EARLY GROWTH RESPONSE OF DIVERSE FAMILIES OF LOBLOLLY PINE TO NUTRIENT AMENDMENTS ON A POOR SITE

S.E. McKeand, J.E. Grissom, D.M. O'Malley, and H.L. Allen'

Abstract:--Open-pollinated families of loblolly pine *(Pinus taeda* L.) from the "Lost Pines" provenance in Texas and the Atlantic Coastal Plain were established on a droughty, infertile site in the Sandhills of North Carolina where half the trees received nutrient amendments and the other half received no fertilizer. Height growth during the first three years has been evaluated as well as foliar nutrient concentrations. Response to fertilizer applications has been large with a 43% increase in height at age three years. The Atlantic Coastal families were significantly taller than the Texas families in both the fertilized and control plots, and no genotype by environment interactions were observed. While no provenance differences for nutrient concentrations were large, family variation was large, but no genetic association between nutrient concentrations and growth were found. Even given the tendency for low genotype by environment interaction for open-pollinated families of loblolly pine, the adaptability of the Atlantic Coastal families to such extreme environmental conditions was surprising. The long-term performance of the trees will be evaluated to see if this trend continues.

Keywords: Adaptability, height growth, *Pinus taeda,* provenance

INTRODUCTION

Geographic and within-provenance variation for growth and adaptive traits in loblolly pine is very large. General trends in productivity variation are that families from southern and eastern coastal sources grow faster than families from northern, western, and interior sources (e.g. McKeand et al. 1989, Wells 1983, Wells and Lambeth 1983, Schmidtling 1994). Variation in other traits such as fusiform rust resistance (Wells and Wakeley 1966, Wells 1985), stem form (McKeand and Jett 1993, Schmidtling and Clark 1988), and wood density (Belonger et al. 1996) can also be very large. Contrasting the response of two very different provenances of loblolly pine such as from the "Lost Pines" region of Texas and the Atlantic Coastal Plain may give us insight into the adaptive significance of different ecophysiological traits.

Previous work indicates that the Texas sources are generally more stable across environments, while productivity of eastern sources depends more on the environment (van Buijtenen 1978). For eastern sources, productivity was high on the better sites, but very low on the droughty sites. The most important mechanism for drought avoidance may be stomatal control;

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[1] Professor, Graduate Student, Research Associate Professor, and Professor, respectively, Department of Forestry, North Carolina State University, Raleigh, NC 27695-8002.

drought-hardy seedlings conserved more water under stress (van Buijtenen et al. 1976), but at the expense of total production (Bongarten and Teskey 1987).

Large genetic differences in productivity among loblolly pine families are being exploited to increase forest productivity in the South. Such productivity differences must result from genetic variation in the ability of trees to acquire and convert solar energy to reduced carbon compounds. The dominant processes determining biomass production of forest stands are light interception, photosynthesis, respiration, and carbon partitioning. Much research has focussed on determining which of these factors has the greatest influence on productivity and how these factors are influenced by environmental stresses (Cannell 1989, Linder 1987). Since light interception and growth efficiency are influenced by soil resource availability, it follows that genetic differences in uptake and utilization of nutrients and water may also contribute to genetic differences in biomass production.

The physiological bases by which genotypes respond to different environments and remain relatively stable in biomass yield are not well understood. Acquisition of resources requires the direct interaction between the genotype and the environment and may explain the relatively high levels of GxE interaction often observed in young stands (Matheson and Cotterill 1990). Results from long-term field trials indicate that for trees at older ages, genotype x environment interactions are less prevalent (McKeand et al. 1990). As full site occupancy is reached, other traits that affect resource utilization and internal recycling of nutrients will become relatively more important. Since these traits involve internal physiological processes, less GxE interaction may be observed.

In this paper, we describe a study designed to assess spatial and temporal variation in response of loblolly pine genotypes to environmental stress. Seedlings have recently completed three growing seasons in the field, and variation in early growth, foliage, and nutritional characteristics are described.

MATERIALS AND METHODS

The study site is located in Scotland County, North Carolina adjacent to the U.S. Forest Service / N.C. State University SETRES (Southeastern Tree Research and Experiment Site) study. The soil is a Wakulla series - sand to greater than 140 feet, sandy, siliceous, thermic Psammentic Hapludult - very infertile, somewhat excessively drained with a total water holding capacity of 7"-8" in a 6.5' profile. The site receives an average annual rainfall of 48". Temperatures average 62°F annually, 79°F summer, and 48°F winter. The existing 10-year-old stand was carefully removed and large block plots of different family-treatment combinations have been established on this droughty, infertile site.

