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GENETIC VARIATION FOR ROOT–SHOOT RELATIONSHIPS AMONG COTTON GERMPLASM*

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McMichael B. L. and Quisenberry J. E. *Genetic variation for root–shoot relationships among cotton germplasm*. Environmental and Experimental Botany **31,** 461–470, 1991.—Twenty-five cotton (*Gossypium* spp.) genotypes were used to evaluate the genetic variability in partitioning of biomass into roots and shoots when plants were grown under conditions of declining soil water and different atmospheric evaporative demands. The entries ranged from primitive race stocks to modern cultivars and were selected on field observations of growth under water stress conditions in the field. Seeds of each genotype were planted in soil (56 kg) in large containers in the greenhouse. Water was added to the soil to bring the water content to field capacity and the plants were allowed to grow with no additional water until they reached the permanent wilting point. Large fans were utilized in the second experiment to reduce the leaf boundary layer resistance and increase the evaporative demand. When the plants of each entry had reached the permanent wilting point, the plants were harvested, the roots washed free of the soil, and the dry weights of both roots and shoots were determined. Information on total water used and days to permanent wilting were also collected for each genotype. Differences were observed in partitioning of total biomass between roots and shoots between experiments and genotypes. There was no significant interaction, however, between entries and experiments. Root–shoot ratios increased in plants grown in the more stressful environment resulting from a significant increase in root dry weights with little change in shoot dry weights. The distribution for root–shoot ratios coincided in general with the distribution for root weights among the entries, with a 59% decrease from the highest to lowest value. The exotic strains also in general had higher root–shoot ratios than the commercial varieties, the *herbaceum* species and the experimental strain (Lubbock dwarf). There was no direct relationship between shoot weights and root weights among the genotypes for either environment. Those plants that grew large tops did not necessarily grow correspondingly large root systems (e.g. T141 has a large root system with a very small shoot compared to the *herbaceum* species, which has a relative large shoot and a small root system). The lack of a correlation between shoot and root growth along with genotypic differences in changes in root–shoot ratios in response to environmental demand may provide an opportunity to exploit the observed variability to improve production for a wide range of growth conditions by altering the root development and function independent of shoot development.

INTRODUCTION

The growth and development of the root system are essential for plants to efficiently extract water and nutrients and to maintain plant productivity over a wide range of environments.

Earlier studies with cotton (*Gossypium hirsutum* L.) have indicated that the growth and morphological development of the root system are under genetic control, but may be modified by environmental influences.[3,6] There is evidence for environmentally mediated differences in the

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development of total root length and the degree of branching in cotton root systems. These differences can be a major factor in the ability of the plant to explore the available soil volume for water and nutrients.[3,6,7]

The partitioning of biomass into roots and shoots is a dynamic process that can impact the productivity and drought tolerance capabilities of the plant since the roots and shoots are in constant competition for available photosynthate. The coordination of the growth between roots and shoots becomes important since the development of either part is dependent on the other.

The total biomass produced by a cotton root system makes up 10–15% of the total biomass produced by the plant in a growing season.[2,4] This information has been determined in a limited number of studies since adequate information regarding the total growth of the root system is difficult to obtain. The interactions between root and shoot growth, as a result of external environmental stimuli such as declining soil water or increased evaporative demand, are not clear. Work by KLEPPE *et al.*[5] and TAYLOR[11] has shown that the distribution of the roots is altered as a result of decreasing soil water. They showed that as rooting depth increased with stress the rooting density decreased, especially in the upper soil layers.

Since the development of the root system of cotton is under genetic control, genetic variability may exist for the partitioning of the total biomass when the plants are grown under similar environmental conditions. If such variability is present, then opportunity for improvement of the root–shoot relationships when plants are subjected to adverse moisture conditions may also be possible.

The objectives of this research were to evaluate root–shoot relationships in genetically diverse cotton germplasm grown in the greenhouse under conditions of declining soil moisture and to determine the impact of different evaporative demands on the partitioning of biomass into roots and shoots.

