from South Carolina. In comparison with the loblolly pine families, the slash pine appeared to have suffered near catastrophic mortality. For example, the mortality of slash pine in HI plots at Kirbyville was as high as 56.2%.

Table 2-3 Summary of F values, p values, and associated degrees of freedom from the mixed model testing for loblolly pine at three sites at different tree ages.

|  | df | DBH |  | Tree Height |  | BAHA[b] |  | VOLHA[b] |  | CM[b] |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Effect |  | F | P | F | P | F | P | F | P | F | P |
| Bogalusa, Age 2 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 1.79 | 0.2518 | 1.31 | 0.3148 | 1.88 | 0.2425 | 1.80 | 0.2504 | 0.39 | 0.5433 |
| F | 5 | 3.96 | **0.0117**[c] | 4.32 | **0.0256** | 3.78 | **0.0143** | 4.18 | **0.0092** | 0.48 | 0.7837 |
| C×F | 5 | 2.02 | 0.1197 | 1.38 | 0.3204 | 2.24 | 0.0901 | 2.46 | 0.0684 | 1.75 | 0.1984 |
| Age 5 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 8.16 | **0.0472** | 2.72 | 0.1766 | 4.49 | 0.1021 | 3.47 | 0.1366 | 2.09 | 0.1862 |
| F | 5 | 2.12 | 0.1413 | 2.93 | 0.0679 | 1.86 | 0.1876 | 2.60 | 0.0922 | 1.02 | 0.4210 |
| C×F | 5 | 3.49 | **0.0448** | 4.55 | **0.0205** | 2.26 | 0.1290 | 2.28 | 0.1265 | 0.69 | 0.6322 |
| Age 10 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 17.08 | **0.0247** | 15.10 | **0.0078** | 10.38 | **0.0174** | 14.09 | **0.0090** | 0.74 | 0.4384 |
| F | 5 | 3.84 | **0.0089** | 3.73 | **0.0103** | 2.16 | 0.0875 | 3.44 | **0.0149** | 0.49 | 0.7825 |
| C×F | 5 | 1.36 | 0.2674 | 1.79 | 0.1462 | 1.47 | 0.2317 | 1.59 | 0.1943 | 1.03 | 0.4289 |
| DeRidder, Age 2 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 27.07 | **0.0133** | 11.06 | **0.0419** | 24.65 | **0.0001** | 22.64 | **0.0002** | 1.60 | 0.2746 |
| F | 5 | 4.05 | **0.0206** | 8.57 | **<0.0001** | 4.15 | **0.0173** | 4.98 | **0.0087** | 0.90 | 0.4926 |
| C×F | 5 | 1.42 | 0.2832 | 1.20 | 0.3384 | 1.35 | 0.2924 | 1.26 | 0.3258 | 0.49 | 0.7850 |
| Age 3 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 51.36 | **<0.0001** | 9.78 | 0.0576 | 50.87 | **<0.0001** | 37.82 | **<0.0001** | 1.81 | 0.2156 |
| F | 5 | 1.02 | 0.4452 | 4.26 | **0.0060** | 1.21 | 0.3541 | 1.91 | 0.1583 | 1.12 | 0.3646 |
| C×F | 5 | 14.82 | 0.2304 | 1.53 | 0.2164 | 1.77 | 0.1768 | 1.66 | 0.2027 | 0.72 | 0.6163 |
| Age 6 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 32.01 | **0.0110** | 7.45 | 0.0698 | 135.39 | **0.0025** | 38.88 | **<0.0001** | 2.09 | 0.1862 |
| F | 5 | 1.38 | 0.2624 | 2.11 | 0.1300 | 1.12 | 0.3965 | 1.39 | 0.2876 | 1.02 | 0.4210 |
| C×F | 5 | 1.04 | 0.4166 | 1.49 | 0.2595 | 1.68 | 0.2043 | 1.87 | 0.1549 | 0.69 | 0.6322 |
| Age 10 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 9.26 | 0.0559 | 12.34 | **0.0030** | 9.10 | **0.0081** | 11.02 | **0.0043** | 1.95 | 0.1998 |
| F | 5 | 3.96 | **0.0232** | 4.44 | **0.0145** | 4.28 | **0.0141** | 4.70 | **0.0101** | 1.29 | 0.2875 |
| C×F | 5 | 1.00 | 0.4549 | 1.07 | 0.4122 | 2.49 | 0.0751 | 2.49 | 0.0756 | 0.85 | 0.5220 |
| Kirbyville, Age 2 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 39.23 | **0.0002** | 14.37 | **0.0053** | 39.86 | **0.0002** | 30.39 | **0.0006** | 1.19 | 0.2818 |
| F | 5 | 28.12 | **<0.0001** | 53.65 | **<0.0001** | 18.51 | **<0.0001** | 21.39 | **<0.0001** | 2.50 | **0.0434** |
| C×F | 5 | 0.67 | 0.6455 | 0.63 | 0.6815 | 0.93 | 0.4737 | 1.13 | 0.3610 | 0.77 | 0.5745 |
| Age 3 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 64.63 | **<0.0001** | 35.34 | **0.0003** | 64.94 | **<0.0001** | 50.99 | **0.0020** | 1.03 | 0.3147 |
| F | 5 | 25.37 | **<0.0001** | 41.19 | **<0.0001** | 15.02 | **<0.0001** | 17.51 | **<0.0001** | 2.19 | 0.0708 |
| C×F | 5 | 1.31 | 0.2790 | 1.46 | 0.2260 | 0.86 | 0.5185 | 0.88 | 0.5016 | 0.82 | 0.5430 |
| Age 10 |  |  |  |  |  |  |  |  |  |  |  |
| C | 1 | 30.10 | **0.0006** | 12.86 | **0.0071** | 22.73 | **0.0089** | 20.57 | **0.0105** | 4.55 | 0.0675 |
| F | 5 | 16.96 | **<0.0001** | 52.00 | **<0.0001** | 9.51 | **<0.0001** | 12.87 | **<0.0001** | 1.65 | 0.1871 |
| C×F | 5 | 2.10 | 0.0857 | 0.76 | 0.5825 | 0.24 | 0.9404 | 0.22 | 0.9502 | 1.84 | 0.1569 |

[a] Effects include family (F); silvicultural intensity (C); site (S); and deployment (D).

[b] BAHA is basal area per hectare; VOLHA is stem volume per hectare; CM is cumulative mortality of loblolly pine stand at each age.

[c] p-Values significant at the 95% level of confidence are shown in bold type.

Table 2-4 Summary of F values, p values, and associated degrees of freedom from the mixed model testing for loblolly pine at three sites at tree ages 2 and 10 year.

| | df | DBH | | Height | | BAHA[b] | | VOLHA[b] | | CM[b] | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Effect[a] | | F | P | F | P | F | P | F | P | F | P |
| Age 2 | | | | | | | | | | | |
| C | 1 | 20.96 | **0.0013**[c] | 9.86 | **0.0118** | 26.70 | **0.0005** | 21.53 | **0.0009** | 0.47 | 0.5510 |
| F | 5 | 22.21 | **<0.0001** | 35.78 | **<0.0001** | 15.38 | **<0.0001** | 17.03 | **<0.0001** | 1.41 | 0.2277 |
| F×C | 5 | 1.22 | 0.3072 | 1.66 | 0.1649 | 1.17 | 0.3548 | 1.60 | 0.1978 | 0.32 | 0.8974 |
| S | 2 | 61.18 | **<0.0001** | 16.82 | **0.0010** | 88.93 | **<0.0001** | 81.76 | **<0.0001** | 13.61 | **0.0009** |
| C×S | 2 | 0.50 | 0.6252 | 0.09 | 0.9124 | 4.79 | **0.0388** | 4.50 | **0.0460** | 1.58 | 0.2446 |
| F×S | 10 | 2.96 | **0.0031** | 2.48 | **0.0195** | 5.02 | **0.0002** | 6.30 | **<0.0001** | 0.72 | 0.7009 |
| F×C×S | 10 | 1.75 | 0.0824 | 2.47 | **0.0198** | 0.89 | 0.5525 | 0.80 | 0.6343 | 0.56 | 0.8436 |
| Age 10 | | | | | | | | | | | |
| C | 1 | 30.32 | **0.0049** | 22.15 | **0.0005** | 13.19 | **0.0329** | 18.20 | **0.0004** | 2.70 | 0.1374 |
| F | 5 | 12.14 | **<0.0001** | 10.80 | **<0.0001** | 11.82 | **<0.0001** | 14.74 | **<0.0001** | 1.41 | 0.2271 |
| F×C | 5 | 1.75 | 0.1507 | 1.49 | 0.2177 | 1.03 | 0.4346 | 1.19 | 0.3579 | 0.78 | 0.5678 |
| S | 2 | 6.67 | **0.0276** | 17.16 | **0.0028** | 10.59 | **0.0016** | 14.00 | **0.0003** | 1.92 | 0.1862 |
| C×S | 2 | 6.53 | **0.0228** | 9.36 | **0.0049** | 1.02 | 0.3897 | 2.22 | 0.1421 | 0.31 | 0.7368 |
| F×S | 10 | 2.01 | 0.0658 | 1.94 | 0.0556 | 1.32 | 0.2570 | 1.60 | 0.1490 | 0.87 | 0.5645 |
| F×C×S | 10 | 1.36 | 0.2381 | 1.35 | 0.2231 | 1.69 | 0.1264 | 1.57 | 0.1631 | 1.17 | 0.3204 |

[a] Effects include family (F); silvicultural intensity (C); site (S); and deployment (D).
[b] BAHA is basal area per hectare; VOLHA is stem volume per hectare; CM is cumulative mortality of loblolly pine stand at each age.
[c] p-Values significant at the 95% level of confidence are shown in bold type.

### II.3.1 Genotype × Silvicultural Intensity Interaction

#### II.3.1.1 Stem Volume

At the three sites, the family effect on stand volume was significant at ages 2 and 10 years (Table 2-3), and loblolly pine family Lob 5 was the top performer (Figure 2-3). For example, at ten years old, family Lob 5 accumulated about 202.9 $m^3$/ha, 227.8 $m^3$/ha and 238 m$^3$/ha respectively at Bogalusa, DeRidder and Kirbyville under the HI treatment. Family Lob 5 even had higher stand volume under the LI treatment than most other families had under the HI treatment at DeRidder and Kirbyville (Figure 2-3 b, c). Furthermore, at DeRidder and Kirbyville, the silvicultural effect on stand volume was significant at all ages, but at Bogalusa, the effect was only significant at age 10 years (Table 2-3). Trees of the same family under the HI treatment generally grew faster than those under the LI treatment (Figure 2-3). For example, stand volume of family Lob 5 was 126.3 m$^3$/ha under LI treatment, but increased to 202.9 m$^3$/ha under HI treatment at Bogalusa (Figure 2-3 a). For the superior family, the high intensity treatment could increase stand productivity by about 61%. However, the interaction of family and silvicultural intensity was not significant at all ages and sites (Table 2-3).

Figure 2-3: Time series plots of VOLHA at Bogalusa, LA; DeRidder, LA and Kirbyville, TX PPINES sites. Dotted lines indicate LI treatment, solid lines indicate HI treatment.

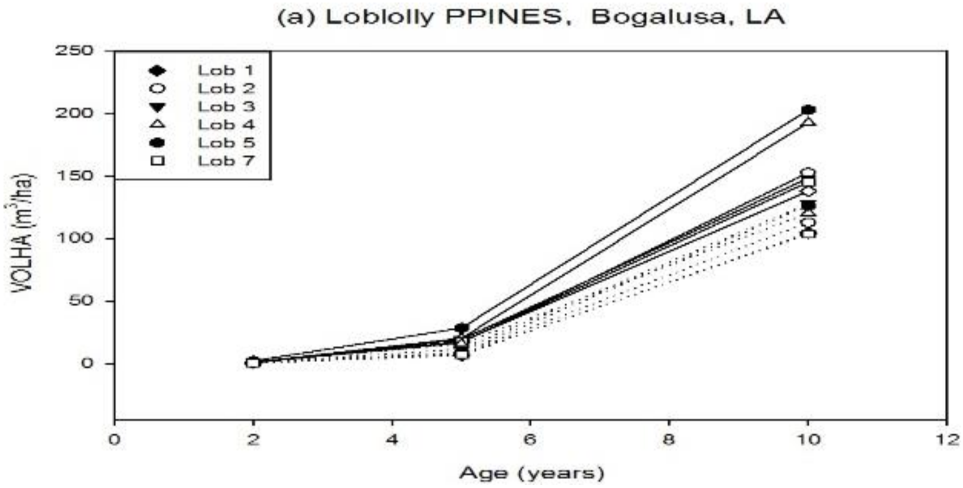
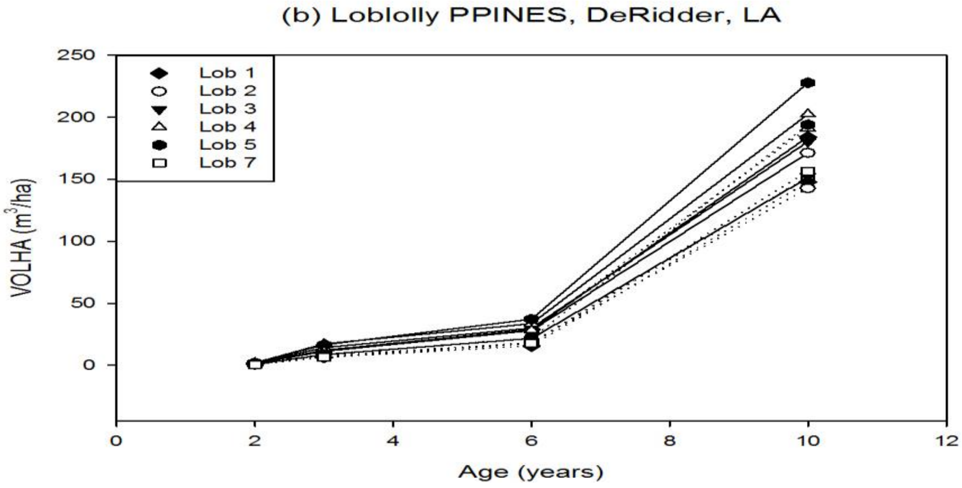


Figure 2-3 Continued



II.3.1.2 Basal Area

At Bogalusa, the family effect on BAHA was only significant at age 2 years, and at Kirbyville, there was a significant family effect at ages 2, 3, and 10 years, but at age 5 or 6 years, the family effect was not significant at either Bogalusa or DeRidder (Table 2-3). Consistent with stem volume, the family Lob 5 had the largest basal area per hectare under the HI treatment achieving 38.4 $m^2$/ha (Figure 2-4). At Kirbyville, the family Lob

5 under the LI treatment was still larger than other families under the HI treatment. (Figure 2-4 c). The family Lob 4 had the second largest basal area among the loblolly pine families (Figure 2-4). Similar to stem volume, the silvicultural effect on basal area was significant at all ages at DeRidder and Kirbyville, but the effect was only significant at age 10 years at Bogalusa (Table 2-3). Trees of the same family under the HI treatment had larger basal area than those under LI treatment generally at all ages (Figure 2-4). However, at DeRidder, the family Lob 4 and Lob 7 had similar basal area per hectare under the two treatments (Figure 2-4 b). However, the interaction effect of genotype and silvicultural intensity on basal area was not significant at the three sites at all ages (Table 2-3).

Figure 2-4: Time series plots of BAHA at Bogalusa, LA; DeRidder, LA and Kirbyville, TX PPINES site. Dotted lines indicate LI treatment, solid lines indicate HI treatment.

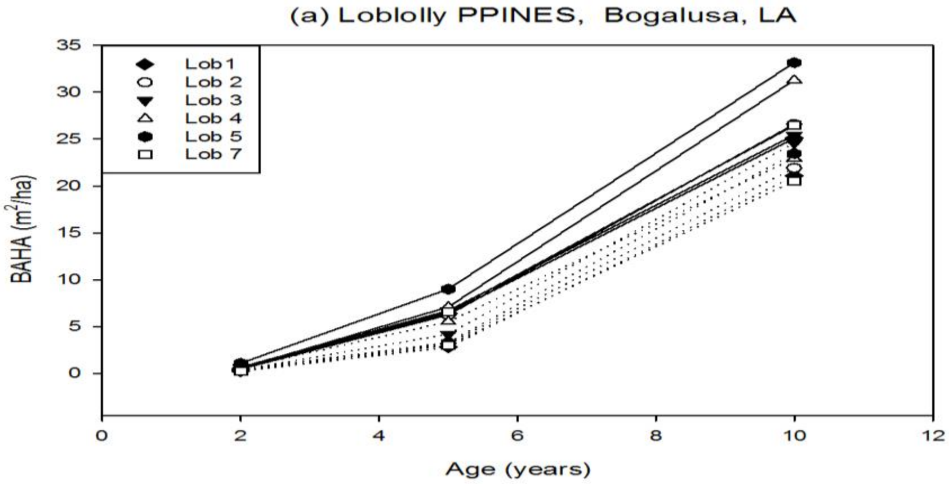
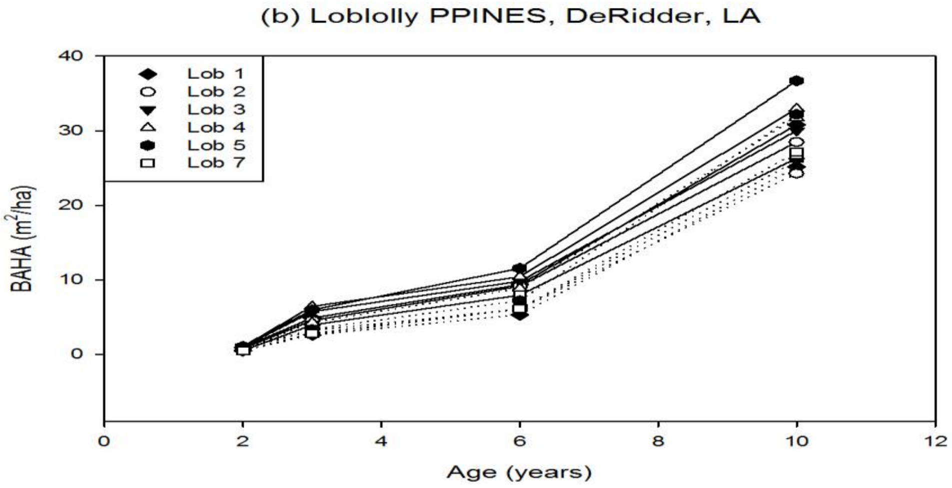
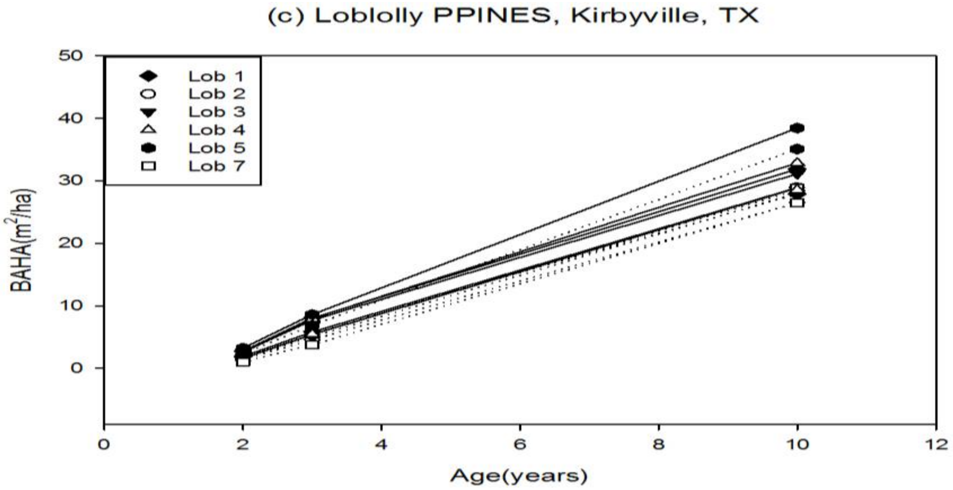


Figure 2-4 Continued


(b) Loblolly PPINES, DeRidder, LA


(c) Loblolly PPINES, Kirbyville, TX

### II.3.1.3 Height

Consistent with stem volume and basal area, the family effect on height was significant at age 2, 3 and 10 years at Bogalusa and DeRidder, and there was a significant family effect at all ages at Kirbyville (Table 2-3). The family Lob 5 was still the greatest for tree height growth at DeRidder and Kirbyville. For example, at Kirbyville, it achieved as high as 13.8 m at age 10 years (Figure 2-6 c). However, at

Bogalusa, the family Lob 4 had the largest height growth under the HI treatment (Figure 2-6 a).

Similar to the family effect, the silviculture effect on tree height was significant only at ages 2 and 10 years at DeRidder, and Bogalusa only had a significant silviculture effect at age 10 years, but there was a significant silviculture effect on tree height at all ages at Kirbyville (Table 2-3). Generally, trees within the same family had higher tree height under the HI treatment at age 10 years (Figure 2-5).

The interaction of family and silvicultural intensity was only significant at age 5 years at Bogalusa (Table 2-3). At Bogalusa, the family Lob 5 was the most sensitive to silvicultural intensity as indicated by the rank change from third to first under the LI and HI treatment, respectively, at age 5 years (Figure 2-5 d).

