PRODUCTIVITY AND BIOMASS PARTITIONING OF NORTH CAROLINA AND OKLAHOMA/ARKANSAS LOBLOLLY PINE ON A DROUGHTY SITE

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INTRODUCTION

The various provenances (seed sources) found within the natural range of loblolly pine (*Pinus taeda* L.), differ in several growth characteristics as well as survivability, and forest managers frequently capitalize on this genetic variability when selecting planting stock. Growth characteristics such as the height and diameter growth rate, branching pattern, and wood specific gravity vary between the different provenances, as does resistance to abiotic factors such as drought and frost and to biotic factors such as insects and diseases. Generally, seed sources from the eastern edge of the range grow faster than those from the western edge of the range, and southern provenances grow more rapidly than northern provenances. As a result of the differences in growth rates between the provenances, productivity of stands can be improved by moving faster-growing seed sources to areas where they outperform local seed sources. However, planting seedlings from a seed source adapted to an environment radically different from that of the planting site can sometimes result in significant mortality, thus offsetting growth gains achieved by planting nonlocal stock. Forest managers thus maximize productivity of their stands by compromising between superior growth and adequate adaptation to the site when selecting a seed source for planting stock.

Forest managers in Oklahoma and Arkansas have chosen to plant seedlings from nonlocal seed sources in order to increase forest productivity. For the past twenty years, loblolly pine from North Carolina Coastal (NCC) seed sources has been widely planted in southeastern Oklahoma in favor of local Oklahoma/Arkansas (O/A) seed sources since NCC trees commonly have a faster growth rate than O/A trees. Forest productivity is thus improved since NCC trees are expected to be larger at harvest than O/A trees, i.e. stands of NCC loblolly pine have a higher volume yield per acre than stands of O/A loblolly pine. In addition, NCC trees reach a merchantable size sooner than O/A trees. However, it is assumed that NCC loblolly pine is poorly adapted to the extreme droughts that occasionally occur in southeastern Oklahoma. As a result, forest managers are very conservative in where they plant NCC loblolly pine, restricting it to soils that maintain higher moisture contents. Yet little testing has been done to ascertain the productivity of NCC sources of loblolly pine on excessively drained soils. If NCC seed sources maintain their greater productivity on droughty sites, potential exists for increasing the productivity of marginal sites in southeastern Oklahoma and southwestern Arkansas.

This study examines the productivity and growth characteristics of two seed sources of loblolly pine from disparate regions, one from coastal North Carolina and one from Oklahoma/Arkansas, growing in southeastern Oklahoma. The site is much more droughty than would be operationally selected for planting of NCC stock, providing an opportunity to determine whether NCC seed sources maintain their growth superiority over O/A sources even on an excessively drained site. Two separate and complete manuscripts have been prepared from the study. The first, "Prediction of branch biomass components for North Carolina and Oklahoma/Arkansas loblolly pine seed sources growing in southeastern Oklahoma", focuses on testing for seed source differences in branch-level relationships between tree dimensions and foliage and branch biomass production. It was prepared in the format of the Forest Science journal. The second, "Productivity and biomass partitioning of North Carolina and Oklahoma/Arkansas loblolly pine growing on a droughty site in southeastern Oklahoma", provides a thorough comparison of the productivity of the two seed sources growing on the dry site selected for this study. It was prepared in the format of the Canadian Journal of Forest Research. Since the second manuscript builds from the results of the first manuscript, the first manuscript will be referred to as "Manuscript 1" when cited within the second manuscript. Both manuscripts will be submitted for publication in the respective journals.

Manuscript I

Prediction of branch biomass components for North Carolina and Oklahoma/Arkansas loblolly pine seed sources growing in southeastern Oklahoma

Abstract

Height and volume have been traditionally used as selection criteria in evaluating seed source productivity; quantification of crown growth dynamics would provide a greater understanding of the basis for productivity differences. In the northwest portion of the range of loblolly pine (*Pinus taeda* L.), there is a particular need to understand productivity differences between North Carolina Coastal (NCC) and local Oklahoma/Arkansas (O/A) provenances since it may be possible to increase productivity of droughty sites by planting NCC sources in favor of O/A sources. The objective of this study was to quantify differences in the branch-level production of foliage and branch (branchwood+bark) biomass of NCC and O/A provenances on an excessively drained site in southeastern Oklahoma using nonlinear regression models. Another set of regression equations that included variables that accounted for the seed sources were developed in order to quantify seed source differences in the relationships between tree and branch dimensions and branch-level foliage and branch biomass production. The relationship between tree and branch dimensions and branch production was found to be similar for the two seed sources. It was found that seed source significantly influenced the amount of foliage per branch; if tree and branch dimensions were held constant, NCC branches would carry approximately 30% more foliage than O/A branches. The distributions of branch biomass did not differ for the two provenances, but their foliage distributions differed in that the NCC source carried more foliage in the upper crown than the O/A source. Since the NCC provenance carried more foliage per branch and foliage biomass in the upper crown than the O/A source, we conclude that the productivity of the NCC provenance was equal to or greater than that of the O/A source on this droughty site.

Introduction

Traditional evaluations of the various seed sources of loblolly pine (*Pinus taeda* L.) have demonstrated that the sources vary in their growth characteristics, but the potential exists for a more comprehensive evaluation of seed source growth differences. Results of seed source studies have served as guidelines for seed source movement, a process in which provenances which have demonstrated the most favorable growth traits are planted in regions where they outperform local sources in order to increase forest productivity (Wells 1983). Tree height growth has been widely used in seed source studies as a selection criterion to identify genetic gains in productivity (McKeand 1988, Sprintz et al. 1989, Knowe and Foster 1989). Some authors have noted that height growth is an advantageous selection criterion since it is correlated with volume production and growth form (Perry et al. 1966, McCutchan 1983, Sprintz 1987). Measurements of total stem volume have also been used to evaluate the productivity of various loblolly pine provenances (van Deusen et al. 1981, Talbert and Strub 1987, Buford 1989). Given the importance of tree form on the profitability of the wood being produced by the various seed sources, quantifying differences in branch and foliage biomass production between provenances is desirable; the traditional selection criteria (height and volume) do not allow such a quantification to be made. Furthermore, better knowledge of crown biomass components, particularly foliage, would enable deeper understanding of the physiological processes that govern growth, most notably photosynthesis. The quantity and distribution of foliage, as well as the crown shape, are important factors in determining a tree's potential for interception of solar energy and assimilation of carbon through photosynthesis (Baldwin et al. 1997, Doruska and Mays

1998). The implication of the correlation between foliage quantity and distribution and photosynthesis is that trees that differ in foliar biomass production and partitioning will differ in photosynthetic capacity, thereby differing in productivity. It is possible that seed sources differ in their partitioning of branch and foliage biomass, so measurements of such characteristics (beginning at the branch level) would be desirable when comparing the productivity of seed sources.

A modeling approach can be employed to gain knowledge about the branch-level foliage and branch biomass production and partitioning of seed sources. It has been proposed that growth models are viable alternatives to traditional selection and genetic gain prediction systems (Knowe and Foster 1989, Rockwood et al. 1995). Non-destructive, indirect measurement of biomass components is a favorable method since it is less time-consuming and expensive than direct measurement (St. Clair 1993). Regression equations (linear and nonlinear) have been developed to estimate the branch-level foliage or branch weight as a function of parameters such as branch basal diameter and the distance of the branch from the top of the tree (relative branch height) (Hepp and Brister 1982, Baldwin 1989, Gillespie et al. 1994, Baldwin et al. 1997).

In addition to providing predictions of biomass components, models can be used to quantify seed source influences on biomass production. Diverse methods of evaluating models have been used to determine the influence of a variety of silvicultural treatments on foliage and branch biomass production, but there is scarce mention in the literature of seed source influences on biomass partitioning being analyzed with models. Van Lear et al. (1986) developed regression equations to predict the dry weights of various above-ground biomass components for trees of two types of sites; one set of equations was developed for a plantation stand and one set for a natural stand. They then compared the biomass curves of the various biomass components by examining parametric hypotheses concerning the exponents of each component curve for the two sites; residual errors from the conditional model were compared with the residual errors from the model with no conditions imposed (the principle of conditional error) to test the hypothesis that the biomass curves were similar for the two different types of sites. In a portion of their study on the impact of thinning and fertilization treatments on foliage quantity and distribution, Gillespie et al. (1994) developed separate sets of regression equations for predicting branch-level foliage weight of stands receiving different fertilization treatments, then conducted an analysis of variance on foliage biomass predictions to determine the effects of the fertilization treatments. Rockwood et al. (1995) developed height-age models for families of slash pine (*Pinus elliottii* var. *elliottii* Engelm.), then used the parameter estimates of the models to interpret family differences in growth dynamics. In summary, given that models have allowed interpretation of differences in growth characteristics in response to other silvicultural treatments, models developed for prediction of biomass components of different seed sources should help identify seed source differences in biomass partitioning, should differences occur.

In the northwestern portion of the loblolly pine range, there is a particular need to determine productivity differences between North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) loblolly pine on droughty sites. Several studies have shown that when planted in common environments, NCC sources frequently produce taller, faster-growing trees than O/A sources (Wells and Wakeley 1966, Wells and Lambeth 1983, Lambeth et al. 1984, Sprintz et al. 1989, Harrington 1991, Douglass et al. 1993).

NCC seed sources are now widely planted in the southeast Oklahoma/southwest Arkansas region, with a 20- to 30-percent gain in volume relative to local sources expected at harvest (Lambeth et al. 1984). However, forest managers avoid planting NCC planting stock on soils with poor moisture-holding capacity to avert excessive drought-related mortality in the NCC seed sources, which evolved in a climate with greater summer rainfall than that of the northwestern portion of the loblolly pine range (Lambeth et al. 1984). Lambeth et al. (1984) have stressed the need to monitor growth of NCC and O/A provenances on a wide variety of sites in the region to verify the accuracy of planting guidelines. A characterization of the relative productivity of NCC and O/A provenances grown on a droughty site (like those commonly avoided by planting guidelines) is desirable, for if the superior productivity of NCC sources is maintained on such sites the potential exists to increase the profitability of managing what are currently deemed marginal sites.

The objectives of this study are: (1) to use a modeling approach to estimate the branch-level foliage and branch (branchwood+bark) biomass production by NCC and O/A seed sources growing on a droughty site in southeastern Oklahoma and (2) to develop a technique to quantify any seed source differences in the foliage and branch biomass production per branch. This study is the first of a pair of studies focusing on characterizing the productivity (as measured by aboveground biomass production and partitioning) of NCC and O/A seed sources grown on a droughty site. The focus of this paper is to describe branch-level differences in crown growth dynamics; the subsequent study will build from the results of this study and test for tree- and stand-level differences in aboveground biomass production and partitioning. The subsequent study will also couple gas exchange measurements with the biomass data to yield a physiological process-based interpretation of the productivity of NCC and O/A seed sources.

