COMPARATIVE PHYSIOLOGY OF LOBLOLLY PINE SEEDLINGS FROM SEVEN GEOGRAPHIC SOURCES AS RELATED TO GROWTH RATE

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Abstract.--Growth, photosynthesis and water relations characteristics were examined in loblolly pine seedlings from seven diverse geographic sources. At the end of the first year, Florida trees were largest in height and dry weight, while Texas and Arkansas trees were smallest. Seed source size rankings were established by the fifteenth week of growth and were correlated with seed weights and both earliness and completeness of bud-set. They were also correlated with net photosynthesis at each of eleven dates during the growing season. This appears to result primarily from differences in leaf area accretion. When photosynthesis was measured on a unit leaf area basis, differences among the provenances were absent, except late in the year when Florida trees were most active.

Few differences in water relations characteristics were shown among the provenances. No differences in osmotic potential at saturation or turgor loss were detected. The degree of osmotic adjustment appeared to be equal, as well. Continental seedlings (Texas, Arkansas and Georgia Piedmont) exhibited greater stomatal conductance than seedlings from coastal origins when drought stress was never imposed, however, in trees pretreated with drought, no provenance differences were observed.

Differences in first year growth rate appear to be due, in part, to differences in seed weight, leaf production, and late season growth and photosynthesis. The measured water relations traits do not appear to be important although other water relations traits may be.

Additional keywords: Genetic differentiation, provenance testing, photosynthesis, water relations, pressure-volume curves, Pinus taeda.

INTRODUCTION

Thirty years of loblolly pine provenance testing have clearly demonstrated the presence of geographic differentiation for growth rate. Principally, trees from south coastal areas, with mild winters and heavy summer rainfall, are faster growing than trees from interior or north coastal regions

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(Wells, 1983; Wells and Wakeley, 1966). Differences are sufficiently great that trees from non-local provenances are often planted to improve productivity. This is particularly true in Arkansas where loblolly pines from coastal North Carolina are now widely planted with projected volume increases of 20-30% over the local stock (Lambeth, et al., 1984).

In this work, we examined some of the possible physiological causes for provenance differentiation in growth rate in the seedling phase. The growth superiority of trees from regions with short, mild winters and wet summers suggests that provenance differences may be due to differences in the duration of growth activities, including photosynthesis, and/or differences in water relations traits. We have, therefore, emphasized these in our initial work. The information obtained may be useful in predicting responses of trees to different environments, thus providing a means for assessing the risks incurred upon planting trees of foreign provenance. Additionally, knowledge of the physiological basis for growth rate differences may be used to design inter-provenance breeding plans which maximize growth by combining complementary components. As our understanding of the physiological basis for growth increases, it may also be possible to select more effectively for rotation-age volume in the juvenile stage.

MATERIALS AND METHODS

Seedlots

Seeds were obtained from seven first generation seed orchards representing different portions of the loblolly pine range (Figure 1). The North Carolina, South Carolina, Florida and Louisiana sources are considered "Coastal", while the Georgia, Arkansas/Oklahoma and Texas sources are considered "interior" or "continental". The Georgia Piedmont and Coastal Louisiana seed orchards had been rogued, while the others had not. The Texas seed orchard was composed of ramets from ortets selected in nursery beds for drought resistance by the Texas Forest Service; most were originally from Bastrop and Lee Counties, Texas. Ortets for the other orchards were selected primarily for phenotypic superiority in volume, and crown and form factors.

Growth and Photosynthesis

In May, 1984, seeds from six seedlots (all except Georgia Piedmont) were sown in DEEPOT containers (646cm^3) in a greenhouse using a randomized complete block design with four replicates. Each replicate contained one plot of 20 trees per seedlot. Seedlings were kept well-watered and fertilized throughout the study period.

Beginning 12 weeks after sowing, and recurring every 10 to 14 days through mid-December, seedling height, root collar diameter and net photosynthesis were measured on the interior six trees from each plot. The number of seedlings with buds was also recorded on each date. In all, measurements were made on eleven dates. Seed weights, based on 500 seeds, were obtained before sowing.