MATERIALS AND METHODS

The cotton germplasm selected for these studies is summarized in Table 1. The genotypes represent exotic cottons from the World Cotton Col-

Table 1. Cotton germplasm used in two greenhouse experiments on biomass partitioning

Primitive race stocks *G. hirsutum* Race						
latifolium	*punctatum*	*richmondi*	*morelli*	*marie galante*	*palmeri*	*yucatense*
T50	T15	T461	T171	T141	T1	T1236
T80	T25	T256	T283	T184		
T151	T45					
T169	T115					
T185						
T252						
Modern cultivars						
G. hirsutum				*G. barbadense*		
"Paymaster 145"				"Pima S-5"		
"Coker 5110"						
"Tamcot CAMD-E"						
"Deltapine 61"						
Other species and experimental strains						
G. herbaceum				*G. hirsutum*		
(designation and origin unknown)				Lubbock dwarf		

lections as well as modern cultivars and one experimental strain. The choice of the genotypes was based on observed performance of biomass production under conditions of declining soil water in studies conducted under field rain-out shelters. All studies were conducted in the greenhouse during the winter months so that the exotic cottons, which are photoperiodic and require long nights to flower, would reproduce. Two experiments were conducted in two different environments. In the first experiment, the air flow in the greenhouse was minimal so that the leaf boundary resistances were high. In the second experiment large oscillating fans were used to move the air in the greenhouse during the times between 0800 and 2000 hr each day at about 4 m/sec to reduce the leaf boundary layer resistances. The planting dates for the two experiments were 24 October 1984 (Experiment 1) and 28 January 1985 (Experiment 2), respectively. Regardless of the experiment, the temperature in the greenhouse was set at 25° C and the night temperatures did not go below that value. Although attempts were made to control daytime temperatures to 25° C, they often rose above 25° C. Daily maximum and minimum temperatures were recorded. Relative humidities were also recorded at a height of 25 cm above the canopy. The height of the sensors was adjusted as the plants grew. The greenhouse environmental data are summarized in Table 2. Plastic pots with a volume of 37.8 l were used for growing the plants in each experiment. Each pot was filled with 56.4 kg of air-dried Amarillo loam soil (fine-loamy, mixed, thermic Aridic Paleustalf). Small holes were cut into the bottom of the pots to facilitate initial drainage. Sufficient water was added to each pot until all drainage terminated. The holes in the bottom of the pots were then sealed, the top of the pots covered with plastic and the pots weighed.

Five seeds were planted per pot in each of five pots in a randomized complete block design. Fourten days after planting, holes were cut in the plastic covering the tops of the pots to allow the hypocotyls to protrude. The plants were also thinned to one plant per pot at that time and the hole in the plastic top was sealed around the hypocotyl to prevent water loss. A relatively small amount of root biomass was produced by the seedlings that were removed since the plants were only 14 days old. By the time the remaining plant was harvested (on average 60–70 days after planting) the root system produced by the 14-day-old seedling that was left at the time of thinning

Table 2. Means for environmental parameters for greenhouse Experiment 1 (no fans) and Experiment 2 (with fans)

Parameter	Experiment 1	Experiment 2
Air temperature (°C)		
Average daily max.	30.6 ± 2.3	33.9 ± 3.3
Average daily min.	25.4 ± 1.1	25.2 ± 1.8
Relative humidity (%)		
Average daily max.	58.9 ± 9.8	62.3 ± 11.7
Average daily min.	40.8 ± 7.5	38.7 ± 8.6
Windspeed (m/sec)		
Average daily max.	0.2 ± 0.05	4.0 ± 1.2*
Average daily min.	0.1 ± 0.06	0.2 ± 0.07
Solar radiation ($MJ\ m^{-2}\ hr^{-1}$)		
Mid-day outdoors	2.95 ± 0.23	3.15 ± 0.16
Mid-day in greenhouse	2.60 ± 0.10	2.85 ± 0.11

* Fans were operated from 0800 to 2000 hr each day in this experiment.

Table 3. Analyses of variance over experiments and means within each experiment for water used, biomass produced, and days to permanent wilting for 25 cotton genotypes grown in two experiments in a greenhouse

		Mean squares		
Source of variation	df	Water used	Biomass produced	Permanent wilting
Experiments (Exp.)	1	83.09*	17.52	8514.7*
Reps/Exp.	8	0.24	21.82	37.0
Genotypes (G)	24	0.18	20.26*	158.0*
G × Exp.	24	0.10	1.15	29.0*
Error	192	0.10	1.57	10.8
			Means	
		kg	g	days
Experiment 1		9.60 a†	18.5 a	72.3 a
Experiment 2		8.45 b	18.0 a	60.7 b

* Statistically significant at the 0.01 probability level.

† Means followed by the same letter are not significantly different at the 0.05 probability level based on an LSD test.

in the pot had decomposed and did not add any significant dry weight to the root system remaining.