Materials and methods

Site description

The study was conducted in a 15-year-old loblolly pine plantation in southeastern Oklahoma, near Broken Bow. The soil on the site is mapped as a Goldston-Carnasaw-Sacul association, which is an upland, gravelly, moderately steep, silt loam soil association with a low water-holding capacity. The average annual rainfall of the area is 49 in (125 cm), and the average annual temperature is 63° F (17° C) (USDA 1974). Rainfall is usually adequate through May, but droughts two to six weeks in duration are common from June through October. The climate through much of the growing season is hot and humid (Stogsdill 1986).

The site was planted in 1983 with NCC 8-01 and O/A mix 4213 seed sources. Prior to planting, the site was subsoiled to improve survivability. One-acre (0.405 ha) split plots arranged in a completely randomized design were established at two adjacent locations. Since the study site was originally established to observe the effects of both planting spacing and seed source on productivity and survival of the two seed sources on a droughty site, two treatments (planting spacing and seed source) were randomly applied to the split plots. Planting spacing was the whole-plot treatment and seed source was the sub-plot treatment. However, since planting spacing effects were beyond the scope of this study, only plots with an 8 ft x 8 ft (2.4 m x 2.4 m) spacing were observed since that spacing best approximated a commercial planting density. Because one spacing was selected, the 0.5-acre (0.202 ha) sub-plots differed only in seed source treatment; therefore, the 0.5-acre sub-plots were considered to be individual, "whole" plots. Thus, for the remainder of this paper "plot" will refer to the 0.5-acre plots originally laid out as sub-plots. In all, five plots planted with the NCC provenance and four plots planted with the O/A provenance were observed in this study.

Data collection

In May 1998, fifteen trees per seed source were destructively sampled for use in model development. To ensure that the sample trees represented the range of tree diameters present on the site, 0.1-acre (0.04 ha) plots were established within each of the 0.5-acre plots in March 1998, and the height and diameter at breast height (DBH) of all trees in the 0.1-acre plots were measured. Four-centimeter diameter classes (<11.0 cm, 11.0-15.0 cm, 15.1-19.0 cm, 19.1-23.0 cm, and >23.0 cm) were established based on the data collected in the 0.1-acre plots. All trees in the 0.1-acre plots were also tagged so their growth and survival could be monitored over time. Three sample trees/seed source were collected from each of the five diameter classes (a total of 15 sample trees/seed source) to adequately represent the study site's range of diameters. Further selection criteria for sample trees were: (1) at least one of the three sample trees/seed source/diameter class was collected from each location, and (2) at least one tree was harvested from each plot.

Measurements collected on each sample tree included DBH, height of every dead branch from the base of the tree, and the diameter of every dead branch. Once those measurements were collected, the sample trees were felled (with ropes used to slow their descent, thus preserving branches), and the tree's total height, height of every live branch from the base of the tree, and diameter of every live branch were measured. Two branches per crown third were randomly subsampled on each of the sample trees for foliage and branch biomass. Foliage was separated from woody branch material on each of the sample branches; foliage from the second growth flush of 1998 was discarded during the separation of foliage and branch material since it was just beginning to develop when the sample trees were collected. The foliage and branch material was then oven-dried to constant weight at 80° C.

Model development

Using the data gained from the destructively sampled branches, nonlinear regression equations were computed for each seed source using the NLIN procedure of the SAS System Version 6.12 (SAS Institute Inc., Cary, NC.). To ensure that the models included only variables that significantly ($P=0.15$) influenced foliage or branch biomass, a stepwise regression procedure was performed during model development. The resulting equations had the following form:

$$Y = B0 * BRDIA^{B1} * (RELHT)^{B2} * (H/D)^{B3} \qquad [1]$$

where Y is either the foliage or branch biomass (g) of an individual branch, BRDIA is the branch diameter (cm), RELHT is the relative height of the branch (m), H is the total tree height (m), and D is the DBH (cm) of the tree. The relative height is the difference between the total height of the tree and the distance of the branch from the base of the tree. This model form is in agreement with models developed by Ek (1979) to predict the branch and foliage biomass of individual branches. It is noteworthy that predictions of foliage biomass apply only to the last growth flush of the previous season and the first growth flush of the current season. Residual analyses revealed that the variance of the residuals was not homogenous in neither the branch biomass model nor the foliage biomass model, so all observations were weighted by the inverse of their squared branch diameters during model development. The non-linear regression equations were used to estimate the foliage and branch biomass for each branch on the sample trees using measurements of their branch diameters, branch heights, total tree height, and DBH. To augment predictions of the branch and foliage weights of all branches of the sample trees, total heights of all trees in the 0.1 acre plots were analyzed with mixed-model analysis of variance.

Models were then developed to identify seed source differences in the relationships between the dependent and independent variables in the previous models. First, the sample branch data used in the development of the above regression equations was pooled for the two seed sources. A dummy variable was then created for seed source and multiplied by all variables in the regression equations in order to create variables that accounted for seed source influence on all variables. Log transformations were performed on all variables to convert them into linear form, resulting in the following model form:

$$\ln Y = B1 + B2(\ln Z) + B3(\ln BRDIA) + B4(\ln Z_{dia}) + B5(\ln RELHT) + B6(\ln Z_{relht}) + B7(\ln(H/D)) + B8(\ln Z_{(H/D)}) \quad [2]$$

where Y is the branch or foliage weight (g) of an individual branch, BRDIA, RELHT, H, and D are as defined in the aforementioned model form, Z is a dummy variable for seed source (that has a value of 1 if an O/A observation and 0 if a NCC observation), Z_{dia} is Z*BRDIA, Z_{relht} is Z*RELHT, and $Z_{(H/D)}$ is Z*(H/D). A stepwise regression procedure was performed to ensure that only variables that significantly (P=0.15) affected the branch or foliage biomass production were included in the regression equations. Upon development of the models, seed source differences in parameter estimates were quantified by converting the linear form of the parameter estimates of any significant dummy variables to their antilog (multiplicative) form, thus yielding the percentage difference between the seed sources in respect to their independent-to-dependent variable relationships.

Results and Discussion

The nonlinear regression equations developed for prediction of the branch-level foliage and branch biomass production of the NCC and O/A seed sources on the study site are provided in Table 1. The models appeared to predict branch biomass better than foliage biomass, as can be inferred from the higher fit indices of the branch equations. The superior ability of the models to predict branch biomass is likely due to the relationship of foliage production to tree moisture and nutrient status and amount of mutual shading, all of which create variability in foliage production (Rachal 1986). In all regression equations, branch diameter had the highest explanatory power, while the H/D variable had relatively low explanatory power. When averaged for the two seed sources, the branch diameter parameter estimates were 2.49±0.34 and the standard errors of these parameter estimates were 0.168±.07. The H/D parameter estimates were -0.02±0.4 and their standard errors were 0.28±0.1. All parameter estimates and their standard errors are provided in Table 1. In the stepwise procedure, it was found that the H/D variable could be removed from the regression equation predicting the branch weight of NCC branches due to its low explanatory power, but it was decided to keep the H/D variable in the model due to its slight contribution to the overall explanatory power of the model and the ease of obtaining height and DBH measurements.

Branch diameter had a positive effect on foliage and branch biomass for both seed sources, hence the positive coefficients for branch diameter in the branch and foliage biomass models for both seed sources (Table 1). This positive effect suggests that with increasing branch size there is an increase in foliage and branch biomass production per branch. Similar results have been previously reported for loblolly pine (Gillespie et al.

1994). Relative height of the branch had a positive effect on branch production for both seed sources, suggesting that larger branches are produced with increasing distance from the top of the tree for both seed sources. By contrast, relative branch height was negatively related to foliage production for both seed sources, implying that branches in the lower crown tend to carry less foliage per branch than branches higher in the crown. This pattern of foliage display has been found in previous studies (Hepp and Brister 1982, Gillespie et al. 1994). Gillespie et al. (1994) attributed the reduction in foliage biomass with increasing crown depth to the increased shading present in the lower crown, which inhibits the ability of foliage to fix carbon and thereby reduces the amount of foliage carried. The effect of the H/D variable contrasted for the two seed sources in the branch and foliage models; in NCC equations H/D had a negative effect and in O/A equations H/D had a positive effect. This result is likely due to the low significance of the H/D variable; since H/D is only slightly significant in the regression equations, the value of the coefficient could possibly be close to zero, either positively or negatively.

No dummy variables were found to be significant in the regression equation developed to identify seed source differences in the relationships between branch biomass production and branch diameter, relative branch height, and H/D. The stepwise procedure removed all dummy variables from the model since they were non-significant at the P=0.15 level. Thus, the relationships between the independent variables and branch biomass production did not significantly differ between the seed sources. This finding illustrates that branches of identical diameter and distance from the top of the tree taken from NCC and O/A trees of equal height and DBH produce similar branch biomass.

A significant dummy variable was found in the model developed to identify seed source differences in the relationships between foliage production per branch and branch diameter, relative branch height, and H/D. The Z variable was found to be significant (P=0.0019) and was included in the model (Table 2), but Z_{brdia}, Z_{relht}, and $Z_{(H/D)}$ were removed from the model since they were not significant at the 0.15 level. The negative value of the Z parameter estimate indicates that the intercept of the NCC seed source foliage regression equation is greater than that for the O/A seed source foliage regression equation (since the dummy variable was assigned a value of 0 for NCC and 1 for O/A). However, the lack of any other significant dummy variables indicates that the slopes of NCC and O/A foliage regression equations are equivalent. The antilog of the Z parameter estimate was 0.711, indicating that if branches with the same branch diameters and relative heights were taken from NCC and O/A trees on the study site of identical heights and DBH's and compared, the O/A branch would have about 71.1% of the foliage carried by the NCC branch. Thus, if all variables in the regression equations developed to predict branch-level foliage biomass were held constant, a NCC branch would tend to carry approximately 28.9 % (100-71.1%) more foliage than an O/A branch.

The branch and foliage biomass distribution patterns within the crowns of the two seed sources were inferred by observing the average branch and foliage weights along the stem. The regression equations were applied to each branch in the 15 trees/seed source destructively harvested in this study, yielding predictions of the branch and foliage weights of individual branches. Since the height of every branch from the stem base was recorded during sample tree measurement, it was possible to couple the branch and foliage weight predictions for each branch with the branch's corresponding height and thereby ascertain the manner in which the predictions of the branch and foliage weights of the individual branches were distributed. The branch and foliage weight predictions for the 15 trees/provenance were averaged for one-meter height classes to provide a representation of the distribution of branch and foliage biomass within the crowns of the NCC and O/A seed sources (Figures 1 and 2). The largest branches and foliage weights were in the lower portion of the crown for both seed sources. Hepp and Brister (1982) found that the maximum dry weight of an individual branch occurs at 20% of the crown length up from the base of the live crown, whereas we found the maximum average branch and foliage weight occurred close to the base of the live crown for both provenances. The foliage distributions of the two seed sources appear consistent with a study conducted by Gillespie et al. (1994) which found that more foliage would be present in the lower crown, such that the foliage would be vertically distributed as a Weibull distribution. The branch biomass of the two seed sources in the present study was distributed in a similar fashion (Figure 1).