Figure 2-5: Family × culture interaction plots for age 5 years tree height of the loblolly pine PPINES sites at Bogalusa, LA. Families within cultures having the same letter are not significantly different at the 95% level of confidence. (Student's t-test)

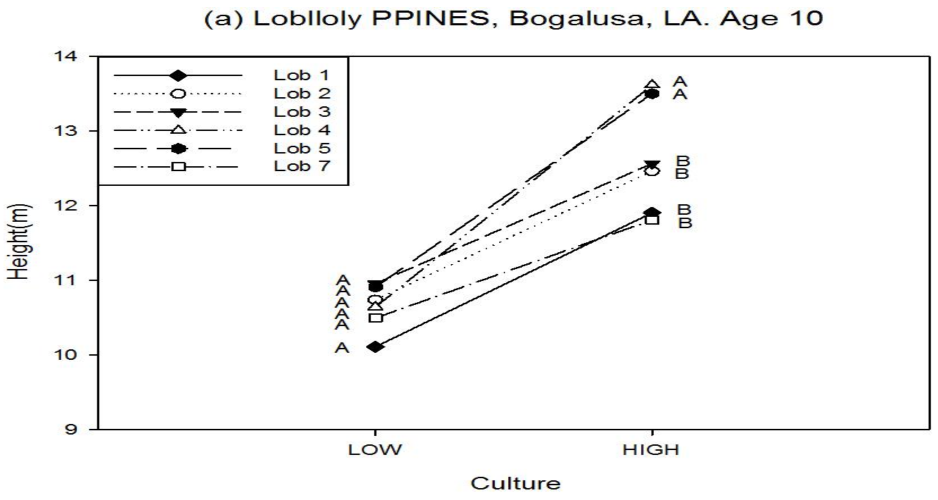
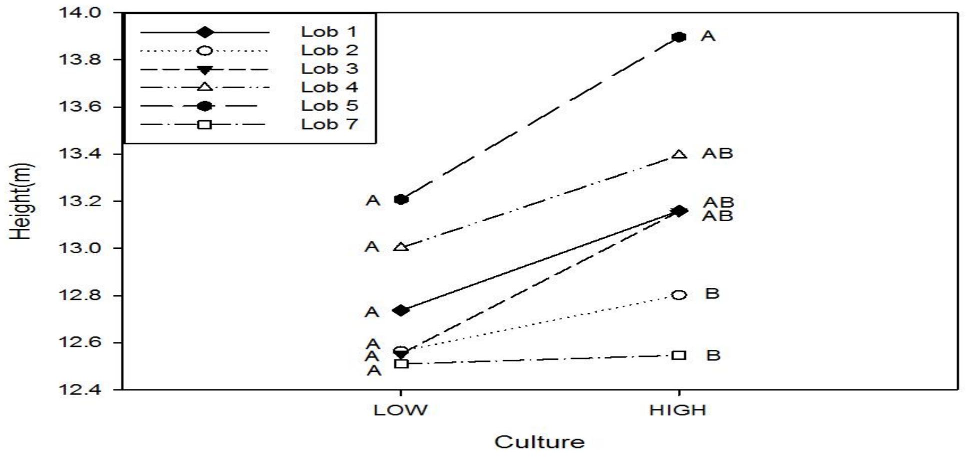
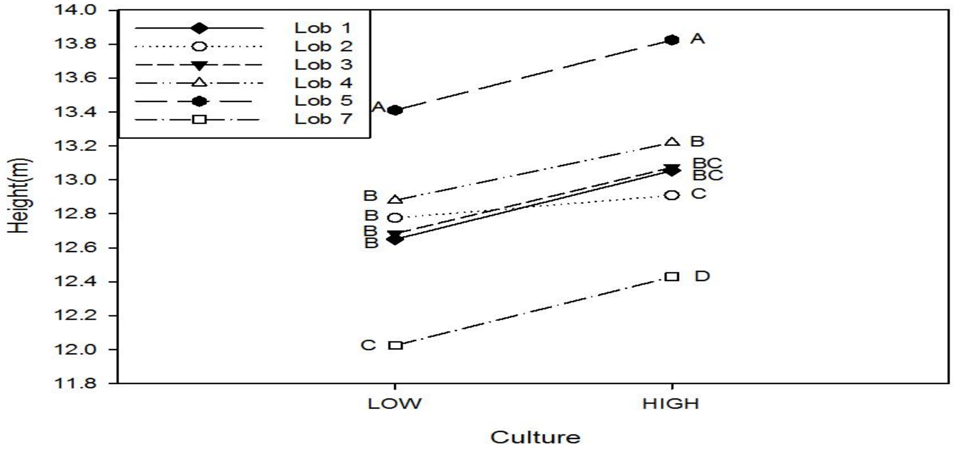

(a) Loblloly PPINES, Bogalusa, LA. Age 10

Figure 2-5 Continued

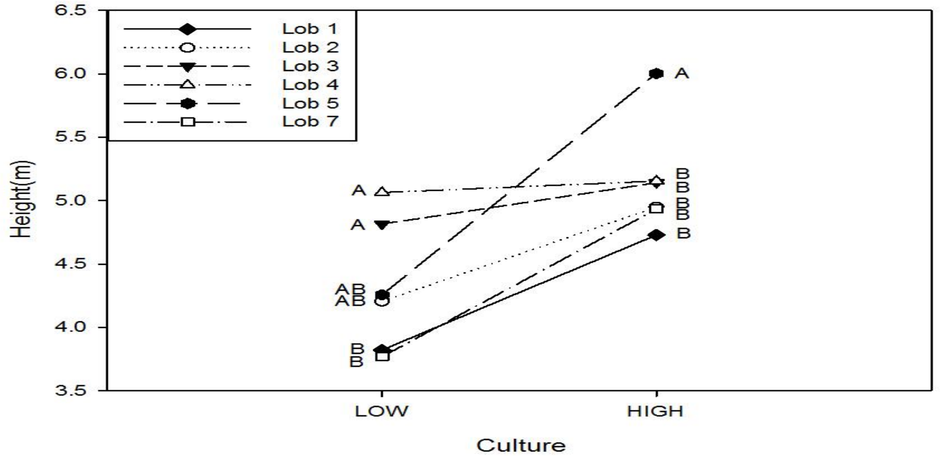
(b) Loblolly PPINES, DeRidder, LA. Age 10



(c) Loblolly PPINES, Kirbyville, TX. Age 10



(d) Loblolly PPINES, Bogalusa, LA, Age 5



#### II.3.1.4 DBH

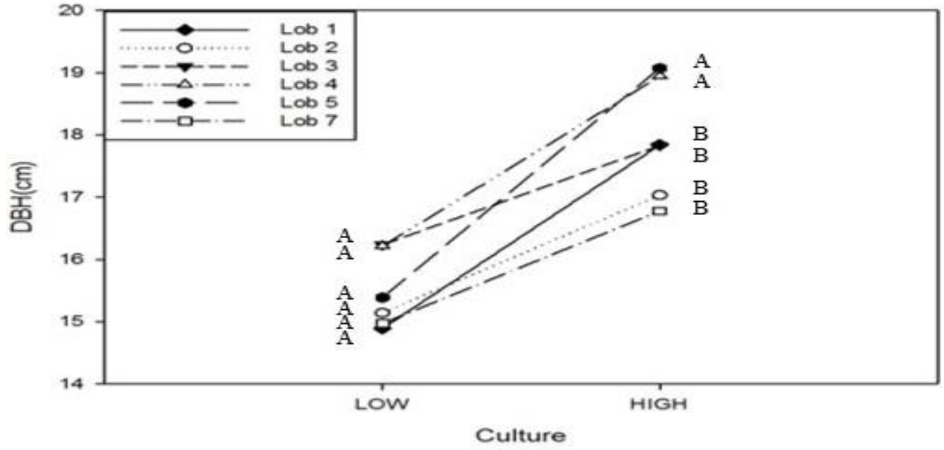
The family effect on DBH showed a similar trend to other growth traits. It was significantly different among families at ages 2, 3 and 10 years at Bogalusa and DeRidder, but at all ages at Kirbyville (Table 2-3). The family Lob 5 was still the top performer for DBH at the three sites, with the greatest average value at Kirbyville of 20.9 cm. Lob 4 was the second greatest family for DBH among the loblolly pine families in most treatment combinations (Figure 2-6).

The effect of silviculture intensity was significant at most ages and sites, except for age 2 years at Bogalusa and age 10 years at DeRidder (Table 2-3). Within the same family, the HI treatment generally increased DBH at age 10 years. For example, every family showed a significant growth increase when the treatment changed from the LI to HI at Bogalusa (Figure 2-6 a).

Similar to tree height growth, a significant interaction between family and silvicultural intensity only occurred at ages 5 years at Bogalusa (Table 2-3). The family Lob 5 was most sensitive to the change of silvicultural intensity (Figure 2-6 d). For example, it ranked fourth under the LI treatment, but increased to first under the HI treatment, so the HI treatment improved the DBH growth by ~77% (Figure 2-6 d).

Figure 2-6: Family × culture interaction plots for age 10 years DBH of the loblolly pine PPINES sites at Bogalusa, LA; DeRidder, LA and Kirbyville, TX. Families within cultures having the same letter are not significantly different at the 95% level of confidence. (Student's t-test)

(a) Loblloly PPINES, Bogalusa, LA. Age 10



(b) Loblolly PPINES, DeRidder, LA. Age 10

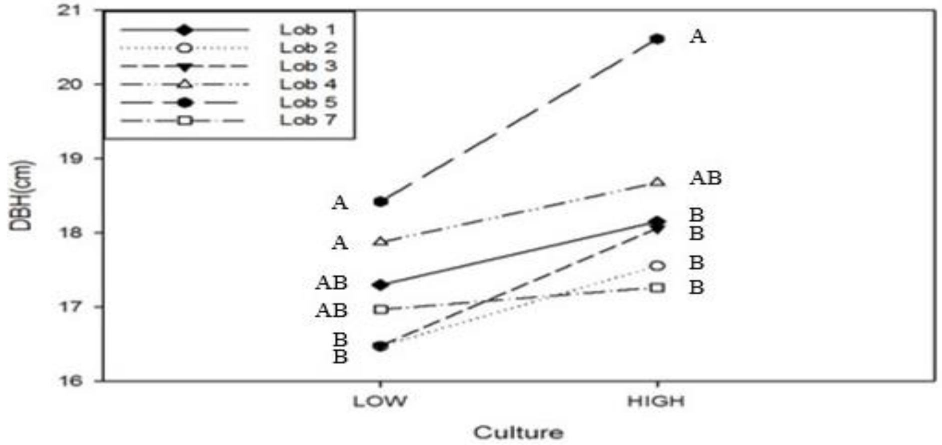
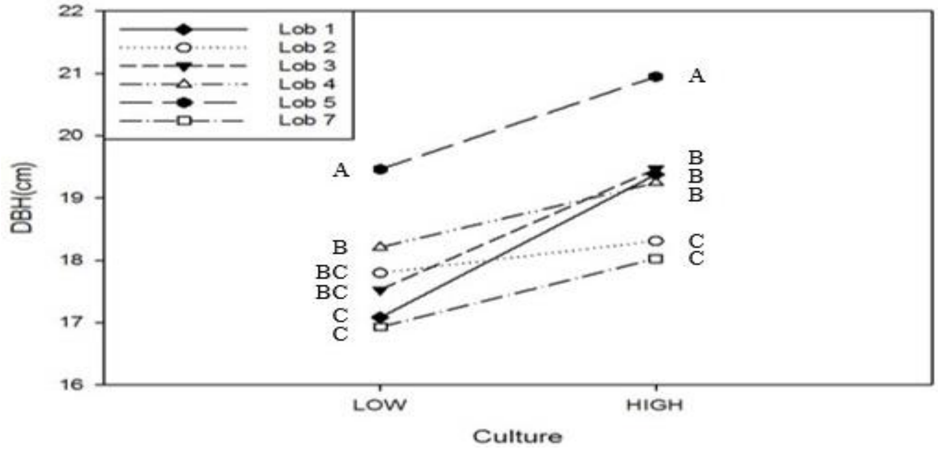
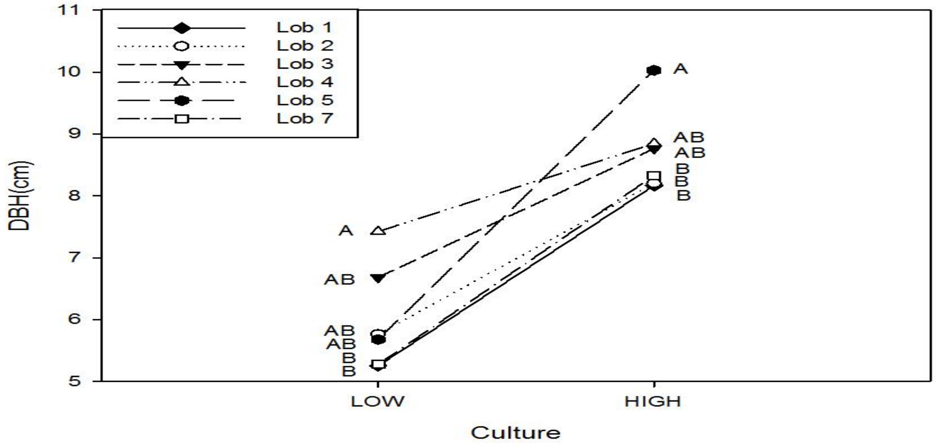


Figure 2-6 Continued

(c) Loblolly PPINES, Kirbyville, TX. Age 10



(d) Loblolly PPINES, Bogalusa, LA, Age 5



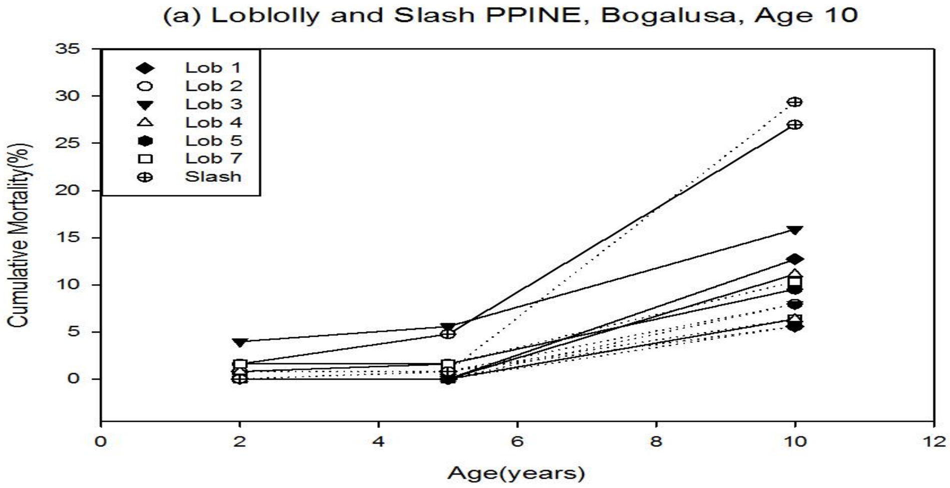
### II.3.1.5 Mortality and Wind Damage

Even though the family and silvicultural intensity effects on tree mortality were not significant at all ages and sites for loblolly pine families (Table 2-3), slash pine had significantly higher mortality than the loblolly pine families at age 10 years ($p<0.0001$)

(Figure 2-7). The family Lob 4 at DeRidder (p=0.0258) had higher mortality than other loblolly pine families (Figure 2-7).

The interaction between family and silvicultural intensity was not significant for all ages and sites (Table 2-3). However, at age 10 years, the family Lob 4 (p=0.0228) at DeRidder, and the family Lob 1 (p=0.0273), Lob 3 (p=0.0361) and Slash pine (p<0.0001) at Kirbyville showed significant differences between the LI and HI treatment (Figure 2-8 b, c).

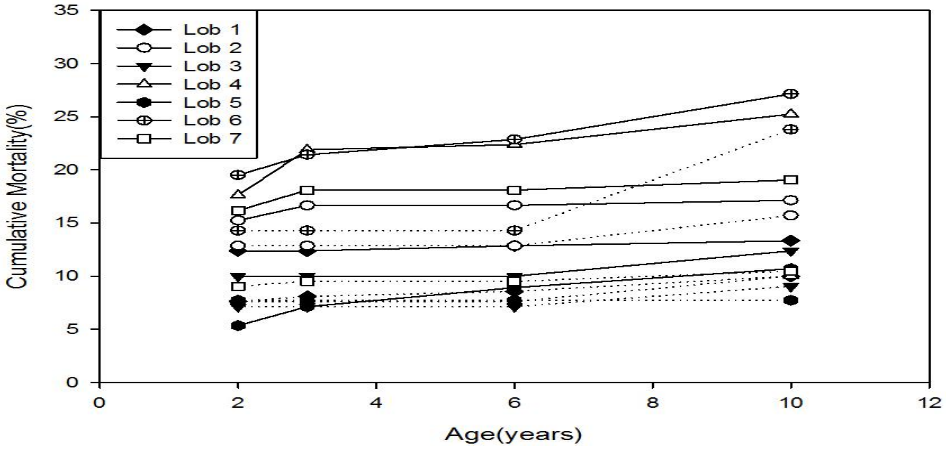
Figure 2-7: Time series plots of mortality for Bogalusa, LA; DeRidder, LA and Kirbyville, TX PPINES site. Dotted lines indicate LI treatment, solid lines indicate HI treatment.



(a) Loblolly and Slash PPINE, Bogalusa, Age 10

Figure 2-7 Continued

(b) Loblolly and Slash PPINES, DeRidder, Age 10



(c) Loblloly and Slash PPINE, Kirbyville, Age 10

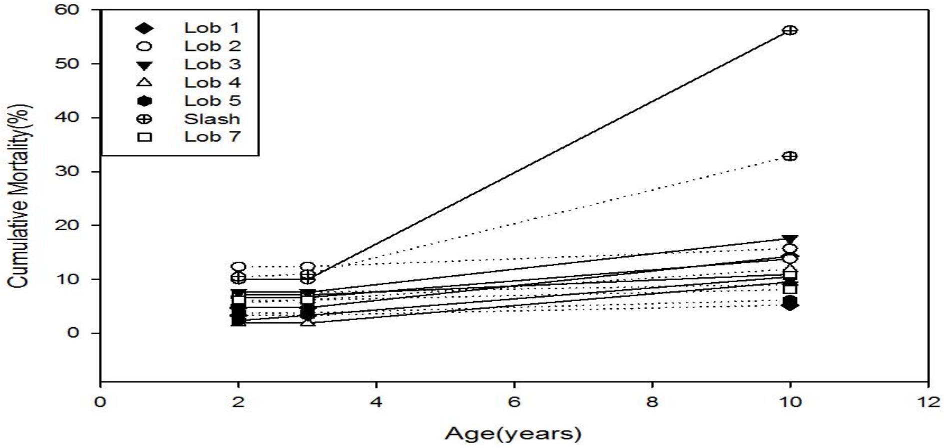
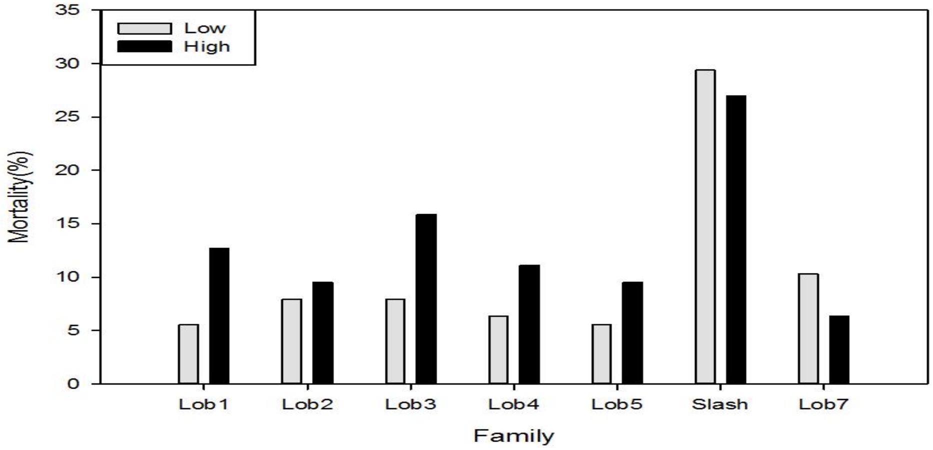


Figure 2-8: Family × culture interaction plots for age 10 years mortality for the PPINES sites at Bogalusa, LA; DeRidder, LA and Kirbyville, TX. Bars within family having an asterisk indicates significant difference at the 95% level of confidence.

(a) Loblolly and Slash PPINE, Bogalusa, Age 10



(b) Loblolly and slash PPINE, DeRidder, Age 10

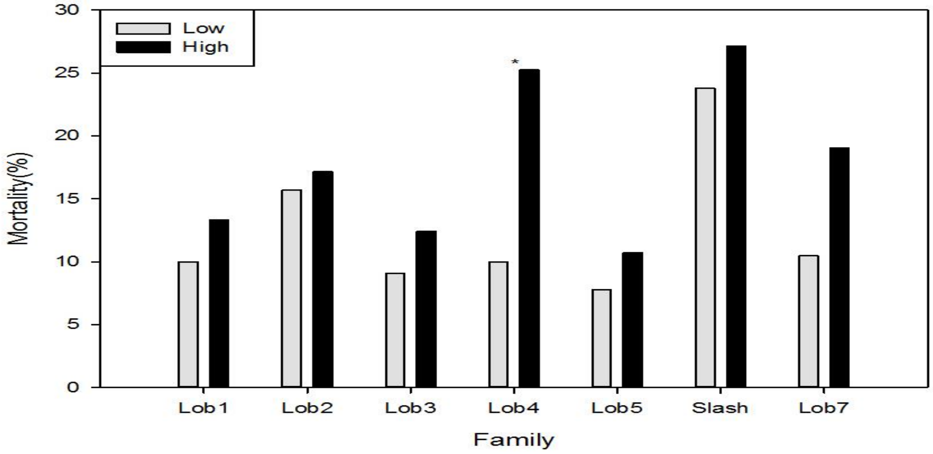
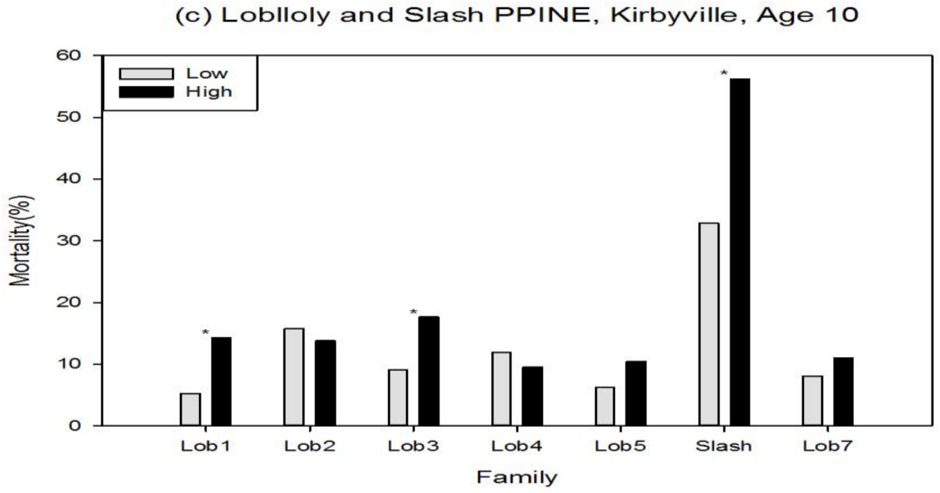
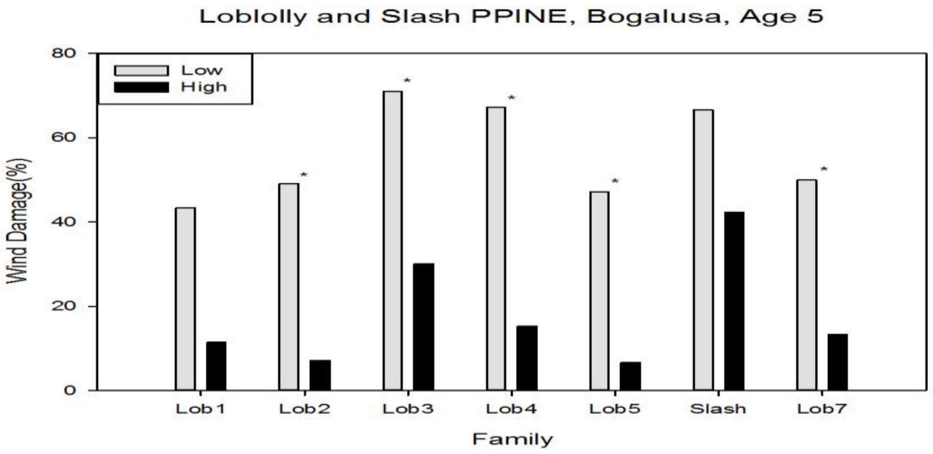


Figure 2-8 Continued



After comparing different reasons (disease, insect, weather, etc.) that can cause tree death, wind damage was only the significant causal agent at the three sites. Hurricane damage at Bogalusa is shown here as an example (Figure 2-9). The family effect on wind damage was significant at age 5 years ($p<0.0001$). For example, the average damage of slash pine was 54.5%, the second high family Lob 3 was 49.3%, and the lowest family Lob 5 was 26.9%. Moreover, the silvicultural intensity effect was also significant ($p=0.0325$). For example, Lob 4 had the largest difference between the two intensities ($p=0.0029$) (Figure 2-9).

Figure 2-9: Family × culture interaction plots for wind damage at age 5 years for the PPINES sites at Bogalusa, LA. Bars within family having an asterisk indicates significant difference among silvicultural treatments at the 95% level of confidence.



### II.3.2 Genotype × Environment Interaction

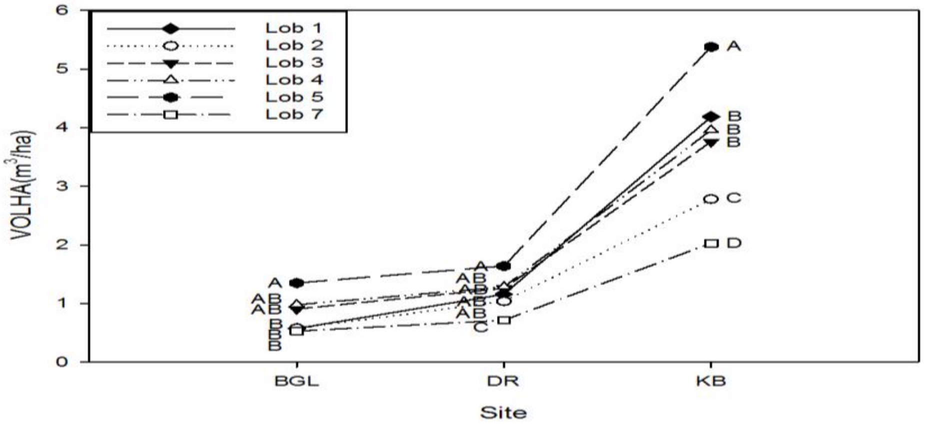
#### II.3.2.1 Stand Growth across Sites

At age 2 years, there was significant interaction of site and loblolly pine family for stem volume, basal area, tree height and DBH, but the effect had become less significant at age 10 years. The significance of these interactions for DBH (p=0.0658) and tree height (p=0.0556) were higher than for basal area (p=0.2570) and stem volume (p=0.1490) at age 10 years (Table 2-4).