Open-pollinated families from the North Carolina and South Carolina Coastal Plain and from the "Lost-Pines" area of Texas were included in the study. Five families with average or slightly above average breeding values for volume production were used. Seeds were sown in containers (10 in^3 RL Super Cells) in the greenhouse in June 1993, and seedlings were field-planted in November 1993.

To facilitate the application of nutrients, a split-split-plot design was used with the two treatments as main plots, provenances as sub-plots, and families within provenances as sub-sub-plots. The experimental design is:

10	blocks
2	provenances
5	families / provenance
2	treatments (optimal water and nutrition, control)
100	trees/b/p/f/t
20000	total trees

Each plot consists of 100 measurement trees planted at 5'x7' spacing. Buffer trees, 40' around each treatment plot, were planted to eliminate the influence of one treatment on another.

Foliar nutrient ratios (Hockman and Allen 1990) have been used to guide annual fertilizer applications to maintain a balanced supply of all nutrients. Our goal has been to supply optimal levels of nutrients to stimulate rapid growth. Fertilizer additions through the first three growing seasons are shown in Table 1.

Competing vegetation has been controlled in all plots by periodic herbicide treatments and mowing. Likewise, insects (especially tipmoths, *Rhyacionia* sp.) were controlled in the first two growing seasons as needed with periodic insecticide applications.

Table 1. Nutrient additions to fertilizer plots (pounds per acre).

Date	Fertilizer	N	P	K	Ca	Mg	S
June 1994	10-10-10	23.3	10.0	19.3	0	0	<0.4
August 1994	10-10-10	23.3	10.0	19.3	0	0	<0.4
March 1995	12-6-6 + micronutrients[1]	37.3	8.0	15.5			
April 1996	Urea + TSP + KMagS	50	5	25	2.5	15	30
	Total	134	33	79	2.5	15	31

Micronutrients included: 0.5 B, 2.0 Cu, 5.0 Fe, 5.0 Mn, 2.0 Zn.

Measurements and Analyses: All trees were measured annually for height and in year 3 for diameter. In January 1997, foliage samples from each plot were taken. Five healthy fascicles from the first flush from the base of the first stem flush from 1996 were sampled from 10 dominant trees in each family plot. After collection, the projected surface area of the foliage (FSA) was measured with an area meter (Delta-T Devices Ltd., Cambridge UK). The needles were then dried for 72 hours at 160°F and average fascicle dry weight (FDW) measured. Specific leaf area (SLA) was calculated as FSA / FDW. After the samples had been ground and sieved through a 1 mm mesh, they were digested using a sulfuric acid-peroxide mix. Foliar nutrient concentrations (N, P, K, Ca, Mg) were estimated for each plot. Analyses for N and P were done colorimetrically using a Lachat QuickChem System IV Colorimeter (Lachat Instruments, Milwaukee, WI). Flame emission spectrophotometry was used to determine K, and absorption spectrophotometry for Mg and Ca concentrations using a Perkin-

Elmer 560 atomic absorption spectrophotometer (Perkin-Elmer Corporation). Elemental concentrations were expressed on a percent dry mass basis.

Analyses of variance were conducted on an individual-tree basis for growth data and on a plot-mean basis for nutrient traits. Blocks and families were considered as random effects, treatments and provenances as fixed effects. Correlations of nutrient concentrations and growth traits on family-means basis were estimated rather than genetic correlations because of the limited genetic sample.

Plot means and within plot standard deviations were calculated for height for each 100-tree family plot. Within-plot standard deviations and coefficients of variation were also subjected to analyses of variance to determine if plot uniformity varied.

RESULTS AND DISCUSSION

Survival and growth of the trees has been excellent in the first three years. Survival averaged 93% after three growing seasons (no treatment or genetic effects), and height averaged 6.5 feet. Deer browse and tipmoth caused some problems in the first two growing seasons, and 12.6% of the trees were damaged and not included in the analyses for growth traits.