While the branch distributions were very similar for the two seed sources, the provenances differed in the proportion of foliage produced in the upper crown relative to foliage produced in the lower crown. Branches in the upper crowns of NCC trees had a high proportion of foliage relative to the foliage on branches in the lower crown, whereas O/A trees had a much lower proportion of foliage biomass in their upper crowns when compared to the foliage on branches in their lower crowns (Figure 2). It has been demonstrated that photosynthesis per unit foliage is increased by proximity to light (Boltz et al. 1986). Since the NCC trees had more foliage in the upper crown than the O/A trees, foliage in upper crowns of NCC trees potentially had greater photosynthate production than foliage in upper crowns of O/A trees. However, greater productivity of the upper crown foliage would not necessarily constitute superior tree-level productivity for the NCC provenance since photosynthesis is also influenced by total leaf area of the tree and the amount of mutual shading present in the lower crown, which tends to be greater in taller trees (Burkhalter 1967, Boltz et al. 1986). Gillespie et al. (1994) found that the distributions of foliage and branch biomass were not altered by thinning and fertilization treatments. In the present study, we found that the branch biomass distributions were not influenced by the selection of NCC or O/A seed sources on a droughty site, but the foliage distributions were influenced by seed source.

The seed sources differed somewhat in their growth forms. The NCC trees were significantly taller than the O/A trees (P=0.0125). The greater height of the NCC provenance is consistent with many other studies that show that trees from East Coast seed sources are taller than trees from western seed sources (Wells and Lambeth 1983, Talbert and Strub 1987, Lambeth et al. 1984, Sprintz et al. 1989, Harrington 1991, Douglass et al. 1993). In addition, the NCC source had a shorter crown length; on average, the length from the base of the live crown (position of the lowest living branches) to the top of the tree was 10 m for the NCC trees and 11 m for the O/A trees (Figures 1 and 2). The finding that the taller NCC trees also had smaller crowns agrees with a previous study in which it was found that selection for small-crown, fast-growth characteristics in tree breeding programs had been effective in improving juvenile log quality of North Carolina families and that these characteristics were exhibited even when North Carolina stock was planted in Mississippi (Campbell et al. 1995).

Conclusions

Predictions of the branch-level foliage and branch biomass production of the NCC and O/A seed sources helped obtain some indication of their growth forms, which contributes to an understanding of the productivity of the two sources on an excessively drained site. In addition, the process developed in this study to quantify the relationships between branch and tree dimensions and the foliage and branch production was a useful method of providing further information about branch and foliage growth dynamics of the two provenances. NCC seed sources have been anticipated to be maladapted to excessively drained sites such as the one observed in this study; however, if the NCC source was maladapted to our site, it did not result in a poorer growth form relative to the local O/A seed source. The distribution of branch biomass for the NCC provenance was very similar to that of the O/A provenance, and the NCC source appeared to carry somewhat more foliage in the upper crown than the O/A provenance. In addition, the growth form of the NCC provenance on the excessively drained site observed in this study was consistent with the form exhibited by NCC trees on sites with greater moisture content; the NCC trees were taller, with a smaller crown. The process of creating dummy variables to account for the seed source treatments and using stepwise regression to test their significance made it possible to isolate any significant seed source effects on branch and foliage biomass production. From this technique, it was found that the seed sources did not differ in branch production dynamics and that the NCC seed source would tend to produce 29% more foliage per branch than the O/A source, given branches of comparable size and location within the crown.

The tendency of NCC branches to produce more foliage than O/A branches and the greater amount of foliage present in upper crowns of NCC trees offer compelling evidence that the NCC trees are more productive than the local source even on the droughty site observed in this study. It is possible that with more foliage per branch, the NCC seed source has a greater density of foliage per tree, which could make it more productive than the O/A seed source. The propensity of NCC trees to carry more foliage in the upper crown than O/A trees could also contribute to superior productivity of the NCC provenance since foliage in the upper crown is exposed to more solar radiation. However, there are numerous tree-level (i.e., number of branches per tree and stem production per tree) and stand-level (i.e., survival) factors to take into account before an accurate assessment of how selection of either NCC or O/A seed sources for planting would affect forest productivity. The subsequent study performed on this site will build from the results of this study and assess above-ground biomass production and partitioning at the stand level to further characterize the productivity of these seed sources on an excessively drained site.

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TABLE 1. Regression coefficients for equations used in prediction of foliage and branch biomass of individual branches of 15-year-old trees from coastal North Carolina and Oklahoma/Arkansas loblolly pine seed sources grown on a droughty study site in southeastern Oklahoma, 1998.[1]

Dependent Variable[2]	Parameter estimates				Standard errors of parameter estimates				Statistics[3]	
	b0	b1	b2	b3	b0	b1	b2	b3	FI	SE
NCBRDWT	0.044	2.524	0.381	-0.069	0.011	0.089	0.057	0.161	0.97	0.179
OABRDWT	0.029	2.777	0.202	0.470	0.013	0.162	0.102	0.249	0.90	0.321
NCFOLDWT	0.205	2.010	-0.213	-0.502	0.084	0.168	0.097	0.316	0.79	0.192
OAFOLDWT	0.040	2.668	-0.558	0.022	0.026	0.253	0.137	0.391	0.75	0.234

[1] The model is:

$$Y = b0 * (Brdia)^{b1} * (Relht)^{b2} * (H/D)^{b3}$$

where:

Y = predicted dry weight (g) of branches or foliage of one branch
Brdia = branch diameter (cm)
Relht = relative height of branch (m)
H = total height of tree (m)
D = diameter outside bark (cm) at 4.5 ft (1.37 m)
b0, b1, b2, b3 = coefficients estimated from data.

[2] NCBRDWT = dry weight of a branch (branchwood+bark) of coastal North Carolina trees
OABRDWT = dry weight of a branch (branchwood+bark) of Oklahoma/Arkansas trees
NCFOLDWT = dry weight of foliage on one branch of coastal North Carolina trees
OAFOLDWT = dry weight of foliage on one branch of Oklahoma/Arkansas trees

[3] FI = Fit Index
SE = Standard error of the estimate

TABLE 2. Significance of variables included in a regression equation developed to quantify effect of seed source upon relationships between branch and tree dimensions and foliage production for 15-year-old coastal North Carolina and Oklahoma/Arkansas loblolly pine trees grown on a droughty site in southeastern Oklahoma [1].

Variable	Parameter estimate	Standard error	Prob. > |T|
Intercept	-2.4899	0.2982	0.0001
Ln(Z)	-0.3414	0.1080	0.0019
Ln(BRDIA)	2.2916	0.1289	0.0001
Ln(RELHT)	-0.2621	0.0893	0.0038
Ln(H/D)	-0.5797	0.2412	0.0173

[1] The model is:

$$\ln Y = B1 + B2(\ln Z) + B3(\ln BRDIA) + B4(\ln RELHT) + B5(\ln(H/D))$$

where:

Y = foliage weight of an individual branch (g)
Z = seed source (value of 1 if O/A and 0 if NCC)
BRDIA = branch diameter (cm)
RELHT = relative branch height (m)
H = total height of tree (m)
D = diameter at breast height (cm)

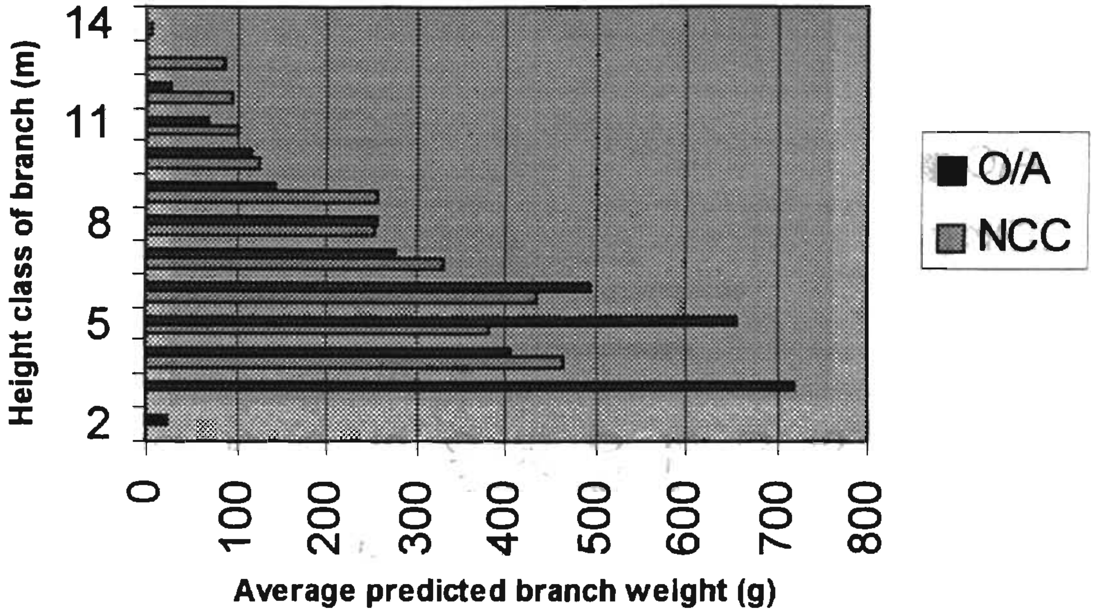

Figure 1. Predictions of the branch weights of individual branches of North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) loblolly pine seed sources averaged for one-meter stem sections. Trees were 15-years-old and grown on a droughty site in southeastern Oklahoma, 1998.

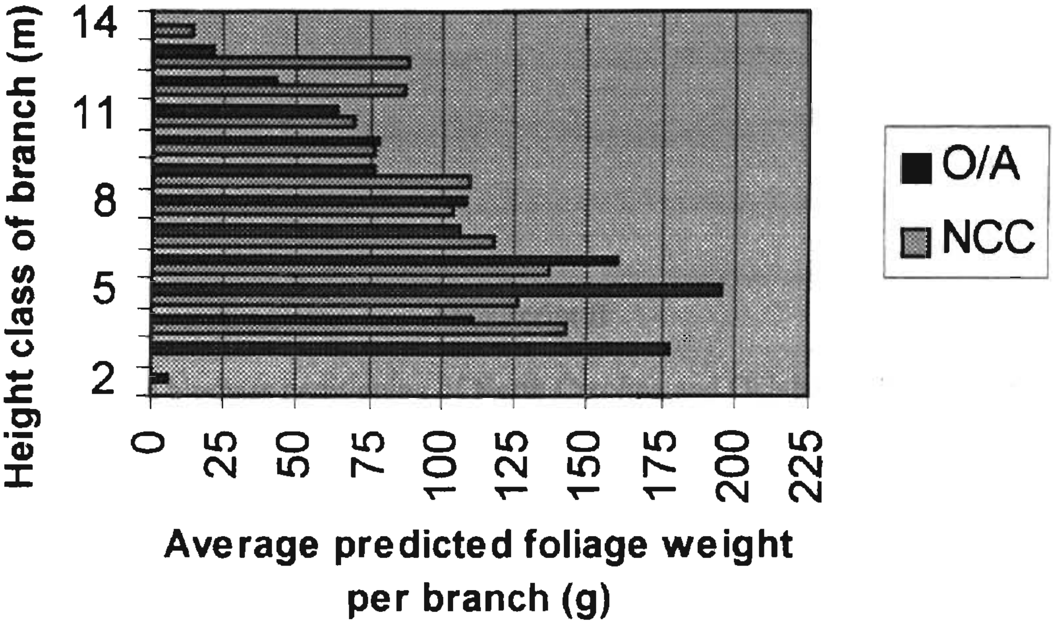

Figure 2. Predictions of the foliage weights of individual branches of North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) loblolly pine seed sources averaged for one-meter stem sections. Trees were 15-years-old and grown on a droughty site in southeastern Oklahoma, 1998.

