Exotic Cottons as Genetic Sources for Drought Resistance[1]

J.E. Quisenberry, W.R. Jordan, B.A. Roark, and D.W. Fryrear[2]

ABSTRACT

As irrigation water becomes more limited and energy costs increase on the Southern Great Plains, more cotton (*Gossypium hirsutum* L.) acreage will be diverted to dryland production. Because water is the most limiting resource for cotton production in this region, production will be positively related to changes which increase the water supply or make more efficient use of water. The purpose of this study was to evaluate plant (shoot) dry matter accumulation in photoperiodic (exotic) cotton strains under irrigated (water optimal) and dryland (water stressed) field conditions, to estimate their water-use efficiency under dryland, and to determine the relationship between field growth parameters, laboratory evaluations of heat tolerance, and greenhouse estimates of root growth. Fifteen photoperiodic strains and one commercial cultivar were planted in irrigated and dryland field tests at Big Spring, Texas and in acrylic tubes in the greenhouse at Temple, Texas. In the Big Spring test, dry weight harvests from both the irrigated and the dryland plots were made at 44, 58, 72, and 86 days after planting (DAP). Soil-water use was measured with a neutron probe in the dryland plots, and leaf discs were taken from both the irrigated and the dryland tests to measure heat tolerance. In the Temple test, shoot dry weight, leaf area, taproot length, and the number of major root laterals were measured 35 DAP. Analyses of variance and regression analyses were used to evaluate the data.

Significant variability was demonstrated among entries for shoot dry weights under both irrigated and dryland conditions, for water-use efficiency in the dryland test, for heat tolerance at Big Spring, and for root growth at Temple. The number of lateral roots measured in the greenhouse was positively associated with shoot dry weights in the dryland plots, but not in the irrigated plots. Root morphology and root growth potentials appear to be important traits in the adaptation of cotton to conditions where limited soil-water availability is a major constraint on plant growth.

Additional index words: Gossypium hirsutum L., Drought tolerance, Heat tolerance, Water-use efficiency, Dry matter accumulation, Root growth.

THE largest acreage of semiarid, non-irrigated cotton (*Gossypium hirsutum* L.) production in the United States occurs in the Southern Great Plains. Cotton is grown in this region because of the high monetary value that is placed on cotton lint compared with a similar quantity of grain. Small increases in the productivity of cotton through genetic or cultural modifications would mean large increases in monetary returns to the producer.

Because water is by far the most important limiting resource for cotton production in this region, productivity must ultimately be tied to modifications in the production system which increase the water supply or make more efficient use of water. Genetic improvement of cotton to allow more efficient use of soil water is especially attractive in view of current efforts to reduce energy consumptive in view of current efforts to reduce energy consumption during production. More efficient cultivars would not require additional production inputs in contrast to physical methods to increase water supply through soil surface or profile modification. Both of the latter are expensive in terms of time and energy.

Under dryland production, efficient use of soil water may be accomplished by several means. High efficiency of use means the water resource is neither over nor under utilized during the production season. Some mechanisms which assist the plant in making efficient use of soil water also increase water-use efficiency; others do not. For example, a deep root system may allow complete utilization of the stored water resource, but the return of harvestable product per unit of water used may be constant over a wide range of total water availability. On the other hand, mechanisms which allow tolerance or avoidance of drought-induced water deficits and the associated loss of fruiting potential (during the critical early-to-peak-bloom period) may allow more efficient use of mid- to late-season rainfall.

Previous work with cotton suggests that, apart from growth habit, little variability exists within currently grown cultivars for traits which may be exploited to enhance drought resistance or improve water use efficiency. Even in the case of growth habit, which is difficult to quantify (17), crop perfromance is closely tied with the seasonal pattern of soil-water availability. For example, Quisenberry and Roark (13) found that early maturing "determinate" cultivars used water less efficiently than "indeterminate" cultivars when severe water deficits developed early in the growing season. However, early maturing types were more efficient under optimal moisture conditions when the growing season was abbreviated by low temperatures. This finding may be partially explained by the inability of the more determinate types to compensate for early, water deficit-induced square and boll loss, if rainfall occurred later in the growing season. Murray and Verhalen (12) and Jordan (8) have pointed out the importance of early season boll set to lint yield and, therefore, water-use efficiency of dryland cotton in situations where insect pressures render late-season bolls unproductive.