At the three sites, the best performing family was Lob 5 and the poorest families were Lob 2 and Lob 7 (Figure 2-10). Some families performed better or worse than others when grown together on the three sites. The varying performance of families across sites could be noticed by scale effect or rank change. For example, at age 10 years, the family Lob 5 had the largest stem volume compared with other families at Kirbyville, but the difference became smaller at DeRidder and Bogalusa, where Lob 5 and Lob 4 were not significantly different from one another (Figure 2-10 b). In terms of rank change, basal area rank of family Lob 1 changed from sixth to fourth to second at Bogalusa, DeRidder and Kirbyville, respectively, at age 2 years (Figure 2-10 c). On the basis of stand growth performance of all the families at the three sites, Lob 1 and 5 had the most sensitive reaction to the site change, Lob 3 and 4 were intermediately sensitive to the site difference, and Lob 2 and 7 had similar stand growth levels at three sites (Figure 2-10). Moreover, from stand growth comparison of the two ages, the productivity level of the three sites changed with the stand development, for example, for the tree height growth, at age 2 years, the level order is Kirbyville > DeRidder > Bogalusa (Figure 2-10 e), while at age 10 years, it turned to DeRidder ≥ Kirbyville > Bogalusa (Figure 2-10 f).

Figure 2-10: Family × site interaction plots for stand growth indices (VOLHA, BAHA, HEIGHT, and DBH) of the PPINES sites at Bogalusa, LA; DeRidder, LA and Kirbyville, TX. Families within sites having the same letter are not significantly different at the 95% level of confidence. (Student's t-test).

(a) Loblolly PPINES, Age 2



(b) Loblolly PPINES, Age 10

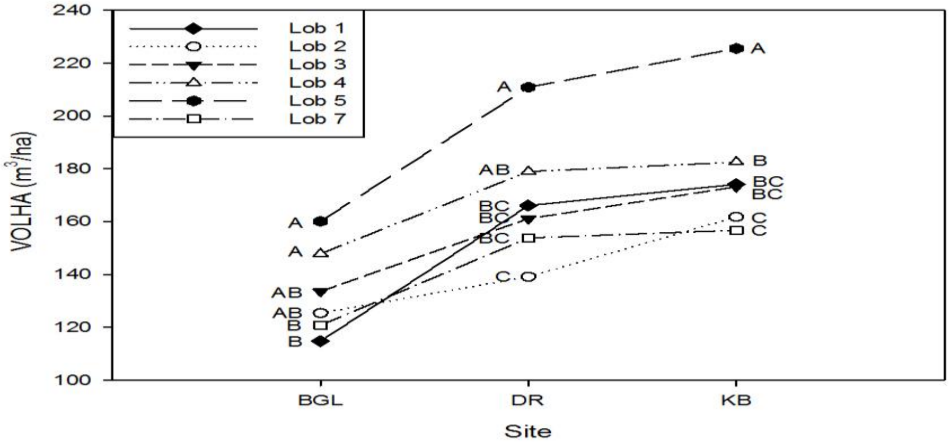
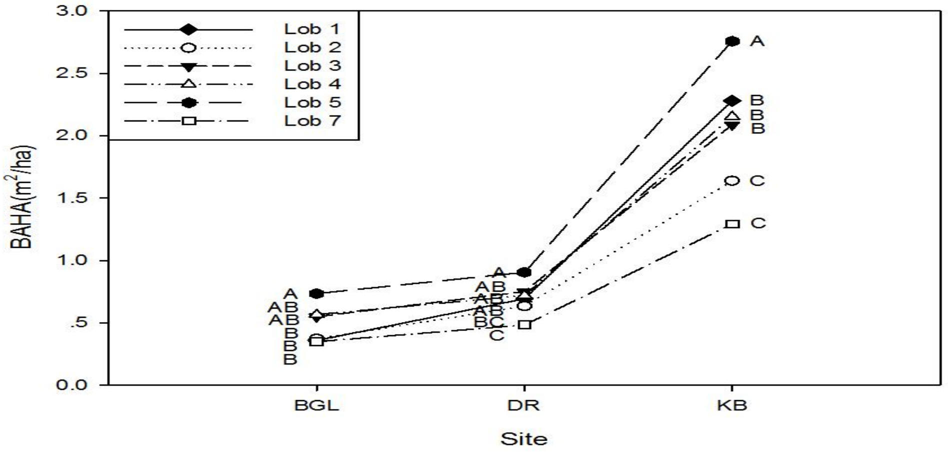
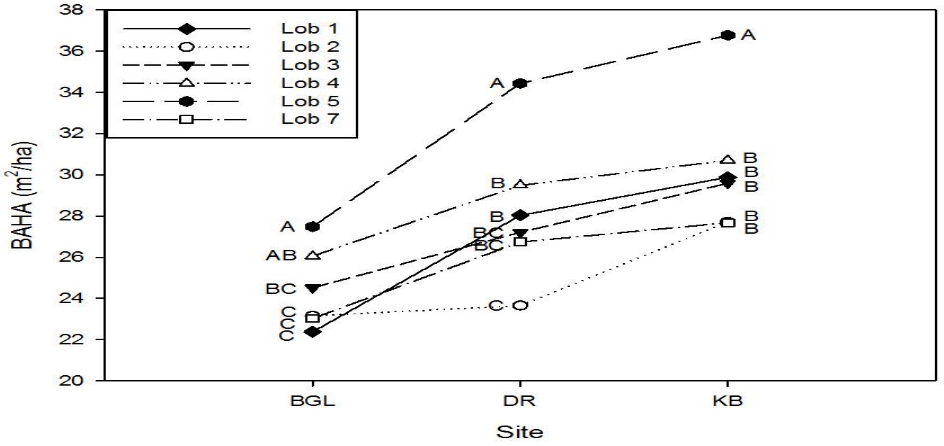


Figure 2-10 Continued


(c) Loblolly PPINES, Age 2


(d) Loblolly PPINES, Age 10

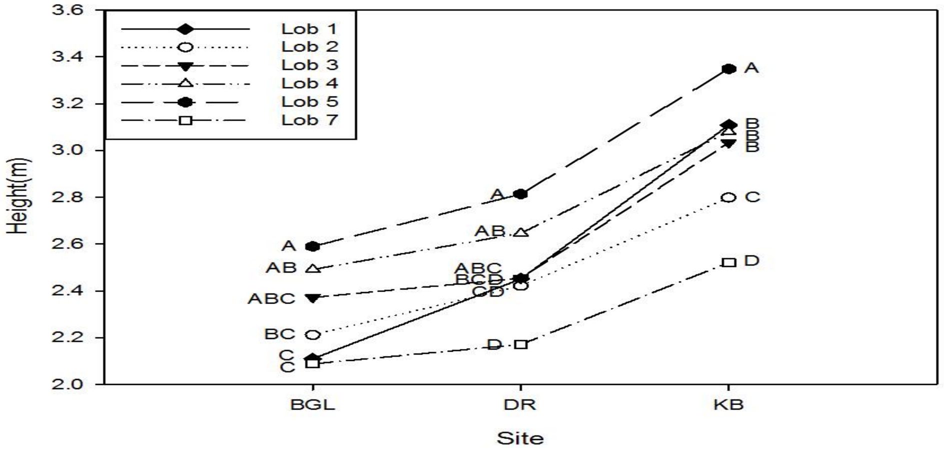
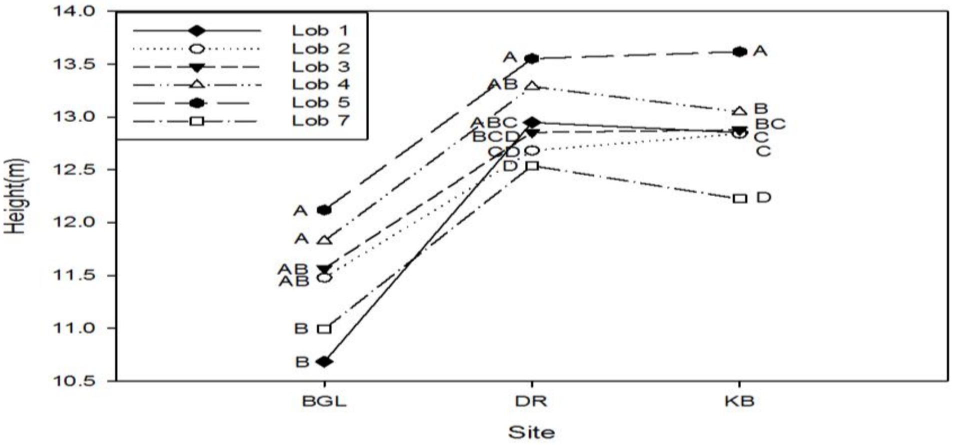
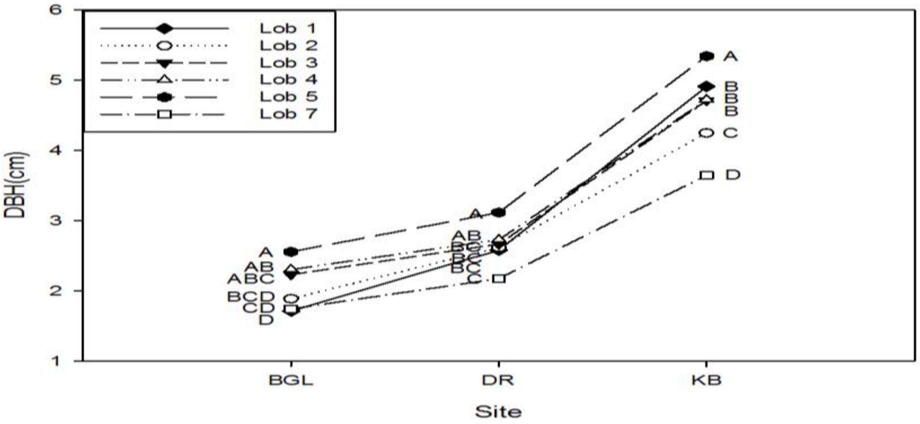

(e) Loblolly PPINES, Age 2

Figure 2-10 Continued

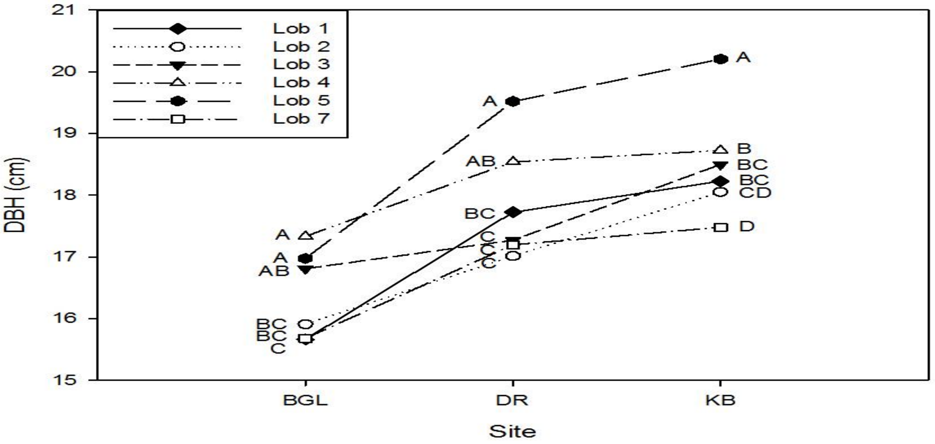
(f) Loblolly PPINES, Age 10



(g) Loblolly PPINES, Age 2



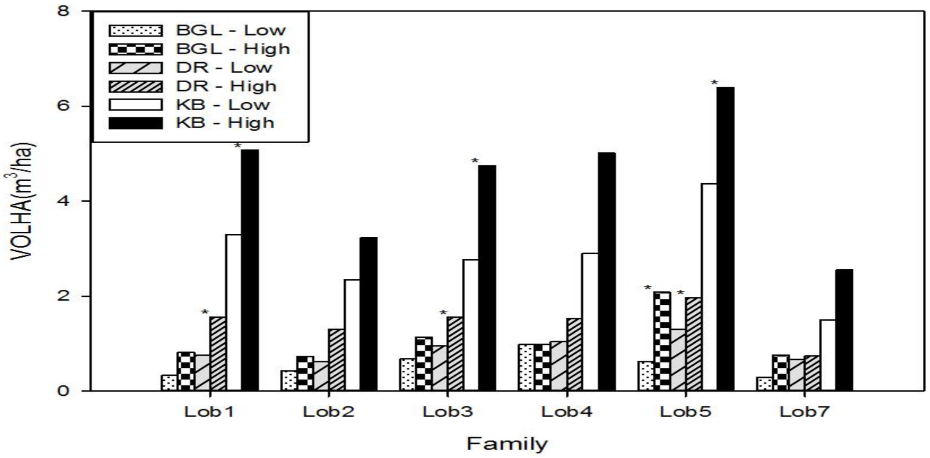
(h) Loblolly PPINES, Age 10



The interaction of family, site and silvicultural intensity on stand growth was only significant for tree height at age 2 years (Table 2-4). Although some families had different responses to the combinations of site and silvicultural intensity, the best performer was consistent across sites. For example, except for basal area growth at DeRidder, family Lob 5 had significantly better performance on all other stand growth traits under the HI treatment (Figure 2-11). However, some families had different responses to the silvicultural intensities among the sites. For example, there was no significant difference on tree height of Lob 4 under the two intensities at DeRidder at age 2 years. However, this family had significantly greater tree height under the HI treatment at Kirbyville (p=0.0070), and under the LI treatment at Bogalusa (p=0.0013) (Figure 2-11 e). Silvicultural intensity could change stand growth comparison among the three sites within family. For example, comparing stem volume difference of Lob 4 between Bogalusa and DeRidder at age 10 years, this difference was larger under the LI treatment than the HI treatment. Moreover, for certain families at some sites, the significance of silvicultural intensity changed with stand age, for example, at Bogalusa, except Lob 5, other families showed no significant difference of DBH under the two intensities at the age 2 years, but the difference grew much stronger at the age 10 years (Figure 2-11 g h).

Figure 2-11: Family × site interaction under different silvicultural intensities for stem volume of the PPINES sites at Bogalusa, LA; DeRidder, LA and Kirbyville, TX. Bars within family having an asterisk indicates significant difference at the 95% level of confidence.

(a) Loblolly PPINES, Age 2



(b) Loblolly PPINES, Age 10

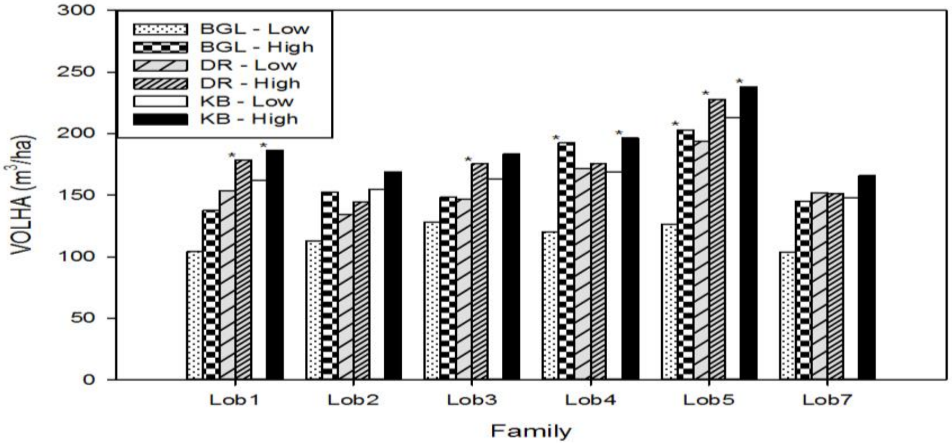
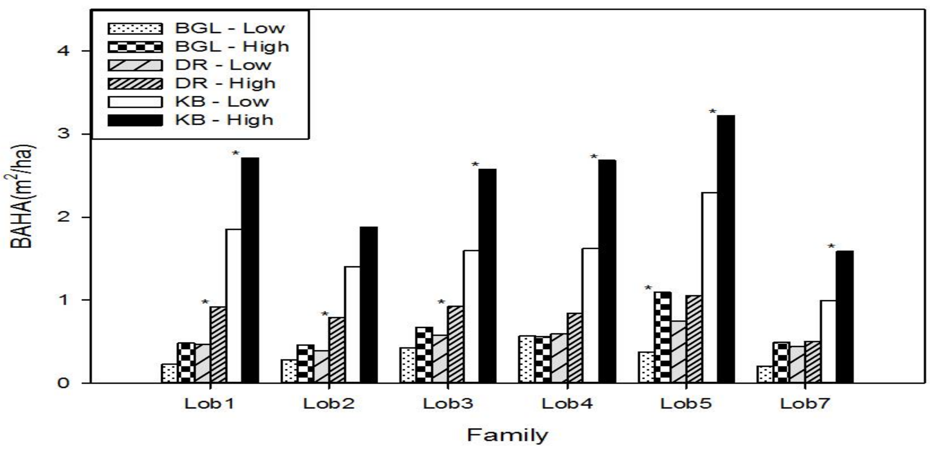
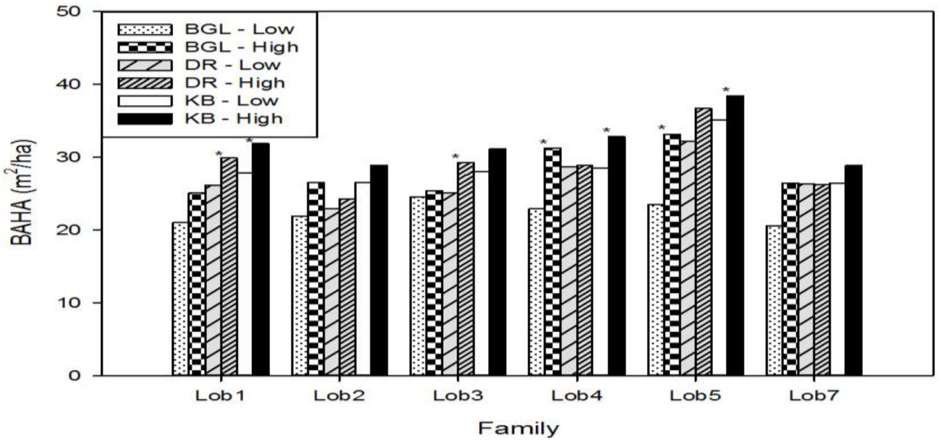


Figure 2-11 Continued

(c) Loblolly PPINES, Age 2



(d) Loblolly PPINES, Age 10



(e) Loblolly PPINES, Age 2

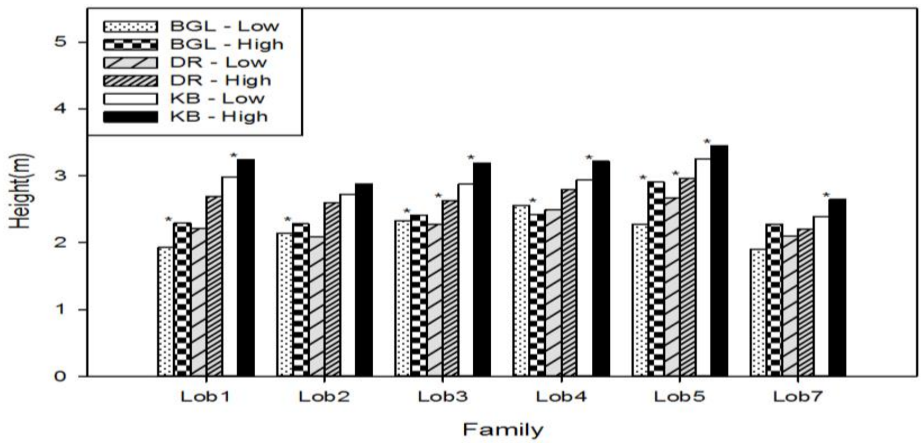
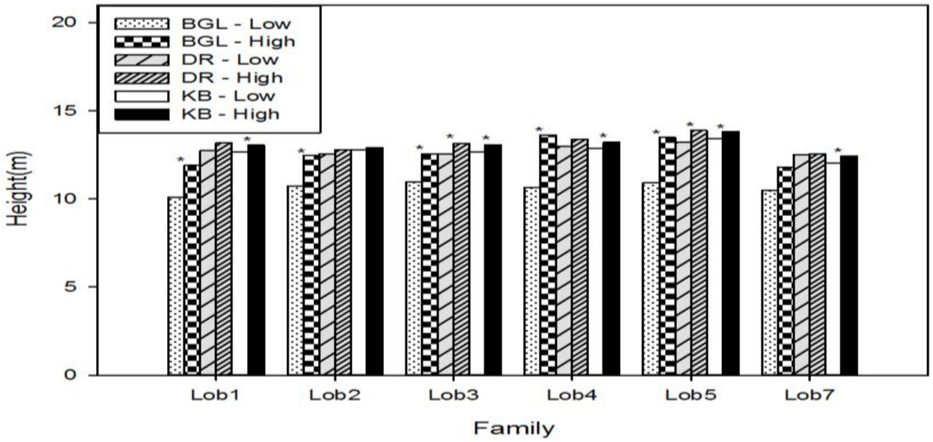
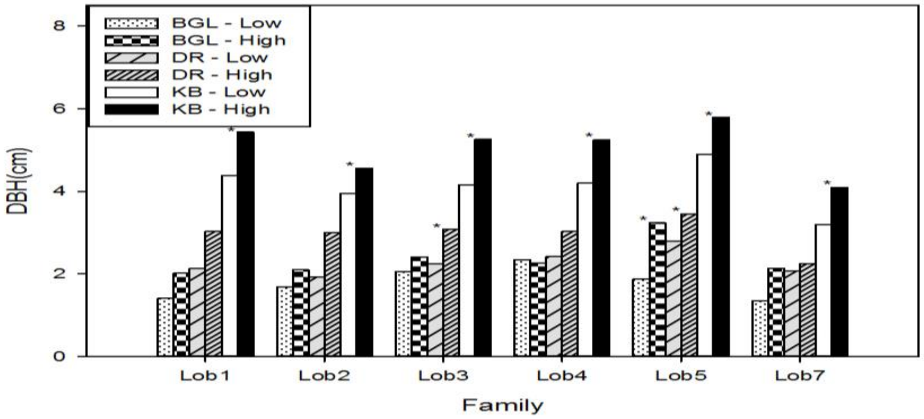


Figure 2-11 Continued

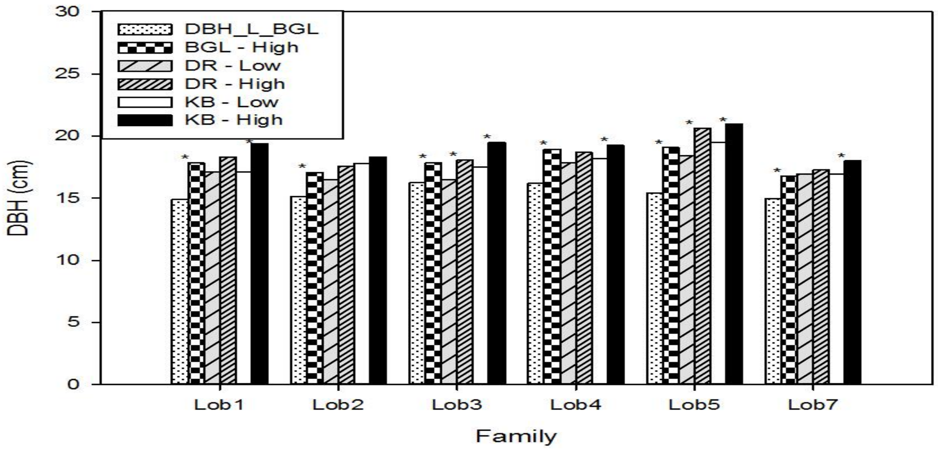
(f) Loblolly PPINES, Age 10



(g) Loblolly PPINES, Age 2



(h) Loblolly PPINES, Age 10

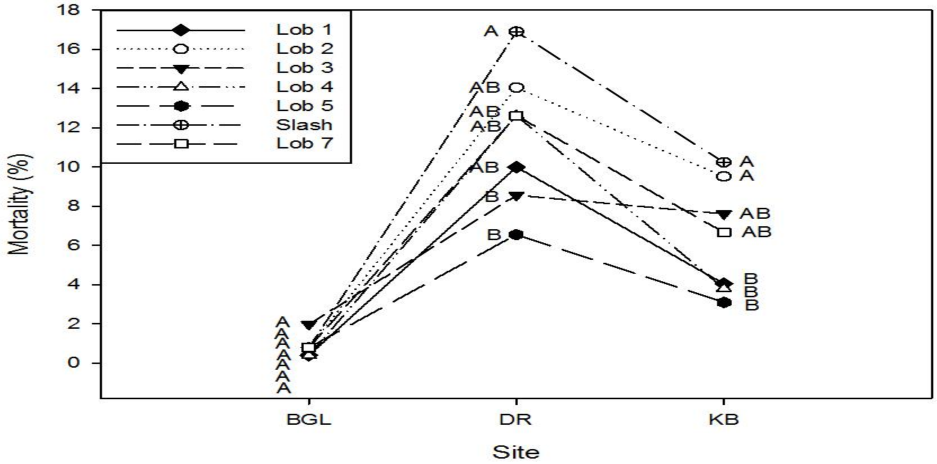


### II.3.2.2 Mortality

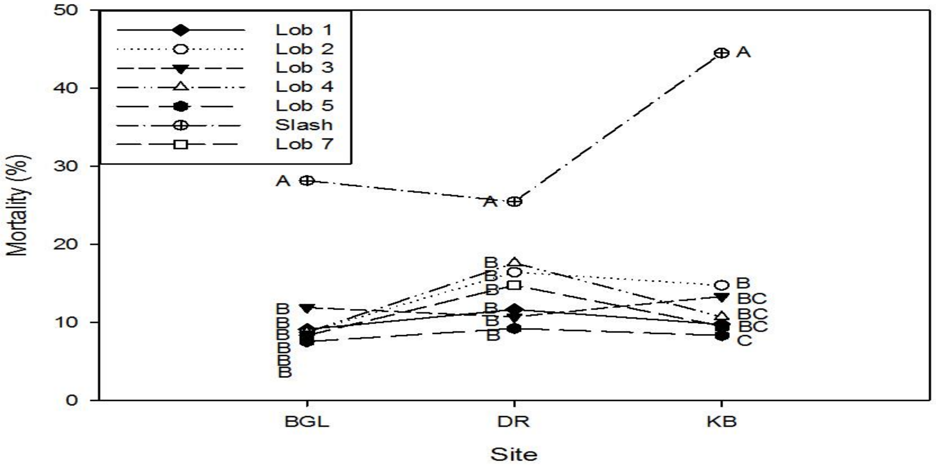
The site effect was significant for tree mortality, but the interaction of family and site was not strong (Table 2-4). At age 2 years, DeRidder had higher mortality than other sites among all the families ($p=0.0009$) (Figure 2-12 a). A site effect was also evident for site scale effects and rank changes in the mortality estimates. For example, slash pine mortality was on the same level to other loblolly pine families at Bogalusa ($p=0.9812$), but its mortality increased to a higher level at DeRidder ($p=0.0062$) and Kirbyville ($p=0.0431$) at age 2 years (Figure 2-12 a). Family Lob 3 ranked second and third at Bogalusa and Kirbyville, respectively, but it decreased to sixth at DeRidder at age 10 years. Moreover, mortality differences between slash pine and loblolly pine families became significantly larger at age 10 years ($p<0.0001$), but the differences among loblolly pine families were strong at age 2 years ($p=0.0009$) (Figure 2-12 b).