Manuscript II

Productivity and biomass partitioning of North Carolina and Oklahoma/Arkansas loblolly pine growing on a droughty site in southeastern Oklahoma

Abstract

Biomass partitioning, gas exchange, and survival of North Carolina Coastal (NCC) and local Oklahoma/Arkansas (O/A) provenances of loblolly pine (*Pinus taeda* L.) were observed on a droughty site in southeastern Oklahoma to assess the validity of planting recommendations in the region. The O/A seed source produced a greater amount of branch and foliage biomass per acre than the NCC source, but the two provenances produced equivalent amounts of stem biomass per acre. Further investigation revealed that the O/A provenance achieved its greater branch and foliage biomass production by virtue of its support of a higher number of live branches per tree. The photosynthetic capacity (P_{max}), needle stomatal conductance of water vapor (g_w), and transpiration rates (E_t), which were periodically measured throughout the year this study was conducted, were similar for the two seed sources, as were survival rates. Given the comparable survival and stem biomass production of the two provenances on this droughty site as well as the NCC provenance's production of wood with less knots, we conclude that planting of the NCC provenance in favor of the local seed source on excessively drained soils in the northwestern portion of the loblolly pine range is a justifiable management option.

Introduction

Seed sources from the eastern portion of the natural range of loblolly pine (*Pinus taeda* L.), particularly those from North Carolina Coastal (NCC) sources, outgrow local seed sources when planted in the western portion of the natural range of loblolly pine. A preponderance of seed source studies has shown that when planted in common environments in southern Oklahoma and Arkansas, NCC seed sources frequently produce taller, faster-growing trees than those produced by local Oklahoma/Arkansas (O/A) seed sources (Wells and Wakeley 1966, Wells and Lambeth 1983, Lambeth et al. 1984, Sprintz et al. 1989, Harrington 1991, Douglass et al. 1993). The height growth superiority of NCC seed sources has been attributed to their ability to grow later into the growing season than other sources and to produce additional growth flushes in years when other sources are restricted in their cycle production (Harrington 1991, Jaywickrama et al. 1995, 1998).

Several authors have suggested that height growth is strongly linked to volume production and growth form (Perry et al. 1966, McCutchan 1983, Sprintz 1987). The implication of this correlation between height growth, volume, and form is that NCC provenances, given their superior height growth, may yield a greater quantity and quality of wood and fiber than western seed sources. Douglass et al. (1993) have identified several NCC families that are adequately adapted to the western portion of the loblolly pine range and produce trees with higher volumes and straighter stems than trees from Oklahoma and Arkansas families. Furthermore, it has been shown that in 29-year-old stands of eastern source trees grown in southwestern Arkansas, stand-level volume growth is allocated to fewer trees than in stands of western seed sources. Thus, stands of eastern seed sources commonly produce stands of larger, more economically valuable trees than those produced by stands of western seed sources (Wells and Lambeth 1983, Talbert and Strub 1987, Tauer and Loo-Dinkins 1990).

Coastal North Carolina seed sources are widely planted across the western edge of the loblolly pine range in favor of local seed sources, but discretion is used when selecting locations for planting nonlocal sources. Since the early 1980's, forest managers have been planting NCC seed sources in Oklahoma and Arkansas in response to studies suggesting that stand productivity would be increased by movement of faster-growing seed sources to areas in which they are sufficiently adapted (Wells 1983, Wells and Lambeth 1983, Duba et al. 1984, Lambeth et al. 1984). Stands of NCC trees are expected to yield a 20- to 30-percent increase in volume at harvest when compared to stands of local seed sources (Lambeth et al. 1984). However, it has been noted that estimates of wood and fiber gains from NCC sources may be somewhat overestimated since the specific gravity of NCC seed sources is lower than that of O/A sources (Byram and Lowe 1988, Tauer and Loo-Dinkins 1990). Another major factor offsetting growth gains from planting of nonlocal seed sources may be mortality. When grown in droughty common environments beyond the western extremity of loblolly pine's range, O/A provenances have demonstrated better survival rates than NCC sources (Long 1980). To minimize the risk of drought-related mortality, forest managers have heeded a recommendation to restrict planting of NCC stock to soils where mortality of NCC seed sources would not be significantly greater than would be expected from O/A sources, i.e. on soils with adequate moisture-holding capacity. Thus, decisions regarding the planting of NCC seed sources in Oklahoma and Arkansas are driven by a compromise between an anticipated gain in growth rate and of a perceived risk of loss to mortality (Lambeth et al. 1984).

The planting guidelines for NCC seed sources in the western fringe of the loblolly pine range may be overly cautious. Although guidelines that discourage the planting of NCC seed sources on droughty soils were developed to minimize mortality, Lambeth et al. (1984) have noted that such planting recommendations are somewhat conservative. They observed that some stands of NCC sources growing on soils more well-drained than the planting recommendations allowed, (i.e., on soils that had soil moisture deficits between 31 and 32 cm in the drought of 1980) exhibited mortality rates similar to stands of local O/A seed sources even during the worst drought ever recorded for the southern Oklahoma-Arkansas area. In addition, it is possible that the higher mortality rates occasionally exhibited by the faster-growing eastern sources could be due to an earlier onset of competition-induced mortality rather than maladaptation to the planting environment, in which case timely thinning and harvesting of stands of NCC sources could capture the trees otherwise lost to mortality (Zobel 1979, Wells and Lambeth 1983, Talbert and Strub 1987, Kung 1989, Tauer and Loo-Dinkins 1990).

A potential for improving the productivity of poorer sites in the western portion of the loblolly pine range may exist. Identification of the most productive seed source that is sufficiently adapted to poor sites is an important pursuit since the profitability of managing such sites is increased by planting of more productive seed sources (Zobel 1979). Since NCC seed sources are more productive than O/A sources wherever they are currently planted, planting NCC stock on excessively drained sites in the western edge of the loblolly pine range could allow more profitable forestry to be conducted on what are now considered marginal sites. The need to monitor growth and survival of stands of NCC and O/A seed sources in order to check the accuracy of the system of matching these two seed sources to proper soils in the southern Oklahoma-Arkansas area has been stressed by Lambeth et al. (1984). The site observed in this study allows such a comparison of the productivity of NCC and O/A seed sources to be made for a droughty site. This paper is one of a series of studies focusing on the growth behavior of the two seed sources on this site, with the overall goal of determining whether or not NCC seed sources can be more productive than O/A seed sources on sites more droughty than what planting guidelines would suggest. In a study previously conducted on this site, regression equations were developed to predict the foliage and branch weights of individual branches of NCC and O/A trees, thus allowing a comparison of seed source differences in the relationships between tree dimensions and foliage and branch production at the individual-branch level (Manuscript 1). The objective of this study was to test the hypotheses that on a droughty southeastern Oklahoma site: (1) total carbon gain of trees from a NCC seed source is greater than the total carbon gain of trees from an O/A seed source and (2) the fraction of total above-ground biomass partitioned into the stem component relative to branches is greater for NCC trees than for O/A trees.

Materials and methods

Site description

A complete description of the study site is given in Manuscript 1; key characteristics of the site will be discussed here. The site was a 15-year-old plantation planted with NCC 8-01 and O/A mix 4213 seed sources in 1983. The site was subsoiled during plantation establishment to improve seedling survival. The soil is a gravelly, silt loam soil with low water-holding capacity (USDA 1974). Droughts are common in the region from June through October; the climate of the region is hot and humid through much of the growing season (Stogsdill 1986). In all, nine 0.5 acre (0.202 ha) plots were observed in this study; five of these plots were planted with the NCC provenance and four were planted with the O/A provenance. The plots were arranged in a completely randomized design at two adjacent locations within the plantation; five plots were at one location and four plots were at the other. All plots were initially planted on an 8 ft X 8 ft (2.4 m X 2.4 m) spacing.

Environment

Various measurements of climatic variables were collected throughout the 1998-1999 growing season to characterize the environment during the year of the study. Daily measurements of temperature, humidity, precipitation, barometric pressure, wind speed, and solar radiation at a weather station located approximately 8 km from the study area were obtained from Mesonet climatological data (1998, 1999).

Gas exchange and plant water relations

Photosynthetic capacity (P_{max}) was measured in July, September, and November 1998 and in February 1999. One tree was sampled from each plot for P_{max} measurement;

trees were selected for observation on the basis of representative size, crown form, and absence of insect, disease, drought, or ice damage. On each sampled tree, a subsample of one branch per crown third (upper, mid, and lower) was harvested for measurement. Immediately after branches were detached from the stem, they were placed in a sealed container of water and measured shortly thereafter to optimize accuracy of measurements (Zhang and Cregg, in press). Measurements were conducted between 800 and 1700 h Eastern Standard Time (EST) at saturating light (PAR 1800 μmol m^{-2} s^{-1}) and controlled CO_2 concentrations (355 ppm) (Whitehead and Teskey 1995, Liu and Teskey 1995, Zhang et al. 1997). No measurements of P_{max} were collected once ambient temperatures exceeded 27° C (80° F), as operational experience revealed that photosynthesis rates were reduced when temperatures reached 29-32° C (85-90° F).

P_{max} measurements, which were paired by seed source, were made using two CO_2 gas analyzers (CI-301 PS, CID Inc.) in an open-system configuration. The gas analyzers were equipped with adjustable light resource attachments (CI-301 LA, CID Inc.) and humidity and CO_2 control units (CI-301 AD, CID Inc.) to control the PAR and CO_2 levels, respectively. On each sampled branch, three needle fascicles from the first flush of growth produced in 1998 were measured. The photosynthetic rates of the fascicles were measured at 40-second intervals with the gas analyzers.

Needle stomatal conductance of water vapor (g_w), transpiration (E_t), needle water potential (Ψ_n), and relative humidity were measured at the time of the P_{max} measurements. The gas analyzers were used to measure g_w and E_t, and Ψ_n was measured with a pressure chamber as described by Ritchie and Hinckley (1975). Relative humidity was measured with a Psychro-Dyne psychrometer (Belfort Instrument Co.).

Biomass

In May 1998, fifteen trees/seed source were destructively sampled to provide data to develop regression equations to predict components of the above-ground biomass of the two seed sources. Fifteen trees/seed source were selected since it was felt that this sample size was the minimum number of trees that would adequately account for the range of diameter classes of each seed source present on the study site. A complete description of the criteria used in sample tree selection to ensure that the fifteen sample trees/seed source were representative of the range of diameters present on the site has been described in Manuscript 1 of this thesis.