Few individual traits have been studied in sufficient detail relative to increased drought resistance to be useful in cotton improvement programs. Roark and Quisenberry (18) detected genetic variability in leaf diffusive

resistance in F_1, F_2, and backcross populations derived from a cross between 'Western Stormproof' and the exotic strain T169 and concluded that improvement of the trait was possible, although heritability was low. Ultrastructural integrity and metabolism of *Gossypium anomalum* Waura ex Waura and Peyritch are less sensitive to water deficits than are those of *G. thurberi* Todaro or *G. hirsutum* (22). In this same vein, genetic differences appear to exist among cultivars for water deficit-induced proline accumulation (B. L. McMichael, USDA-SEA-AR, Lubbock, TX, personal communication) and for leaf and square abscission (personal observation). The relevance of these traits to drought resistance of water-use efficiency remains unknown.

The purpose of this study was to evaluate plant (shoot) dry matter accumulation in photoperiodic (exotic cotton strains under irrigated (water optimal) and dryland (water stressed) field conditions, to estimate their water-use efficiency under dryland, and to determine the relationship between field growth parameters, laboratory evaluations of heat tolerance, and greenhouse estimates of root growth.

MATERIALS AND METHODS

Shoot growth. Fifteen nonflowering (photoperiodic) strains and one cultivar, 'Blightmaster', were planted in 1978 in randomized complete block designs under two soil-water regimes at Big Spring, Texas. Blightmaster is a cultivar developed specifically for production in the nonirrigated, semiarid Southern Great Plains. The nonflowering strains were chosen from the world collection of approximately 1000 strains of *Gossypium hirsutum* L. maintained by the USDA-SEA-AR cotton program at College Station, Texas. The Texas and race designations of the strains are listed in Table 1.

The two soil-water regimes consisted of fully-irrigated and dryland tests located in the same field about 30 m apart. The soil type [previously described by Burnett et al. (3)] was an Amarillo sandy clay loam (Aridic Paleustalfs).

Water was applied to the irrigated test when tensiometer readings fell below -0.5 bar at a soil depth of 46 cm in any plot to assure that growth was not limited by soil-water deficits. About 100 mm of irrigation water was applied at planting and at 45, 56, and 65 days after planting (DAP) for a total of about 400 mm during the test.

Four replications in each test were planted on 23 May 1978 and plots were thinned after emergence to seven plants/m. Plots in the irrigated test consisted of single rows 15 m long with 1 m between rows. Each row was divided into four 3 m sections, one of which was harvested on each of four different dates (44, 58, 72, and 86 DAP) to provide growth data. A section on the end of each plot and between each section was not harvested and used as a border. Because of poor stands in one of the irrigated replications, only three were used for analysis. In the dryland test, plots for each entry and replication consisted of 9 rows 10 m long with 1 m between rows. These rows were as follows: border, test entry, border, border, test entry, border, border, test entry, and a border row. All border rows were Blightmaster. This design was used because of shortage of seed for the exotic stocks and to provide consistent plant competition for available soil water. Each of the two outside rows planted to the test entry were divided into two 3 m sections, one of which was sacrificed on each of the four sampling dates to provide growth data. A border section was maintained between the harvest sections and the end of the row. One aluminum access tube was placed in the center row of each plot, and soil water was measured periodically at the 40, 60, and 80 cm depths with a neutron probe calibrated

for this soil. At planting, all plots were at or near field capacity in the top 40 cm of the soil profile, all plots had some water available at 60 cm, and none had appreciable water available at 80 cm or below.

Heat Tolerance. Leaf discs were collected from dryland plots on 25 July (63 DAP) and from irrigated plots on 26 July (64 DAP) for a laboratory evaluation of heat tolerance using a procedure similar to that described by Sullivan (19) and more recently used by Martineau et al. (9, 10). The collection apparatus consisted of a custom-made stainless steel punch machined to hold a 16 mm glass collection tube. The bottom of the glass tube was covered with nylon mesh held in place with a strong elastic band.

Three samples were collected at random within the plot from the upper expanded leaves between 0700 and 1000 hours each day. Each sample consisted of 10 leaf discs 1.0 cm in diam. After collection, the tubes were placed in test-tube racks within insulated chests containing about 6 cm of tap water at temperatures between 23 and 26 C. The nylon mesh retained the discs within individual sample tubes, yet allowed the entry of water to keep the discs fully hydrated while in the field.