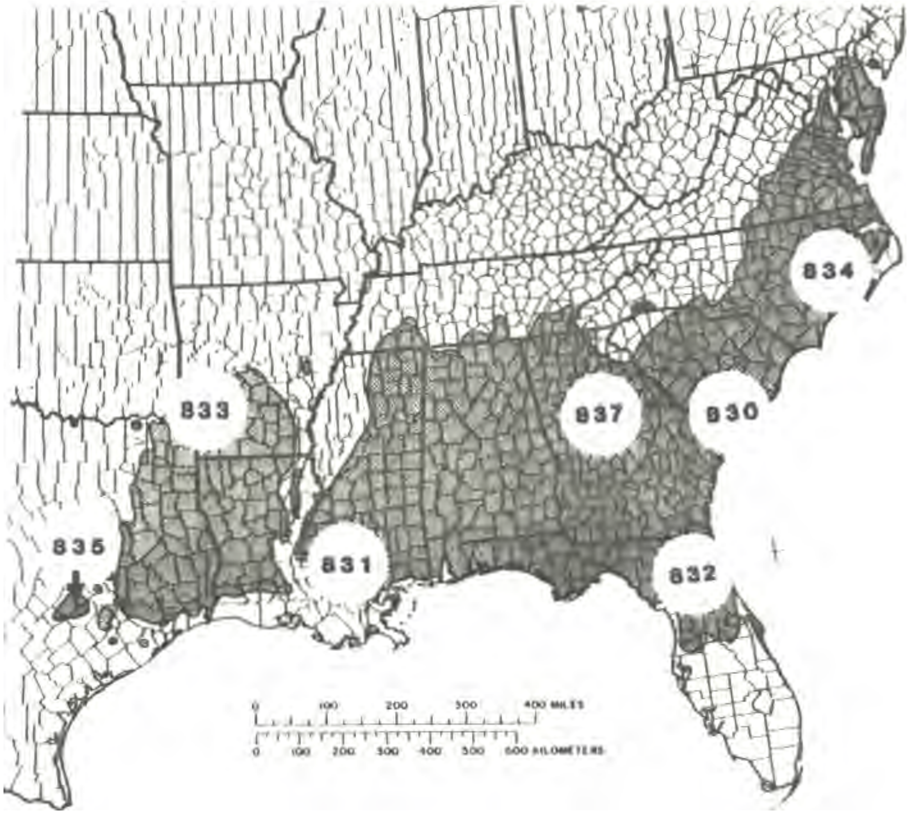

Figure 1.--Locations of the seedlots used in this study. Shaded area represents the natural range of loblolly pine.

Net photosynthetic rates were obtained under steady-state conditions. Trees were placed in a cuvette in which the temperature was maintained at 30°C, relative humidity at 50%, light at 1500 pmol m^{-2} s^{-1} (middle of the cuvette; equivalent to full sun light) and CO_2 concentration at 340 ppm. Carbon dioxide (1%) was pumped continuously from a compressed gas cylinder into the chamber to maintain the CO_2 level at 340 ppm. Steady-state equilibrium was achieved when a constant flow of CO_2 maintained the prescribed cuvette CO_2 concentration. Because the volume of CO_2 pumped into the chamber displaced an equal volume of air having the ambient CO_2 concentration, the rate of CO_2 fixation was calculated as the product of the CO flow rate and the difference in CO_2 concentration between the pumped and displaced gases (Griffiths and Jarvis, 1981). Approximately one hour was required to achieve steady-state equilibrium for each sample of six trees from a seedlot-replicate combination. For each measurement period 24 observations (six seedlots x four replications) were made over two days.

The cuvette, constructed of clear Lexan, measured 47 x 21 x 41 cm in length, width and height, respectively. Only the shoot portion of the tree was enclosed within the chamber. Light was provided from above by a sodium vapor lamp, and from the sides by two incandescent lamps. Temperature was controlled with two copper, radiator type heat exchange units controlled by Neslab thermostats (Portsmouth, NH). Relative humidity was regulated by a Honeywell dehumidifier control (H46C 1000) which directed chamber air through a desiccator column as required.