The plants were grown without additional water being added until the third true leaf from the top of the plant was observed to wilt and did not recover overnight. This was taken to be the "permanent wilting point" for the plant. The date for the "permanent wilting" for each plant was recorded. At this point the plant tops were harvested and separated into leaves, stems and fruit. The tissue, along with any leaves that had been shed and collected during the course of the experiment, was dried at 80° C for at least 24 hr and the dry weights measured. After the tops in each pot were harvested, the soil mass containing the root system was placed on a fine mesh (40 mesh) screen and the roots washed free of the soil and collected on the screen. The roots were then dried at 80° C for at least 24 hr and the dry weights determined.

The results were analyzed using an Analysis of Variance for a randomized complete block design.

RESULTS AND DISCUSSION

The environment for the second experiment was experimentally altered by increasing the air movement across the plants during the day with the large fans. This increased air movement reduced the boundary layer resistances to water evaporation from the leaf surfaces and resulted in a more stressful environment. This fact was demonstrated by the increase in the total amount of water used and the decrease in the days to permanent wilting for Experiment 2 (Table 3).

There were no significant differences in total biomass produced across all genotypes between the two experiments (Tables 3 and 4). There were, however, differences in the partitioning of the total biomass between roots and shoots. Shoot dry weights were lower for Experiment 2 but the difference was not significant (5.4% reduction, Tables 5 and 8). Root dry weights were significantly higher for Experiment 2 (18.7% increase, Tables 6 and 8). Therefore, there was a significant increase in the root–shoot ratio for Experiment 2 owing to an increase in root dry

Table 4. Means for total biomass for 25 cotton genotypes grown in the greenhouse

Genotype	Total biomass (g) Experiment 1	Experiment 2
T80	20.31	19.45
T256	20.44	19.72
T283	20.24	19.74
T461	20.00	20.66
T1236	18.28	17.13
G. herbaceum L.	20.19	19.64
T171	19.93	18.84
T15	20.86	19.84
T184	17.57	16.37
T252	20.23	18.97
T1	18.76	19.24
T25	19.33	17.84
T45	18.96	18.82
T141	16.70	16.89
T115	16.69	16.12
Coker 5110	19.36	17.86
T151	17.88	18.26
T50	18.93	18.34
Pima S-5 (*G. barbadense*)	18.00	16.98
Paymaster 145	18.17	16.71
T185	17.40	16.67
Tamcot CAMD-E	16.45	16.70
T169	16.32	16.67
Lubbock dwarf	15.84	15.97
Deltapine 61	16.90	16.71
Means	18.55	18.00
LSD (0.05)	1.01	0.99

Table 5. Means for 25 cotton genotypes for shoot weight for two planting dates

Genotype	Shoot dry weight (g) Experiment 1	Experiment 2
G. herbaceum	18.30	17.23
T15	18.07	17.07
T461	17.31	17.69
T80	18.14	16.72
T256	17.61	16.42
T283	17.46	16.48
T50	17.09	16.17
Coker 5110	17.54	15.58
T45	16.40	16.41
T171	17.16	15.45
T252	17.16	15.41
T151	16.06	16.02
T1	15.85	15.94
T25	16.70	14.90
Pima S-5 (*G. barbadense*)	16.38	15.06
Paymaster 145	15.91	14.35
T1236	15.95	14.01
T169	15.05	14.51
DPL 61	14.67	14.50
Tamcot CAMD-E	14.60	14.49
T185	14.78	13.94
Lubbock dwarf	14.38	14.15
T115	14.24	12.97
T184	13.62	12.43
T141	13.04	12.83
Means	16.12	15.25
LSD (0.05)	1.87	1.82

weights without a significant decrease in the shoot dry weights (Tables 7 and 8, respectively). Increases in root biomass have been shown to occur in cotton as well as other species as a result of water stress.[4]

There were significant differences between the genotypes for all traits (shoot weight, root weight and root–shoot ratios) (Table 8) across experiments. There were no significant interactions, however, between genotypes and experiments for all traits except root–shoot ratios. The significant interaction for root–shoot ratios was a result of changes in the magnitude of the differences of the means between experiments and not due to differences in the growth rate of the species.