Figure 2-12: Family × site interaction plots for tree mortality of the PPINES sites at Bogalusa, LA; DeRidder, LA and Kirbyville, TX. Families within sites having the same letter are not significantly different at the 95% level of confidence. (Student's t-test)

(a) Loblolly and Slash PPINES, Age 2



(b) Loblolly and Slash PPINES, Age 10



The family×site×silvicultural intensity interaction was not strong at either age for mortality (Table 2-4). However, some families did have different mortality levels under the two intensities at different sites. At age 2 years, silvicultural intensity only had significant effect on mortality of Lob 3 at Bogalusa (p=0.0210) (Figure 2-13 a), however, at age 10 years, Lob 4 (p=0.0228) at DeRidder, slash pine (p<0.0001), Lob 1 (p=0.0273) and 3 (p=0.0361) at Kirbyville all had strong responses to the change of silvicultural intensity (Figure 2-13 b). Moreover, the instability of family mortality could also be indicated by the scale effect or rank change. For example, the mortality difference between Lob 3 and 4 was not significant either at DeRidder (p=0.8314) or Kirbyville (p=0.5234) under the LI treatment, but the two families differed significantly at DeRidder (p=0.0049) and to less degree at Kirbyville (p=0.0727) under the HI treatment.

Figure 2-13: Family × site interaction under different silvicultural intensities for mortality of trees at the PPINES sites at Bogalusa, LA. Bars within family having an asterisk indicates significant difference at the 95% level of confidence.

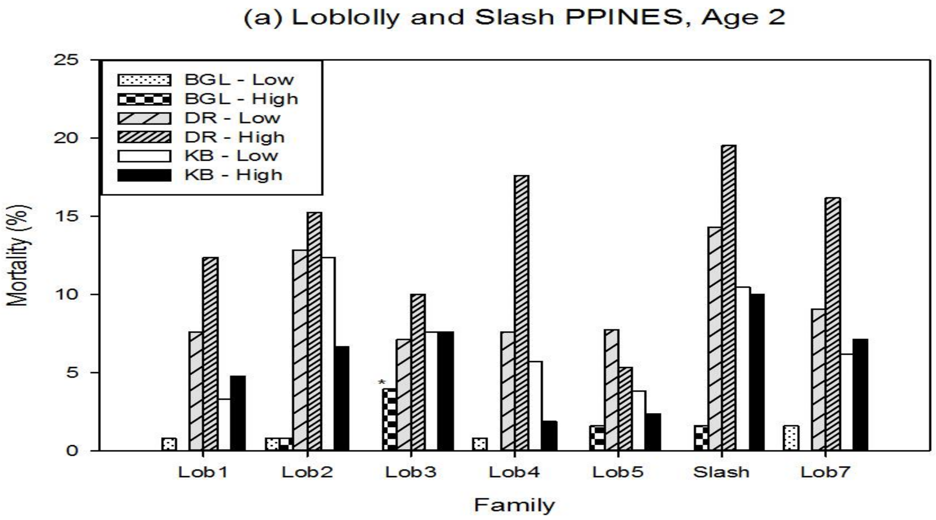
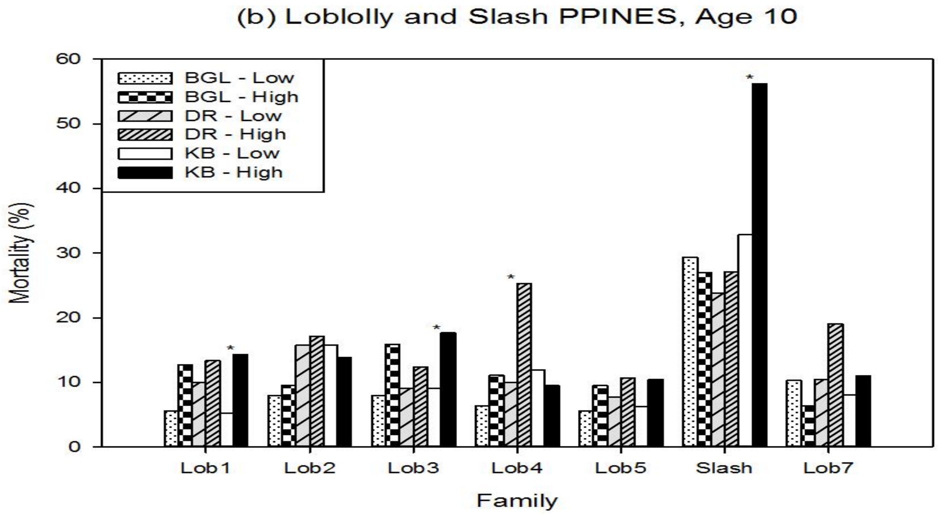


Figure 2-13 Continued



## II.4 Discussion

Loblolly pine is by far the most important tree species to industrial forestry in eastern Texas and Louisiana. The growth of pine families introduced from other regions, in particular those loblolly pine families deemed superior, needed to be examined under different silvicultural intensities at different sites in the WG area. Moreover, slash pine has been identified as needing less silvicultural input than loblolly pine on many sites and could be a preferred choice for low intensity silviculture (Jokela *et al.*, 2004). This study quantified the combined effect of silvicultural intensity and family on stand growth of full-sib loblolly pine families. The interaction of family and site (G × E) was also tested in this study at two levels: family × site and family × site × silviculture. The range of contrasting elite genotypes, silvicultural intensity and site location made a variety of interactions evident. Therefore, this study could detect strong growth differences of loblolly pine families to various environmental conditions in the WG area by using relevant statistical technologies and experimental design.

### II.4.1 Genotype × Silvicultural Intensity Interaction

Implementing integrated management regimes that incorporate genetic gains along with silvicultural practices that optimize resource availability is the key to enhancing productivity of southern pine plantations (Fox *et al.*, 2007). In my study, there was a significant family effect on stand growth (Table 2-3), which means growth increased from genetic gains. Lob 5 is the superior family from the Atlantic Coastal Plain, and it had showed best performance in EG-PPINES (Roth *et al.*, 2007; Staudhammer *et al.*, 2009). In the WG-PPINES, this family continued to have the best performance among loblolly pine families which indicated its strong adaptive ability in the South (Figure 2-3). Lob 4 is the elite family from Livingston Parish in southeastern Louisiana which is close to Bogalusa, and it also showed second best performance at Bogalusa and Kirbyville (Figure 2-3 a, c). However, at DeRidder which is located in western Louisiana, this family was unresponsive to silvicultural intensity, primarily because of the high mortality of Lob 4 under the HI treatment at DeRidder (Figure 2-10 b). Lob 1 and 3 are elite families from Texas and had intermediate performance at DeRidder and Kirbyville, but the growth of Lob 1 ranked last at Bogalusa (Figure 2-5). Though Lob 2 is also an elite family from Texas, it performed poorly at DeRidder and Kirbyville and it had intermediate growth at Bogalusa (Figure 2-5). Lob 7 is the poor family from Texas and it continued to show the least amount of production at all sites

(Figure 2-5). Therefore, on the basis of performances of loblolly pine families in the WG-PPINES, both exotic elite families had better performance than indigenous families.

I also found that the significance of the family effect changed with stand development. The effect was significant at ages 2, 3 and 10 years, but not at ages 5 or 6 years. However, in the EG-PPINES, the family effect was strong from age 2 to 7 years (Staudhammer *et al.*, 2009). It is possible that this result is due to the increased mortality and damage caused by repeated hurricane incidence for all three sites from age 5 to 10 years.

Many studies have demonstrated the significant influence that silvicultural treatments, such as weed control and fertilization, can have on loblolly pine productivity (Jokela *et al.*, 2010). This study is the first to test the effect of different silvicultural intensities on first-generation of full-sib loblolly pine families in the WG region. The silvicultural treatments had a strong effect on stand growth in the WG-PPINES (Table 2-3). My result suggests that more intensive regime would improve production of pine plantations in the WG region.

For the EG-PPINES series, Roth et al. (2007) found a significant family and silvicultural intensity interaction on stem volume at age 3 and 5 years, but no significant interaction at age 2 years. In the WG PPINES series, there was no significant family×silviculture interaction on stem volume at any age (Table 2-3). However, there were significant scale effects on stem volume at Bogalusa and Kirbyville and rank changes at DeRidder between the two intensities (Figure 2-5). This supports the hypothesis that if an elite family shows better growth performance under low silvicultural practices, then it will show better growth response to high silvicultural intensity. The distinctive family growth differences found in stem volume or other growth traits for the range of imposed silvicultural treatments likely reflects differential nutrient demands (Jokela and Martin, 2000). Therefore, a fast growing family, which may have higher resource requirements than a slow growing family, was most responsive to the intensive silvicultural treatment. This result also corresponded with previous studies about loblolly pine in the South, which suggested that intensive silviculture can increase the genetic gains or family performance difference, and better performing families tend to be most responsive to silvicultural treatment (McKeand *et al.*, 1997; Roth *et al.*, 2007).

### II.4.2 Genotype × Site Interaction

Some studies have suggested that the likelihood of G × E interactions may increase with intensified genetic selection (Bridgwater *et al.*, 2005), and increased silvicultural intensity (McKeand *et al.*, 2006). Therefore, it was expected that the significant G × E interactions would be evident in the elite full-sib families under intensive silvicultural treatments. My result showed strong G × E interaction at age 2 years, but it became less significant at age 10 years (Table 2-4). Strong G × E interaction is an indication of variation in genetic response to variations in soil, climate, pests, and diseases. To some degree, given the large differences of the site environments, such as soil, edaphic conditions and precipitation between sites, particularly Bogalusa and Kirbyville, it is surprising that these site conditions had consistent effects on overall growth. However, the G × E interaction was indicated by a few rank change or scale effects among the loblolly pine families and the three sites. For example, family Lob 1 ranked differently in stem volume at the different sites (Figure 2-12 b), but its rank at DeRidder and Kirbyville was the same, perhaps indicating that it could show good performance in the range of its native environment, but it would have very poor stand growth at Bogalusa where it was far from its native environment.

This study also tested how silvicultural intensity influenced the G × E interaction. My result suggested that the LI treatment could increase growth differences of families among sites. For example, under the LI treatment, Lob 7 had a strong growth difference between Bogalusa and DeRidder, but this difference became non-significant under the HI treatment. This may be because if the more intensive treatment can improve site condition, then it would decrease environment difference among sites. Therefore, estimates of the family performance should be combined with the specific silvicultural treatments and the growth environment.

### II.4.3 Mortality

At the three sites of WG-PPINES, hurricane (i.e., tropical cyclones with sustained winds$\geq$119 km hour$^{-1}$) was an important external factor which likely caused much of the tree mortality, because of the low appearance of diseases and insects in the sites. Moreover, the cumulative mortality increased significantly from age 3 to 10 years which overlapped with five large hurricanes (Rita, Katrina (2005); Humberto (2007); Ike, Gustav (2008)) that have struck the three research sites. Many studies have indicated that hurricanes can cause massive economic damage to forests. For example, in 2005, winds from Hurricane Katrina damaged 22 million $m^3$ of timber with an estimated value of $1.4 –2.4 billion (US) (Johnsen *et al.*, 2009).

The relative effect of high wind on trees may vary by species or for different genotypes. Comparing the pine species and loblolly pine families, slash pine had significantly higher mortality than the loblolly pine. This result disagreed with some previous studies that found slash pine was resistant to hurricane winds (Platt *et al.*, 2000; Johnsen *et al.*, 2009) or slash pine was more tolerant of hurricane damage than loblolly pine (Johnsen *et al.*, 2009). These prior studies were an examination of older trees which suggests ontogeny may be important in determining slash pine sensitivity to wind damage. Moreover Roth et al. (2007) reported intraspecific variation in slash pine sensitivity to wind damage for family plots, which suggest my results might reflect the sensitivity of the slash families planted at the sites.

Intraspecific sensitivity to wind damage was also apparent for the loblolly pine families. For example, according to the results about wind damage at Bogalusa at age 5 years, Lob 5 had the lowest wind damage among the loblolly pine families. Some studies have found that taller trees were more likely to have wind damage than shorter trees (Foster and Boose, 1992; Stanturf *et al.*, 2007). Therefore, it is surprising that Lob 5 which was the fast growing family that had greatest tree height, but still had the lowest wind damage. It was also noted that species native to the coastal plain are possibly better adapted to the regime of hurricane disturbance there (Gresham *et al.*, 1991). But Lob 5 was introduced from South Carolina. Thus, there should be other factors contributing to the resistance of Lob 5 to wind damage in the sites. Generally, four factors are related to the wind damage including climate, soils, topography, and stand conditions (Wilson, 2004). Because all the families were at Bogalusa, stand attributes would determine the susceptibly to wind damage. Lob 5 had larger basal area and tree height than the other loblolly pine families which likely made it capture more wind. However, it was also likely to have a deeper and larger root system than the other families and a lower height-to-diameter ratio, which can increase the resistance of trees to wind damage (Roth *et al.*, 2007).

On the basis of above discussion, wind damage had strong influence on stand growth in pine plantation in the WG area, and it was difficult to predict tree resistance to wind damage just considering tree height and original environment. Therefore, only if taking both family traits and environment characteristics into account, forest managers can make a judicious decisions on plantation management.

## II.5 Conclusion

In this study, significant family and silvicultural effects were found in the WG-PPINES. Therefore, landowners using the recommended intensive management practice could increase stand production of southern loblolly pine plantations significantly over lower intensity management methods. Moreover, we found evidence that slash pine suffered greater damage and mortality than loblolly pine in response to hurricanes.

I also found the superior loblolly family had the largest response to the site and silvicultural treatment changes, and that site and silviculture effect may change with stand development for certain families. These findings also have some implications to forestry professionals. First, for forest resource managers, high performing families may need less site-specific management plans but higher levels of silvicultural intensity to realize genetic gains. Second, for forest breeders, the estimation of genetic gain may change with stand development.

Currently, it is unclear how the site environment, family and silvicultural treatment interact to affect southern loblolly pine growth, and how the effects of these factors change with time and space. For example, how the family Lob 5 outgrows other families, why this superior family has a sensitive response to site and treatment changes, and why some families show no significant response to the treatment changes? These kinds of questions need to be examined from the perspective of tree physiology and genetics analysis in the future.

# CHAPTER III

# FINDING IDEOTYPES BY EXAMINING INTERACTIONS AMONG SILVICULTURAL INTENSITY, GENOTYPE, AND ENVIRONMENT FOR FULL-SIB LOBLOLLY PINE FAMILIES

## III.1 Introduction

In a review of the agronomic literature, Newton et al. (2009) reported that many studies have found a significant effect of intergenotypic competition on agronomic crop yield. However, in forestry only a few studies have analyzed the effect of intergenotypic competition for tree species (Perry, 1985; Knowe *et al.*, 1994; Foster *et al.*, 1998; Staudhammer *et al.*, 2009), or specifically on loblolly pine (*Pinus taeda L.*) (Staudhammer *et al.*, 2009). A deeper understanding of intergenotypic competition is important because it can reduce the biases in the progeny tests of tree breeding programs (Pavan *et al.*, 2011), and the mixing of crop varieties with complementary interactions can lead to enhanced yield and pest resistance (Adams *et al.*, 1973; Staudhammer *et al.*, 2009).

In studies conducted by tree breeding programs, there are two factors which may limit the ability of a traditional progeny test to identify how genotypes interactions affect growth. First, single-tree plots are the most common method used in family-level genetic selection programs. Though it is an efficient mixed layout for testing a large number of families, breeders can only estimate the performance of genetic material in the operational plantings. It may be difficult to correctly predict the growth performance in the future deployment environment where there may be new competitive conditions, like growing in pure family block, growing with different and specific neighboring tree genotypes, or growing under different cultural treatments. Second, in progeny tests, the selection criterion is based on the juvenile tree growth in mixed plots. Results from many locations in the southeastern United States have demonstrated that growth performance of loblolly pine families changed with stand development (Jokela *et al.*, 2004; Martin and Jokela, 2004)). In a previous study, some families were found that could have different performance comparison with their peer families at age 2 and 10 years in the Western Gulf area. Therefore, the selection criterion by tree juvenile growth may not correctly reflect the stand production at the end of tree rotation.

Evaluating growth with different types of competition can be facilitated by using the ideotype concept. The concept of ideotype is a biological model of a plant that explicitly describes the phenotypic characteristics of high-productivity plants (Donald, 1968; Martin *et al.*, 2001; Dickmann *et al.*, 2010). There are two main categories of ideotypes (Donald and Hamblin, 1976; Cannell, 1978). One of them is crop ideotype which can efficiently exploit locally available resources, and would not compete strongly with neighboring trees. Thus, the crop ideotype will produce the greatest yield per area (Cannell, 1978). The second category is the competitive ideotype, which could rapidly exploit site resources by aggressively expanding its crown and root system. This ideotype would have the greatest individual tree growth. Therefore, with the different growth strategies, the competitive ideotype could result in superior phenotypes when growing with the crop ideotype or when inter-tree competition is low, with the result being that the yield of a crop ideotype in a pure stand would be negatively correlated with their yield in a mixture of families (Martin *et al.*, 2001). Comparing the growth performance of individual genotypes between pure and mixed plot in long-term block-plot trials will effectively solve the two problems listed above (Staudhammer *et al.*, 2009; Gould *et al.*, 2011). For example, a series of replicated experimental trials of loblolly and slash pine were installed in four sites of Eastern Gulf area, with controlled genotype, planting density, and silvicultural intensity. Result showed that there were significant intergenotypic competitive interactions for the stand growth (Roth *et al.*, 2007). Meanwhile, the growth comparison between pure and mixed plots led to the identification of crop and competitive ideotypes (Staudhammer *et al.*, 2009). In this Western Gulf study, the identified competitive ideotype from the Eastern Gulf was also planted at all three sites.

Previous studies have found that families or ideotypes within loblolly pine differ in growth and biomass accumulation (McCrady and Jokela, 1998; Roberts, 2002; McKeand *et al.*, 2006; Chmura *et al.*, 2007; Roth *et al.*, 2007; Staudhammer *et al.*, 2009). Therefore, there is a need to determine how morphological and physiological properties of loblolly pine affect the growth of families or ideotypes. This analysis process can also help to reveal whether designation of a crop and competitive ideotypes is valuable, increase understanding of the factors that contribute to forest productivity, and then forest management could be improved by better focusing silvicultural activities towards maximizing the most important factors (Will *et al.*, 2005).

Many studies have found loblolly pine stand growth was correlated with the light interception at the stand-level (Cannell, 1989; Dalla-Tea and Jokela, 1991; McCrady and

Jokela, 1998; Will *et al.*, 2005; Chmura and Tjoelker, 2008). Some leaf traits and crown structure properties can influence tree light interception. Of these factors, total leaf area is one of the most important properties for light interception (Wang and Jarvis, 1990). In a 25-yr-old loblolly pine forest of the southern North Carolina, one study observed a strong positive linear relationship between light interception and leaf area index (LAI) (Campoe *et al.*, 2013). Another study also found that the loblolly pine stemwood growth was positively and linearly related to LAI across treatments and stands (Albaugh *et al.*, 1998). Leaf area also affects canopy transpiration, respiration, and photosynthesis efficiency (Clinton *et al.*, 2011; Gspaltl *et al.*, 2013).

Many previous studies have used LAI to understand the growth of southern pine forests under various types and intensities of silvicultural treatments. For example, one study of a 16 years old loblolly pine plantation in south Florida, found that LAI explained >95% of the total variation in stemwood biomass production among all silvicultural treatments (Jokela and Martin, 2000), but there are few studies that have examined the LAI variation in full-sib genotypes of southern loblolly pine. In 4-year-old half-sib loblolly pine stands, there was significant family variation in LAI and light interception, and these differences were associated with contrasting family performance (McCrady and Jokela, 1998; McGarvey *et al.*, 2004). However, a previous study of a 3-year-old loblolly pine stand in Western Gulf area found no significant differences between superior and average loblolly families on specific leaf area and leaf area density for two of three sites examined (Chmura *et al.*, 2007). In a companion study, I found that the family growth differences changed with stand age. Thus there is a need to examine the LAI difference again when the crowns are closed. Moreover, in some long-term studies, the relationship between stemwood biomass increment and LAI was strong at LAI <3.0, but was considerably more variable at higher LAIs (Jokela et al., 2004).

Nitrogen (N) is the nutrient that most commonly limits growth of southern pine (Fox *et al.*, 2007). Foliar N could reflect many aspects of plant growth. First, it could be an effective index of plant nutrient limitation, because it correlates with increased growth response to the addition of a limiting nutrient. Second, in southern loblolly pine, studies have consistently found that foliar N levels were positively associated with foliage biomass production, annual height growth, and chlorophyll concentrations (Zhang *et al.*, 1997; Xiao *et al.*, 2003; Chmura and Tjoelker, 2008). Foliar N was also important in determining foliage development and tree growth in subsequent years since approximately 75% of the N contained in leaves is re-translocated and used for new foliage growth (Zhang and Allen, 1996).