Estimates of leaf areas on each of the sample dates were obtained from regressions of height on leaf area developed at the end of the study. In this way photosynthesis per unit area could be estimated without destructive sampling. Such regressions are subject to errors because of leaf and internode growth subsequent to each measurement. However, these errors may be roughly compensating and of minor importance, particularly near the end of the study, when growth was terminating.

Analysis of variance was used to test for seedlot differences on each measurement date. Differences between dates within seedlots were analyzed by paired t-tests.

Water Relations

Water relations measurements were also taken on trees grown in DEEPOTS in a greenhouse. Eight blocks, each containing one plot of 20 trees from each of six seedlots (coastal South Carolina excluded), were used. Trees in four of the blocks were kept near field moisture capacity by watering on alternate days (high moisture regime). Trees in the other four blocks were subjected to recurring drought cycles; rewatering occurred only when flaccid shoot tips were observed in early morning (low moisture regime). Before the first measurements were taken, trees in the low regime had experienced eight drying cycles and were approximately one-third the size of the trees in the high moisture regime.

Stomatal conductances were determined for each seedlot, in both high and low moisture regimes, under three different humidity conditions. Steady-state methodology was employed. A cuvette measuring 15 x 20 x 15 cm was constructed of glass, Lexan and propafilm-c. Individual seedlings were placed in the cuvette, and dry air was introduced, displacing the moist chamber air. When a constant flow of dry air maintained the chamber air at a prescribed relative humidity, steady-state equilibrium was achieved. Transpiration and stomatal conductance were calculated from the water lost in the displaced air.

The prevailing environmental conditions included a temperature of 30°C, and light at 1500 umol m^{-2} s^{-1} . Measurements were made at relative humidities of 77%, 54% and 31%, which corresponded to absolute humidity deficits of 7, 14 and 21 g/cm^3, respectively. For each seedlot seven to nine seedlings were sampled, individually, in each the high and low moisture regimes. Differences between seedlots, moisture regimes and humidity treatments were assessed by analysis of variance.

Pressure-volume curves were also developed to examine differences in turgor loss points, osmotic potentials at saturation, and osmotic adjustment

(Tyree and Hammel, 1972). Seedlings were cut near the root-collar and placed in water in a dark closet overnight to insure full saturation. Xylem water potentials, measured with a Scholander pressure bomb, and relative water contents (the proportion of total shoot water content) were then periodically recorded as the seedlings were allowed to dry. The curves were plotted as the inverse of xylem water potential versus relative water deficit (RWD), the proportion of water lost (Figure 2). Turgor loss points were estimated visually for each seedling. Osmotic potentials at saturation were estimated for each seedlot-moisture regime combination as the intercepts of linear regression lines based on all points beyond turgor loss (Figure 2). Osmotic adjustment was determined as the difference in osmotic potentials between trees in the high and low moisture regimes. Differences between seedlots were tested with analyses of variance.