Several measurements used for regression equation development were collected on each sample tree. First, measurements of the stem diameter at breast height (DBH), height of every dead branch from the base of the tree, and the diameter of every dead branch were taken. Trees were then felled (with ropes used to slow their descent, thus minimizing loss of branches), and the tree's total height, height of every live branch from the base of the tree, and diameter of every live branch was measured. The bole was sawn into 1-meter sections after all branches had been measured and removed. The sections were weighed in the field with a hanging scale, and the inside- and outside-bark diameters of the top and bottom of each stem section were measured. Disks approximately 1 in. (2.54 cm) in thickness were then cut from the top and bottom of each stem section and weighed in the field with the hanging scale.

The data collected from the 15 sample trees/seed source were fitted to nonlinear model forms so a comparison of the biomass accumulation and partitioning patterns of the two seed sources could be made. The NLIN procedure of the SAS System Version

6.12 (SAS Institute Inc., Cary, NC.) was used to fit the data to the models. Separate sets of coefficients were developed for the two seed sources to best isolate seed source effects on biomass production and partitioning patterns. The resulting equations were evaluated on the basis of standard fit statistics and graphical examinations of the residuals.

Regression equations for predicting the dry weights of a tree's total branch and total foliage were developed. First, the branch-level dry weights of branch and foliage on the sample trees were predicted using equations developed in a study previously conducted on this site (Manuscript 1); these equations are provided in Table 1. The branch and foliage weight predictions yielded by those equations were summed for each sample tree to get the total branch weights and total foliage weights of the sample trees. The total branch weight, height, and DBH data collected on each sample tree were fit to a non-linear model that predicted the total dry weight of branch biomass (branchwood+bark) for a tree using DBH and total height measurements as inputs. Similarly, total foliage weight, height, and DBH data were fit to a non-linear model which predicts the total dry weight of foliage for a tree using DBH and height inputs. The models developed for branch and foliage weight prediction are given in Table 2.

Models for predicting the dry weights of stems were also developed. First, the disks taken from the 1-meter stem sections of the sample trees were oven-dried at 100° C to a constant weight. The disk dry weights were combined with the green weights of the disks that had been taken in the field to calculate dry weight:green weight ratio of the disks. Since two disks had been obtained from each stem section, the dry weight:green weight ratios of the two disks were condensed into one ratio to properly convert the green weights of the stem sections into dry weights. To condense the ratios, the following formula was used to obtain a weighted average of the two dry weight:green weight ratios/stem section:

$$WDR = \frac{(ALD^2 * LDR) + (AUD^2 * UDR)}{(ALD^2 + AUD^2)} \qquad [1]$$

where

WDR = weighted dry weight:green weight ratio for a 1-meter stem section

ALD = area (cm^2) of the top surface of the disk taken from the lower end of a stem section

LDR = dry weight:green weight ratio of the disk taken from the lower end of a stem section

AUD = area (cm^2) of the top surface of the disk taken from the upper end of a stem section

UDR = dry weight:green weight ratio of the disk taken from the upper end of a stem section

The green weights of each 1-meter stem section were then multiplied by the weighted dry weight:green weight ratio to get the dry weights of each stem section. The dry weights of the stem sections were then summed for each sample tree to get their total stem dry weights. The stem dry weights, total heights, and DBH measurements for all sample trees were fit to a nonlinear model, resulting in a model that predicted the total dry weight of a stem using the DBH and height of a tree as inputs. The models developed for stem weight prediction are listed in Table 2.

The models developed for stem, branch, and foliage weight prediction were applied to all trees within 0.1 acre (0.04 ha) plots, and all predicted biomass weights were converted to per-acre values. In March 1998, 0.1 acre plots were established within each 0.5 acre (0.202 ha) plot, and the DBH and height of each tree within the 0.1-acre plots were measured. These measurements were used as inputs in the regression equations to predict the branch, foliage, and stem weight of every tree within the 0.1-acre plots. These tree-level predicted biomass weights were then summed for each 0.1-acre plot to yield the total branch, foliage and stem weights of the plots. To express these predictions of biomass components on the per-acre basis (which is most pertinent to forest managers), branch, foliage, and stem weight/acre for each 0.5-acre plot were then calculated by applying an expansion factor of 10 to the biomass weights predicted for each of the 0.1-acre plots. Using the appropriate conversion factors, the per-acre branch, foliage, and stem weights were converted to the per-hectare basis and will be reported as such for this paper.

Specific leaf area (SLA) was measured on the 15 trees/seed source used in the development of the regression equations. From each crown third of all sample trees, 50 fascicles of needles were randomly sampled for SLA determination since leaf area is such an important determinant of forest productivity (Shelton and Switzer 1984, Teskey et al. 1987). Since SLA is defined as the ratio of leaf area and needle weight (Hager and Sterba 1985), the first step in SLA determination was to calculate the leaf area of the 50-

fascicle samples. The leaf area per fascicle was calculated using the following equation (Bingham 1983):

$$A = 2RL(N + \pi) \qquad [2]$$

where

A = fascicle area (cm^2)

R = average radius of needles (cm)

L = average length of the fascicle (cm)

N = number of needles per fascicle

$\pi = 3.141592654$

All measurements required for use of the equation were collected using the procedures outlined by Bingham (1983). The leaf area values calculated for each fascicle within the 50-fascicle samples were then summed to yield the leaf area for the entire sample. All samples were oven-dried at 80° C to constant weight, and the leaf area of each sample was divided by its ovendry weight to provide the SLA of each 50-fascicle sample. Thus, SLA measurements were obtained for each crown third of all trees used in model development.

Several additional measurements were taken on each of the 15 sample trees/seed source used for regression equation development to provide information on the quality of wood produced by trees of the NCC and O/A seed sources. The number of live and dead branches was counted on each of the sample trees and expressed as the number of knots/log and a half (the number of branches/24 ft (7.32 m) of stem length). Wood quality of the two seed sources was further characterized by measuring wood specific gravity (grams of dry wood/cm^3 of green volume) of all disks removed at one meter above the base of the stem. The 15 trees/provenance from which the specific gravity data was gathered is close to a reported suggested optimum sample size for specific gravity analysis (Jett 1989). The dry weight of all disks was obtained through the procedures previously mentioned. Each disk was then soaked in water until weight gain ceased; disk volume at 100% moisture content (as measured with a Delmhorst J-2000 moisture meter) was then ascertained by displacement. Specific gravity was thereby expressed as the ovendry weight of the wood divided by the weight of the displaced water (Tauer and Loo-Dinkins 1990, Haygreen and Boyer 1996).

To augment the predictions of per-acre weights of the components of above-ground biomass derived from the regression equations, stand density and survival data were collected. Trees/acre (TPA) for each plot was calculated by expanding the tree count made in the 0.1-acre plots in March 1998 by a factor of 10. Survival of trees from 1998 to 1999 was obtained by comparing the tree tally made in the 0.1-acre plots in March 1998 to one made in April 1999; mortality rates were calculated as the percentage of tagged trees in the 0.1-acre plots that were dead in the 1999 tally.

Statistical Analysis

Analysis of all treatment effects of interest were determined by analyses of variance (ANOVA's) made using the MIXED procedure of SAS System Version 6.12 (SAS Institute Inc., Cary, NC.). Various models were used in the analyses depending on the treatments being assessed, and they will be discussed in detail below. When an

ANOVA indicated significant treatment effects, least-square means were calculated and separated by the LSMEANS procedure and DIFF option in SAS. The DIFF option separated means by invoking a t-test to evaluate significant differences between the least-square treatment means, thus allowing multiple comparisons of the treatment means.

For analyses of seed source differences in P_{max}, g_w, and E_t, the experiments were treated as randomized complete block designs (RCBD's) with subsampling. Since the P_{max}, g_w, and E_t observations were paired, the plots that were paired when measurements were taken were considered as blocks. Seed source was the treatment, and blocks were the experimental units that received the treatment. Since P_{max}, g_w, and E_t measurements were taken for each crown third, crown levels were treated as subsampling units. Separate analyses of P_{max}, g_w, and E_t were conducted for each month in which measurements were taken to determine whether seed source differences occurred during the growing season. Analysis of variance procedures were performed on a mixed model with the following effects: seed source, block, crown level, and all possible interactions between seed source, block, and crown level. Seed source and crown were considered to be fixed effects, and block and all interactions with block were considered to be random effects.

Although Ψ_n measurement collection was similar to that for the P_{max}, g_w, and E_t measurements, only one pressure chamber was used, preventing pairing of the Ψ_n measurements. Instead, a 2 x 2 factorial treatment structure (with planting location and seed source as the two treatments) arranged in a completely randomized design (CRD) was considered for the analysis of Ψ_n. Seed source and location were the treatments, and plots (with a location x seed source interaction nested within) were the experimental units receiving the treatments. Crown levels were considered subsampling units. Analysis of variance procedures were performed on a mixed model with the following effects: (1) seed source, (2) location, (3) crown, (4) all possible interactions between seed source, location, and crown, and (5) seed source X location nested within plot. Seed source, location, crown, and all their possible interactions were considered fixed effects; seed source X location nested within plot was considered a random effect. SLA measurements were taken in a similar fashion as the Ψ_n measurements, so the same model was used in SLA analysis.

Branch weight/ha, foliage weight/ha, stem weight/ha, TPA, percentage of mortality from 1998-1999, specific gravity, number of knots/log and a half, and the heights and DBH's of trees within the 0.1 acre plots were analyzed as a 2 x 2 factorial treatment structure arranged in a CRD. Planting location and seed source were the two treatments, and plots (with seed source X location interaction nested within) were the experimental units receiving the treatments. Analysis of variance procedures were performed on a mixed model with the following effects: seed source, location, seed source X location, and seed source X location nested within plot. Seed source, location, and seed source X location were fixed effects, and seed source X location nested within plot was a random effect.

Results

Environment

The climate during the study, a period spanning from February 1998 to February 1999, was marked by a pronounced drought during July and August. For the two months combined, there was only 3.04 in (7.72 cm) of precipitation. Temperatures were high during these two months; there were 11 consecutive days in which air temperatures exceeded 100° F (37.8° C). For July and August combined, temperatures exceeded 100° F for 21 days. However, the hot, dry summer was followed by a wet fall. From September to November, a total of 22.3 in (56.5 cm) of rain fell. The total precipitation for the February 1998-February 1999 period was 48.7 in (123.8 cm).

Gas Exchange

In the analyses of P_{max}, no significant differences attributable to seed source were found for any month (Figure 1). Both seed sources showed similar trends in P_{max} over the growing season. During the hot and dry month of July, P_{max} values were at their lowest; in the much cooler and wetter September, the P_{max} values were at their highest. P_{max} values dropped from September to November, but were slightly greater in February 1999. In September only, a marginally non-significant (P=0.0966) crown x seed source interaction was found. Comparison of least-square means for all possible crown x seed source interactions showed that for the NCC seed source, the lower crown had significantly lower (P=0.0552) P_{max} than the upper crown. In November, a significant (P=0.0189) crown effect was found. For both seed sources, the lower crown had a significantly lower P_{max} than both the mid (P=0.0064) and upper (P=0.0509) crown (Figure 2).