Following collection, samples were removed to the laboratory where they were rinsed in tap water and two changes of distilled water for a total of 1.5 hours to remove possible surface contaminants and solutes from the cut surface of the discs. Excess water was removed by shaking, and the sample tubes were slipped into dry 25 × 200 ml culture tubes. Two tubes were placed in a covered water bath maintained at 50.0 ± 0.01C for 45 min while the remaining tube was kept as a control at room temperature (28 ± 1 C). After the 45 min period, the sample tubes were removed from the larger culture tubes and inverted and the discs were washed into the culture tubes with distilled water to give a final volume of 40 ml. The culture tubes were periodically mixed by inversion. Electrical conductivity of the efflux solution was measured after 6 hrs with a YSI Model 31 Conductivity Bridge equipped with a plastic, diptype cell. After measurement, the heat-treated samples were again heated in a pressure cooker at 1.02 atm for 15 min to release all cellular solutes and electrical conductivity was again measured after cooling.

Cellular damage due to the 50 C heat treatment was calculated from conductivities as follows:

$$\% \text{ cellular damage} = \frac{\text{heated} - \text{control}}{\text{boiled} - \text{control}} \times 100$$

The absence of cellular damage, expressed as (100 − % damage), was taken as a measure of heat tolerance.

Root-Shoot Growth. A greenhouse experiment was conducted at Temple, Texas during the period of 23 May to 25 June 1979 to gather data on the root and shoot growth of these entries. Seeds were scarified with a razor blade, treated with Captan, and germinated in Petri dishes on moist filter paper in the dark. When the radicles emerged, seedlings were transplanted into a commercial peat-vermiculite potting mixture contained in 7 × 240 cm acrylic plastic tubes and placed in a greenhouse. The potting mixture had been wetted with tap water from the surface several times prior to planting to avoid settling during the experiment. Immediately after planting, 800 ml of nutrient solution were added. Thereafter, plants were watered daily with tap water and nutrient solution was added twice weekly. Greenhouse temperatures reached 35 ± 3 C during the day and 25 ± 2 C during the night.

The acrylic tubes were placed in wooden racks at an angle of 15° from vertical so roots would be visible along the lower surface (21). The entire rack with tubes was insulated with 2.5 cm thick reflective styrofoam panels which could be removed for measurement of root growth. Temperatures within the rack remained constant at 26 ± 1 C. Plants were harvested at 35 DAP when the tap root of the fastest growing entry neared the bottom

Table 1. Analyses of variance for shoot dry weights of 16 cotton entries grown under dryland and irrigated moisture regimes at Big Spring, Texas.

| Source | df | Days after planting | | | |
		44	58	72	86
		mean squares			
Moisture level (M)	1	0.7	643.6**	3,575.4**	7,912.9**
Reps/M (R/M)	5	2.1	11.8	23.9	13.9
Entries (E)	15	1.6**	19.1**	62.2**	78.2**
E × M	15	0.7	7.4*	35.7**	43.4**
E × R/M	75	0.4	3.3	12.5	18.9

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

of its tube. Data collected at harvest included shoot dry weight, leaf area, taproot length, and the number of strong, downward-growing lateral roots appearing against the lower surface of the tube at a distance of 1 m from the surface of the potting mixture. The tubes were arranged in the greenhouse in a randomized complete block design with nine single-plant replicates.

Analyses. Analyses of variance were used to evaluate differences among entries for the traits measured. Linear correlations were used to determine interrelationships among the traits.

RESULTS AND DISCUSSION

Precipitation prior to planting (15 Oct. 1977 to 23 May 1978) was 140 mm with 43 mm of that total occurring on 19–20 May 1978. Rainfall during this test (86 days) totaled only 86 mm, an extremely dry test environment.

A computer simulation of the average pattern of soil-water availability in the dryland plots is shown in Fig. 1. Soil-water available to the plant represents the total amount in the profile which, in this case, extended to only 60 to 80 cm below the soil surface. The simulation was based on a water budget similar to that proposed by Richardson and Ritchie (15) using our soil-water estimates to fix the upper and lower limits of availability. Pan evaporation, rainfall, and shoot dry matter (from which LAI was estimated) were collected on-site during the growing season. Soil evaporation was a major component of total water use since LAI did not exceed 0.6 on the dryland plots at 86 DAP. Total modeled water use was 167 mm which is in good agreement with that measured for individual genotypes (152 to 172 mm, Table 3).

Shoot Growth

Dry matter differences between treatments were not detected until later than 44 DAP (Table 1, Fig. 2). Water stored in the profile and rainfall apparently allowed relatively water-stress-free growth in both treatments during that period even though water was added to the irrigated plots at planting. Average dry weights at 44 DAP for the entries in the irrigated plots were 2.0 g/plant compared with 2.1 g/plant in the dryland plots. These data further suggest that downward and lateral root growth of plants in dryland plots was rapid enough to maintain shoot growth in a "water non-limited" situation, even though only about 160 mm of available water remained in the profile at this time.