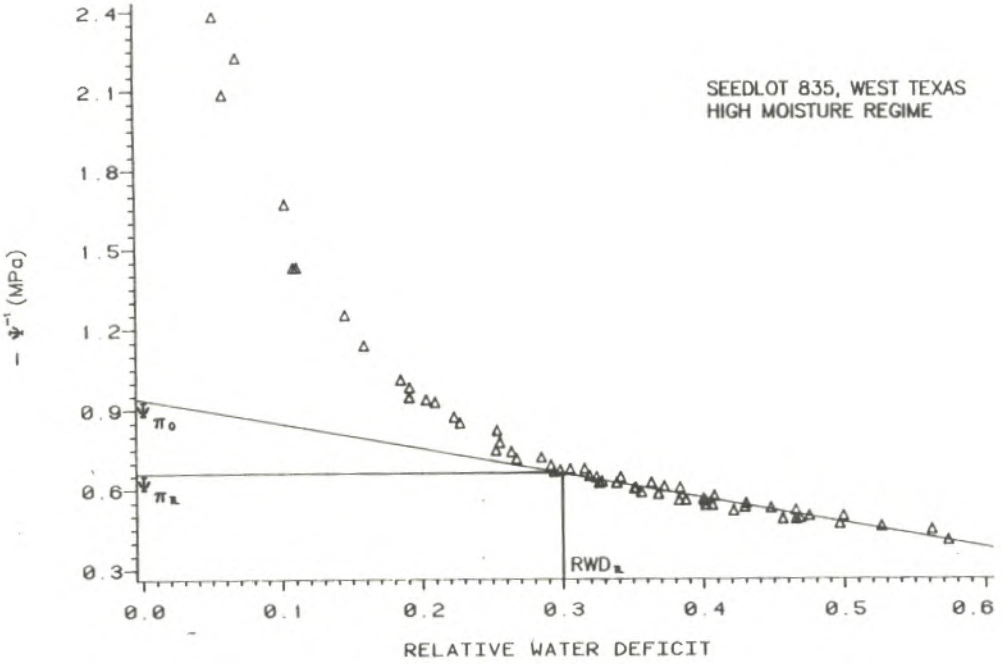

Figure 2.--A sample pressure-volume curve indicating the osmotic potential at saturation (ψ_0), and at turgor loss (ψ_{t1}), and the relative water deficit at turgor loss (RWD_{t1}). This plot was constructed from the combined data of six sampled trees.

RESULTS

Growth

Of the seedlings monitored for photosynthesis, those from each of the Coastal Plain origins grew faster than those from Arkansas or the Lost Pines region of Texas. Seedlings from Florida grew fastest, achieving 50% greater height and dry weight than seedlings from Arkansas, which, on average, were smallest (Figure 3).

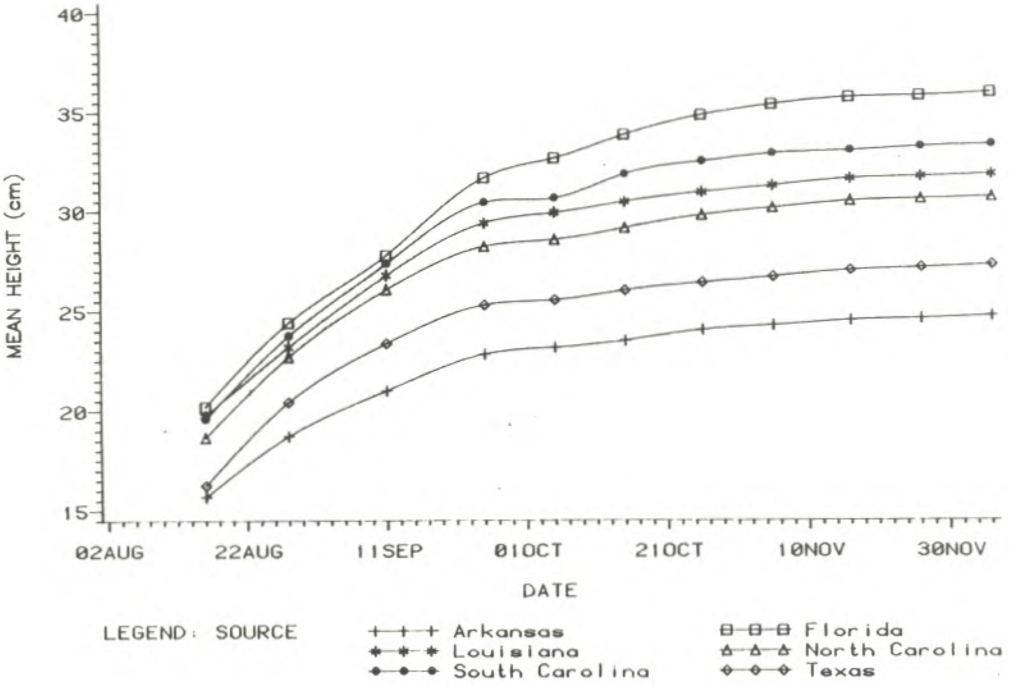

Figure 3.--Height growth in the first year for loblolly pines from six provenances.

