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Response to Drought Stress in a Subset of the U.S. Peanut Mini-core Evaluated in Oklahoma, Texas, and Virginia

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ARTICLE INFORMATION

ABSTRACT

In many parts of the world, limited water and climate change are significant challenges to the future of peanut production, and much work remains in developing heat- and drought-tolerant cultivars. To this end, we evaluated 21 accessions of the U.S. peanut mini-core under water-limited conditions in 2018 and 2019 in Oklahoma, Texas, and Virginia. These accessions were identified as potentially exhibiting phenotypic extremes for ten drought stress traits, and therefore may be useful for identifying genetic markers associated with drought tolerance. Results indicated that plant wilting and paraheliotropism (leaf folding) were less affected by genotype by environment interactions than SCMR (SPAD chlorophyll meter readings), flower counts, yield, TSMK (total sound mature kernels), and seed weight. No differences among genotypes were observed with canopy temperature, canopy temperature depression, or NDVI (normalized difference vegetation index). Paraheliotropism was moderately correlated ($|r|$ = 0.40 to 0.52, $P < 0.01$) with SCMR and flower counts in the Southwest; SCMR was also correlated with yield and TSMK (r = 0.48, $P < 0.01$). Despite environmental differences between subhumid Virginia and the semiarid Southwest, the locations shared genotypes at the extremes for most traits. This information may be useful for future studies by highlighting traits associated with drought tolerance that may be more stable in different production environments, as well as divergent genotypes for those traits.

INTRODUCTION

Climate change and limited water are significant challenges to the future of peanut production. In the southwestern U.S. peanut production area, an estimated 35% of the southern High Plains will not be able to support irrigated agriculture within 30 years at current depletion rates of the Ogallala Aquifer (Scanlon *et al.*, 2012). In addition, global warming is expected to add additional demands on the aquifer (Rosenberg *et al.*, 1999). Recurring and severe droughts have also occurred in the southeastern U.S. (Branch and Kvien, 1992; Strzepek *et al.*, 2010), which produced 65% of U.S. peanuts from 1980-2019 (USDA-ERS, 2021). The importance of drought-tolerant peanuts also extends beyond producing profitable yields under

limited water. Higher levels of aflatoxin contamination are observed under drought conditions (Sanders *et al.*, 1985; Holbrook *et al.*, 2000, 2009; Arunyanark *et al.*, 2009, 2010; Girdthai *et al.*, 2010). Despite this, few drought-tolerant peanut cultivars are available.

In peanut, up to 153 marker-trait associations and quantitative trait loci associated with drought-tolerance have been identified, but many of them have minor effects (Ravi *et al.*, 2011; Gautami *et al.*, 2012; Pandey *et al.*, 2014, 2021). Multiple physiological processes mediate drought tolerance, making breeding and phenotyping for this trait especially difficult (Cattivelli *et al.*, 2008; Ravi *et al.*, 2011). Yield and seed quality traits, such as shelling percentage and 100-seed weight, are frequently used to assess drought resistance (Nageswara Rao *et al.*, 1989; Branch and Kvien, 1992; Faye *et al.*, 2015; Pandey *et al.*, 2021). However, yield data are difficult to procure for large mapping populations (Nigam *et al.*, 2005) and may be less reliable as an indicator for multiple locations due to significant genotype x environment interactions (Arunyanark *et al.*, 2008). As a result, surrogate physiological traits associated with drought tolerance are now used to screen larger numbers of genotypes (Pandey *et al.*, 2014, 2021).

Soil plant analysis development measurement (SPAD) or SPAD chlorophyll meter readings (SCMR) are one of the most widely measured physiological traits, perhaps due to the ease of data collection (Upadhyaya, 2005; Rowland and Lamb, 2005; Lal *et al.*, 2006; Arunyanark *et al.*, 2008; Songsri *et al.*, 2008; Balota *et al.*, 2012; Singh *et al.*, 2014; Luis *et al.*, 2016). Several studies with peanut have demonstrated SCMR as a relatively stable trait that correlates well with transpiration efficiency, a trait generally regarded as a reliable indicator of drought tolerance, but one that is difficult to measure on a large scale (Nageswara Rao *et al.*, 2001; Upadhyaya, 2005; Sheshshayee *et al.*, 2006; Arunyanark *et al.*, 2008). Canopy temperature, canopy temperature depression (CTD), and normalized difference vegetation index (NDVI) have also been used for phenotyping drought tolerance (Rucker *et al.*, 1995; Holbrook

et al., 2000; Jongrungklang *et al.*, 2008; Nautiyal *et al.*, 2008; Balota *et al.*, 2012; Singh *et al.*, 2014; Luis *et al.*, 2016). Visual indicators of drought stress, such as wilting and leaf color were significantly correlated with aflatoxin contamination (Holbrook *et al.*, 2000; Luis *et al.*, 2016) and are also promising as surrogate traits. Lastly, another visible trait, leaf folding or paraheliotropism, is an adaptation present in some peanut genotypes to reduce solar radiation under drought stress (Matthews *et al.*, 1988; Chapman *et al.*, 1993).