At the other harvest dates (58, 72, and 86 DAP), significant differences in dry weights did exist between the soil-water regimes (Table 1). Entry and entry × water-level interactions were detected for the last three
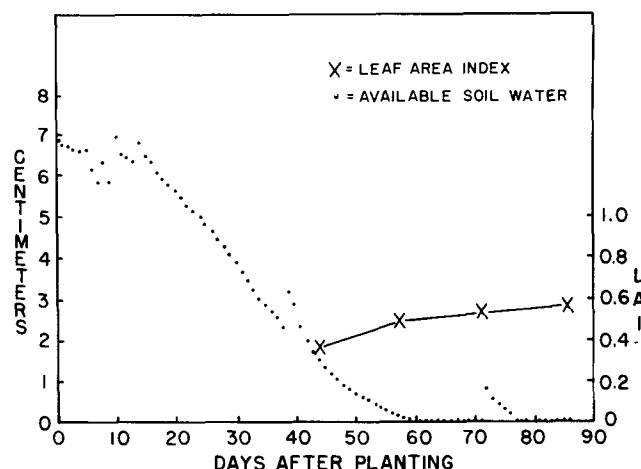

Fig. 1. A simulation of the water available to the plant over time for the soil profile of the dryland plots at Big Spring, Texas. Leaf area index (LAI) was estimated from dry matter samples using data provided in Ritchie and Burnett (16).
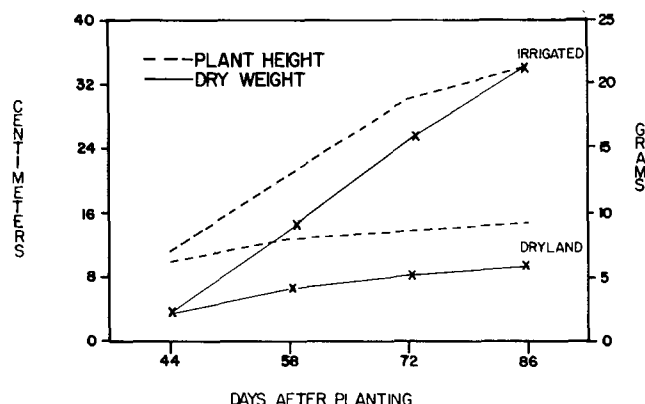

Fig. 2. Plant heights and shoot dry weights at four dates after planting for the irrigated and dryland plots.

harvest dates. The significant entry × water level interactions indicated that the entries were not all growing at the same relative rates under the two water regimes (Table 2). Correlation coefficients between irrigated and dryland means for dry weights at each of the last three harvest dates (58, 72, and 86 DAP) were 0.61, 0.59, and 0.57, respectively. Those correlation coefficients were significant at the 0.05 probability level. The coefficients suggest that, although some interactions for dry weights did occur among entries between the two moisture regimes, those entries with the most rapid growth in the irrigated plots also tended to grow more rapidly in the dryland plots.

Means averaged over entries showed that increase in height and dry-matter accumulation were nearly linear under both moisture regimes, although the actual rates were greatly reduced in the dryland plots (Fig. 2). Means for the entries averaged over moisture regimes for 44 DAP and for separate moisture regimes for the last three harvest dates are shown in Table 2. T147 appeared to grow rapidly in both moisture regimes, while T169 grew more rapidly in the irrigated test than in the dryland test.

Table 2. Means for shoot dry weights of 16 cotton entries, two moisture regimes, and four dates after planting.