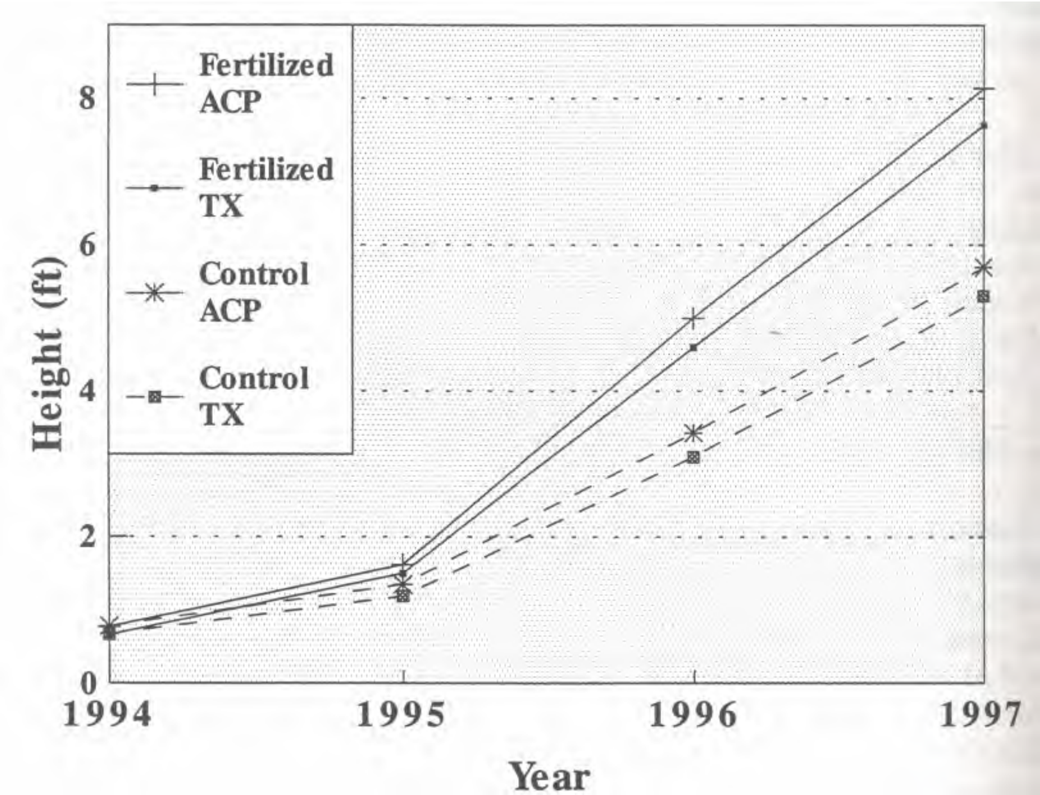


Figure 1. Mean tree heights during the first three growing seasons in the field for trees from the Texas and Atlantic Coastal Plain provenances in the fertilized and control plots. Initial height of seedlings at planting was measured in 1994.

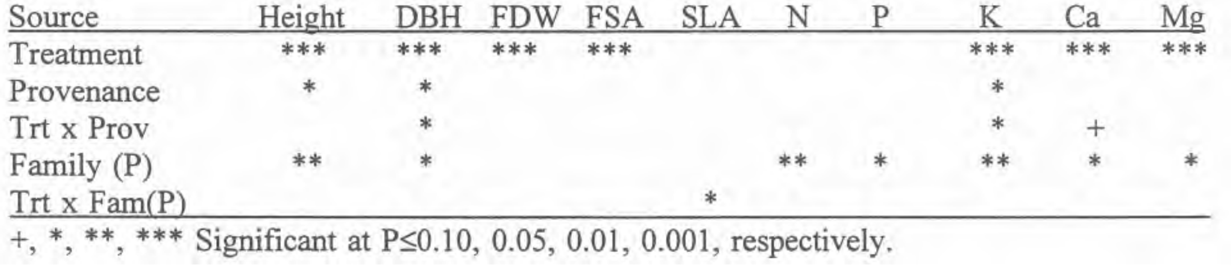
Fertilizer Response. The growth responses to fertilizer amendments were very large and significant each year (Table 2). Height was 23%, 47%, 43% greater in the fertilized plots for years one, two, and three, respectively (Figure 1). Although this is an excessively well-drained site, from the results of the nutrition x irrigation study adjacent to this trial, we know that the primary limit to productivity is nutrition (Albaugh et al. 1997). The huge increase in productivity in the first three growing seasons is possible since all potential nutrient limitations (i.e. more than just N and P) were ameliorated.

One of the most dramatic effects of the nutrition amendment was the increase in uniformity within the 100-tree family plots. The average within-plot coefficient of variation for third-year height was 26.3% for the control plots and 14.3% for the fertilized plots. The within plot standard deviations for height were also significantly different and were 1.43' and 1.12' for the control and fertilized plots, respectively. While increased uniformity typically results from nutritional amendments on very poor sites, the dramatic differences in uniformity was surprising.

