DROUGHT TOLERANCE IN SIX SWEETGUM CLONES

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Abstract.--Sixteen ramets each of three good and three poor sweetgum phenotypes were exposed to two watering levels for four weeks in a greenhouse. Response parameters focused on stomatal conductance and biomass partitioning to explain possible mechanisms of drought tolerance. Water stress caused significant declines in stomatal conductance. Clones showed little interaction with watering treatment for conductance but exhibited considerable variation within treatments. Analysis of allometric growth indicated an increase in root dry matter at the expense of leaf dry matter in stressed trees. Clones generally did not vary significantly in their relative partitioning of biomass. Clonal responses were independent of ortet field performance.

Keywords: Liquidambar styraciflua L., water stress, stomatal conductance, allometric growth, biomass partitioning.

INTRODUCTION

Site adaptability, good sprouting ability, and relatively high productivity should propel sweetgum (Liquidambar styraciflua L.) into a more prominent position in the southeast United States, particularly for fiber and fuel production in short-rotation, intensive plantations. However, drought can limit tree growth (Bassett 1964, Kramer 1983), especially on well-drained sites. Clones exhibiting a genetically controlled mechanism to tolerate drought should perform better under water stress. Identification of characteristics that impart drought tolerance could allow early screening of genotypes for use on drought-prone sites, thus increasing yields (Kellison et al. 1979, Hennessey et al. 1988).

Several response mechanisms enable trees to tolerate dehydration and maintain a suitable water balance for continued growth. Stomatal regulation allows plants to conserve water at a cost of reduced photosynthesis. Pezeshki and Chambers (1986) found sweetgum to have relatively high stomatal sensitivity, allowing partial stomatal closure at relatively high water potentials to reduce desiccation while affording some positive photosynthesis

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during prolonged drought. Furthermore, trees which partition a greater proportion of carbohydrate to root growth are more capable of delaying dehydration by increasing absorptive area and the volume of soil explored for available water. Kitchens (1985) found that Piedmont sweetgum possesses drought tolerant characteristics such as decreased shoot-root ratios and lower stomatal conductances as compared to coastal sweetgum.

Little work has been conducted to characterize the intraspecific variation in drought tolerance for sweetgum. Therefore, the objectives of this study were to: 1) evaluate the impact of water stress on leaf conductance and biomass partitioning by clone, 2) quantitatively compare clonal variation with respect to watering treatment, and 3) establish whether drought response of young rooted cuttings might explain observed differences in ortet field performance.

METHODS

Study Design

A vegetative propagation procedure similar to that for *Eucalyptus* (Zobel et al. 1983) was used to root stump-sprout cuttings. Mother trees on a moderately-well to poorly drained site in southeast Virginia were selected for 14-year height by identifying the tallest and shortest individuals in the tallest and shortest three families, respectively. Sprouts were collected and transported to a greenhouse in Raleigh, North Carolina in June 1988. Fifteen-cm cuttings were dipped into a 0.3% IBA solution, stuck in flats of vermiculite:perlite (1:1 by volume), and placed under an intermittent mist system. After seven weeks, cuttings with the greatest root development from each clone were transplanted individually to tall, plastic pots (2.7 liter) containing sand. Mist was gradually reduced over a three-week period and nutrient solution was applied daily. One week prior to treatment initiation the most uniform 16 ramets of each clone were placed on the greenhouse experimental apparatus to acclimate to the well-watered regime. A single row of buffer trees reduced edge effects.

A split-plot design with two watering treatments as main plots and six clones as subplots was replicated eight times (i.e. 96 study trees). Each clone was represented once and arranged randomly within each treatment-replication combination. Clones were subdivided by ortet field performance as good: 310, 316, 338, and poor: 312, 340, 353.

Watering Treatments and Environmental Conditions

Based on a preliminary study, non-stress and stress watering treatments received nutrient solution four times and one time daily, respectively. Deionized water was applied once weekly to avoid salt accumulation. A drip-irrigation system delivered the treatments at approximately 300 ml increments which allowed equal soil wetting because drip-point was exceeded. Watering treatments were initiated in October. Supplemental incandescent lighting (100 Watt bulbs) extended the natural photoperiod to 18 hours. Greenhouse temperature ranged from 18 to 30 C, and relative humidity varied between 10 and 95%.

Measurements

Using a Licor model LI-1600, leaf resistances were obtained at midday nine times during the study, measuring the fourth leaf from the apex on all trees. Initial and final height of the largest shoot was measured from bud origin to the uppermost node. Trees were harvested after four weeks to obtain oven-dry (70 C, 60 h) weights of leaves, stems, and roots.