Provenance differentiation in height was apparent by the first measurement, 12 weeks from sowing. At that time, seedlings from Texas and Arkansas were already significantly shorter than seedlings from Coastal sources. This early size difference may be related to seed weight as seeds from Texas and Arkansas averaged 2.7 mg, compared to 3.4 mg for seed from Coastal sources. Significant differences in height at 12 weeks were also detected among the

Coastal provenances (Louisiana and Florida seedlings being taller than North Carolina seedlings), but they were not related to seed weight. The early difference between Coastal and Continental seedlings in height growth was accentuated by differences in bud-set later in the study. Compared with Coastal trees, those from Texas and Arkansas began bud-set earlier, and more of them had terminal buds at the end of the study (Table 1). Among the Coastal seedlings, those from Florida showed significantly less bud-set than the others. Overall, provenance differences in bud-set closely parallelled final tree heights and dry weights, although provenance differences in seedling height were readily apparent well before the first seedlings set buds.

At the end of the study, provenance differences in height more or less mirrored differences in root collar diameter, total dry weight and dry weights of leaves, stems and roots (Table 1). By contrast, Florida and Texas seedlings, which represented the extremes in size, had the greatest shoot-root ratios. However, shoot-root ratios vary with seedling size (Ledig and Perry, 1965) and time of bud-set (Carmen and Willett, 1976). Therefore, the shoot-root ratios calculated here may not be indicative of the real differences in the relative growth of shoots and roots. This essential information may only be obtained by sampling shoot and root weights throughout the study period.

Table 1.--Growth measurements at the end of the first growing season for lobllolly pines from six provenances.[a]

Source	Height	Dry weight	Shoot-root	Bud-set
	cm	g		% of seedlings
SC	33.3^{ab}	3.7^{ab}	0.52^{a}	45.8
LA	31.8^{b}	3.5^{abc}	0.49^{b}	50.0
FL	35.9^{a}	4.2^{a}	0.64^{a}	12.5
AR	24.7^{d}	2.8^{c}	0.52^{b}	87.5
NC	30.6^{bc}	3.6^{ab}	0.46^{b}	41.7
TX	27.2^{cd}	3.1^{bc}	0.46^{b}	58.3

[a] Means not having a superscript in common differ at the 5% level of significance.

Photosynthesis

The seasonal pattern of seedling net photosynthesis was similar for each of the six examined seedlots. From August 15 photosynthesis rose slowly until October 1, then rapidly to a maximum in late October. Thenceforth, net photosynthesis fell until levelling off in November (Figure 4). The rise in