To be useful for peanut breeding, genotypes at the phenotypic extremes of these surrogate traits need to be identified (Shekoofa *et al.*, 2013). Preliminary work identified candidate accessions with divergent phenotypes from the U.S. mini-core. The goal of this project was to evaluate the accessions in three peanut production environments, spanning subhumid southeastern Virginia to semiarid southwestern Oklahoma and the southern Texas High Plains.

MATERIALS AND METHODS

A total of 21 core collection (CC) accessions from the U.S. mini-core collection, in addition to seven reference genotypes, were evaluated in 2018 and 2019 in Oklahoma, Texas, and Virginia (Table 1). The 21 accessions were selected from a 2017 study of the broader mini-core because they exhibited divergent phenotypes for traits associated with drought tolerance (data unpublished). The seven reference genotypes included the following: runner breeding line C76-16 (Holbrook *et al.*, 2013) and cv. Tamrun OL11 (Baring *et al.*, 2013); Spanish cv. Tamspan 90 (Smith *et al.*, 1991); Valencia cvs. New Mexico Valencia C (Hsi, 1980) and TamVal OL14 (Burow *et al.*, 2019); and Virginia cvs. Walton (Balota *et al.*, 2021; tested as 08X09-3-14-1) and Wynne (Plant Variety Protection 201500288). C76-16 (Holbrook *et al.*, 2013; Luis *et al.*, 2016; Bhogireddy *et al.*, 2020; Wang *et al.*, 2021) and Walton (Balota *et al.*, 2021) have demonstrated drought tolerance, and New Mexico Valencia C (Bhogireddy *et al.*, 2020) was recently shown to have poor drought tolerance.

Table 1. Reference peanut genotypes and characteristics of U.S. mini-core genotypes selected for traits associated with drought tolerance in Oklahoma, Texas, and Virginia.

Genotype[a]	PI No.	Subspecies[b]	SCMR[c]	Flowers[c]	Fold[c]	Wilt[c]	CT[c]	CTD[c]	NDVI[c]	Yield
C76-16	—	*hypogaea*	—	—	—	—	—	—	—	—
New Mexico Valencia C	565461	*fastigiata*	—	—	—	—	—	—	—	—
Tamrun OL11	665017	*hypogaea*	—	—	—	—	—	—	—	—
Tamspan 90	550721	*fastigiata*	—	—	—	—	—	—	—	—
TamVal OL14	689039	*fastigiata*	—	—	—	—	—	—	—	—
Walton	695073	*hypogaea*	—	—	—	—	—	—	—	—
Wynne	674760	*hypogaea*	—	—	—	—	—	—	—	—
CC053	493729	*fastigiata*	—	Lowd	—	High	—	—	High	—
CC068	493880	*fastigiata*	—	—	Low	—	—	—	—	—

Table 1. Reference peanut genotypes and characteristics of U.S. mini-core genotypes selected for traits associated with drought tolerance in Oklahoma, Texas, and Virginia.

Genotype[a]	PI No.	Subspecies[b]	SCMR[c]	Flowers[c]	Fold[c]	Wilt[c]	CT[c]	CTD[c]	NDVI[c]	Yield
CC075	493938	*fastigiata*	—	—	Low	High	—	—	Low	Low
CC080	494018	*fastigiata*	Low	High	—	—	Low	—	—	—
CC112	497517	*fastigiata*	Low	—	—	High	—	—	—	High
CC157	502120	erect	—	—	High	—	—	—	—	Mid
CC189	339960	erect	—	Low	Low	—	Low	—	—	—
CC208a	274193	spreading and bunch, bunch	High	—	—	—	—	—	—	Low
CC230	290594	spreading, bunch	—	—	—	—	—	Low	—	Mid
CC246	343398	spreading and bunch	Low	High	—	High	—	Low	—	High
CC342	298854	spreading	—	—	High	—	High	—	High	High
CC388	162655	erect	—	—	—	Low	Low	—	—	High
CC458	268996	spreading	Low	High	High	—	Low	High	—	—
CC529	319768	spreading and bunch, bunch	High	Low	High	—	Low	—	—	—
CC535	296558	bunch	—	—	—	—	—	—	High	—
CC546	259836	spreading and bunch	Low	—	—	—	—	Low	—	Low
CC553	157542	bunch	High	—	—	—	—	Low	—	—
CC588	403813	erect	Low	High	Low	High	—	Low	—	Low
CC650	478819	erect	—	—	High	Low	—	—	—	High
CC678	476636	spreading and bunch	—	Low	—	—	—	High	Low	—
CC812	323268	spreading and bunch	High	Low	High	—	High	—	High	High

[a] Seven reference genotypes and 21 U.S. mini-core accessions (listed by core collection number). CC208 not planted in Texas in 2018.