Statistical Analysis

Analysis of variance was used to test effects of treatment, clone, ortet field performance, and interactions of treatment x clone and treatment x performance on leaf conductance (inverse of resistance), initial and final height, and total dry weight. Duncan's multiple range test was used to detect significant differences among clone means.

Relative partitioning of biomass among plant organs has been shown to change with increasing plant size (Ledig and Perry 1965). Regression parameters were compared to detect differences in dry matter allocation to leaves, stems, and roots using the allometric equation (Bongarten and Teskey 1987):

$$\log (0) = a + b \log (W)$$

where 0 is the organ dry weight, W is the total plant dry weight, and a and b are constants. Covariance analysis was used to adjust organ dry weight for plant total dry weight and to test significance for watering treatment, clone, and ortet performance differences in regression intercepts and slopes (Freund and Littell 1981, Bongarten and Teskey 1987). A significant difference among regression intercepts indicates a difference in the adjusted treatment or clone means if slopes are similar. A significant difference among regression slopes indicates a change or difference in the relative allocation of dry matter to the plant organ. Where heterogeneity of regression slopes for clones within treatment was significant, pairwise comparisons using the studentized range statistic were performed (Zar 1984).

RESULTS AND DISCUSSION

Stomatal Conductance

For each of the nine measurement days during the study, non-stress trees showed greater stomatal conductance (cm/s) than stressed trees ($p<0.025$) (Figure 1). For both treatments the gradual decline in conductance may have been attributed to increasing stress with increasing plant size. Because both treatments exhibited very similar reductions, the decrease is more likely to have resulted from changing environmental conditions (e.g. light, temperature) caused by lateness in the growing season.

Conductance response patterns among clones were similar within each watering regime, but mean values differed considerably (Figure 2). Clone 340 showed consistently greater conductance than the highly uniform response of the other five clones within the non-stress treatment ($p<0.05$). Conductance for clone 312 decreased sharply relative to the other clones. Clone 353 maintained consistently low relative conductance. Clones of good ortet performance (310, 316, and 338) showed intermediate conductances. Separation among clonal conductances was greater within the stress treatment (Figure 2), but individual clonal response remained consistent with those just described except for clone 316 which showed a large reduction in conductance with stress.

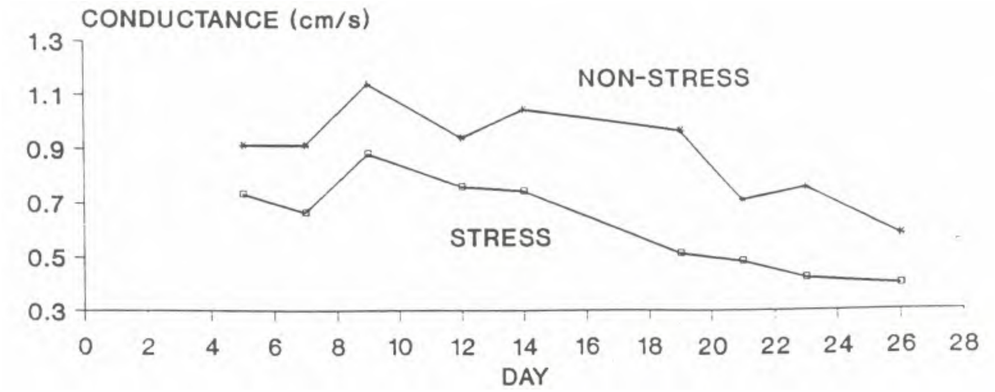

Figure 1. Stomatal conductance as affected by watering treatment across 6 L. styraciflua clones (n=48).