No significant differences attributable to seed source were found in the analyses of E_t, g_w, or Ψ_n; the trends in E_t, g_w, and Ψ_n were similar for the two seed sources throughout the study. E_t values followed a trend similar to that exhibited by P_{max} values for most measurement periods (Figure 3); however, there was a decrease in E_t in February instead of a slight increase as in the P_{max} trends. As with the analysis of P_{max}, a significant (P=0.0056) crown effect was found in only November for E_t. Comparison of the E_t least-square means for each crown third showed that the lower crown had significantly lower E_t than both the mid (P=0.0018) and upper (P=0.0209) crown in November. The trend in g_w over the growing season contrasted somewhat from the P_{max} and E_t trends; g_w values were at their lowest in the dry month of July, increased from September to November, then declined by February 1999 (Figure 4). Similar to the analyses of P_{max} and E_t, a significant crown effect on g_w (P=0.0052) was found only in November. Comparison of g_w least-square means showed that there were differences within the crown identical to those found for both P_{max} and E_t in November, with the lower crown having significantly lower g_w than the mid (P=0.0015) and upper (P=0.0366) crown. Ψ_n values were low in July, plateaued at a higher level from September to November, then declined again by February 1999 (Figure 5). Interestingly, the Ψ_n values were lower in February than in July 1998 even though February had had more precipitation than July. Analyses of Ψ_n values by month revealed no significant seed source effects on Ψ_n; however, there were significant crown effects for every month ($P=0.0069 \pm 0.013$) in which measurements were taken. The general trend in Ψ_n in the crowns of the two seed sources over the measurement period, as assessed by comparisons of Ψ_n least-square means by each crown third, was that the lower crown had a greater Ψ_n than both the mid and upper crown levels.

Biomass

The analyses of the measures of the components of above-ground biomass of the NCC and O/A provenances revealed significant differences attributable to seed source (Table 3). Branch weight/ha was found to be significantly greater (P=0.0078) for the O/A source than the NCC source. Foliage weight/ha was also found to be significantly greater (P=0.0163) for the O/A source than the NCC source. However, the seed sources did not significantly differ (P=0.6812) in stem weight/ha.

The two seed sources differed somewhat in wood quality and growth form. Specific gravity did not differ for the two seed sources (P=0.6235), but there was a significant difference in the number of knots per log and a half (Table 3). The O/A source had a significantly greater (P=0.0279) number of knots. The NCC and O/A seed sources did not differ (P=0.6897) in SLA (Table 3); there was also no difference in SLA between the crown levels across the two seed sources (P=0.4198). There was a significant difference between the seed sources in total tree height; trees from the NCC source were significantly taller (P=0.0125) than trees from the O/A source (Table 3). The DBH of the two seed sources was not significantly different (P=0.4601); the NCC provenance had a mean DBH of 17.7 cm and the O/A provenance had a mean DBH of 16.1 cm.

The NCC and O/A sources did not significantly differ in stand density or survival at age 15. The difference in TPA for the two sources was not significant (P=0.5891); the NCC source had a mean of 523 TPA and the O/A source had a mean of 565 TPA (Table

3). The two sources also did not differ (P=0.2440) in mortality rates from 1998 to 1999. The NCC source experienced a 2 % mortality rate, and the O/A source had a 0.5 % mortality rate (Table 3).

Discussion

The lack of any significant differences in P_{max} suggests that the photosynthetic apparatus of the NCC and O/A seed sources exhibit similar characteristics throughout the growing season (Schaberg et al. 1998). The physiology of the needles of the two seed sources was similar, so the two provenances had the same potential for producing photosynthate and thereby, by inference, for producing biomass. However, in addition to the photosynthetic capacity, the productivity of the two seed sources would also be influenced by leaf area and the photosynthetic rates per unit of foliage (Teskey et al. 1987). In this study, the O/A provenance had more leaf area (as inferred from the combination of foliage weight/ha and SLA) than the NCC source, which gave it a larger amount of area in which photosynthesis can occur. However, it has been demonstrated that trees with greater leaf areas commonly exhibit greater mutual leaf shading, which decreases average photosynthesis per unit leaf area (Burkhalter et al. 1967, Boltz et al. 1986). Thus, although the O/A provenance had a greater leaf area, its photosynthetic rates per unit leaf area were likely moderated at the crown level by the increased mutual leaf shading associated with larger leaf areas. It has been proposed that photosynthetic rates per unit leaf area are increased by greater proximity of foliage to light (Boltz et al. 1986). The study conducted previously on this site revealed that on average NCC trees carried higher proportions of foliage biomass in their upper crowns than O/A trees (Manuscript 1). Thus, the crowns of NCC trees likely have more foliage with high photosynthetic rates per unit leaf area than crowns of O/A trees. Since E_t is strongly influenced by the amount of leaves exposed to incoming solar radiation, the lack of any significant differences in crown-level E_t for the two seed sources suggests that although the total leaf areas are different for the two seed sources, a comparable amount of solar radiation is intercepted by the foliage of the two provenances at the tree-level due to a combination of proximity of foliage to light and mutual leaf shading within the crowns (Boltz et al. 1986, Kramer and Boyer 1995). Given that the foliage of both seed sources had equivalent photosynthetic capacities, that the NCC source had less total leaf area but more leaf area in direct sunlight, and that the O/A source had more total leaf area but more mutual shading, it is likely that the two seed sources had equal stand-level abilities to carry out photosynthesis and thus to produce biomass.

The two seed sources differed in overall above-ground biomass production and in the proportions of biomass allocated into the various components of above-ground biomass. The O/A provenance produced more foliage and more branch biomass/ha than the NCC provenance. This finding was somewhat unexpected, since a study conducted previously on this site determined that on an individual-branch basis the NCC source produced 29% more foliage per branch (Manuscript 1). It appears that the greater branch and foliage biomass production by the O/A seed source is more closely related to its branch production/tree than its foliage production/branch. The O/A seed source had approximately 20% more branches per tree (as measured by the number of knots per log and a half) than the NCC seed source; the O/A provenance in turn had 26% more branch weight/ha and 24% more foliage weight/ha than the NCC seed lot. Campbell et al. (1995) found that the selection for small-crown, fast-growth characteristics in tree breeding programs had been effective in improving juvenile log quality of North Carolina families and that these characteristics were exhibited even when North Carolina stock was planted in Mississippi. Relative to local Mississippi sources, the NCC stock had a lower number of limbs/tree. The results of this study are consistent with their findings in that the NCC provenance had a smaller crown (as measured by number of knots/log and a half) than the local O/A seed source, even when planted on an excessively drained site in southeastern Oklahoma. The two seed sources did not differ, however, in their production of stem biomass/ha. It is apparent from these results that the O/A seed source exceeds the NCC source in total above-ground biomass, or in total carbon gain. However, it is also obvious that the NCC seed source partitions more biomass into its stem component relative to the branches, since it produced an amount of stem biomass comparable to that produced by the O/A seed source with significantly less branch biomass. In summary, the analyses of the above-ground biomass components suggest that the superior growth form of NCC trees relative to O/A trees is maintained even on a soil with low water-holding capacity.

Since the specific gravity measurements were equivalent for the two seed sources, the wood properties (such as strength and stiffness) would likely be similar for both seed sources; yield of pulp per volume would also be similar for the two seed sources (Byram and Lowe 1988, Haygreen and Bowyer 1996). The results of this study differ from a study done by Tauer and Loo-Dinkins (1990) in which it was determined that eastern seed sources had significantly lower specific gravities than northwestern seed sources when planted in southwest Arkansas. Our finding that the specific gravity did not differ between the two provenances also contrasts with studies that assert that genotype x environment interaction in specific gravity is not operationally meaningful for southern pines (Byram and Lowe 1988, Lowerts and Zoerb 1989). It is possible that the contrast between the results of the above studies and this one is attributable to edaphic and climatic factors, which were possibly stressful enough to mask genetic effects on specific gravity. None of those studies specified the soil type of the test areas, but it is probable that the test plantings were not done on shallow, rocky soils with poor moisture-holding capacity such as the soil in this study. In addition to the poor moisture-holding capacity of the soil on our test site, prolonged summer droughts are common in the test area. It has been proposed that differences in the latitude of seed source origin determine the timing of spring growth initiation, with southern sources initiating growth earlier in the spring than northern sources (Byram and Lowe 1988). NCC and O/A provenances originate from areas that lie along virtually the same latitude and have similar spring rainfall patterns, so it is likely that earlywood production initiates at about the same time for the two seed sources. It is also assumed that that summer drought initiates latewood production (Byram and Lowe 1988, Cregg et al. 1988). The onset of drought may be especially severe on this site since drought is accentuated by the poor moisture-holding ability of the soil. As a result, both seed sources likely make the transition to latewood production at virtually the same time, resulting in similar specific gravities.

The equivalent survival of the two seed sources on this site contradicts some studies that suggest that eastern seed sources could not be planted on highly droughty sites in the western edge of the loblolly pine range without mortality significantly greater than what would be expected of local seed sources (Long 1980, Lambeth et al. 1984). The lack of any significant differences in plant water relations suggests that the two seed sources are similar in their ability to survive on the droughty site. There were no seed source differences in Ψ_n, suggesting that the two provenances had similar water uptake abilities. Root system architecture may be similar for the two seed sources. E_t and g_w

also did not differ for the two seed sources at any time during the study. It has been suggested that trees with greater drought resistance will demonstrate a more rapid decline in leaf conductance than less resistant trees as soil moisture is depleted (van Buijtenen et al. 1976, Bongarten and Teskey 1986). The lack of any difference in g_w trends throughout the growing season, particularly in response to the drought that occurred in July, suggests that the NCC and O/A provenances are not significantly different in their drought resistance when both are grown in an area of recurring drought. Bongarten and Teskey (1986) tested the drought resistance of seedlings from diverse origins (which included seedlings from both NCC and O/A) and found no difference in leaf conductances among the various seed lots when seedlings were exposed to recurring drought. In that study, it was implied that trees from diverse origins experience comparable drought conditioning when grown in areas with recurring drought; the conductance and evapotranspiration responses of the two seed sources in this study are consistent with those in that study. In addition to genetic factors, the subsoiling operation done at stand establishment likely improved survival of both seed sources, since subsoiling (a common site preparation in the southeastern Oklahoma-southwestern Arkansas area) improves the condition of shallow, rocky soils by breaking up the soil layers, concentrating organic matter near seedlings, and improving soil aeration and water-holding capacity (Wittwer et al. 1986, Fallis and Duzan 1995). Wittwer et al. (1986) proposed that drought survival could be improved by the increase in soil moisture gained by subsoiling. Fallis and Duzan (1995) found that subsoiling was particularly effective in improving early survival and height growth up to age 19 on the harsher, drier sites encountered in Oklahoma. Furthermore, the stage of stand development cannot be discounted when considering mortality rates of the two seed sources. Measures of TPA for the two seed sources were not significantly different. It is likely that at age 15 years neither seed source was experiencing competition-induced mortality. If the NCC seed source performs on this excessively drained site as it has on sites with greater water-holding capacity, its mortality rate will increase at an earlier age than that of the O/A source (Wells and Lambeth 1983, Tauer and Loo-Dinkins 1990). We intend to monitor this site to observe such trends should they occur.