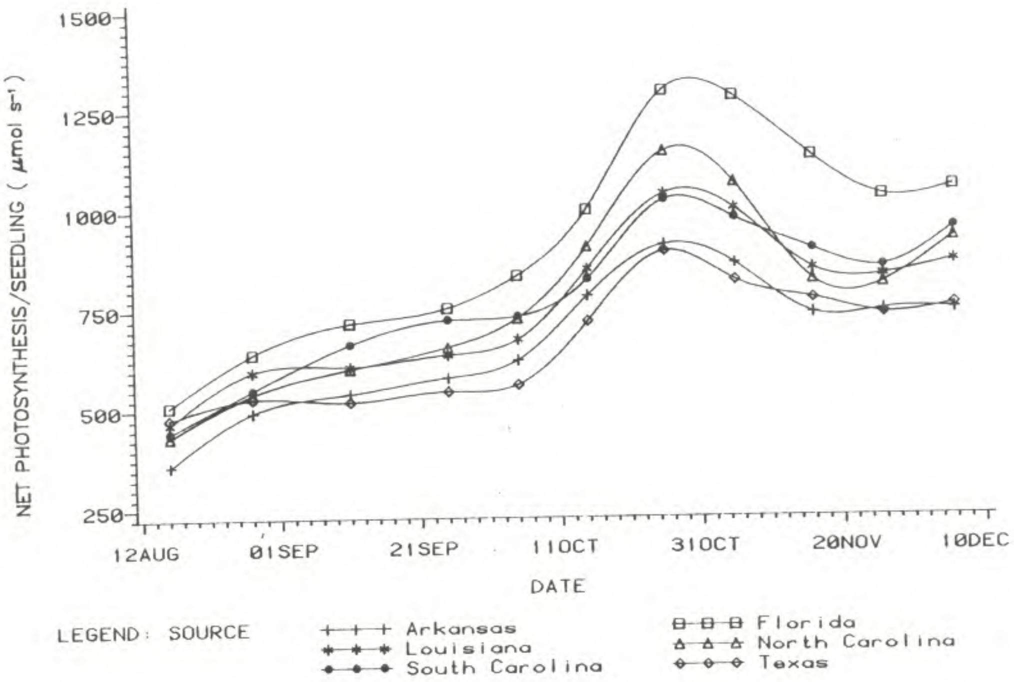

Figure 4.--Seasonal course of net photosynthesis per seedling. Each point represents a mean of 24 trees.

net photosynthesis through October resulted primarily from accretion of leaf area. The increases were modest through early October as respiration from the production of new needles largely offset the increased photosynthetic capacity. However, when the rate of new leaf production declined, net photosynthesis rose dramatically. The decline in net photosynthesis after October was apparently related to internal physiological changes, and is common in temperature zone trees entering the winter season (Ledig, 1976).

When leaf area effects were removed by considering net photosynthesis on a unit leaf area basis, maxima were observed in August and late October, while minima occurred in early October and after mid-November (Figure 5). The decline in net photosynthesis per leaf unit area from August to early October probably resulted from increased respiration due to leaf production. The increase in photosynthesis thereafter until late October reflected a reduction in leaf production. Finally, the decline after late October indicated a transition in physiological activity associated with the onset of winter, as mentioned previously.

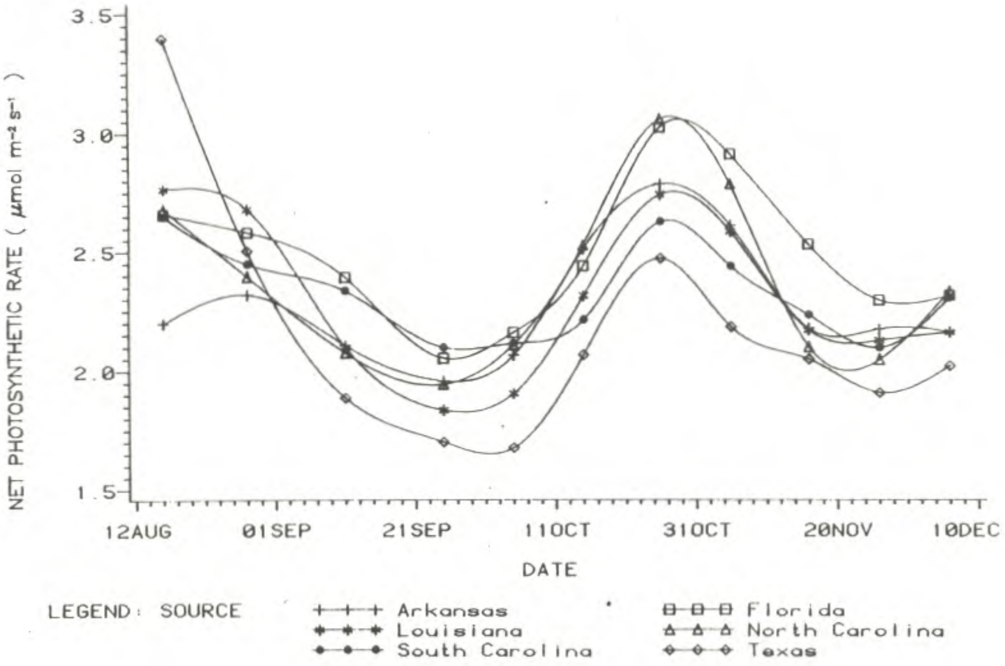

Figure 5.--Seasonal course of net photosynthesis per unit leaf area. Each point represents a mean of 24 seedlings.