The species *G. herbaceum* L. had the highest shoot weight averaged across both experiments, while the exotic genotype T184 had the highest root weight (Tables 9 and 10, respectively). It is significant to note that T184 and T141 had the lowest shoot weights as well as the highest root weights of the 25 genotypes that were evaluated. These particular genotypes are of the race marie galante, and have been designated as so-called "tree cottons" due to their growth habits.[1] From the present results it is obvious that they shifted a larger percentage of their total biomass pro-

Table 6. *Means for 25 cotton genotypes for root weight for two planting dates*

Genotype	Root dry weight (g) Experiment 1	Experiment 2
G. herbaceum	1.89	2.41
T15	2.70	2.77
T461	2.69	2.97
T80	2.18	2.72
T256	2.83	3.30
T283	2.79	3.26
T50	1.84	2.18
Coker 5110	1.82	2.28
T45	2.29	2.42
T171	2.77	3.39
T252	3.03	3.56
T151	1.82	2.24
T1	2.91	3.30
T25	2.63	2.94
Pima S-5 (*G. barbadense*)	1.61	1.92
Paymaster 145	1.96	2.36
T1236	2.33	3.12
T169	1.57	2.16
DPL 61	2.08	2.21
Tamcot CAMD-E	1.61	2.21
T185	2.20	2.74
Lubbock dwarf	1.44	1.82
T115	2.44	3.14
T184	3.95	3.94
T141	3.66	4.06
Means	2.35	2.79
LSD (0.05)	0.49	0.44

Table 7. *Means and mean differences for 25 cotton genotypes for root/shoot ratios for two experiments*

Genotype	Root/shoot ratio Experiment 1	Experiment 2	Exp. 2–Exp. 1
T1236	0.147	0.223	0.076
T115	0.172	0.245	0.073
T171	0.163	0.221	0.058
T252	0.178	0.231	0.053
T185	0.144	0.197	0.053
Paymaster 145	0.121	0.165	0.044
T169	0.104	0.148	0.044
Coker 5110	0.104	0.146	0.042
T256	0.161	0.201	0.040
T25	0.157	0.197	0.040
T80	0.123	0.162	0.039
T283	0.160	0.198	0.038
G. herbaceum	0.103	0.139	0.036
T141	0.280	0.316	0.036
Lubbock dwarf	0.101	0.130	0.029
T184	0.289	0.318	0.029
Pima S-5 (*G. barbadense*)	0.099	0.127	0.028
T50	0.107	0.134	0.027
T151	0.114	0.140	0.026
Tamcot CAMD-E	0.127	0.152	0.025
T1	0.183	0.208	0.025
T15	0.150	0.164	0.014
T461	0.156	0.168	0.012
DPL 61	0.151	0.153	0.002
T45	0.155	0.147	−0.008
Means	0.149	0.186	
LSD (0.05)	0.026	0.028	

Table 8. *Analyses of variance for shoot weight, root weight, and root–shoot ratios for* 25 *cotton genotypes grown in two greenhouse experiments*

		Mean squares		
Source of variation	df	Shoot weight (g)	Root weight (g)	Root/shoot
Experiments (Exp.)	1	44.23	11.41	0.079*
Reps/Exp.	8	19.07	0.75	0.001
Genotypes (G)	24	18.49*	3.59*	0.023*
G × Exp.	24	1.14	0.10	0.001*
Error	181	1.28	0.11	0.0004
		Means		
Experiment 1		16.12 a	2.35 b	0.149 b
Experiment 2		15.25 a	2.79 a	0.186 a

* Statistically significant at the 0.05 probability level.
Means followed by different letters are different at the 0.05 probability level based on an LSD test.

Table 9. *Means averaged over two experiments for* 25 *cotton genotypes for shoot dry weight*

Genotype	Shoot dry weight (g)
G. herbaceum	17.77
T15	17.57
T461	17.50
T80	17.43
T256	17.02
T283	16.97
T50	16.63
Coker 5110	16.56
T45	16.41
T171	16.31
T252	16.29
T151	16.04
T1	15.90
T25	15.80
Pima S-5 (*G. barbadense*)	15.72
Paymaster 145	15.31
T1236	14.98
T169	14.78
Deltapine 61	14.59
Tamcot CAMD-E	14.55
T185	15.36
Lubbock dwarf	14.27
T115	13.61
T184	13.03
T141	12.94
LSD (0.05)	1.85

Table 10. *Means averaged over two experiments for* 25 *cotton genotypes for root dry weight*