Conclusions

This study provided evidence that when planted on a droughty site in the northwest portion of the loblolly pine range, an O/A seed source could produce more total biomass than a NCC source, but the NCC source may produce an equivalent amount of stemwood biomass while partitioning less biomass into branches than the O/A source. The O/A provenance had a greater total carbon gain than the NCC source, as illustrated by its greater foliage weight/ha and branch weight/ha production and equivalent stem weight/ha. However, the NCC seed source partitioned more of its above-ground biomass into the stem component relative to branches than the O/A source had, as indicated by its comparable stem weight/ha and significantly less knots/log and a half.

The different growth habits of the two seed sources on a droughty site has management implications. Given the greater total above-ground biomass production of the O/A seed source, it could be advantageous to plant the O/A seed source on droughty sites when pulp yield is the management objective. By contrast, if sawtimber production on droughty sites is desired, it may be preferable to plant the NCC provenance. Its survival, specific gravity, and stem production/ha was comparable to that of the local O/A source on the droughty site observed in this study, and its stems tended to have significantly less knots/log and a half. The tendency to produce less knots is an important growth characteristic where sawtimber production is concerned, since wood with less knots is typically higher in value. Furthermore, with less branches/tree for the NCC source, its pruning costs would be lower.

When the rising demand for wood products and the shrinking land base from which wood can be harvested are considered, the need for planting the most productive planting stock possible on lands being managed for wood products production is apparent. This study has provided some evidence that forest managers may have more flexibility in which soils can be planted with NCC loblolly pine in the southeast Oklahoma-southwest Arkansas region than has been traditionally considered. The NCC seed source, although it was not the best producer of total above-ground biomass when compared to the local source, exhibited equivalent survival and produced stems with less knots (which may be a preferable growth characteristic for sawtimber production) even on an excessively drained site. However, it must be stressed that before such broad claims of the superior productivity of NCC over O/A on droughty sites can be made with greater certainty, a wider variety of NCC and O/A provenances need to be tested and the growth of the two seed sources should be studied throughout a rotation on a larger number of excessively drained sites.

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TABLE 1. Regression coefficients for equations used in prediction of foliage and branch biomass of individual branches of 15-year-old trees from disparate seed sources grown on a droughty study site in southeastern Oklahoma, 1998.[1] Adapted from Manuscript 1.

Dependent Variable[2]	Parameter estimates				Statistics[3]	
	b0	b1	b2	b3	FI	SE
NCBRDWT	0.044	2.524	0.381	-0.069	0.97	0.179
OABRDWT	0.029	2.777	0.202	0.470	0.90	0.321
NCFOLDWT	0.205	2.010	-0.213	-0.502	0.79	0.192
OAFOLDWT	0.040	2.668	-0.558	0.022	0.75	0.234

[1] The model is:

$$Y = b0*(Brdia)^{b1} * (Relht)^{b2} * (H/DBH)^{b3}$$

where:

Y = predicted dry weight (g) of branches or foliage of one branch
Brdia = branch diameter (cm)
Relht = relative height of branch (m)
H = total height of tree (m)
DBH = diameter outside bark (cm) at 4.5 ft (1.37 m)
b0, b1, b2, b3 = coefficients estimated from data.

[2] NCBRDWT = dry weight of a branch of coastal North Carolina trees
OABRDWT = dry weight of a branch of Oklahoma/Arkansas trees
NCFOLDWT = dry weight of foliage on one branch of coastal North Carolina trees
OAFOLDWT = dry weight of foliage on one branch of Oklahoma/Arkansas trees

[3] FI = Fit Index
SE = Standard error of the estimate

TABLE 2. Regression coefficients for equations used in prediction of components of above-ground biomass of 15-year-old trees from disparate seed sources grown on a droughty study site in southeastern Oklahoma, 1998.[1]

Dependent Variable[2]	Parameter estimates			Statistics[3]	
	b0	b1	b2	FI	SE
NCBRDWT	7.445	3.367	-1.076	0.94	0.129
OABRDWT	4.411	3.392	-0.839	0.92	0.184
NCFOLDWT	73.836	2.832	-1.678	0.97	125.1
OAFOLDWT	43.399	3.348	-2.048	0.97	167.1
NCSTMDWT	36.629	1.825	0.819	0.99	628.8
OASTMDWT	40.355	1.692	0.933	0.98	1401

[1] The model is:

$$Y = b0*(DBH)^{b1} * (HT)^{b2}$$

where:

Y = predicted dry weight (g) of branches, foliage, or stem of one tree
DBH = diameter outside bark (cm) at 4.5 ft (1.37 m)
HT = total tree height (m)
b0, b1, b2 = coefficients estimated from data.

[2] NCBRDWT = dry weight of branches on coastal North Carolina trees
OABRDWT = dry weight of branches on Oklahoma/Arkansas trees
NCFOLDWT = dry weight of foliage on coastal North Carolina trees
OAFOLDWT = dry weight of foliage on Oklahoma/Arkansas trees
NCSTMDWT = dry weight of stem of coastal North Carolina trees
OASTMDWT = dry weight of stem of Oklahoma/Arkansas trees

[3] FI = Fit Index
SE = Standard error of the estimate

TABLE 3. Effect of seed source upon biomass partitioning, wood quality, and survival of 15-year-old plantation-grown loblolly pine in southeastern Oklahoma.

Seed Source[1]	Total ht (m)	branch wt (kg ha^{-1})	foliage wt (kg ha^{-1})	stem wt (kg ha^{-1})	specific gravity $\left(\frac{\text{g dry wood}}{\text{cm}^3\text{ green volume}}\right)$	knots per log $\left(\frac{\text{\# knots}}{\text{7.3 m stem length}}\right)$	SLA[2] ($\text{cm}^2\ \text{g}^{-1}$)	# trees ac^{-1}	% mortality (1998-1999)
NCC	12.3 *a*	11,766 *b*	5,277 *b*	74,021 *a*	0.47 *a*	52 *b*	124.4 *a*	523 *a*	2.0 *a*
O/A	11.6 *b*	15,920 *a*	6,971 *a*	77,275 *a*	0.46 *a*	65 *a*	127.8 *a*	565 *a*	0.5 *a*

Note: means within a column followed by different letters differ significantly at $P < 0.05$

[1] NCC = North Carolina Coastal loblolly pine
O/A = Oklahoma/Arkansas loblolly pine

[2] SLA = specific leaf area, pooled for all crown thirds

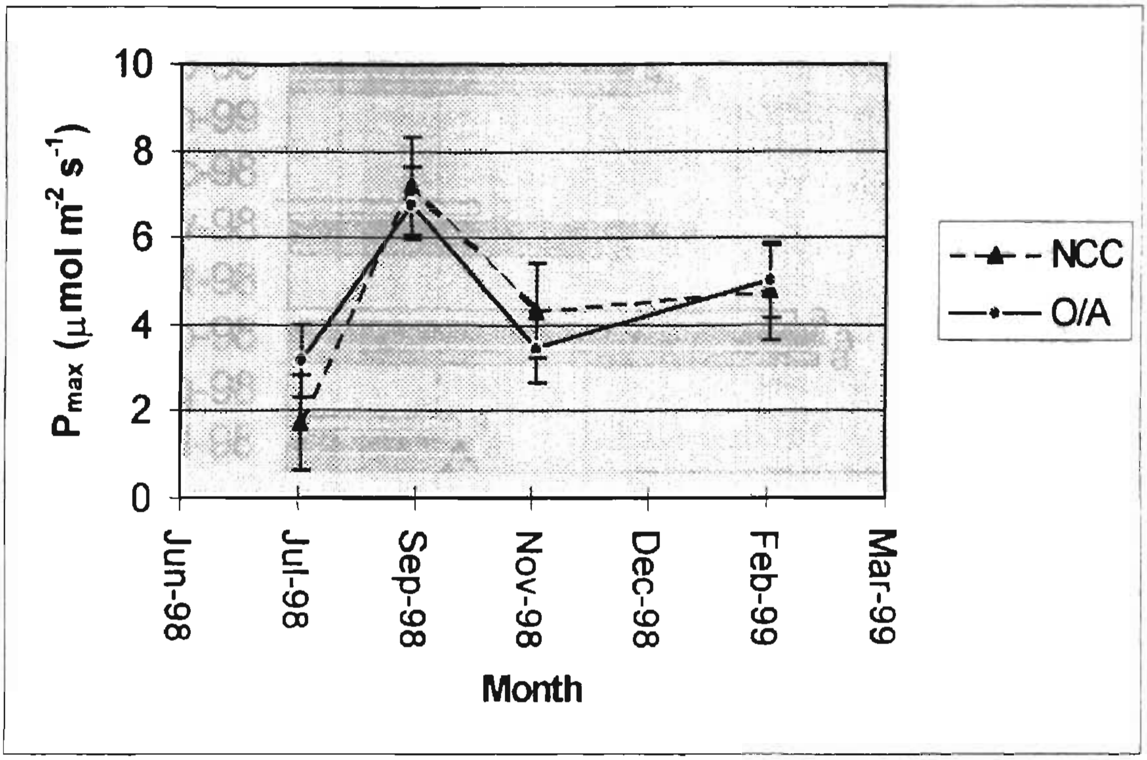

Figure 1. Trends in P_{max} (averaged for separate measurements taken in the upper, mid, and lower crown) for North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) provenances of loblolly pine grown on a droughty site in southeastern Oklahoma. No significant differences ($P<0.05$) attributable to seed source were observed during any month in which measurements were collected. Error bars indicate standard errors of observations.