		Days after planting						
		44	58		72		86	
Entries	Race	Pooled	Irrig.	Dryl.	Irrig.	Dryl.	Irrig.	Dryl.
T1	palmeri	1.6 de†	7.3 bc	3.8 bc	13.9 abc	5.1 b	21.0 ab	5.3 bcd
T25	punctatum	2.3 abcd	12.9 a	5.1 ab	15.6 abc	5.8 b	19.4 ab	7.1 b
T102	latifolium	2.3 abcd	8.5 abc	3.5 bc	19.2 ab	5.1 b	23.7 ab	5.4 bcd
T111	marie-galante	2.0 abcd	8.1 abc	2.5 bc	16.4 abc	3.8 c	21.8 ab	4.6 bcd
T133	morrilli	1.7 cde	6.3 abc	4.1 bc	8.0 bc	4.3 bc	13.1 b	4.9 bcd
T141	marie-galante	1.1 e	5.0 c	2.1 c	6.7 c	3.0 c	14.6 ab	3.3 d
T147	morrilli	2.4 abc	10.9 ab	6.3 a	20.1 a	8.3 a	29.0 a	9.3 a
T169	latifolium	2.6 ab	8.8 abc	5.0 ab	19.0 ab	5.1 b	28.6 a	6.1 bc
T174	latifolium	1.9 bcd	5.7 c	3.5 bc	11.1 bc	3.8 c	14.6 ab	3.9 cd
T254	morrilli	1.9 bcd	10.2 abc	3.1 bc	16.3 abc	4.6 bc	25.7 ab	4.9 bcd
T265	morrilli	2.6 ab	9.8 abc	4.2 bc	19.8 a	4.7 bc	22.3 ab	6.4 b
T284	morrilli	2.1 abcd	8.9 abc	3.7 bc	16.7 abc	5.6 b	25.8 ab	5.6 bcd
T292	morrilli	1.6 de	5.3 c	3.4 bc	8.9 bc	5.3 b	13.0 b	5.7 bcd
T295	morrilli	2.6 ab	6.1 c	4.3 ab	15.6 abc	5.0 bc	20.5 ab	6.9 b
T461	richmondi	2.2 abcd	11.4 ab	4.5 ab	18.9 ab	5.9 b	26.1 ab	7.1. b
Blightmaster	latifolium	2.7 a	10.1 abc	4.7 ab	23.8 a	5.7 b	25.1 ab	6.1 bc
Mean	--	2.1	8.5	4.0	15.6	5.1	21.5	5.8

† Means within columns followed by one or more of the same letters were not significantly different at the 0.05 probability level (based on Duncan's Multiple Range Test).

T292 and T133 appeared to grow relatively faster in the dryland test than in the irrigated test.

In a previous analysis of growth rates among cottons, El-Sharkawy et al. (4) and Muramoto et al. (11) concluded that differences in dry matter accumulation rates among cultivated cottons and most wild species were associated with variations in seed or cotyledon size, and not with photosynthetic rates of leaves. Because dry-matter accumulation is strongly associated with leaf area, the initial advantage of larger cotyledons, magnified with time, could account for some significant differences in growth.

Our results verify that significant differences in dry-matter accumulation do exist within exotic strains of *Gossypium hirsutum* L., but leaf areas were not measured to confirm the findings of El-Sharkawy et al. (4) and Muramoto et al. (11). Limited data (not reported) suggest that the smaller-seeded races used in this study accumulated dry matter at slower rates than did the larger-seeded entries, but differences in leaf size and in leaf initiation rates have also been observed (B. L. McMichael, USDA-SEA-AR, Lubbock, TX, personal communication). Because leaf size, initiation rate, and initial cotyledon size may all influence the rate of leaf area development (and dry-matter accumulation), a detailed analysis of the primary factor(s) responsible for growth differences among these strains must await further study.

Dry weights for the dryland plots at 86 DAP, water used during the 86 days, and water-use efficiency (WUE) at 86 DAP for the dryland treatment are shown in Table 3. T147 produced significantly higher per plant dry weights than any of the other entries. Compared to the commercial cultivar, Blightmaster, T141 produced significantly less dry matter. Blightmaster and T295 used more water than T25 or T284, but this may have been the result of small differences in initial soil-water availability among plots. WUE was highest on T147 and T25 and lowest on T141 and T174. Blightmaster was intermediate between the extreme types.

Differences among entries in WUE were primarily due to differences in the rate of dry-matter accumulation, rather than to differences in water use. This conclusion is borne out by the significant linear correlation (r = 0.98) between dry matter and WUE (Table 3).

Because root weights were not included in the estimates of plant (shoot) dry weights, absolute estimates of water-use efficiency could not be made, nor could possible partitioning differences between shoots vs. roots be estimated. The significant differences between shoot dry weights per unit of water used suggest that variability for WUE exists in this cotton germplasm.

Heat Tolerance

Cellular damage from the heat treatment ranged between 12 and 52% for the dryland plots and 8 and 32% for the irrigated plots (Table 4). These results suggest that the water deficits experienced by plants in dryland plots did not "harden" leaf tissues to high temperature even though it is likely that leaf temperatures of the dryland plants were higher than those under irrigation. Leaf temperatures were not measured, but elevated leaf temperatures are often associated with stomatal closure and wilting, especially in an arid, high-radiation environment such as this location. At the time of sampling, plants in dryland plots were wilted at midday and abscission of some leaves had occurred.