Genotype	Root dry weight (g)
T184	3.95
T141	3.86
T252	3.30
T283	3.12
T1	3.11
T171	3.08
T256	3.07
T461	2.83
T25	2.80
T115	2.79
T15	2.74
T1236	2.73
T185	2.47
T80	2.45
T45	2.36
Paymaster 145	2.16
Deltapine 61	2.15
G. herbaceum	2.15
Coker 5110	2.05
T151	2.03
T50	2.01
Tamcot CAMD-E	1.91
T169	1.87
Pima S-5 (*G. barbadense*)	1.77
Lubbock dwarf	1.63
LSD (0.05)	0.47

duction to the roots during their early stages of growth. In general, all of the species fell within the distribution (means) of the cultivated species of *G. hirsutum* L. for shoot weight. Most of the exotic race stocks of *G. hirsutum* had higher root weights than either of the other two species or the commercial varieties. The extremely early fruiting experimental strain, Lubbock dwarf, had the smallest root weight (Table 10).

The distribution of root–shoot ratios between the genotypes averaged across both experiments showed that T184 had the highest root–shoot ratio, and the *G. barbadense* genotype, Pima S5, had the lowest (Table 11). This distribution coincides with the distribution for root weights (Table 10) for the 25 genotypes since there was a greater change in root weights between the genotypes (59% decrease from highest to lowest value) than for shoot weights (27% decrease from highest to lowest value). The exotic *G. hirsutum* genotypes generally had higher root–shoot ratios compared with either of the commercial varieties, the *G. herbaceum* genotype, or the experimental strain (Lubbock dwarf).

Table 11. *Means averaged over two experiments for* 25 *cotton genotypes for root/shoot ratios*

Genotype	Root/shoot ratio
T184	0.304
T141	0.298
T115	0.209
T252	0.205
T1	0.196
T171	0.192
T1236	0.185
T256	0.181
T283	0.179
T25	0.177
T185	0.171
T461	0.162
T15	0.157
DPL 61	0.152
T45	0.151
PM 145	0.143
T80	0.143
Tamcot CAMD-E	0.140
T151	0.127
T169	0.126
Coker 5110	0.125
T50	0.122
G. herbaceum	0.121
Lubbock dwarf	0.116
Pima S-5 (*G. barbadense*)	0.113
LSD (0.05)	0.020

There was, with the exception of one genotype (T45), an increase in the root–shoot ratio when plants of each entry were grown in the more stressful environment (Experiment 2, Table 7). The exotic genotype T1256 had the largest shift in root–shoot ratio (51%) between the two experiments. This particular genotype was collected on the Yucatan Peninsula of Mexico and was found growing on beaches and dunes near the Gulf of Mexico[12] and should be relatively salt tolerant. This genotype may have the ability to adapt to saline environments by shifting its root–shoot ratio to favor root growth by some mechanism such as osmotic adjustment.

The ability of a plant to change significantly its root–shoot ratio may be only one part of the overall mechanism[5] that a plant uses to tolerate environmental stress. The relative contribution of such a phenomenon to the observed response is not known. For example, it was observed in this study that there was a greater relative increase in the root–shoot ratio of the exotic genotype T169 than for the genotype T25 when the plants were grown in the more stressful environment (Experiment 2, Table 7). This indicates a greater percentage increase in root biomass for T169 since shoot biomass did not differ significantly between the two genotypes. Quisenberry *et al.*[9] observed that T25 had a higher water-use-efficiency under stress conditions than did T169. Thus the increase in root biomass of T169 did not appear to enhance root activity in terms of more efficient water extraction for increased biomass production. Another contributing factor in this case might be the observations by Quisenberry *et al.*[10] and Peterschmidt and Quisenberry[8] that T25 maintains a higher leaf water potential under stress conditions for a longer period of time than does T169, and that T25 closes its stomates at much higher leaf water potentials than does T169. Thus, T25 tends to conserve water and maintain turgor and continued growth. Therefore, the increase in root–shoot ratio of T169 may have