Significant provenance differences (0.1 level) in net photosynthesis per seedling were found on only five of the eleven measurement dates. However, provenance rankings were consistent throughout the study leading to large differences in total CO_2 assimilation (the areas under the curves in Figure 4). The rankings of the seedlots in total net assimilation closely corresponded to their rankings in mean seedling size, seedlings from Florida having the largest values and those from Texas and Arkansas the smallest. This correspondence is expected because of the dominating influence of leaf area on total net photosynthesis.

When calculated on a unit leaf area basis, differences among the provenances in net photosynthesis were detected only on one date near the end of the study, and the seedlot rankings, in general, did not correspond well with those for mean seedling size. The late-season net photosynthetic rates were an exception. Florida seedlings, which had the greatest late season growth, also showed a significantly slower decline in net photosynthetic rate. Thus, it appears that differences in leaf area accretion are primarily responsible for differences in net assimilation and growth among the seedlots. Differences in photosynthetic rate appear to be relatively unimportant except that the longer period of high photosynthetic rate found in Florida seedlings may account for their greater late-season growth.

Stomatal Conductance

Stomatal conductances at three absolute humidity deficits are shown in Figure 6 for droughted and non-droughted seedlings. Trees which had never been subjected to drought had conductances which were more than twice as great as those which had. In the trees which had never been subjected to drought, stomatal conductance declined markedly as the absolute humidity deficit increased from 7 to 14 g/m (equivalent to a change from 77% to 54% relative humidity at 30°C), while the droughted trees showed little stomatal response

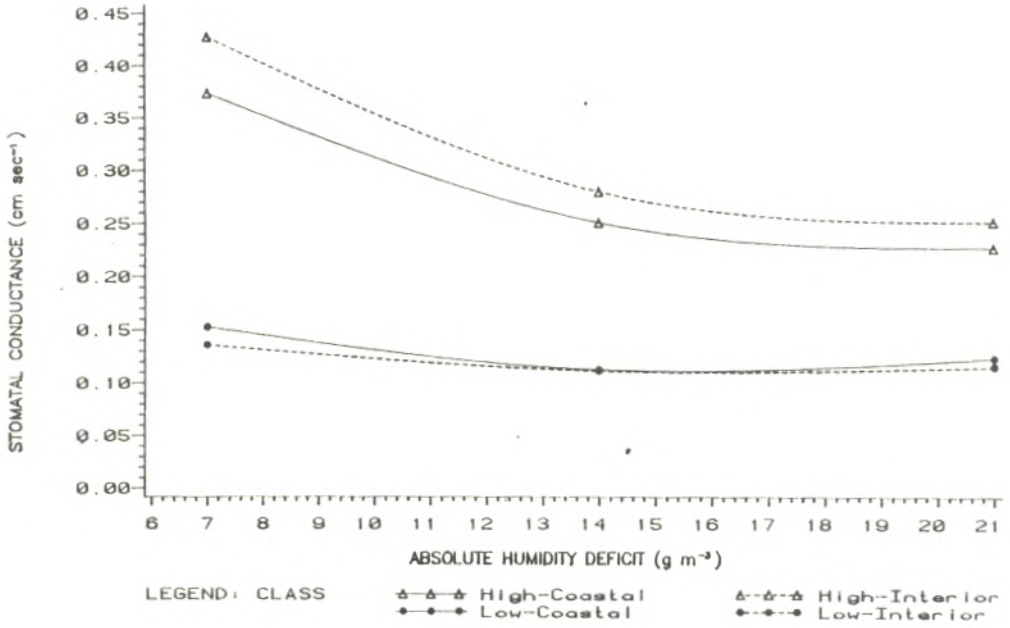

Figure 6.--Stomatal conductances, at three absolute humidity deficits, for Coastal and Interior loblolly pines seedlings grown under moist and droughty regimes.

to changing absolute humidity deficit. Curiously, among the trees which had never been droughted, those from the three interior origins (Texas, Arkansas, and Georgia) had consistently greater stomatal conductance. After drought pretreatment, though, no differences in stomatal conductance were observed among the seedlots.