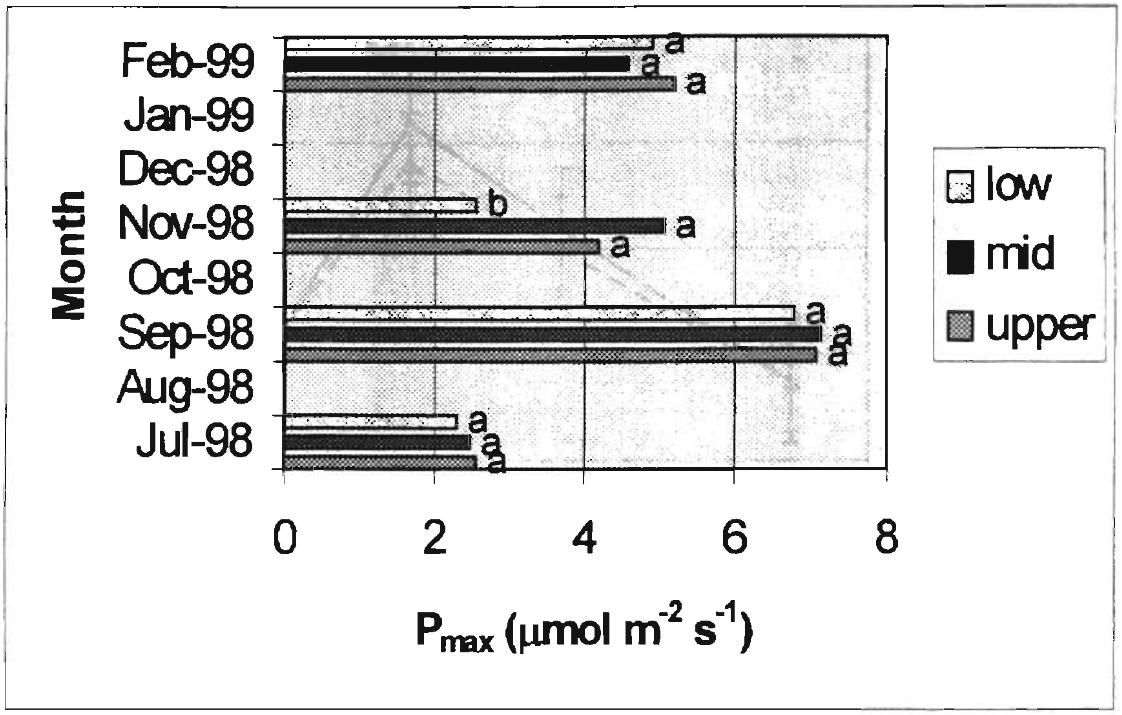

Figure 2. Comparison of the photosynthetic capacity (P_{max}) of the crown levels of North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) provenances of loblolly pine grown on a droughty southeastern Oklahoma site. P_{max} values were pooled for the two seed sources. Within each month, columns followed by different letters significantly differ at $P<0.05$.

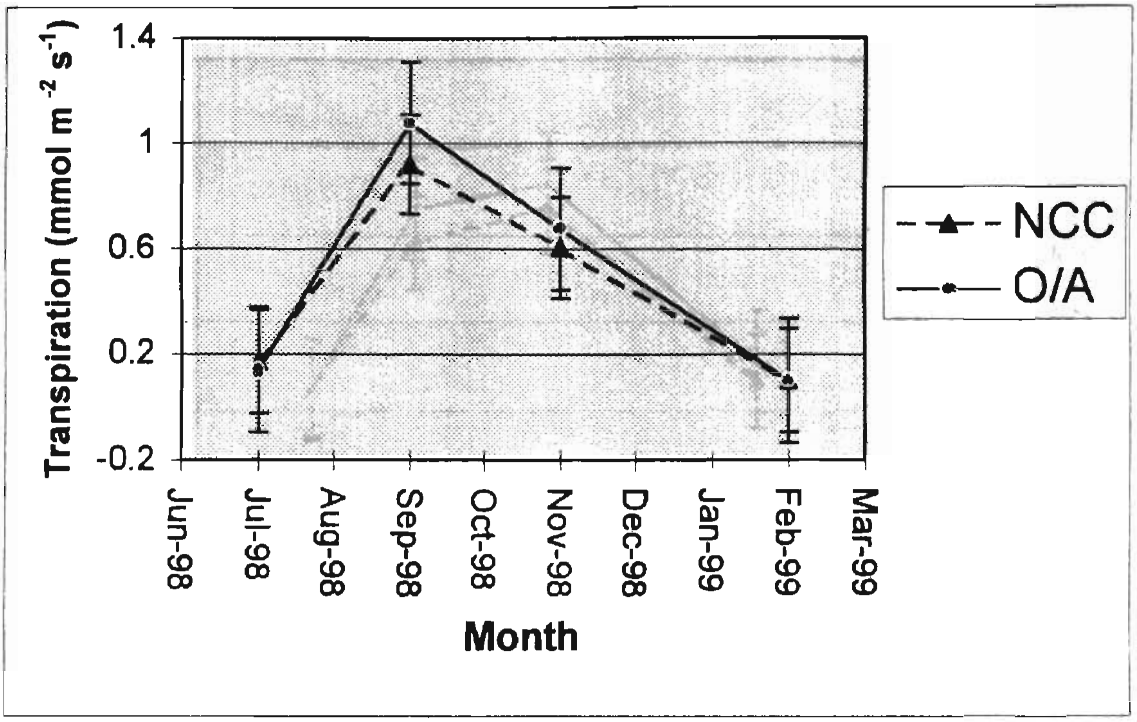

Figure 3. Trends in E_t (averaged for separate measurements taken in the upper, mid, and lower crown) for North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) provenances of loblolly pine grown on a droughty site in southeastern Oklahoma. No significant differences ($P<0.05$) attributable to seed source were observed during any month in which measurements were collected. Error bars indicate standard errors of observations.

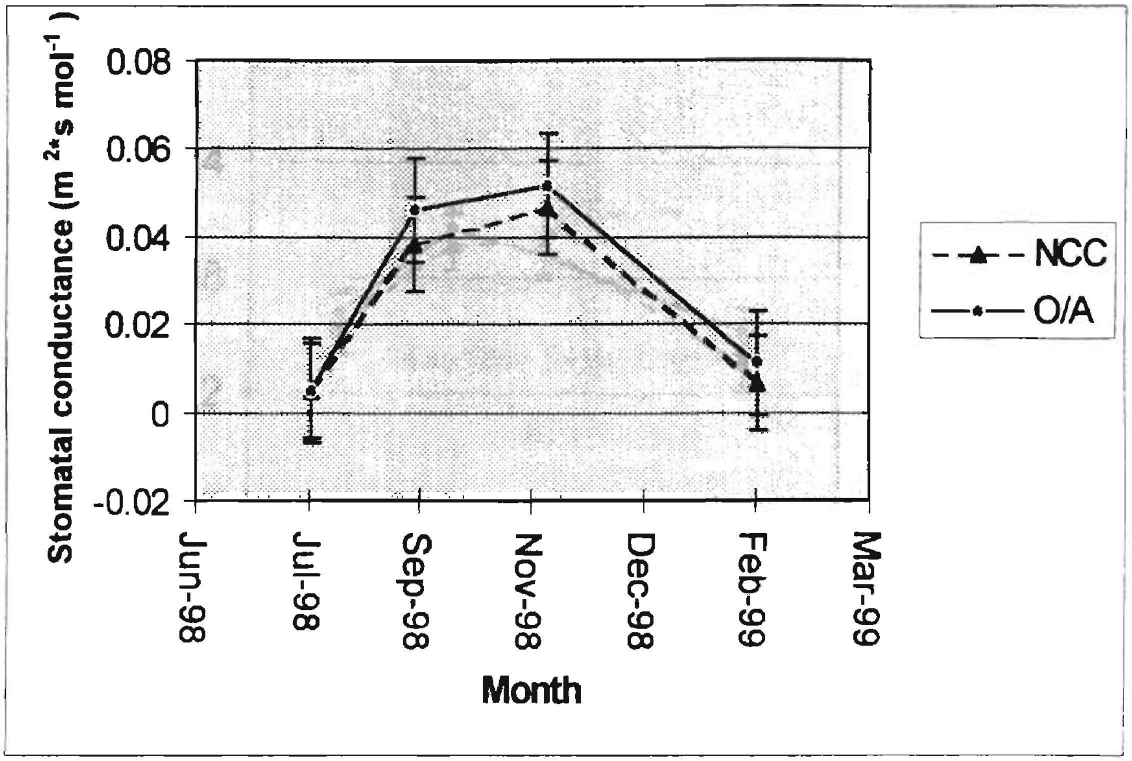

Figure 4. Trends in g_w (averaged for separate measurements taken in upper, mid, and lower crown) for North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) seed sources grown on a droughty site in southeastern Oklahoma. No significant differences ($P<0.05$) attributable to seed source were observed during any month in which measurements were collected. Error bars indicate standard errors of observations.

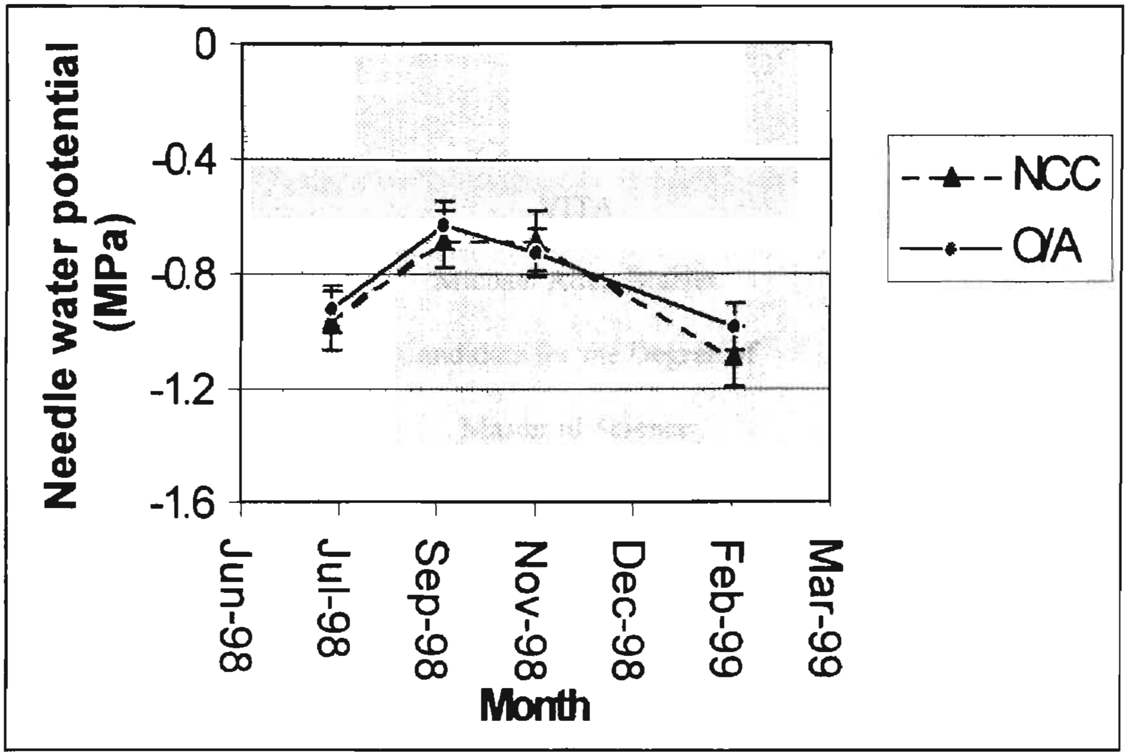

Figure 5. Trends in Ψ_n (averaged for separate measurements taken in the upper, mid, and lower crown) for North Carolina Coastal (NCC) and Oklahoma/Arkansas (O/A) provenances of loblolly pine grown on a droughty site in southeastern Oklahoma. No significant differences ($P<0.05$) attributable to seed source were observed during any month in which measurements were collected. Error bars indicate standard errors of observations.

VITA

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Master of Science

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