Studies examming the variation in foliar N response to fertilization among full-sib families of southern loblolly pine are very limited, and the results are variable. In the open-pollinated families of 3-yr-old slash pine, and 4- and 5-yr-old loblolly pine, researchers have found that improved and unimproved genotypes had different foliar nutrient and growth performance response to intensive management (Xiao *et al.*, 2003; McGarvey *et al.*, 2004). But another study of loblolly pine seedlings found no foliar N difference between the examined families (Samuelson, 2000). These mixed results may be because of the differences in stand age, variation in tree genotype and the intensity of silvicultural treatments.

In this study, the effects of silviculture treatments and deployment in mixed vs. pure plots on loblolly pine family performance were examined, allowing for the identification of different ideotypes among the families in long-term block-plot plantings. Moreover, my study compared the LAI and foliar N differences between crop and competitive ideotypes. From this comparison, the family and silviculture effect on LAI and foliar N, and effect of LAI and foliar N on stand growth were examined in the 11-yr-old full-sib loblolly pine. The following hypothesis were tested:

H1: The competitive ideotype from the Eastern Gulf studies will be the competitive ideotype in the Western Gulf.

H2: High silvicultural treatment will amplify the performance differences of the families in mixed plots because of greater resource acquisition by competitive ideotypes.

H3: LAI and foliar N will be positively correlated with stand growth because these indicate photosynthetic capture.

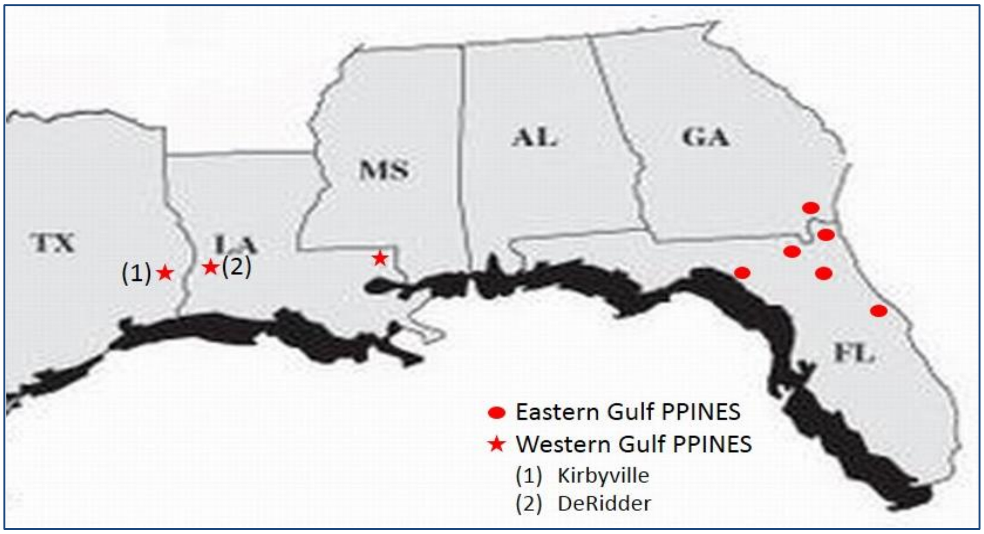
## III.2 Methods

### III.2.1 Experimental Description

Data for this study came from the Pine Productivity Interactions on Experimental Sites (PPINES) trials which are distributed throughout the southeastern United States. PPINES studies are a set of large-scale experimental installations that serve as field laboratories for addressing questions related to the productivity and sustainability of intensively managed plantations of loblolly and slash pine (Staudhammer *et al.*, 2009). These studies are also a part of the Forest Biology Research Cooperative (FBRC) coordinated by the University of Florida. PPINES has two series of sites, one is located in the Eastern Gulf (EG) area and the other is in the Western Gulf (EG) area. Here this study reports results from the WG-PPINES series.

The WG-PPINES locations were established in eastern Texas and western Louisiana (Figure 3-1). The experiment consists of two sites: Kirbyville, Texas (30º 35' N, 93º 59' W) and DeRidder, Louisiana (30º 51' N, 93º 21' W) (Figure 3-1). A third WG-PPINES site near Bogalusa, Louisiana was not examined for this study because of difficulties in accessing the site for the LAI and foliar nitrogen measurements.

Figure 3-1: The distribution of PPINES sites.



Hot and humid summers and mild winters characterize the climate of this region (Table 3-1). The two sites differ in their soil drainage classification and texture in the surface and subsurface layers. The Kirbyville site is a moderately well drained site, and DeRidder is a somewhat poorly drained site. DeRidder has a silt loam surface and sub-surface soil texture, while Kirbyville has a fine sandy loam surface soil and sandy clay loam subsurface soil (Chmura *et al.*, 2007).

Table 3-1: Mean values for the study period (2002-2012) of climatic data(1) for two experimental sites in the West Gulf Coastal Plain area.

| Site | Average Temperature (℃) | Annual Precipitation (mm) |
|---|---|---|
| DeRidder, LA | 19.8 | 1563 |
| Kirbyville, TX(2) | 19.8 | 1365 |

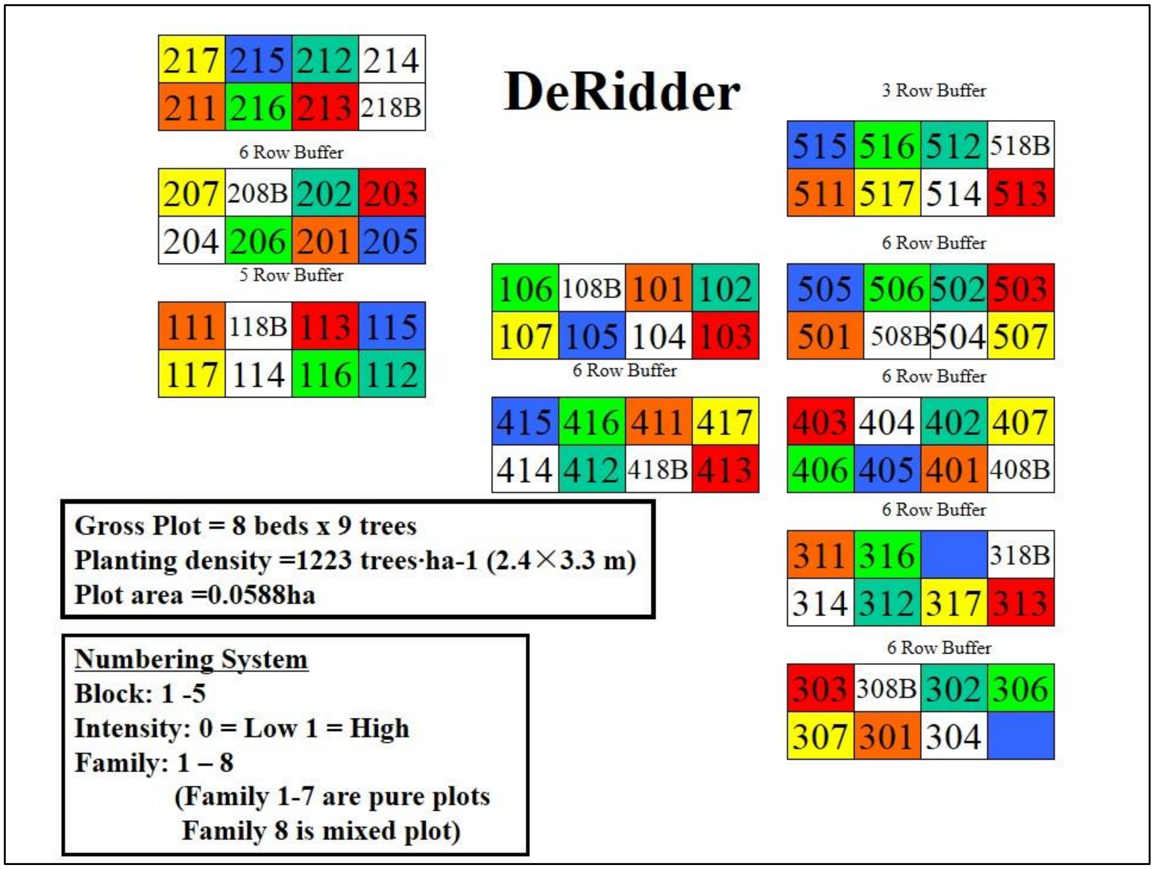
(1) From the nearest recording station, NOAA, National Oceanic and Atmospheric Administration

(2) Town Bluff Dam, Texas

### III.2.2 Experimental Design

The PPINES data used in this study were obtained from two loblolly pine installations. Each installation was established as a randomized complete block design in five blocks with treatments applied in a split-split plot design. Each block was first split into two zones of different cultural regime intensity. Therefore, the two contrasting silviculture intensities—low intensity (LI) and high intensity (HI) were assigned as a main-plot factor. Then each zone was split into eight plots, which were the experimental units for the analysis (Figure 3-2). Seven of the plots were pure-planted with a single family loblolly pine (six plots) and one slash pine family, and one plot was established with a proportional mixture of all seven families, which allowed for a family × deployment comparison.

Figure 3-2: The experimental design at the DeRidder site.



DeRidder

217 215 212 214
211 216 213 218B

6 Row Buffer

207 208B 202 203
204 206 201 205

5 Row Buffer

111 118B 113 115
117 114 116 112

106 108B 101 102
107 105 104 103

6 Row Buffer

415 416 411 417
414 412 418B 413

3 Row Buffer

515 516 512 518B
511 517 514 513

6 Row Buffer

505 506 502 503
501 508B 504 507

6 Row Buffer

403 404 402 407
406 405 401 408B

6 Row Buffer

311 316 318B
314 312 317 313

6 Row Buffer

303 308B 302 306
307 301 304

**Gross Plot = 8 beds x 9 trees**
**Planting density =1223 trees·ha-1 (2.4×3.3 m)**
**Plot area =0.0588ha**

**<u>Numbering System</u>**
**Block: 1 -5**
**Intensity: 0 = Low 1 = High**
**Family: 1 – 8**
**(Family 1-7 are pure plots**
**Family 8 is mixed plot)**

III.2.3 Treatment Description

The experimental sites were established between November 2001 and January 2002. At establishment, all plots received initial site preparation of single pass bedding, and were sprayed with Arsenal® (imazapyr) and Garlon™ (triclopyr) to control the herbaceous and woody vegetation. Establishment fertilization was at the level of 280.5 kg ha$^{-1}$ of diammonium phosphate (51 kg ha$^{-1}$ N and 56 kg ha$^{-1}$ P) at the time of planting for all sites and both silvicultural treatments. LI and HI treatments differed at the beginning of second growing season when the LI treatment did not receive any additional fertilization or weed control, while the HI treatment received competing vegetation control until canopy closure. In addition, fertilizer additions continued for the HI treatment, with rates determined for each site based on yearly analyses of foliar nutrient concentrations on the basis of critical foliage nutrient concentrations given in Gregoire and Fisher (2004). The cumulative fertilization amounts are presented in Table 3-2.

Table 3-2: Total fertilizer elemental application (kg $ha^{-1}$) up to age 3 in the three sites

| **Site** | **Intensity** | **N** | **P** | **K** | **Ca** | **Mg** | **S** | **B** | **Cu** |
|---|---|---|---|---|---|---|---|---|---|
| **DeRidder, LA** | High | 302 | 123 | 66 | 33 | 27 | 61 | 0.5 | 3 |
| | Low | 50.5 | 55.5 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Kirbyville, TX** | High | 258 | 157 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Low | 50.5 | 55.5 | 0 | 0 | 0 | 0 | 0 | 0 |

At the end of the second growing season, foliar nutrient concentrations in the HI treatment were on average higher by 43% for N and 32% for K, and lower by 6% for P than in the LI treatment. Sulfur, B, and Mn foliar concentrations were 29%, 50%, and 12% higher in HI than in LI, respectively. Concentrations of other micronutrients did not differ between the two cultural treatments (Chmura *et al.*, 2007). All sites received monthly tip moth (*Rhyacionia* spp.) control with Mimic™ (tebufenozide) during the first growing season.

Seedlings were raised in 66 ml Ray Leach “Cone-tainer”™ cells (Stuewe & Sons, Inc. Corvallis, Oregon, USA) in 2001. In this research, genetic entries are alpha numerically coded using the prefix letter “Lob” for loblolly pine. There were 72 trees (8 beds × 9 trees) in each individual sub-plot, with the inner 42 trees designated as the measurement plot. Each area of one sub-plot is 0.0588 ha. Only one planting density of 1223 trees·ha$^{-1}$ (2.4×3.3 m) was used in the western series of the PPINES locations (Chmura *et al.*, 2009), while two densities were used in the EG-PPINES. Silvicultural treatment main-plots were separated by eight rows of buffer trees within a block (Figure 3-2).

### III.2.4 Measurement

#### III.2.4.1 Forest Inventory Data

Growth analysis was based on the stand inventory data-tree height and diameter at 1.3 m (DBH). These data were collected for all families in the experiment at the end of the second and tenth growing period (ages 2 and 10 years) at all sites. The hypotheses were tested for these age classes.

#### III.2.4.2 Leaf Area Index

Stand LAI was estimated with an LAI-2000 Plant Canopy Analyzer (Li-Cor, Inc, 1991) in March, 2013. In each sub-plot, 16 LAI measurements along two transects (8 on each one) were made at a height of 1.3m between 0700 and 1000 MST or 1700 and 2000 MST using a 45° view cap. At the same time, above canopy light measurements were collected in an open field which was close to the study site and had a minimum distance of 3.5 times the adjacent canopy height. The 16 measurements were averaged to estimate the stand LAI. In order to decrease the effect of ongoing needlefall on changes in LAI, all the measurements of one site were done within one or two days of another.

### III.2.4.3 Foliage Nitrogen Concentration

One dominant tree, free of any visible defects, was randomly sampled for foliage N concentration (FN) from each subplot, and eight needle samples were collected from each fully elongated needle cohort which was current-year flush in the upper one-third of the live crown. The sampling time was in March 2013 following the 11th growing season, about 8 years after fertilization at each site.

Needles were scanned with a LI-3100C Area Meter (Li-Cor, Inc., Lincoln, Nebraska, USA). Needles were then oven-dried at 65℃ for at least 48 hours, ground and analyzed for N concentration with an NC analyzer (Flash EA 1112, Thermo Election, Milan, Italy). The foliar N concentration (FN) was expressed on a leaf mass ($N_m$, mg $g^{-1}$) basis.

### III.2.4.4 Volume and Basal Area Analyses

Response variables of interest included tree DBH (cm), tree height (m), basal area per hectare (BAHA; $m^2$ $ha^{-1}$), volume per hectare (VOLHA; $m^3$ $ha^{-1}$), and cumulative mortality (CM; %). The relevant variables were calculated using the following equations.

[1] $\text{Basal Area} = 0.00007854 \times \text{DBH}^2$

[2] $\text{Tree Volume} = (0.00395569\times(\text{DBH}^{1.8945})) \times (\text{tree height}^{0.9288}) \times 0.000056$

(Clutter et al. 1984)

This study included stand growth data at ages 2 and 10 years. Basal area and volume were first calculated on a tree-level basis. Then the family-level estimates of basal area, volume, height and DBH were scaled to per hectare and per tree bases to obtain estimates of BAHA, VOLHA, tree height and DBH. Tree mortality was calculated on a per-subplot basis by family. Tree mortality was assessed as the proportion of dead tree in the subplot.

#### III.2.4.5 Annual Increment of Basal Area and Growth Efficiency

Using the DBH data at age 10 years, the ten largest trees were selected for DBH measurement in March, 2013 at age 11 years. According to the DBH data at age 10 and 11 years, the periodic annual increment (PAI) of BAHA was calculated as the difference between the two year's basal area. To determine the canopy's efficiency in converting LAI into growth, the PAI was divided by LAI (PAI/LAI) as an estimate of growth efficiency.

### III.2.5 Statistical Analysis

The change in response variable was modeled as a function of interactions of block, family, deployment and silvicultural intensity. To test for differences in tree-level and stand-level attributes among treatment, separate analyses were performed for the two-level attributes (LAI and FN).

#### ① Intergenotypic Competitive Interactions and Identification of Ideotype

To support crop and competition ideotype identification, and test the deployment effect on the tree-level attributes tree height, DBH, BAHA and VOLHA, separate ANOVAs were performed for three sites. The basic model was:

$$[3] \qquad Y_{iklmr} = \mu + G_k + C_l + D_m + b_i + GC_{kl} + GD_{km} + bG_{ik} + CD_{lm} + bC_{il} + GCD_{klm} + bGC_{ikl} + bCD_{ilm} + bGCD_{iklm} + \varepsilon''''_{(iklm)r}$$

where $Y_{iklmr}$ is the response variable (tree height, DBH, BAHA, and VOLHA ) of the rth tree in the ith block, mth deployment, kth genotype and lth silvicultural intensity (m=1, 2); $D_m$ is the fixed effect of mth deployment; $GD_{km}$ is the interaction effect of mth deployment and kth genotype; $CD_{lm}$ is the interaction effect of mth deployment and lth silvicultural intensity; $GCD_{klm}$ is the interaction effect of kth genotype, mth deployment and lth silvicultural intensity; $bCD_{ilm}$ is the random effect of lth silvicultural intensity, mth deployment in the ith block; $bGCD_{iklm}$ is the random effect of kth genotype; lth silvicultural intensity; mth deployment in ith block; $\varepsilon''''_{(iklm)r}$ is the random error of rth tree in ith block, kth genotype, lth silvicultural intensity, mth deployment; and all other variables are as previously defined.

To test the deployment effect on the stand-level attributes cumulative mortality, an ANOVA was performed for three sites. The basic model was:

$$[4] \qquad Y_{iklm} = \mu + G_k + C_l + D_m + b_i + GC_{kl} + GD_{km} + bG_{ik} + CD_{lm} + bC_{il} + GCD_{klm} + bGC_{ikl} + bCD_{ilm} + bGCD_{iklm} + \varepsilon'''''_{(klm)i}$$

where $Y_{iklm}$ is the stand level variable proportion of death of the trees in the ith block, kth genotype, lth silvicultural intensity, mth deployment; $\varepsilon''''_{(klm)i}$ is the random error of the ith block in kth genotype, lth silvicultural intensity; and mth deployment and all other variables are as previously defined.

② LAI

In this study, the LAI is the stand-level LAI. Therefore, to understand the relationship of LAI with stand growth, the analysis was conducted using a model similar to eq. 3. But the analysis was just focused on crop and competitive ideotype.

③ Foliar N concentration

The N concentration per leaf area was calculated from the experimental result of foliar N amount and the specific leaf area ($m^2g^{-1}$) of needles at age 1 year. Then the stand level N content was estimated by using the following formula:

$$[5]\ Stand\ Foliar\ Nitrogen\ Concentration\ (FN) = N\ (g \cdot m^{-2}) \times LAI(m^2 \cdot m^{-2})$$

The statistical analysis was conducted using a model similar to eq. 3 to understand the relationship of foliar N with stand growth.

Analyses were conducted in mixed-models framework using the SAS procedures MIXED and GLIMMIX (Littel *et al.*, 2006). First, the studentized residuals and Cook's D influence of the response variable data were calculated to find outliers. Then these outliers were deleted to increase the least squares coefficients. Second, the data were tested for normality using the Kolmogorov-Smirnov test in the SAS UNIVARIATE procedure. If the data were not significantly different from normal distribution ($P>0.05$), they were analyzed with the MIXED procedure. If data did not fit the normal distribution, a log transformation would be used on the data to result in approximately normal data. Then, the GLIMMIX procedure was used to analyze the data. Third, in the data of stand growth at ten years old, only a subset of tree heights was collected. The PROC NLIN procedure was used to predict the height value from DBH, family and silvicultural intensity.

To test the assumptions of proper model specification and homogeneous variation necessary for analysis of variance, probability plots of residuals versus predicted values was conducted, and then Bartlett's test method in PROC GLM was used to make the equal variance test. Where models proved significant effects ($P < 0.05$), least squares means were generated between levels of the factors of interest.

## III.3 Result

### III.3.1 Stand Growth

There were no significant main effects on interactions at age 2 years, while some factors became significant with stand age. For example, at 10 years, interactions of deployment×family, and deployment×site×silvicultural intensity were strong in VOLHA, tree height, and DBH.

Table 3-3 Summary of F values, statistical significance, and associated degrees of freedom from the mixed model testing for loblolly pine growth at ages 2 and 10 years.

| | df | DBH | | Tree Height | | BAHA[b] | | VOLHA[b] | | CM[b] | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Effect[a] | | F | P | F | P | F | P | F | P | F | P |
| Age 2 | | | | | | | | | | | |
| D | 1 | 2.81 | 0.1223 | 2.62 | 0.1345 | 0.24 | 0.6399 | 0.28 | 0.6091 | | |
| D×C | 1 | 0.40 | 0.5403 | 0.50 | 0.4938 | 0.40 | 0.5442 | 0.49 | 0.5048 | | |
| D×F | 5 | 0.65 | 0.6602 | 0.27 | 0.9293 | 0.45 | 0.8101 | 0.28 | 0.9243 | | |
| D×C×F | 5 | 1.41 | 0.2451 | 1.47 | 0.2097 | 1.12 | 0.3562 | 1.09 | 0.3763 | | |
| D×S | 1 | 1.07 | 0.3345 | 0.88 | 0.3797 | 0.95 | 0.3600 | 1.18 | 0.3109 | | |
| D×C×S | 1 | 0.44 | 0.5282 | 1.58 | 0.2504 | 0.00 | 0.9963 | 0.02 | 0.8957 | | |
| D×F×S | 5 | 0.82 | 0.5435 | 1.00 | 0.4244 | 0.40 | 0.8487 | 0.51 | 0.7707 | | |
| Age 10 | | | | | | | | | | | |
| D | 1 | 1.25 | 0.2846 | 0.04 | 0.8550 | 29.63 | **0.0011**[c] | 23.33 | **0.0024** | 11.54 | **0.0026** |
| D×C | 1 | 1.18 | 0.2967 | 0.69 | 0.4227 | 0.08 | 0.7846 | 0.15 | 0.7112 | 1.92 | 0.1797 |
| D×F | 5 | 11.61 | **<0.0001** | 3.23 | **0.0133** | 13.88 | **<0.0001** | 12.33 | **<0.0001** | 1.98 | 0.0948 |
| D×C×F | 5 | 0.50 | 0.7767 | 2.32 | 0.0570 | 0.96 | 0.4455 | 0.96 | 0.4481 | 1.87 | 0.1194 |
| D×S | 1 | 0.86 | 0.3999 | 7.77 | **0.0167** | 0.80 | 0.4142 | 1.53 | 0.2724 | 1.92 | 0.1797 |
| D×C×S | 1 | 7.88 | **0.0250** | 31.52 | **0.0001** | 7.76 | 0.0536 | 10.49 | **0.0370** | 0.0003 | 0.9874 |
| D×F×S | 5 | 0.76 | 0.5794 | 0.40 | 0.8482 | 0.72 | 0.6129 | 0.37 | 0.8699 | 1.87 | 0.1194 |

[a] Effects include family (F); silvicultural intensity (C); site (S); and deployment (D).

[b] BAHA is basal area per hectare; VOLHA is stem volume per hectare; CM is cumulative mortality of loblolly pine stand at age 10 year.

[c] p-Values significant at the 95% level of confidence are shown in bold type.

### III.3.1.1 DBH and BAHA

At age 2 years, the deployment effect on DBH (p=0.1223) and BAHA (p=0.6399) was not significant, but the same effect on BAHA increased strongly at age 10 years (p=0.0011) (Table3-3). The interaction of deployment and family on DBH (p<0.0001) and BAHA (p<0.0001) also became strong at age 10 years (Table 3-3). Among the loblolly pine families, Lob 4 (p=0.0253) and Lob 5 (p=0.0005) had significantly larger DBH in the mixed plots than the pure plots, whereas Lob 7 (p=0.0035) had smaller DBH in the mixed plots at age 10 years (Figure 3-3). For BAHA, except for Lob 7, all other families showed significantly larger growth in the mixed plots at age 10 years. For example, the BAHA difference between mixed and pure plots of Lob 5 ($p<0.0001$) was about 12.46 $m^2$/ha. Moreover, comparing the mixed and pure plots, the range of DBH and BAHA became narrower from age 2 to 10 years (Figure 3-3).

Figure 3-3: Family × deployment interaction for DBH and BAHA of the WG-PPINES sites. Data points within deployments having the same letter are not significantly different at the 95% level of confidence using Student's t-test.