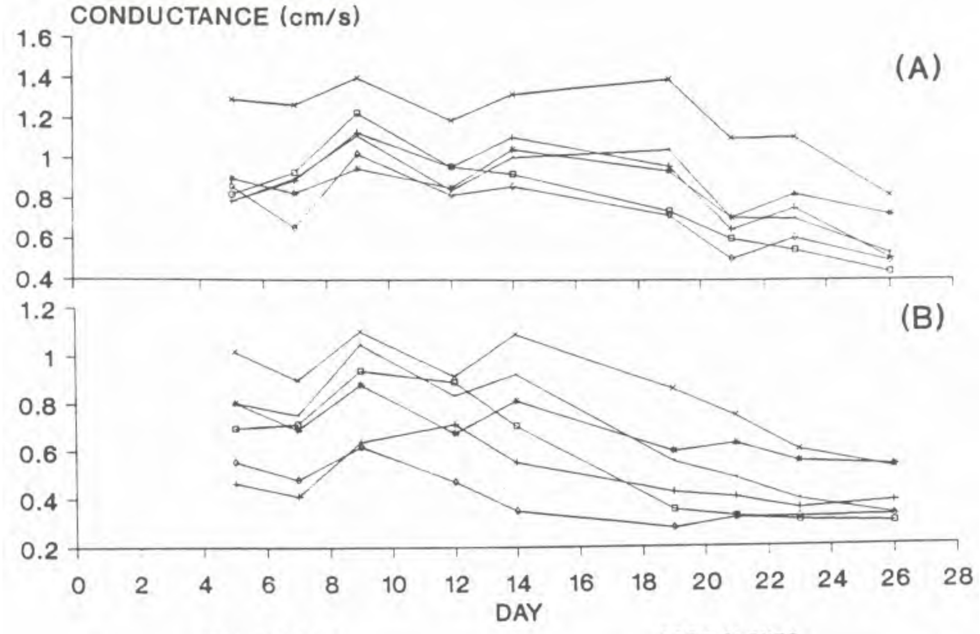

Figure 2. Stomatal conductance for 6 **L.** styraciflua. clones (n=8) as affected by watering treatment: (A) non-stress and (B) stress.

The interaction of clone x treatment was not significant for stomatal conductance at any measurement date. Separation of the interactive effect of plant size x treatment from the clone x treatment effect was difficult due to initial size differences among clones (Table 1). Because larger plants tend to possess greater leaf area, transpiratory losses and degree of water stress will be greater when compared to smaller trees with less leaf area. However, clones 340 and 312 were of comparable initial size (Table 1), but their conductance responses were different (Figure 2). Because it was able to maintain the highest conductance (Figure 2) and total dry weight production (Table 1) relative to watering treatment, clone 340 reflected a high degree of drought tolerance compared to other clones tested (Kelliher and Tauer 1986).

The effect of ortet field performance and performance x treatment interaction were not significant for stomatal conductance at any measurement date. Conductance for poor performers was higher than good performers early in the study, but the values converged within two weeks (Ehlert, unpublished data). Conductances among non-stress good-performers were not significantly different for most measurement days.

Table 1. Initial height, final height, and total dry weight by L. styraciflua clone as affected by watering treatment (n=16 for initial height; n=8 for final height and dry weight). Values within a column followed by the same letter are not significantly different at p<0.05.

Clone	Initial Ht. (cm)	Final Ht. (cm)		Total Dry Wt. (g)	
		Non-stress	Stress	Non-stress	Stress
Good: 310	4.63 b	32.54 a	23.44 a	6.04 b	5.03 b
316	9.92 a	39.78 a	21.88 a	9.61 a	6.53 ab
338	1.86 be	31.55 a	18.24 a	6.39 b	5.22 b
Poor: 312	5.12 b	33.05 a	23.36 a	7.88 ab	5.49 ab
340	5.21 b	31.66 a	19.79 a	10.13 a	7.75 a
353	0.74 c	15.41 b	5.31 b	3.14 c	2.21 c
Combined	4.58	30.66	18.95	7.20	5.44

Biomass Partitioning

All clones except 310 exhibited greater total dry weight when well-watered as compared to water-stressed (maximum p<0.07). Combined clonal mean for total dry weight was greater for non-stress as compared to the stress treatment (p<0.01) (Table 1).

Watering treatment affected biomass partitioning among plant components. Allometric regression parameters for leaves and roots were significantly altered by watering treatment (Table 2). Treatment differences across clones were detected for the intercepts of leaves and roots (p<0.001) with no effect on slope (Table 2). Regression parameters for stems were not different by treatment. Thus, for a given total weight, water-stressed cuttings generally had lower leaf weights and greater root weights than well-watered plants.

Table 2. Significance levels for analysis of watering treatment differences in allometric growth of leaves, stems, and roots of 6 L. styraciflua clones. (* indicates $p<0.05$).