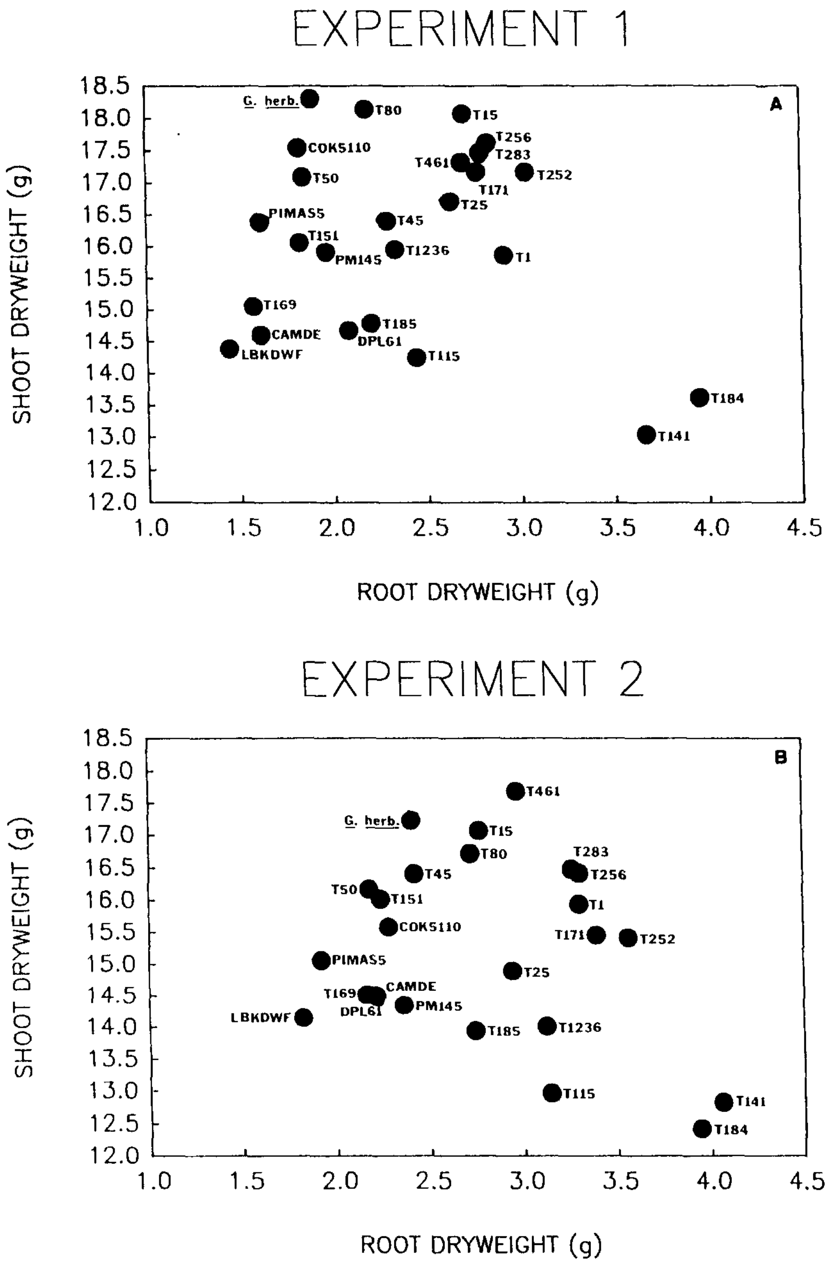

FIG. 1. Relationship between shoot dry weight and root dry weight for 25 cotton genotypes for two experiments in a greenhouse (A = Expt 1, B = Expt 2).

allowed the plant to survive somewhat longer but did not result in more efficient use of the water since there may have been significant differences in the rate of water transpired.

The relationship between shoot production and root production for the 25 genotypes grown under both environments showed that there was no direct correlation between shoot weights and root weights across genotypes grown in either environment (Fig. 1). This lack of correlation indicates that for a given environment genotypes that have large shoots do not necessarily have large root systems. For example, the *G. herbaceum* genotype had relatively large shoots in both environments, but the root system of this genotype was no larger than other genotypes such as DPL61 or T169 which had much smaller shoot weights. The genotypes T184 and T141 had relatively large root systems and the smallest shoots of all the genotypes. The lack of a relationship between root weight and shoot weight across environments should, however, provide an opportunity to exploit the variability in the cotton root systems independent of the variability in the shoots for possible improvement of root system morphology and traits associated with more efficient uptake and utilization of water and nutrients.

In conclusion, we have shown that significant variability exists in cotton germplasm for partitioning of total biomass into roots and shoots in plants grown in different environments. In general, all genotypes partitioned a greater amount of biomass into root systems when grown under conditions of high evaporative demand. Genotypic differences in shifts in root–shoot ratios in response to environmental changes may provide the opportunity, however, to develop plants for improved production under a wide range of growth conditions by having the capability of altering root system morphology and function independent of the capability for changing shoot characteristics in the same species.

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