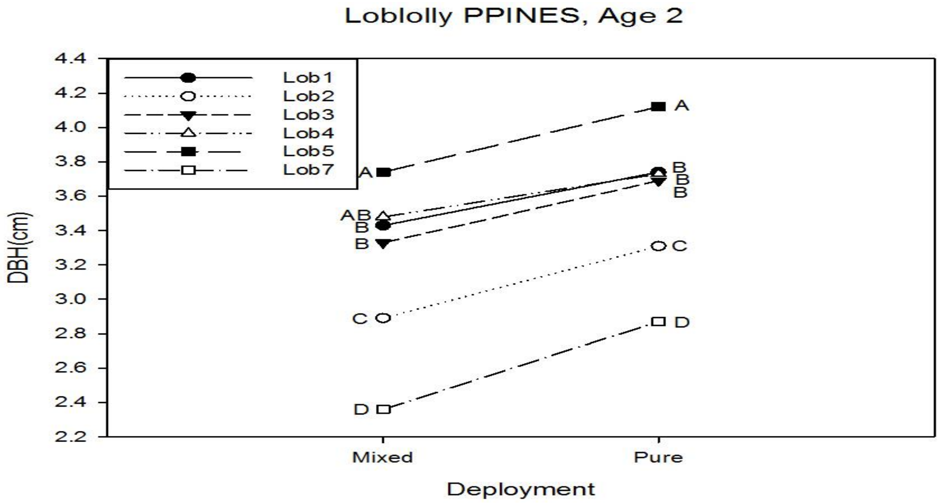
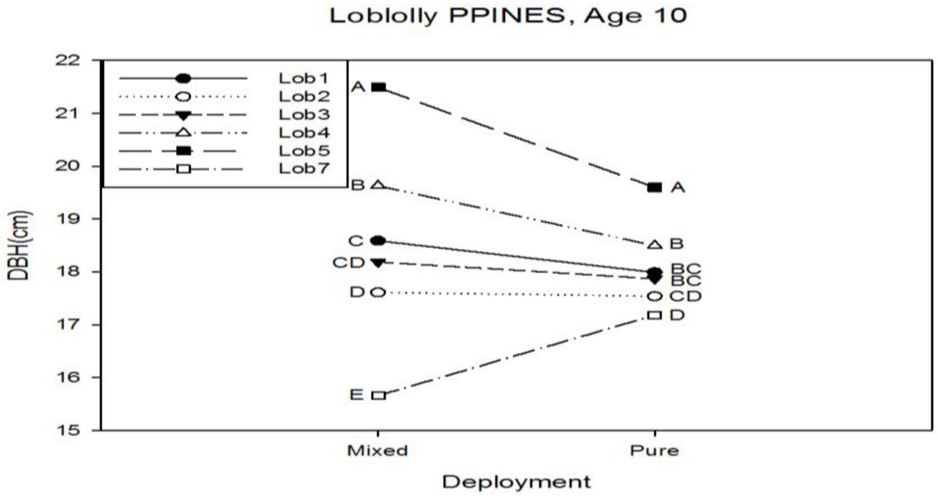
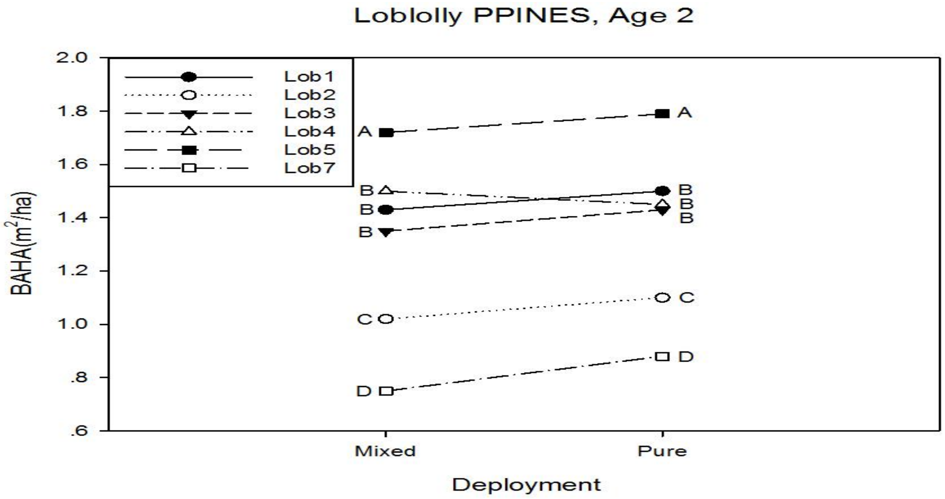
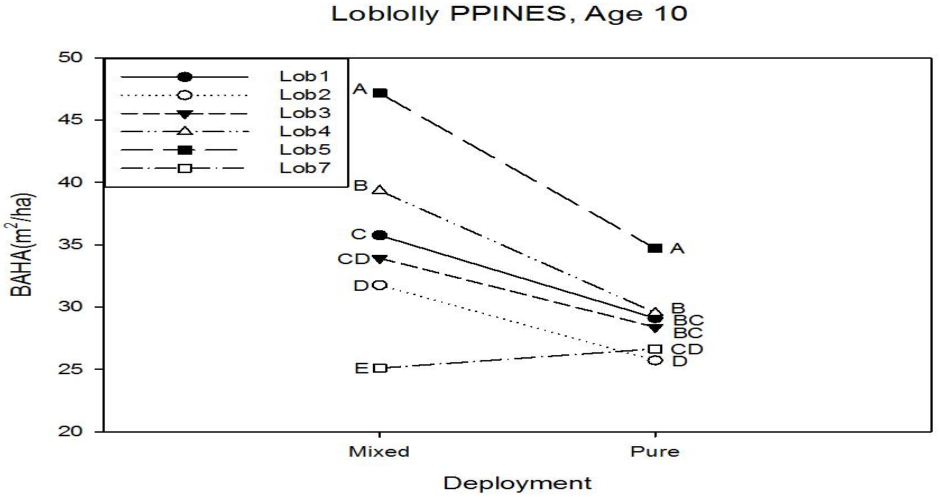


Figure 3-3 Continued







Though the interaction of deployment×family×silviculture was not significant (Table 3-3), the silvicultural intensities showed strong influence on certain combinations of family and deployment. For example, family Lob 1 (p=0.0491) and Lob 4 (p=0.0182) showed strong DBH differences between the two deployments under the LI treatment, but there were no significant differences under the HI treatment (Figure 3-4). However, Lob 7 (p=0.0157) showed more significant DBH difference at age 10 years under the LI treatment than under the HI treatment (Figure 3-4). For BAHA, family Lob 1 (p=0.0005) continued to show significant BAHA difference between the two deployments under the LI treatment, and Lob 2, Lob 3, Lob 4, and Lob 5 had the strong BAHA difference under the both intensities (Figure 3-4). However, Lob 7 showed no significant difference under either the LI (p=0.5097) or HI (p=0.5146) treatments (Figure 3-4).

Figure 3-4: Family × deployment interaction under different silvicultural intensities for DBH and BAHA of the WG-PPINES sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.

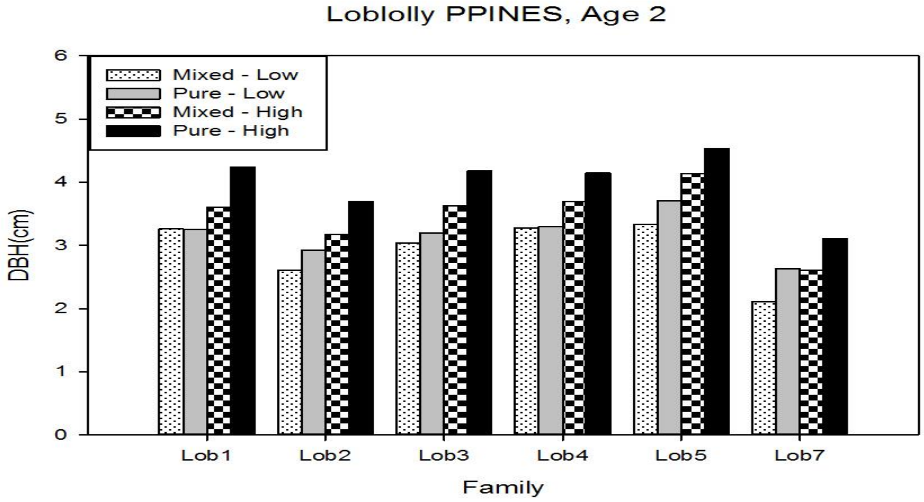
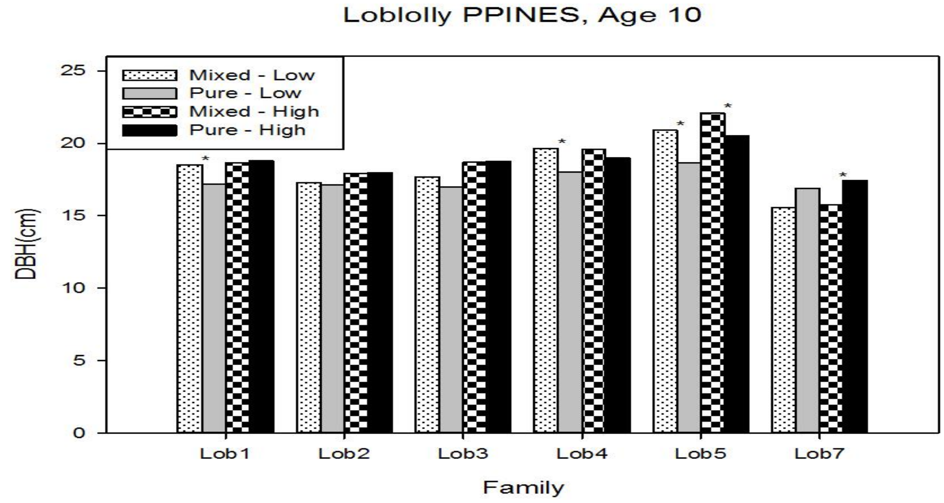
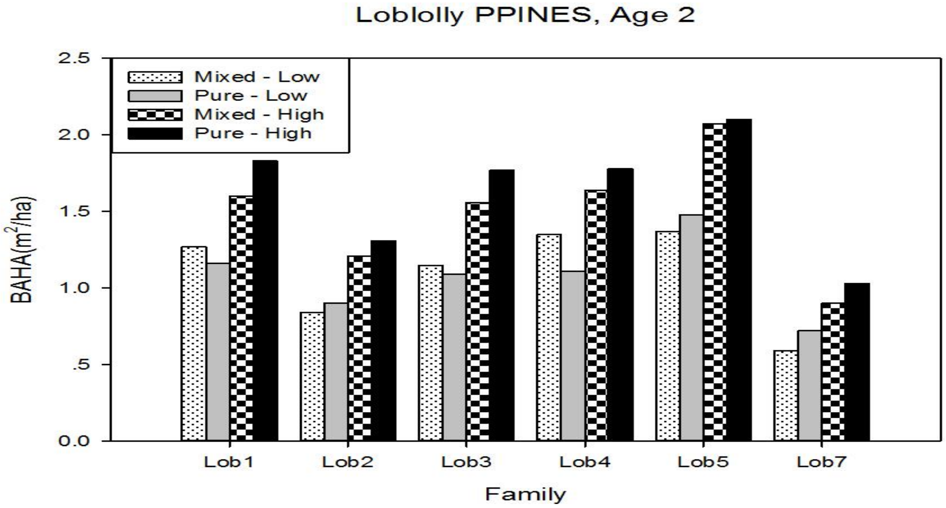
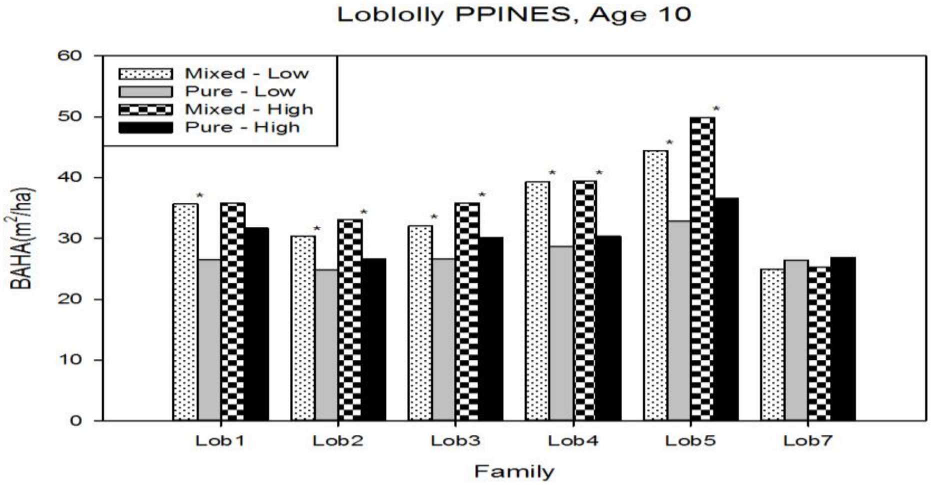


Figure 3-4 Continued







Similar to the effect of silviculture, the site effect can influence the interaction of family and deployment, and this influence appeared as early as age 2 years. For example, at DeRidder, there were no strong DBH differences between the mixed and pure plots at age 2 years. However, at Kirbyville, family Lob 1 (p=0.0471), Lob 2 (p=0.0219) and Lob 7 (p=0.0450) showed significant differences between the two deployments (Figure 3-5). At age 10 years, Lob 7 continued to show significant DBH differences at Kirbyville (p=0.0018) (Figure 3-5). However, Lob 4 showed significant DBH differences at DeRidder (p=0.0343), and no strong differences at Kirbyville (p=0.1316). There were significant differences between the two deployments for DBH at both sites for Lob 5 (p=0.0197, p=0.0004 respectively) at age 10 years. For BAHA, except for Lob 7, all other families showed significant BAHA differences between the mixed and pure plots at the both sites at age 10 years (Figure 3-5). For example, at Kirbyville, Lob 5 (p=0.0004) in the mixed plots had about 13.84 $m^2$ more BAHA than the pure plots (Figure 3-5).

Figure 3-5: Family × deployment interaction at different sites for DBH and BA. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.

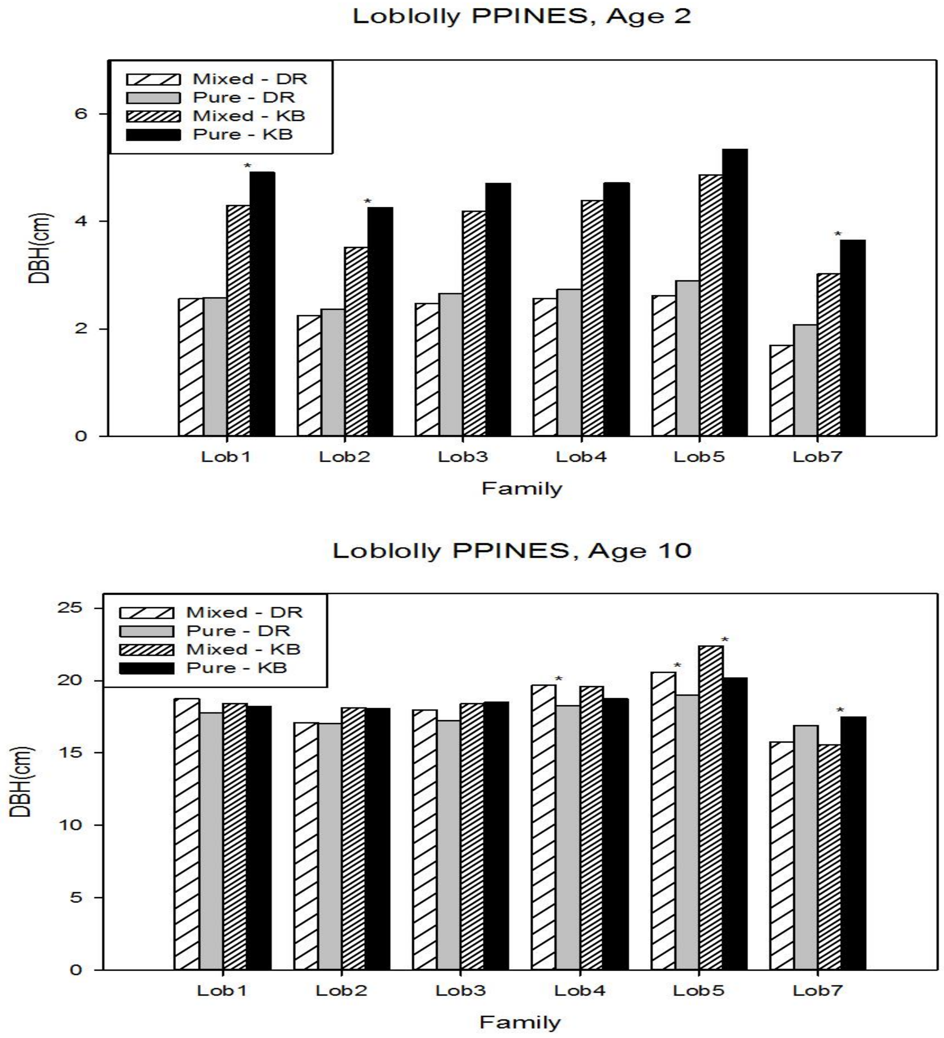
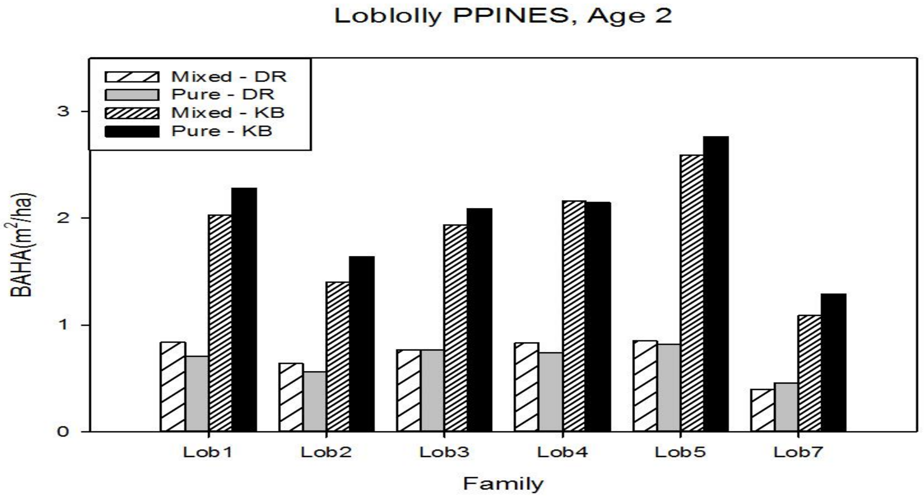
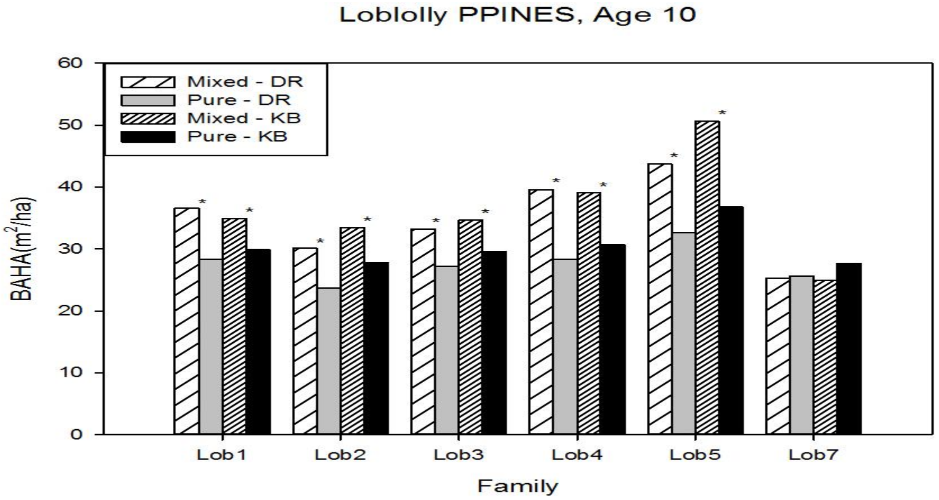


Figure 3-5 Continued


Loblolly PPINES, Age 2


Loblolly PPINES, Age 10

### III.3.1.2 Stem Volume

At age 2 years, the deployment effect (p=0.6091) on VOLHA was not strong. However, with the stand development, there was a strong deployment effect (p=0.0024) at age 10 years (Table 3-3). The interaction of deployment and family (p<0.0001) was also very significant at age 10 years (Table 3-3). Among the families, except for Lob 7 (p=0.4375), other families showed significant VOLHA differences between the mixed and pure plots. For example, the VOLHA difference of Lob 5 ($p<0.0001$) was about 78.82 $m^3$/ha, thus the mixed deployment increased VOLHA by about 37.2% (Figure 3-6). Moreover, consistent with DBH and BAHA, the pure deployment narrowed the range of VOLHA compared with the mixed deployment (Figure 3-6), and the scale effect of deployment was also significant among the loblolly pine families. For example, the VOLHA difference of Lob 2 and Lob 7 became significantly larger in the mixed ($p=0.0002$) than pure plots ($p=0.9215$) (Figure 3-6).

Figure 3-6: Family × deployment interaction for VOLHA of the WG-PPINES sites. Data points within deployments having the same letter are not significantly different at the 95% level of confidence using Student's t-test.