Pressure-volume Curves

Four water relations parameters were estimated from pressure-volume curves: osmotic potential at saturation (ψ_0), osmotic potential at turgor loss (ψ_{tl}), relative water deficit at turgor loss (RWD_{tl}), and the change in osmotic potential with declining water content (slope). These parameters are shown in Table 2. No seedlot differences were detected for any of the parameters. However, trees in the high moisture regime differed significantly from those in the low moisture regime in each of the four parameters. Droughted trees had greater initial osmotic potentials, but lower osmotic potentials at turgor loss than non-droughted trees. Furthermore, the droughted trees reached turgor loss at lower water contents than the non-droughted trees. Such differences between droughted and non-droughted trees are common and are termed "osmotic adjustment." The seedlots could not be shown to differ in their degree of osmotic adjustment, either.

Table 2.--Pressure-volume curve parameters for seedlots and moisture regimes.

Water Regime	Source	Water potential (MPa)		RWD_{tl}	Slope
		Saturation	Turgor loss		
HIGH	LA	-1.03	-1.47	0.29	-0.099
	FL	-1.03	-1.41	0.26	-0.102
	AR	-1.02	-1.48	0.29	-0.098
	NC	-1.23	-1.53	0.29	-0.081
	TX	-1.00	-1.42	0.28	-0.107
	GA	-1.01	-1.44	0.28	-0.106
	MEAN	-1.05	-1.46	0.28	-0.099
LOW	LA	-1.00	-1.58	0.34	-0.108
	FL	-0.98	-1.57	0.34	-0.114
	AR	-0.96	-1.53	0.32	-0.123
	NC	-0.96	-1.61	0.35	-0.114
	TX	-0.99	-1.55	0.37	-0.116
	GA	-0.88	-1.59	0.36	-0.142
	MEAN	-0.96	-1.57	0.35	-0.120

DISCUSSION

When undamaged by winter cold or ice or biotic agents, loblolly pines of Coastal origin grow faster than those of Continental origin over a wide range of sites. Similarly, southern loblolly pines outgrow northern ones (Wells and Wakely, 1966; Wells, 1983). In our work we have sought to determine the causes for these well documented trends in order to better understand the risks incumbent with seed transfer and to assess opportunities for improving growth rate with inter-provenance hybrids.

In the investigations considered here, the seedlings conformed to the expected geographic differences in growth rate. The differences among seedlots in total growth were well correlated with differences in total net photosynthesis; however, the correlation resulted primarily from differences in leaf area and is of little value in selection or breeding. Differences between Coastal and Interior seedlings in early growth rate may, however, be due to the much smaller seed weights and earlier bud-set of the latter. Furthermore, the superiority of the trees from Florida may result, in part, from their longer period of high photosynthetic activity. Although differences in photosynthesis per unit leaf area or partitioning of photosynthate are often suggested as causes for differences in growth rate, we could not show significant differences among seedlots in either respect.

The growth measures presented here are based on high levels of moisture and nutrients and cannot be considered to simulate field conditions. Differences among the seedlots in growth rate may also be due to factors affecting growth during water or nutrient stress (Cannell et al., 1978). In our investigations we have also considered some of the factors that might affect growth during periods of drought stress, including (1) changes in stomatal conductance with increasing evaporative demand, (2) differences in osmotic potential, and (3) differences in osmotic adjustment (the latter two may result in differential stomatal closure with increasing water loss). Although measured with great precision, no differences among seedlots for these characteristics was detected. Other drought resistance characteristics which might affect growth rate, such as rapid stomatal closure in response to water stress and longer and deeper roots, have been shown to differ among seedlots from the Western Gulf region (van Buijtenen et al., 1976), but these were not examined in this work.

It is obvious that at this point in time our knowledge of the physiological basis for growth rate differences is incomplete, and we are not in a position to make recommendations applicable to field conditions. However, this is a rather new area of research endeavor, and, if considered holistically, promises to offer faster, more effective methods of selection and improved breeding strategies.

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