Fertilization effects on foliage dry weight and projected surface area were large and significant (Table 2), but they were very small for specific leaf area. For the fertilized plots, average fascicle dry weight was 144 mg and projected surface area was 4.1 cm^2/fascicle. As expected, the foliage in the control plots had significantly less mass (118 mg) and surface area (3.4 cm^2/fascicle). Since foliage production is so critical for stemwood production (Vose and Allen 1988), it is not surprising that the fertilized trees had heavier, larger needles. In future years, we will assess total foliage production on a whole tree basis to better evaluate treatment effects on leaf area - stemwood production.

Foliar nutrient concentrations for nitrogen and phosphorus were not different in the fertilized and control plots (Table 2), even though 134 lbs/a of N and 33 lbs/a of P were applied in the first 3 years (Table 1). We explain this as a dilution effect of having much greater foliage production in the fertilized plots compared to the control plots. Potassium in the fertilized plots (0.38%) was lower than in the control plots (0.47%) even though 79 lbs/a K was applied. Again, dilution effects appear to be the main reason that the faster growing trees had lower concentrations of K. Very little calcium and magnesium was applied in the first three growing seasons (Table 1), so the higher concentrations in the control (Ca: 0.19%, Mg: 0.068%) versus the fertilized plots (Ca: 0.14%, Mg: 0.055%) was also due to dilution.

Table 2. Significance levels for main effects tested in the analyses of variance for growth, foliage, and volume traits at age three years.



Source	Height	DBH	FDW	FSA	SLA	N	P	K	Ca	Mg
Treatment	***	***	***	***				***	***	***
Provenance	*	*						*		
Trt x Prov		*						*	+	
Family (P)	**	*				**	*	**	*	*
Trt x Fam(P)					*					

+, *, **, *** Significant at P≤0.10, 0.05, 0.01, 0.001, respectively.

Provenance and Family Variation. As expected, the five families from the Atlantic Coastal Plain grew faster than the five Texas families (Figure 1). We anticipated that under the harsher environmental conditions in the control plots that the Texas families would perform relatively better. However, the ACP families were superior in both environments, and the provenance by treatment interactions for height in all three years were not close to being significant. Although there was a provenance by treatment interaction for DBH (Table 2), there was no provenance rank change in the two environments, only a difference in the magnitude of the differences (greater in the fertilized plots).

Families within provenances also differed for growth traits (Table 2). The family means for the ACP families varied from 5.2' to 5.8' in the control plots and from 8.6' to 10.2' in the fertilized plots. The Texas families also differed in the control plots (4.7' to 5.0') and in the fertilized plots (7.8' to 8.6'). The marked difference in productivity between the drought-hardy Lost Pines families and the ACP families is illustrated by the lack of overlap of the family means for height.

The lack of genotype by environment interaction both at the provenance and family level was surprising. Given the magnitude of the imposed environmental differences and the young age of the trees, differential performance of the families in the two treatments were expected. This result reinforces the tenet of the stability of open-pollinated families of loblolly pine.

In general, provenance differences were minimal for foliage traits and nutrient concentrations. Only for potassium, did the two provenances differ (TX: 0.41%, ACP: 0.44%). The ACP had higher concentrations for K in both treatments, despite the significant provenance by treatment interaction; only the magnitude of the differences changed.

Family differences within provenance were significant for all foliar nutrient concentrations but not for FDW, FSA, and SLA. Genetic variation in nutrient concentrations is common in loblolly pine (e.g. Li et al. 1991, Vasquez 1993), but the association with productivity variation has been poor (McKeand and Svensson 1997). In the present study, family differences in foliar nutrition were not correlated with any growth or foliage trait (data not shown).

Future Work. This experiment will be a long-term (-20 years) field laboratory for ecologists, physiologists, and geneticists to study the bases for trees' responses to environmental stress. Future work will emphasize both above- and below-ground production and physiological processes and how they interact to affect productivity. Not only will traditional quantitative genetic analyses be conducted to evaluate genetic control for these traits, but genomic mapping to determine the significance of major gene control is also an integral part of the study. Megagametophytes for each of the 20,000 individuals in the trial are in cold storage (-80°C) and DNA will be extracted and genomic maps developed to determine marker - trait associations. Using the open-pollinated families in such a manner will allow us to determine if major genes with high breeding value (O'Malley and McKeand 1994) are associated with adaptive response to environmental stress.

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