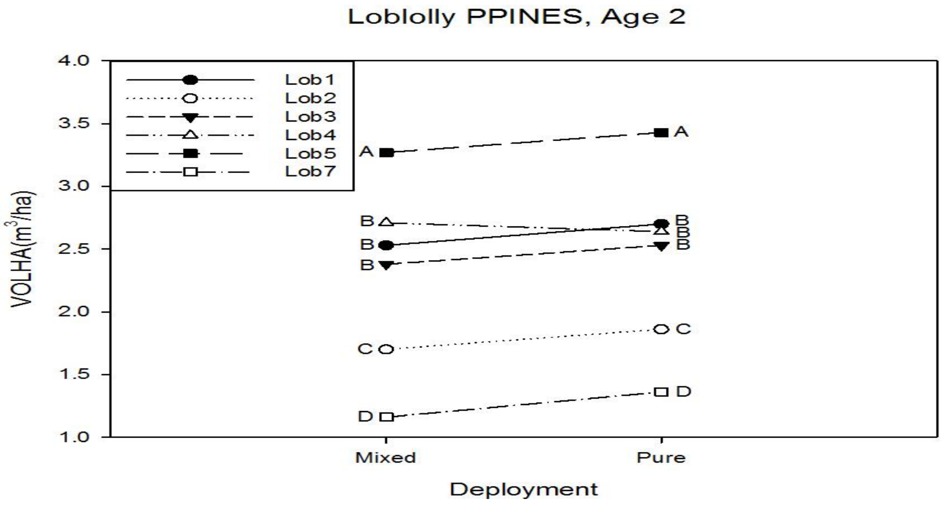
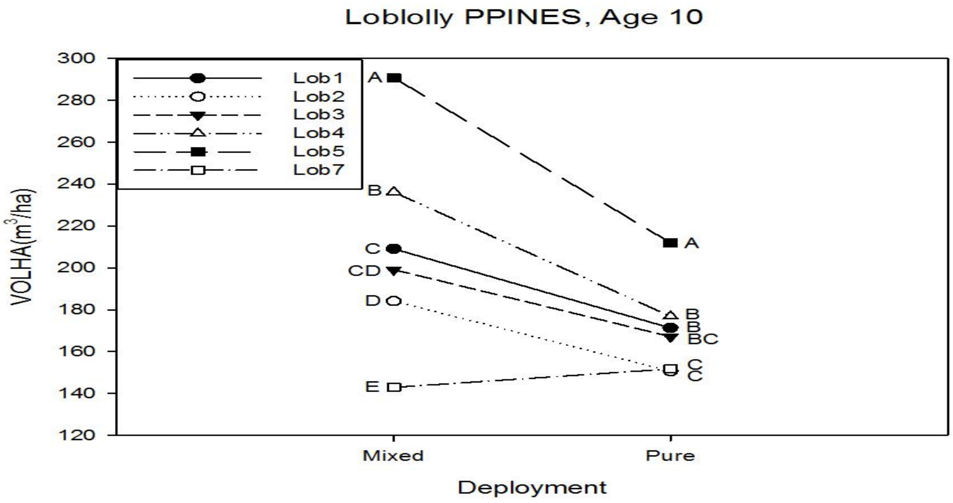
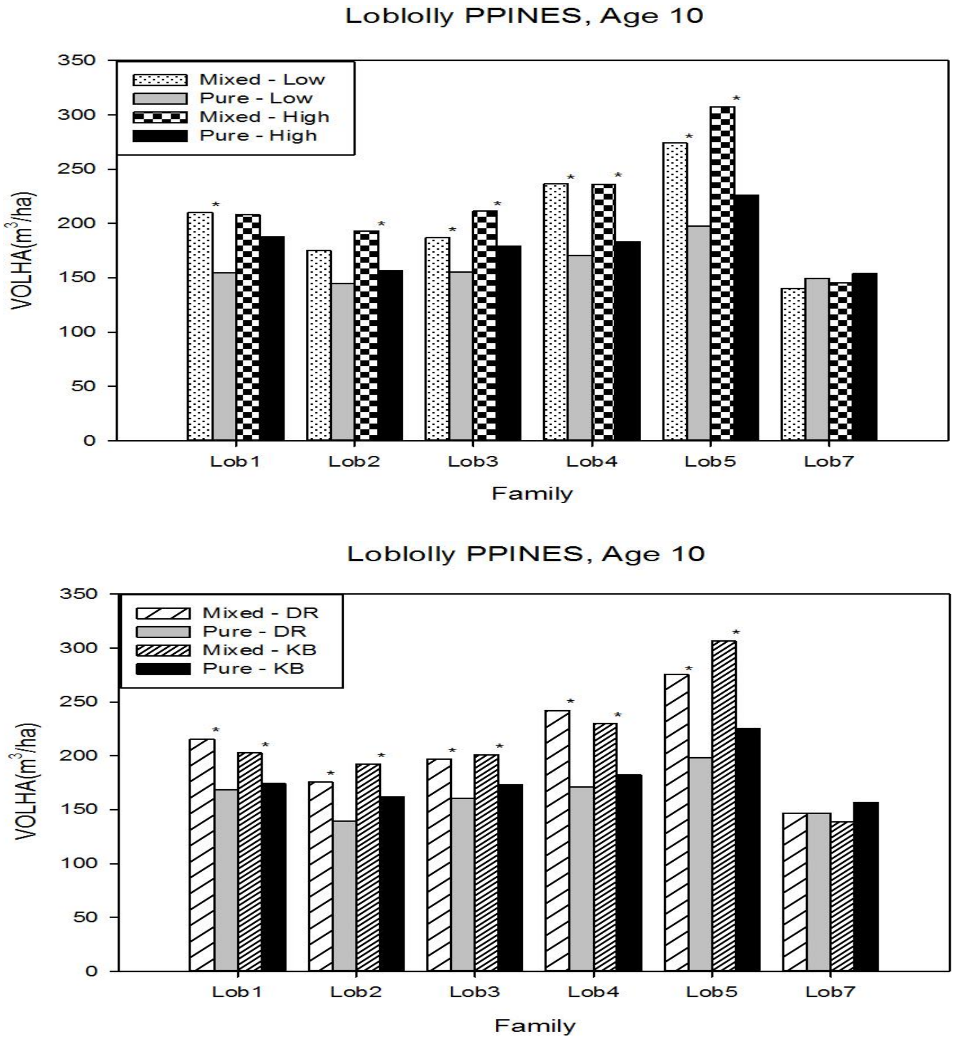


Figure 3-6 Continued



The interaction of deployment×family×silviculture was not significant (Table 3-3). Comparing ages 2 and 10 years, the deployment effect under each treatment became significant with stand age. For certain families, silvicultural intensity can influence the interaction of family and deployment at age 10 years. For example, family Lob 1 had significant VOLHA difference between the two deployments under the LI treatment (p=0.0014), but this difference became non-significant under the HI treatment (p=0.1938). However, Lob 2 showed more significant difference under the HI treatment (p=0.0250) than the LI treatment (p=0.0581), and Lob 3, Lob 4, and Lob 5 showed strong differences under the both treatments (Figure 3-7). There was also no strong interaction of deployment×family×site for VOLHA at both ages (Table 3-3). Similar to BAHA, except for Lob 7, all other families had significantly higher VOLHA in the mixed plots than the pure plots at both sites at age 10 years (Figure3-7). However, after comparing the P values, the differences at DeRidder were more significant than at Kirbyville.

Figure 3-7: Family × deployment interaction under different silvicultural intensities and at different sites for VOLHA of the WG-PPINES sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.



### III.3.1.3 Height

The main effect of deployment was not significant for tree height (Table 3-3). However, the interaction of family and deployment (p=0.0133) was strong at age 10 years for tree height. Among the loblolly pine families, only family Lob 5 (p=0.0606) showed relatively strong response to the two types of deployment, and tree height of Lob 5 in the mixed plot was greater than the pure plots. However, there was no significant difference between the two deployments for other families.

Figure 3-8: Family × deployment interaction for tree height of the WG-PPINES sites. Data points within deployments having the same letter are not significantly different at the 95% level of confidence using Student's t-test.

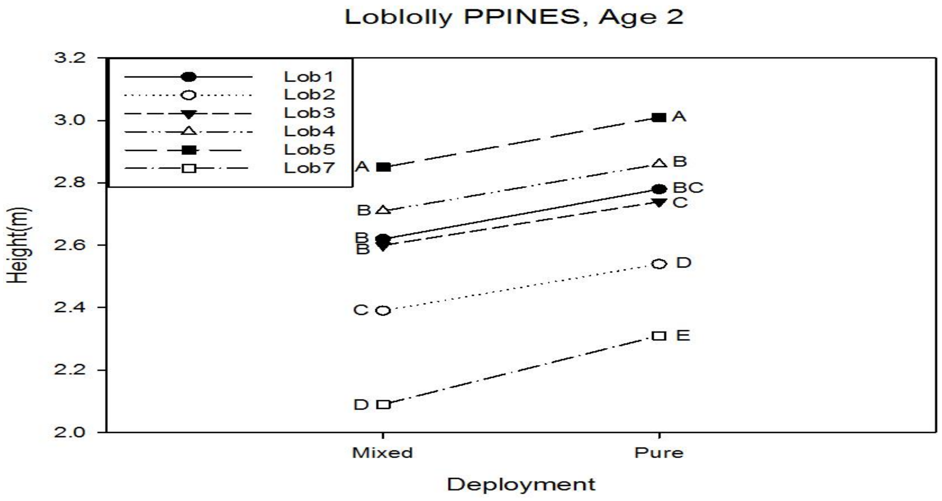
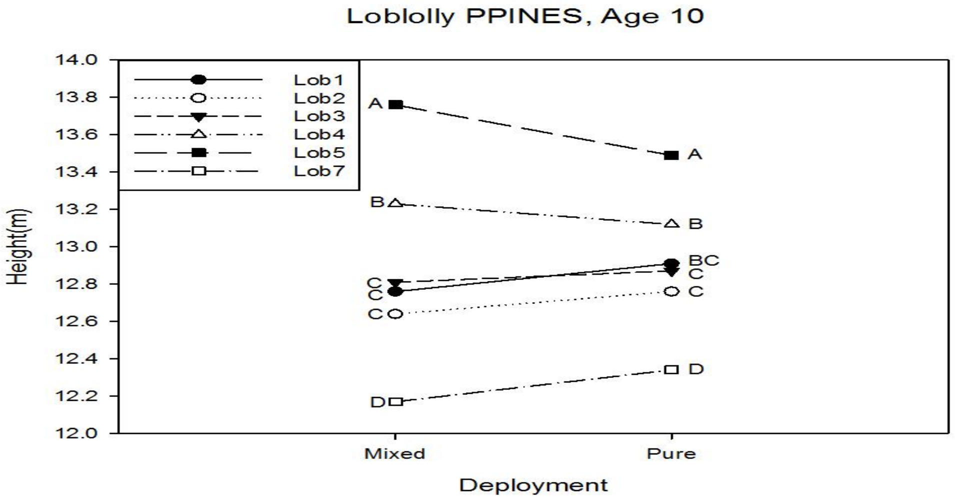


Figure 3-8 Continued



With the stand development, the significance of deployment×silviculture×family interaction increased from age 2 years (p=0.2097) to age 10 years (p=0.0570) (Table 3-3). For example, at age 10 years, Lob 1 (p=0.0536) showed relatively larger height difference to the two deployments under the HI treatment (Figure 3-9). However, for Lob 5 (p=0.0186), there was a significant height difference under the LI treatment. Moreover, the interaction of deployment×site×family was not strong at both ages (Table 3-3). In the loblolly pine families, only Lob 1 (p=0.0324) had significant height difference between the two deployments at Kirbyville at age 2 years. At age 10 years, there was significant height difference for Lob 5 (p=0.0062) at DeRidder (Figure 3-9). However, Lob 7 (p=0.0412) had the strongest difference at Kirbyville among the families (Figure 3-9).

Figure 3-9: Family × deployment interaction under different silvicultural intensities and at different sites for tree height of the WG-PPINES sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.

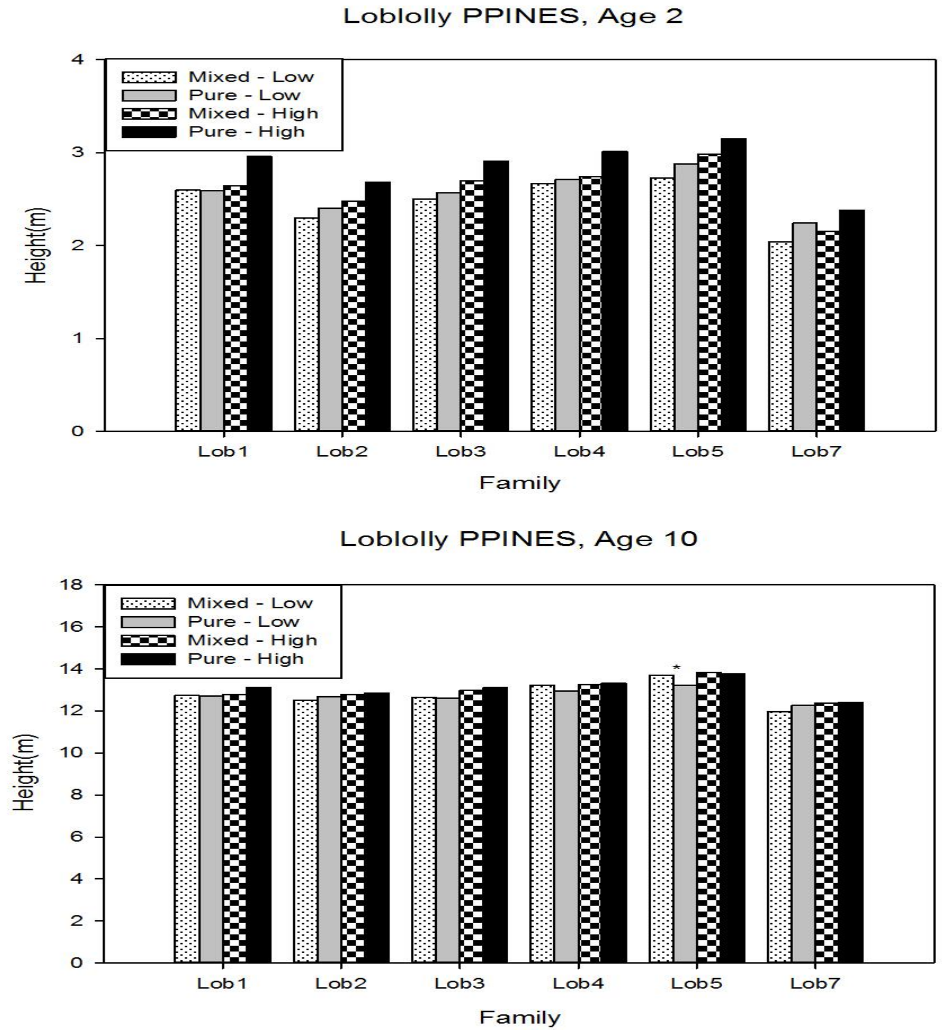
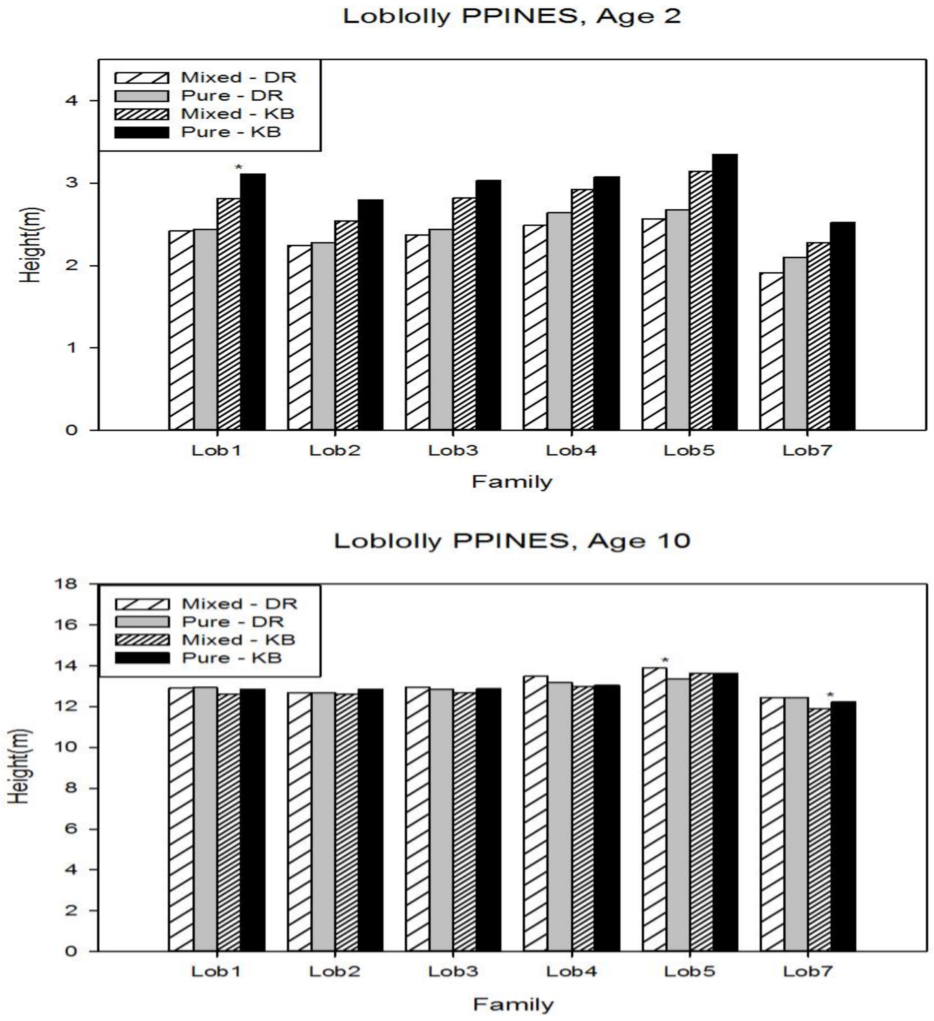


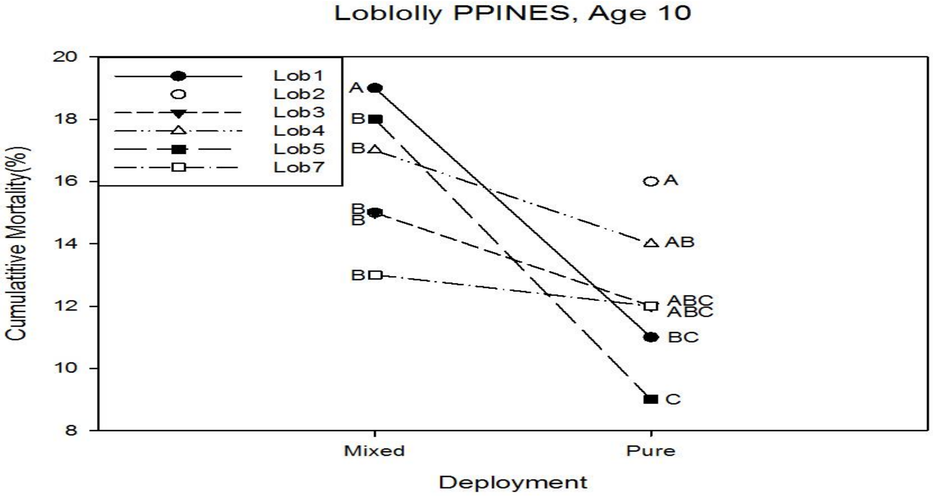
Figure 3-9 Continued



### III.3.1.4 Cumulative Mortality

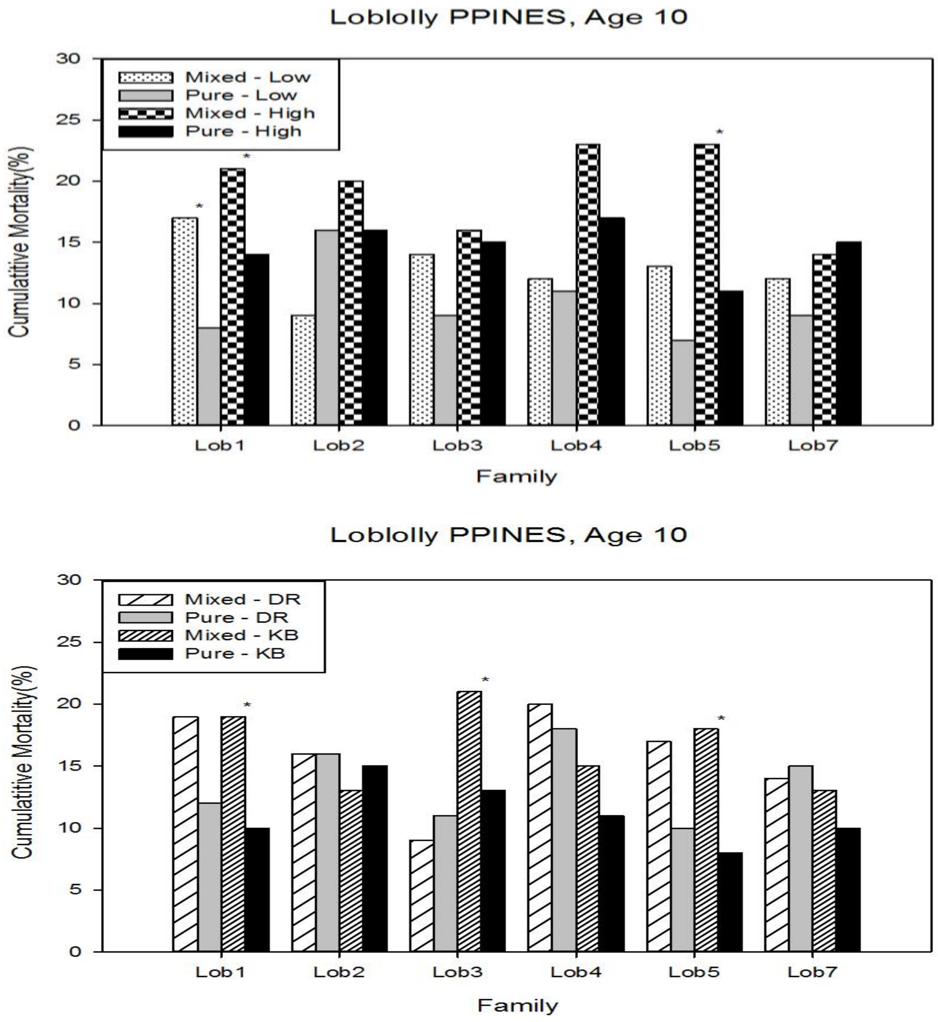
There was a significant deployment effect (p=0.0026) on mortality after 10 years growth (Table 3-3). Generally, the mixed plots had higher mortality than the pure plots at the two sites. In the loblolly pine families, Lob 1 (p=0.0044) and Lob 5 (p=0.0028) showed strong mortality differences between the two deployments. For example, the mortality of Lob 5 in mixed plot was about 50% higher than in pure plots. Moreover, there were significant rank changes between the two deployments. For example, Lob 5 ranked sixth on cumulative mortality in the pure plots, but the rank increased to second in the mixed plots (Figure 3-10).

Figure 3-10: Family × deployment interaction for tree mortality of the WG-PPINES sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.



The interactions of family×deployment×silviculture, and family × deployment×site were not significant for cumulative mortality at age 10 years. However, for some specific families, silvicultural intensity and site can influence the mortality responses to the two deployments. For example, between the two deployments, there was a significantly higher mortality under the HI treatment (p=0.0018) for Lob 5 than under the LI treatment (p=0.1039) (Figure 3-11). Moreover, in terms of site effect, families Lob1 (p=0.0181), Lob 3 (p=0.0447) and Lob 5 (p=0.0118) showed strong mortality differences to the deployment at Kirbyville (Figure 3-11). However, no loblolly pine families showed significant mortality differences between the mixed and pure plots at DeRidder (Figure 3-11).

Figure 3-11: Family × deployment interaction for tree mortality under different silvicultural intensities and at different sites of the WG-PPINES sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.



### III.3.2 Physiological Traits

This study also examined the effects of family, silvicultural intensity and site on the LAI and FN of crop and competitive ideotypes. There were strong differences of LAI and FN between the two ideotypes (Table 3-4).

Table 3-4: Summary of F values, statistical significance, and associated degrees of freedom from the mixed model testing for loblolly pine LAI and FN at age 10 years.

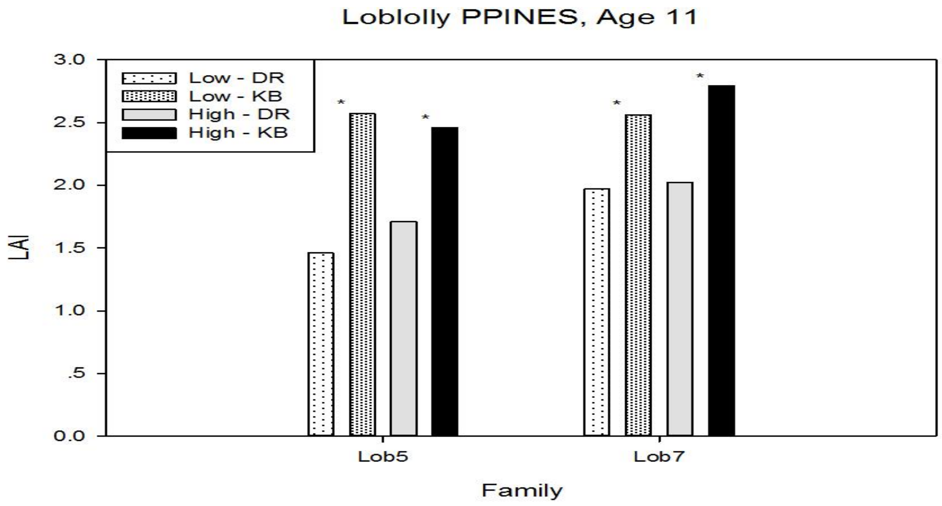
| | df | LAI | | Foliar Nitrogen | | Stand FN | |
|---|---|---|---|---|---|---|---|
| Effect[a] | | F | P | F | P | F | P |
| F | 1 | 15.22 | **0.0080** [b] | 9.86 | **0.0085** | 10.02 | **0.0085** |
| S | 1 | 30.71 | **0.0023** | 1.43 | 0.2553 | 13.28 | **0.0034** |
| F×S | 1 | 2.98 | 0.1353 | 0.84 | 0.3789 | 0.07 | 0.7903 |
| C | 1 | 0.52 | 0.5002 | 0.65 | 0.4354 | 0.25 | 0.6289 |
| F×C | 1 | 0.78 | 0.4120 | 1.50 | 0.2446 | 0.57 | 0.4650 |
| S×C | 1 | 0.13 | 0.7446 | 0.15 | 0.7047 | 0.45 | 0.5144 |
| F×C×S | 1 | 11.01 | **0.0161** | 0.38 | 0.5483 | 0.40 | 0.5389 |

[a] Effects include family (F); silvicultural intensity (C) and site (S).
[b] p-Values significant at the 95% level of confidence are shown in bold type.