Total ionic solutes per unit leaf area (as estimated from conductivity measured on boiled samples) averaged nearly twice as great for dryland plots, but the increase was not uniform among lines. For example, the increase in total conductivity between irrigated and dryland plots of T265 was 325 μmho/cm^2, while that for T1 was only 142 μmho/cm^2.

The importance of the apparent differences among lines in solute accumulation between treatments is unknown at this time. The differences may be in part a reflection of the degree of inhibition of leaf expansion which could differ among lines. Leaf area and vegetative growth are known to be the parameters of growth which

Table 3. Shoot dry weights, total water used, and water-use efficiency (WUE) of 16 entries on dryland plots—86 days after planting.

Entries	Dry weights	Water used	WUE
	g	mm	g/mm
T147	9.3 a*	159 bc	0.058 a
T25	7.1 b	153 c	0.047 ab
T461	7.1 b	158 bc	0.045 abc
T295	6.9 b	164 ab	0.042 bcd
T265	6.4 b	163 abc	0.039 bcde
T169	6.1 bc	161 bc	0.038 bcde
Blightmaster	6.1 bc	172 a	0.035 bcdef
T292	5.7 bcd	162 abc	0.035 bcdef
T284	5.6 bcd	152 c	0.037 bcde
T102	5.4 bcd	156 bc	0.035 bcdef
T1	5.3 bcd†	161 bc	0.033 bcdef
T254	4.9 bcd	153 c	0.032 bcdef
T133	4.9 bcd	157 bc	0.031 cdef
T111	4.6 bcd	158 bc	0.029 def
T174	3.9 cd	156 bc	0.025 ef
T141	3.3 d	156 bc	0.021 f
Mean	5.8	159	0.036

* Means within columns followed by one or more of the same letters were not significantly different at the 0.05 probability level (based on Duncan's Multiple Range Test).

are perhaps the most sensitive to internal water deficits (2, 6). Because the assay procedure uses a constant surface area per sample, the actual number of cells sampled may have differed widely among lines and between treatments. The relation of cellular volume to total ionic content is not known.

One alternative explanation to account for differences in total ionic solutes is that mineral ion uptake and accumulation may differ among lines. Genetic variability in ion-uptake efficiencies is known to exist for several ions-crop species combinations. It is doubtful, however, that this mechanism could account for the large differences between treatments. Most mineral ions are accumulated from the soil solution suggesting a strong association between water supply and nutrient availability (at least for major mineral nutrients). Viets (23) concluded that water-stressed plants may have lesser supplies available, especially if the mineral nutrients are concentrated in the upper portion of the soil profile (which dries most rapidly during drought). Such a moisture condition did exist during the term of this study. Other recent evidence (1, 5, 7) suggests that osmotic adjustment in water-stressed plants results primarily from accumulation of internally generated organic solutes.

Regardless of the amount of cause of solute accumulation, there appeared to be no quantitative relation between total conductivity and cellular damage (r = 0.28 for the irrigated plots; r = 0.09 for dryland).

Root-Shoot Growth

Genetic variations in shoot growth as measured by either leaf-area development or dry-weight accumulation during the 35-day period were significant (Table 5). Within this germplasm, T25 and T169 had the most vigorous shoot growth while T254 had the least. A significant correlation (r = 0.54) was calculated between the shoot dry weights in this study and shoot dry weights at 44 DAP in the Big Spring field study. Variability also existed among entries for taproot length and number of laterals

Table 4. Total electrical conductivity of leaf samples and cellular damage caused by heat treatment on 16 cotton entries grown under irrigated and dryland moisture regimes at Big Spring, Texas.

	Irrigated		Dryland	
Entry	Total conductivity	Damaged cells	Total conductivity	Damaged cells
	μmho/cm²	%	μmho/cm²	%
T1	255 abc*	17 cdef	397 efgh	19 def
T25	254 abc	32 a	438 bcde	38 ab
T102	233 bcde	25 ab	379 gh	52 a
T111	221 de	18 bcd	418 defg	32 bcd
T133	270 a	9 fgh	454 bcd	35 abcd
T141	252 abcd	22 bc	471 abc	36 abc
T147	187 fg	11 defgh	356 h	25 bcdef
T169	209 ef	16 cdef	416 defg	30 bcd
T174	229 cde	17 cdef	432 bcdef	35 abcd
T254	176 g	15 cdefg	382 fgh	18 def
T265	180 g	12 defgh	505 a	12 f
T284	213 ef	8 gh	382 fgh	29 bcde
T292	226 cde	8 h	425 cdefg	17 ef
T295	263 ab	10 efgh	475 ab	34 abcd
T461	229 cde	17 bcde	436 bcde	22 cdef
Blightmaster	276 a	19 bcd	504 a	29 bcde
Mean	230	16	429	29

* Means within columns followed by one or more of the same letters were not significantly different at the 0.05 probability level (based on Duncan's Multiple Range Test).