Clone	Leaves		Stems		Roots	
	intercept	slope	intercept	slope	intercept	slope
Good: 310	.379	.442	.966	.363	.174	.032 *
316	.003 *	.866	.404	.980	<.001 *	.639
338	.472	.580	.229	.754	.148	.914
Poor: 312	.010 *	.808	.198	.045 *	.039 *	.041 *
340	.112	.262	.157	.585	.004 *	.362
353	.013 *	.405	.116	.439	.061	.601
Combined	<.001 *	.149	.428	.408	<.001 *	.847

Watering treatment effect on the allometric parameters of individual clones deviated from general trends observed for all clones (Table 2). Three clones showed significant treatment differences among leaf intercepts (316, 312, and 353), and four clones had differing root intercepts (316, 312, 340, and 353). Clonal regression parameters were not different between treatments for stems. No treatment differences were detected for any regression parameter of clone 310 or 338 (Table 2). Clone 340 responded uniquely, exhibiting no treatment effect on leaf biomass but a significant increase in stress treatment root weight, imparting further evidence of drought tolerance (Table 2).

Similar allometric response patterns of increased root weight at the expense of leaf weight were found under low nitrogen treatment for sweetgum seedlings and rooted cuttings by Cunningham (unpublished data) and for loblolly pine seedlings by Li (1989). However, loblolly pine seedlings exposed to dry soil conditions allocated proportionately more biomass to roots at the expense of stems rather than needles (Bongarten and Teskey 1987).

Significant clonal effects were observed for the allometric parameters within watering treatment. Differences were observed among intercepts of leaves and stems of well-watered clones ($p<0.02$) (Table 3), which indicated variation in biomass partitioning to leaves and stems (Table 4). Analysis of heterogeneity of individual regression slopes for leaves and stems indicated that all slopes were highly similar except for those of clone 353. As total dry weight increased, clone 353 allocated proportionately less biomass to Leaves and more to stems relative to other clones (Ehlert, unpublished data). This response may seem attractive, but growth for clone 353 was significantly lower than other clones (Table 1). Clone 312 exhibited the largest leaf weight and smallest stem weight compared to the other clones when well-watered (Table 4), thus providing a large transpirational surface and perhaps explaining its rapid decline in stomatal conductance (Figure 2).

Clonal effects were detected for intercepts of leaf, stem, and root within the stress treatment, but slopes did not differ (Table 3). Therefore, the relative distribution of dry matter to each component was similar among clones, but the amounts allocated varied (Table 4). A preferential partitioning of biomass to roots was an apparent response to the stress treatment (Table 4). Compared to other clones, 316 exhibited a particularly greater root biomass production to compensate for the increased water deficits (Table 4).

Partitioning of biomass among clones was independent of ortet field performance.

Table 3. Significance levels for analysis of clonal differences in allometric growth of leaves, stems, and roots within watering treatment. (* indicates $p<0.05$).

	Non-stress			Stress		
	leaves	stems	roots	leaves	stems	roots
intercept	<.001 *	.019 *	.443	.002 *	.051	.017 *
slope	.035 *	.013 *	.097	.942	.351	.221

Table 4. Adjusted (least square) mean dry weight (g) among leaves, stems, and roots within watering treatment for 6 L. styraciflua clones. Values within a column followed by the same letter are not significantly different at $p<0.05$. (# indicates that the value should not be compared to others because of its significantly different regression slope).

Clone		Non-stress Treatment			Stress Treatment		
		leaves	stems	roots	leaves	stems	roots
Good:	310	2.90 b	2.16 b	1.21 a	2.01 b	1.63 a	1.11 b
	316	3.22 ab	1.89 bc	1.21 a	1.90 b	1.34 ab	1.55 a
	338	3.36 a	1.79 c	1.18 a	2.49 a	1.17 b	1.08 b
Poor:	312	3.52 a	1.61 c	1.18 a	2.23 ab	1.26 b	1.26 ab
	340	3.29 ab	1.95 bc	1.08 a	2.15 ab	1.47 ab	1.15 ab
	353	2.16 c #	3.38 a #	1.19 a	1.88 b	1.70 a	0.97 b

CONCLUSIONS

When water stressed the **six** sweetgum clones exhibited reduced stomatal conductance and increased dry matter allocation to roots compared to leaves. This indicated the influence of available soil moisture on tree growth and physiology. Clonal variation in conductance and dry weight partitioning was evident and suggested intraspecific differences for drought tolerance. The characteristics examined did not explain observed differences in ortet field performance. The artificial study conditions, young plant material, and small number of genotypes qualify these results. Examination of a larger number of clones, particularly from families proven to be fast growers and under field conditions could prove successful in identifying clones with desirable drought tolerance characteristics.

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