#### III.3.2.1 Leaf Area Index (LAI)

Family (p=0.0080) and site (p=0.0023) effects were significant for LAI at age 11 years (Table 3-4). For example, Lob 7 had 14.2% larger LAI than Lob 5, and there was 44.7% higher LAI at Kirbyville than DeRidder (Figure 3-13). However, the silvicultural intensity (p=0.5002) had no significant effect on LAI (Figure 3-13). Moreover, the interaction of family×silviculture×site (p=0.0198) was significant for LAI (Table 3-4). For each family, silvicultural intensity had different effects on the interaction of family and site. For example, Lob 5 had relatively higher LAI difference between the two sites under the LI treatment (p=0.0004) than the HI treatment (p=0.0057). However, for Lob 7, there was the higher LAI under the HI treatment (p=0.0004) than the LI treatment (p=0.0204).

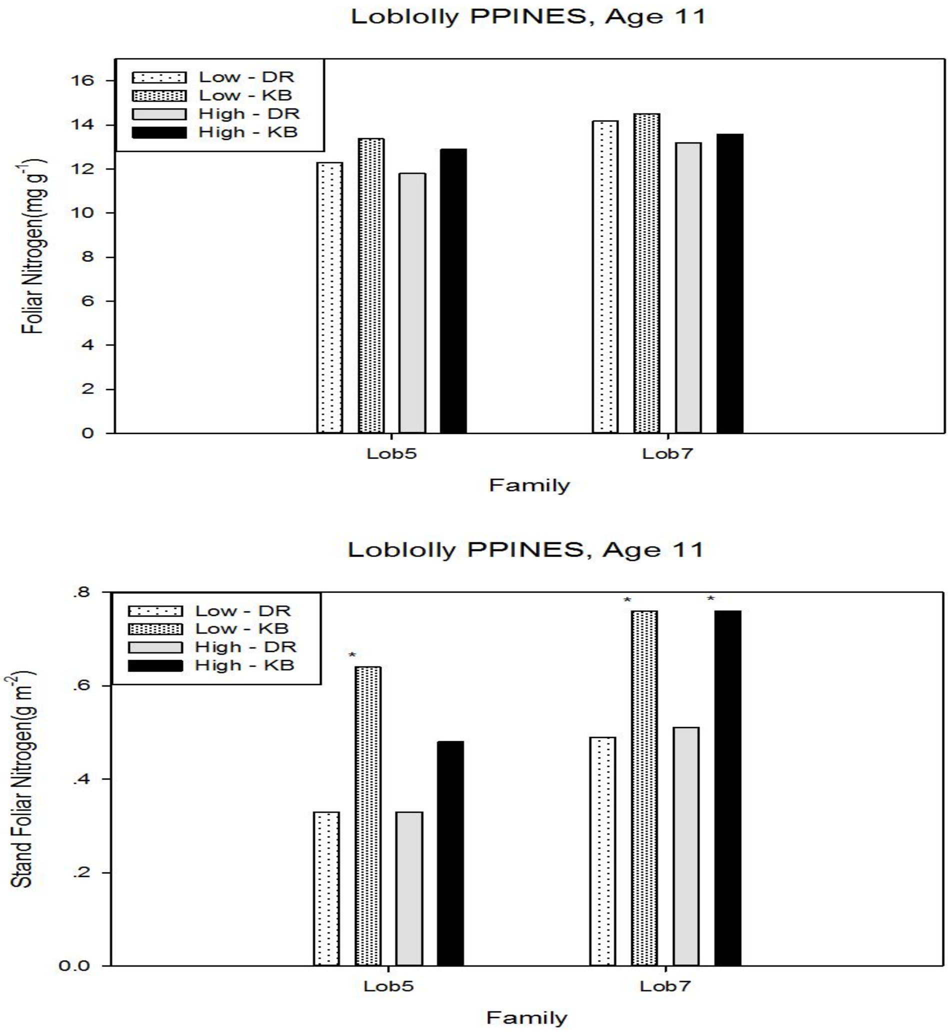
Figure 3-12: Interaction of family, site and silvicultural intensity on LAI at DeRidder and Kirbyville sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.



III.3.2.2 Foliar Nitrogen Concentration (FN) and stand FN

In this study, foliar N was expressed on a leaf mass (FN, mg $g^{-1}$) and area (stand FN, g $m^{-2}$) basis. Among all the fixed factors, only family (p=0.0085) had a significant effect on the FN at age 11 years (Table 3-4). Family Lob 7 had about 10.3% higher FN than the Lob 5. However, the site (p=0.2553) and silvicultural intensity (p=0.4354) effects and the interaction of these factors had no strong influence on FN. For stand FN, family (p=0.0085) effect was still significant, and silvicultural intensity (p=0.6289) was still not significant. However, site (p=0.0034) had a strong effect on stand FN. Under the LI treatment, both Lob 5 (p=0.0256) and Lob 7 (p=0.0337) had significant response of stand FN to the site difference. Under the HI treatment, only Lob 7 (p=0.0465) showed clear stand FN difference between the two sites.

Figure 3-13: Interaction of family, site and silvicultural intensity on FN and stand FN at DeRidder and Kirbyville sites. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.



### III.3.2.3 Annual Increment of Basal Area

Comparing BA annual growth, Lob 5 had significantly larger change than Lob 7 between the 10th and 11th growing seasons (Figure 3-12). However, neither the site nor silvicultural intensity effect were significant for BA annual growth. For BA growth efficiency (PAI/LAI), Lob 5 still showed significantly higher efficiency than Lob 7, and loblolly pine families at DeRidder were more efficient than at Kirbyville (Figure 3-12).

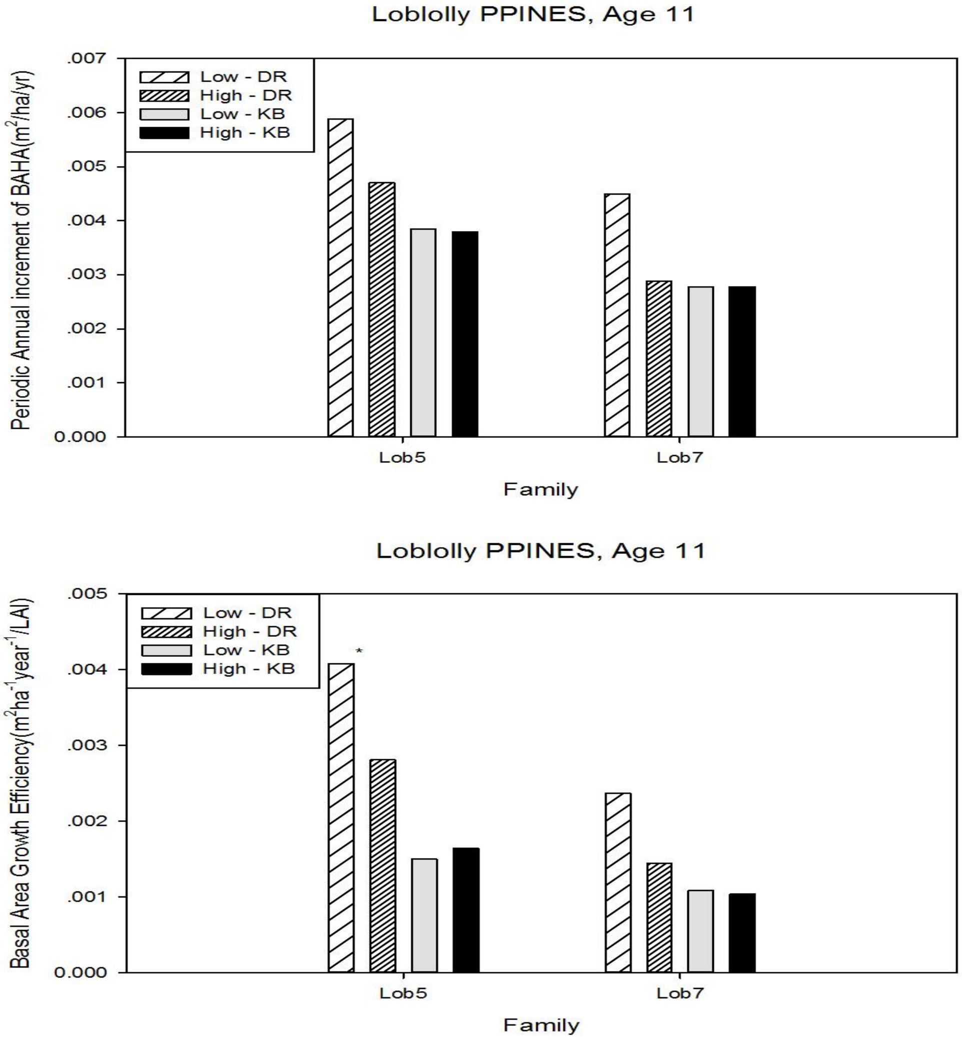
Table 3-5: Summary of F values, statistical significance, and associated degrees of freedom from the mixed model testing for loblolly pine annual increment of BAHA and BA growth efficiency at age 11 years.

| | df | BA annual increment | | Light Use Efficiency | |
|---|---|---|---|---|---|
| Effect[a] | | F | P | F | P |
| F | 1 | 8.57 | **0.0272**[b] | 12.20 | **0.0045** |
| S | 1 | 5.18 | 0.0629 | 21.42 | **0.0006** |
| F×S | 1 | 0.37 | 0.5659 | 3.13 | 0.1027 |
| C | 1 | 3.10 | 0.1027 | 3.21 | 0.0988 |
| F×C | 1 | 0.06 | 0.8100 | 0.01 | 0.9101 |
| S×C | 1 | 2.90 | 0.1136 | 3.81 | 0.0750 |
| F×C×S | 1 | 0.09 | 0.7651 | 0.21 | 0.6541 |

[a] Effects include family (F); silvicultural intensity (C) and site (S).

[b] p-Values significant at the 95% level of confidence are shown in bold type.

Figure 3-14: Family × site × silvicultural intensity interaction on annual increment of BAHA and BA growth efficiency at DeRidder and Kirbyville sites at age 11 years. Bars within family having an asterisk indicates significant differences at the 95% level of confidence.



## III.4. Discussion

In a previous study in the WG-PPINES, I had demonstrated the significant family and silviculture effect on stand growth, and strong responses of superior families to changes of site and silvicultural treatment. This research examined intergenotypic competition in the mixed plots, family and site effects on intergenotypic competition, identification of ideotypes among the elite loblolly pine families, and correlation of LAI and FN with ideotype performance. The significant effects of factors and the interactions in my study can reflect the clear growth differences of ideotypes, strong influence of intensive silvicultural treatments, and the high statistical power.

### III.4.1 Intergenotypic Competition

Comparing stand growth of the mixed plots and pure plots, stand growth differences developed rapidly among families in the mixed plots. This was likely because the loblolly pine families varied in competitive ability, particularly in the capture and use of light, water or nutrients. In a previous study, I found that Lob 5 and Lob 4 were fast growing families in the WG-PPINES, and Lob 2 and Lob7 were slow growing families. In the mixed plots of this research, the fast growing families showed significantly larger VOLHA than the slow growing families at age 10 years (Figure 3-6). In the EG-PPINES, Staudhammer et al. (2009) found that the same fast growing family (Lob 5) as in my research also showed the best performance in the mixed plots of the Eastern Gulf area. For Douglas-fir, Gould et al. (2011) also reported that in mixed plots, the growth difference of fast growing families and slow growing families was much larger than in pure plots.

In my study, the fast growing families also had higher stand growth in mixed plots than pure plots, and the slow growing families had lower stand growth in mixed plots. For example, Lob 5 had 9.6% larger DBH in mixed plots than pure plots, and Lob 7 had 9.7% smaller DBH in mixed plots. Therefore, on the basis of comparison of all the growth traits, Lob 5 and Lob 7 clearly showed growth patterns of competitive and crop ideotype, respectively. Lob 4 also showed growth characteristics of a competitive ideotype, but not as clear as Lob 5. Moreover, there was no rank change of stand growth between the two deployments, which means the elite and poor families were the same in the mixed and pure plots. Staudhammer et al. (2009) also found the similar growth trend between mixed and pure plots in EG-PPINES.

The intergenotypic competition was also indicated by the mixed plots having wider ranges in stand growth. For example, the BAHA difference of the fastest and slowest growing families in the mixed plots was 22.07 $m^2$/ha, but it decreased to 8.99 $m^2$/ha in the pure plots (Figure 3-3). This result suggested that the performance of fast growing families was at the expense of the slow growing families. Therefore, it is likely that the differences of fast and slow growing families would be larger if there were less available resources in the environment. My study results showed support for this assertion. For example, there was a significant stem volume difference between Lob 1, the fast growing family, and Lob 2, the slowing growing family, under the LI treatment in mixed plots, but this clear difference disappeared under the HI treatment.

Silvicultural intensities can have different influences on the ideotypes' growth comparisons between the two deployments. For example, there was a strong tree height difference for Lob 5, the competitive ideotype, under the LI treatment, but not under the HI treatment (Figure 3-9). Staudhammer et al. (2009) also found competitive ideotype had higher DBH in mixed plots when contrasting a narrow and wide spacing treatment. However, the change trend of stand growth from the LI to the HI treatment was opposite for crop ideotype. For example, Lob 7, the crop ideotype, had significant difference of DBH between mixed and pure plots under the HI treatment, but not the LI treatment. Therefore, the two ideotypes showed different response to the silvicultural intensities. For the competitive ideotype, the LI treatment increased growth and competition in both pure and mixed plots, but the competitive ideotype could best take advantage of this increased competition in mixed plots, not in pure plots. Therefore, deployment response was more obvious under the extreme competitive environments created by the low culture plots. On the other hand, although silvicultural practices may compensate for the growth loss of crop ideotype in mixed plots to some degree, my previous study found that Lob 5, the competitive ideotype, benefited most from the HI treatment. Meanwhile, the HI treatment increased stand growth of crop ideotype in pure plots, because of less inter-tree competition. Thus, there was more growth difference between the two deployments under the HI treatment for the crop ideotype.

Comparing the stand growth at age 2 and 10 years, the growth differences and ability to identify ideotypes increased with stand age. The result showed that there were no significant deployment effects on any stand growth traits at age 2 years, but it became stronger at age 10 years (Table 3-3). Intergenotypic competition in mixed plots had similar characteristics of natural thinning in pure plots. With stand development, individual trees had higher growth requirements, thus the competition among the individual trees became more intense. However, my result indicated that the effect of intergenotypic competition was stronger than the effect of natural thinning in pure plots at age 10 years. For example, the cumulative mortality of mixed plots was higher than the pure plots, and Lob 5 had the highest mortality in the mixed plots which had 50% higher mortality than the pure plots. This result was against my hypothesis, that competitive ideotype should suppress the growth of crop ideotype because of high competitive ability of competitive ideotype. Because of the low occurrence of insects and diseases in the study sites, the mortality differences may be explained by the hurricane effect which may have had a stronger effect on the trees with large crowns when they stood well above neighboring trees. Chmura et al. (2007) reported that the Lob 5 had the largest crown volume at age 5 years, and when surrounded by smaller trees in the mixed plots, this might have resulted in greater damage.

For certain growth traits of specific families, the deployment effects were influenced by the sites. The interaction of site and deployment had significant effect on Height at the age 10 years. Lob 7, the crop ideotype and slowest growing family, only had significant DBH and Height differences between the two deployments at Kirbyville. Lob 4 and Lob 5, the competitive ideotypes, both showed strong DBH differences at DeRidder between the two deployments. Comparing site condition between Kirbyville and DeRidder, there was a moderately well drained and sandy loam soil in Kirbyville, but DeRidder was a poorly drained silt loam soil. From my previous study, Kirbyville had relatively higher production than DeRidder. Therefore, Kirbyville had a better growth environment than DeRidder for loblolly pine. This study suggests that the competitive ideotypes had stronger response to the deployment effect at DeRidder where there was an average growth environment, but there was a clearer deployment effect for the crop ideotype at Kirbyville which had a better growing environment. This result corresponded to the previous finding, that the deployment response was more obvious for the competitive ideotype under the LI treatment, but more significant for the crop ideotype under the HI treatment.

### III.4.2 BA Annual Growth and Physiological Traits of Crop and Competitive Ideotypes

This study found that the plots under the LI treatment had relatively higher BA growth efficiency than the HI treatment. Jokela and Martin (2000) also found the silviculturally treated loblolly pine plots tended to have lower levels of stemwood growth efficiency than the untreated controls from age 7 to 16 years. It should be noted that the plots under the HI treatment stopped receiving fertilization at the age of 3 years. Therefore, the less growth efficiency under the HI treatment may be caused by higher nutrient demands and reduced nutrient supply, coupled with increased maintenance respiration (Jokela and Martin, 2000) and increased biomass allocation to fine roots following the end of the fertilizer treatment (Albaugh *et al*. 1998).

Family effects had a significant influence on LAI, FN and stand FN. The crop ideotype had 14.2% higher LAI, 10.3% more FN, and 41% more stand FN than the competitive ideotype. Furthermore, in the same site at DeRidder, Chmura and Tjoelker (2008) found the average loblolly pine family had significantly higher area basis foliar nitrogen concentration (stand FN) than the fast growing family at only age 4 years, but this difference became non-significant or opposite direction at Kirbyville and other ages. Foliar N concentration can reflect the future stand growth (Zhang and Allen, 1996), therefore, it is possible that slow growing family Lob 7 may outgrow the faster growing family Lob 5 in the next half of the loblolly pine rotation if there are no large changes in the environment.

Pine stand growth is mainly determined by the amount of solar radiation intercepted, the photosynthetic efficiency of the canopy, and the allocation of fixed carbon to stemwood (Vose and Allen, 1988). LAI and foliar N can be positively related with the intercepted radiation and the photosynthetic efficiency, respectively. I hypothesized that Lob 5, the competition ideotype, would have characteristics that indicated greater resource acquisition (Martin *et al*. 2001), either N or light. However, Lob 5 had lower LAI and foliar N than Lob 7. Therefore, this suggested that the fast growing family is more efficient with its site resources than the slowing growing family. Specifically, more carbon allocation to stem growth than other biomass components (e.g. roots, branches) may explain the better growth performance of Lob 5 with less LAI and foliar N than Lob 7.

Many other southern pine studies have found that fertilization increases foliar N concentrations (Martin and Jokela, 2004; Sayer et al., 2004). However, at the same sites as in this study others found that the silvicultural intensity effect was not significant for foliar N as early as age 4 years (Chmura and Tjoelker, 2008), and I have found this continued to age 11 years (Table 3-4). The research sites were fertilized for the last time in 2005, and my foliar nitrogen measurement was made in 2013. Gough et al. (2004) reported that the rise and subsequent return of foliar N to non-fertilized levels following fertilization occurred within a time frame of just over 100 days. Chmura and Tjoelker (2008) also reported that the fertilization effect was only detected for one month after fertilization. This may explain why the silvicultural intensity effects were not significant for FN and stand FN (Figure 3-13). Although the silvicultural intensity was not significant, foliar N of families Lob 5 and Lob 7 generally remained above the critical concentrations of 12 mg $g^{-1}$ reported for loblolly pine (Jokela, 2004) under the two intensities.

In the same sites as this study, Chmura and Tjoelker (2008) found that average family had much significantly higher mass basis foliar N (FN) than superior family at age 4 and 5 years, but the family difference became less significant for area basis foliar N (stand FN). At age 11 years, the family Lob 7 also had both significantly higher FN and stand FN than Lob 5, but the significances were equivalent for the two variables (Table 3-4). Therefore, the stand FN might more directly reflect the family difference with stand age. Moreover, for both FN and stand FN, Kirbyville only had significantly higher stand FN than DeRidder (Figure 3-13), and my previous study found that there was better stand growth of loblolly pine at Kirbyville. Thus, on the basis of the foregoing results, stand production might be more positively correlated with stand FN across sites than for different families within a site.

## III.5 Conclusion

Based on the comparison of stand growth between mixed and pure plots under the two silvicultural intensities at two research sites, the fast growing family, Lob 5, showed significantly better performance in the mixed plots than pure plots and the slow growing family, Lob 7 grew better in the pure plots. Therefore, I can draw the conclusion that Lob 5 is a competitive ideotype, and Lob 7 is a crop ideotype. Moreover, the loblolly pine families showed significant growth differences between the two deployments under the LI treatment.

I also found the deployment effects were non-significant at age 2 years, while at age 10 years, the scale effects of stand growth were significant among the loblolly pine families between the two deployments. Thus in the progeny test, this may affect the accuracy of prediction of fast growing families. Moreover, the high mortality in mixed plots may also influence predictions of family ranks.

At the current stage of stand development, the LAI and FN differences between the two ideotypes did not explain the difference in their annual increments. Indeed, the results suggest that the crop ideotype will have greater growth in the future. With the stand development, continued measurement of stand growth and the physiological traits of competitive and crop ideotypes may be required to determine why the two ideotypes differ.

# CHAPTER IV

# SUMMARY

Loblolly pine is one of the major timber species in the United States, and accounting for more than half the total volume of southern pine growing stock (Schultz, 1997). The production per hectare of loblolly pine has increased by over four times over the past 50 years (Fox *et al.*, 2007).  These productivity gains are attributable to the adoption of intensive silvicultural practices and breeding of elite tree families (Aspinwall *et al.*, 2011). New elite families achieve more and more genetic gain from the development of breeding technology (McKeand *et al.*, 2003b). Therefore, there is a need to know how new elite families of loblolly pine interact with intensive silvicultural treatments and the local environment. Moreover, identification of ideotypes in new elite families is able to improve the ability of progeny test to identify genotypes interactions on growth. The WG-PPINES series had seven pine families, two levels of silvicultural intensities, two deployments and three locations in the WG area. Therefore, the experimental design has enabled researchers to detect fixed effects of family, silvicultural intensity, deployment, site and the interactions among them. By examming these factors, my study can help to resolve how to best deploy elite families in the Western Gulf area.

## IV.1 Combined Effect of Genotype and Silvicultural Intensity

In this study, the significant family and silviculture effect were found in the WG-PPINES. Therefore, for landowners, using the recommended intensive management practice could increase the stand production of southern loblolly pine plantations significantly over lower intensity management methods. Moreover, the superior family had the largest response to the silvicultural treatment changes, and the silviculture effect may change with stand development for certain families. These findings also have some implications to forestry professionals. First, for forest resource managers, high performing families may need higher levels of silvicultural intensity to realize genetic gains. Second, for forest breeders, the estimation of genetic gain may change with stand development.

## IV.2 Genotype×Environment Interaction

In the WG-PPINES series, strong G × E interaction was only detected at age 2 years, and became less significant with stand age. However, for some specific genotypes, there was still G × E interactions which was indicated by scale effects or rank changes at age 10 years. Moreover, silvicultural intensity can also influence the G × E interaction. Particularly, the fast growing family showed more significant G × E interaction under the HI treatment. Therefore, it is important to know how elite families will respond to intensive silvicultural treatments in a new growth environment. However, from this study in the WG area, I found that silvicultural intensity had a larger influence than the change of growth location.

## IV.3 Identification of Ideotype

In the WG-PPINES, loblolly pine family Lob 5 is fast growing family among the tested pine families, and it also showed growth characteristics of competitive ideotype that had better growth in the mixed plots. Lob 7 is slow growing family, and it showed higher production in the pure plots than mixed plots, which indicated that Lob 7 is a crop ideotype. Furthermore, for the two ideotypes, this study found that silvicultural intensities and site locations had different effects on growth comparison between the two deployments. The LI treatment increased the growth difference of fast growing family between pure and mixed plots, while the LI treatment had the opposite effect on the growth comparison of the slow growing family. There was more significant deployment effect at Kirbyville, which had greater growth overall.

Forest managers need to know how elite pine families will respond to intensive silvicultural treatments in a new environment (Roth *et al.*, 2007). In addition, since Lob 5 is a competitive ideotype and may outgrow its peer families in mixed plots, breeders may need to be careful about estimating its growth potential in single-tree plots of a progeny test.

## IV.4 Physiological Properties of Ideotypes

Comparing the morphological and physiological properties between different ideotypes can contribute to better understanding of growth strategies of different ideotypes. This study found that slow growing family had significantly higher FN, stand FN and LAI than fast growing family. Although the slow growing family had much less production than the fast growing family, the LAI and FN result more closely reflect future stand growth (Zhang and Allen, 1996). Therefore, these results suggest either that the slow growing family may outgrow the fast growing family in the future, or that the fast growing family has an allocation strategy towards wood growth that makes it outcompete other families. In addition, in comparing the mass basis foliar N or FN, this study also found the area basis of foliar N or stand FN was more correlated with stand growth across sites, but not across families within a site.

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