Table 5. Characteristics of root and shoot growth of 16 cotton entries grown in a greenhouse and harvested after 35 days of growth.

	Shoot		Root	
Entry	Dry weight	Leaf area	Tap length	Laterals†
	g	cm²	cm	no.
T1	2.7 abc*	366 bcde	191 abcd	4.0 bc
T25	3.3 a	527 a	196 ab	9.3 a
T102	2.3 abcde	378 bcde	169 abcde	4.6 b
T111	1.7 de	316 cde	166 bcde	0.8 c
T133	2.2 bcde	364 bcde	177 abcde	2.7 bc
T141	1.8 cde	303 de	173 abcde	1.3 bc
T147	2.3 bcde	462 abc	176 abcde	4.6 b
T169	3.3 a	482 ab	193 abc	3.9 bc
T174	2.2 bcde	332 cde	147 e	1.0 c
T254	1.5 e	277 e	163 cde	1.1 c
T265	2.3 abcde	380 bcde	165 bcde	3.0 bc
T284	2.6 abcd	383 bcde	172 abcde	1.7 bc
T292	2.1 bcde	367 bcde	178 abcde	1.8 bc
T295	2.6 abcd	419 abcd	198 a	2.2 bc
T461	2.2 bcde	295 de	175 abcde	3.4 bc
Blightmaster	2.9 ab	325 cde	178 abcde	2.3 bc
Mean	2.4	374	176	3.0

* Means within columns followed by one or more of the same letters were not significantly different at the 0.05 probability level (based on Duncan's Multiple Range Test).
† The number of strong, downward-growing lateral roots observed against the lower face of the acrylic tube 1 m below the surface.

observed. Although not clearly illustrated by these data, those entries exhibiting vigorous shoot growth also appeared to produce more vigorous roots. For example, both taproot length and number of laterals were high for T25, but low for T254.

The association between shoot and root vigor is shown more clearly by the correlation matrix presented in Table 6. Correlations between all possible pairs of variables were significant demonstrating the close coupling of shoot and root growth under these conditions. Roots were

not recovered, thus preventing a more rigorous examination of the variability in dry-matter partitioning between shoot and root.

The significant correlation of taproot length to number of laterals suggests more rapid growth of all roots, not only the taproot. The points of origin of the laterals observed at the 1 m depth were not rigorously determined, but observation suggested origin within 15 cm of the surface. It is not known whether the frequency of these first-order lateral roots differed among entries, but that could be an alternative explanation for variation in lateral root numbers at that depth.

Correlations of All Measured Traits

Interpretations of correlations among variables must be made in light of the pattern of soil-water availability which existed during this study. The lack of significant treatment (moisture level) effect on dry matter accumulated between planting and 44 DAP may be taken as evidence for the absence of water limitations to growth during that period. Water deficits developed after 44 DAP such that significant reductions in growth rates (height and dry matter, Fig. 2) occurred by 58 DAP and were accentuated with time. By 86 DAP, all entries had depleted essentially all of the soilwater available to the plant in the dryland plots (Fig. 1).

Also, growth of these photoperiodic strains under non-inductive photoperiods allowed an evaluation of growth response to water supply without the possible confounding effects introduced by variations in fruiting pattern

Table 6. Linear correlation coefficients for traits presented in Table 5.

Traits	Leaf area	Taproot length	Root laterals
		r	
Shoot dry weight	0.77**	0.67**	0.66**
Leaf area	--	0.63**	0.76**
Taproot length	--	--	0.56*

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

and intensity. In this situation, the major sinks for photosynthate were limited principally to leaves and roots.

Linear correlation coefficients among all possible pairs of traits measured in all experiments are shown in Table 7. The plant dry weights from all harvest dates were significantly correlated for both water treatments. This indicates that the accumulation of dry weight is entry specific; and in general, those entries with genetic potential for rapid growth rates performed better in spite of low soil-water availability. The entry × moisture level interactions (Table 1) were due to changes in relative growth rates among lines and not to changes in entry ranking.

The implications of these results seem clear. Drought resistance, as expressed by dry-matter yield, is due to the early growth advantage expressed under conditions of non-limiting soil water. The low total soil-water availability, coupled with the high evaporative demand, may have caused plant-water deficits to develop so rapidly that a differential expression of growth sensitivity to low water potential was prevented. An extension of this line of reasoning would permit the conclusion that screening for drought resistance could be carried out under conditions of optimal soil water. These findings tend to support a previous conclusion that selection for lint yield in cotton for production in stressful environments is more efficient if conducted under optimal environmental conditions (14).

Cellular damage from heat showed consistent, though nonsignificant, negative correlations with dry-matter yield from dryland plots. Similar negative correlations were found with yield in irrigated plots with only the correlation of 86 DAP significant at the 10% level. These results are similar to those reported for soybeans [Glycine max (L.) Merr.] by Martineau et al. (9, 10) where correlations between cellular damage and yield were consistently negative among experiments although the association was often not strong enough for statistical significance to be demonstrated. Sullivan and Ross (20)

Table 7. Linear correlation coefficients for traits in all experiments under the two moisture regimes. Days after planting (DAP).

	Experiments							
	Shoot growth				Heat tolerance		Root-shoot growth	
Moisture regime	44 DAP	58 DAP	72 DAP	86 DAP	Conductivity	Percent damaged cells	Taproot length	Root laterals
Irrigated								
58 DAP	0.55*	--	0.73**	0.70**	0.37**	-0.32	0.15	0.62*
72 DAP	0.83**	0.73**	--	0.87**	0.13	-0.29	0.09	0.26
86 DAP	0.63**	0.70**	0.87**	--	0.11	-0.48†	0.13	0.19
Conductivity	-0.01	0.37	0.13	0.01	--	0.28	0.11	0.57*
Percent damaged cells	-0.16	-0.32	-0.29	-0.48†	0.28	--	0.43	0.14
Taproot length	0.24	0.15	0.09	0.14	0.11	0.43	--	0.56*
Root laterals	0.32	0.62*	0.26	0.19	0.57*	0.14	0.56*	--
Dryland								
58 DAP	0.67**	--	0.84**	0.90**	-0.10	-0.09	0.44†	0.63**
72 DAP	0.49*	0.84**	--	0.92**	-0.20	-0.39	0.32	0.50*
86 DAP	0.64**	0.90**	0.92**	--	-0.22	-0.17	0.45†	0.57*
Conductivity	0.03	-0.10	-0.20	-0.22	--	-0.09	0.05	0.24
Percent damaged cells	0.18	-0.09	-0.39	-0.17	-0.09	--	0.10	-0.13
Taproot length	0.23	0.44†	0.32	0.45†	0.05	0.10	--	0.56*
Root laterals	0.32	0.63**	0.50*	0.57*	0.24	-0.13	0.56*	--

†,*,** Significant at the 0.10, 0.05, and 0.01 probability levels, respectively.

reported a significant correlation between sorghum [*Sorghum bicolor* (L.) Moench] grain yield and heat tolerance, but their correlations for experiments conducted in different environments were often striking (C. Y. Sullivan, personal communication). The present data are regarded as suggestive that heat tolerance may be causally related to field performance, although much additional work will be required to establish the value of heat tolerance to performance in stressful environments.

The correlations of root vigor (root length and root laterals) with dry-matter production after 44 DAP were consistent for dryland, but not for irrigated plots. The stronger correlations with root laterals could be rationalized because of the greater differences in numbers of laterals than in taproot lengths (Table 5). The significant correlations between root characteristics and dry-matter yield under dryland conditions suggest that overall root vigor may have allowed some types to be better competitors for limited soil water. The experimental design was such that consistent competition between rows was provided by Blightmaster. In this situation, where all entries should have been capable of extending roots to the bottom of the wetted profile (60 to 80 cm), competition between adjacent rows for water may be strongly related to the frequency and vigor of lateral roots. For irrigated plots, the loss of significance in the correlation between root laterals and dry matter after 58 DAP and the low correlation values in general suggest that differences in root characteristics do not influence yield when ample water is available.

CONCLUSIONS

We have demonstrated that significant genetic variability exists among exotic strains of *Gossypium hirsutum* L. for shoot dry-matter accumulation, heat tolerance, and shoot and root growth. Estimates of root and shoot growth conducted in the greenhouse under non-inductive photoperiods were related to early season field performance when water was not limiting to growth. Root morphology and root growth potentials appear to be important for the adaptation of cotton to conditions where limited soil-water availability is a major constraint to growth.

The low total water available to the plant and the pattern of water availability during this study are believed to have precluded the expression of other drought-resistance mechanisms which may be important to both dry-matter accumulation and lint yield in a full-season situation.

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