[b] Subspecies listed by the U.S. National Plant Germplasm System GRIN-Global online database (https://npgsweb.ars-grin.gov/gringlobal/search). Growth habit (erect, spreading-bunch, bunch) listed by GRIN given for PIs without subspecies information.

[c] Drought resistance-associated traits: soil plant analysis development chlorophyll meter reading (SCMR) chlorophyll, leaf folding (paraheliotropism), plant wilting, flower production, canopy temperature (CT), canopy temperature depression (CTD), and normalized difference vegetation index (NDVI).

[d] Trait classes were determined in separate 2017 study of the mini-core in the three states (unpublished data).

In Oklahoma, the experiments were conducted at Oklahoma State University's Caddo Research Station in Fort Cobb. In 2018, entries were planted in a randomized complete block design (RCBD) with four replications/blocks on 18 May. Half of the field was harvested at 134 days after planting (DAP) on 28 September; the remainder was harvested two weeks later on 12 October. In 2019, entries were planted on 17 May using a RCBD, however, three blocks were in a water-restricted field, and two blocks were in a field with normal irrigation. The irrigated field was harvested 141 DAP, but due to logistical and weather delays, the water-restricted field was harvested 172 DAP. In Texas, the experiments were conducted at the USDA-ARS Cropping Systems Research Laboratory in Lubbock. Entries were planted using a RCBD with four blocks in 2018

and 2019 under water-deficit conditions. Planting and harvest dates were 17 May and 8 November (176 DAP) in 2018 and 14 May and 17/18 October (157-158 DAP) in 2019, respectively. In Virginia, the experiment was conducted at Virginia Tech's Tidewater Agricultural Research and Extension Center (TAREC) in Tidewater. Three blocks arranged in a RCBD were each planted in an irrigated field and a water-restricted field. Rain-out shelters covered the water-restricted fields from 16 July 2018 and 15 July 2019 for 6 weeks and were removed on 30 August 2018 and 27 August 2019. In 2018, the irrigated plots were planted on 17 May and harvested on 9 September (116 DAP), and the water-restricted plots were harvested at 125 DAP. Planting and harvest dates in 2019 were 30 April and 10 September (134 DAP). Plots in all states were managed for weeds and diseases following their respective University Extension recommendations. In all states, water-restricted plots were irrigated to 25% evapotranspiration (ET) replacement from approximately 40 to 105 DAP (weather permitting in Oklahoma and Texas). This growth period includes the pod-filling stage (Boote, 1982), a time that is especially susceptible to water stress (Nageswara Rao *et al.*, 1985, 1989).

Ten traits associated with drought resistance were measured, but the specific traits measured varied among states depending on equipment availability and labor (Table 2). SCMR readings were taken by recording the mean from four representative plants in each plot. The 4th fully expanded leaf from the top of the mainstem of each of four plants was measured in Oklahoma and Virginia; the 4th fully expanded leaf from lateral branches were measured in Texas. SCMR readings were taken with a SPAD 502 Plus (Spectrum Technologies, Aurora, IL) in Oklahoma, and a SPAD-502 (Minolta, Tokyo, Japan) in Texas and Virginia. In Oklahoma and Texas, fresh, non-wilted flowers were counted in the morning within a representative 1.86-m section inside each plot (Oklahoma) or within the entire plot (Texas). An Agri-Therm II (model 100L, Everest Interscience, Chino Hills, CA) was used to measure afternoon (13:00 to 16:00) canopy temperature and canopy temperature depression (CTD). Normalized difference vegetation index (NDVI) was measured in Texas and Virginia with the GreenSeeker Handheld Crop Sensor (Trimble Agriculture, Sunnyvale, CA). In Oklahoma and Texas, paraheliotropism was rated in the afternoon using the following scale: 0, no folding; 1, 10% leaves folded; 2, 30% leaves folded; 3, 50% leaves folded; 4, 70% folded; 5, 90% folded; and 6, 90% folded but with leaves closed tightly and puckered around leaf margins. Plant wilting was also rated in the afternoon with the following scale in Oklahoma and Texas: 1, no wilting; 2, 25% of plants wilted; 3, 50% wilted; 4, 75% wilted; and 5, 100% leaves wilted and ca. 50% leaves brown for >90% plants within plot. In Virginia, a wilting scale from 0-5 was used (Sarkar *et al.*, 2021). After harvest, pods were dried in a forced-air dryer to approximately 7% moisture by weight and separated from soil and plant debris with a peanut cleaner. One 200-g sample of pods from each plot was used to determine the percentage of total sound mature kernels (TSMK) following USDA-AMS (2019) guidelines. To simplify grade collection from diverse genotypes, TSMK for all entries was determined using the smallest screen for Spanish/Valencia kernels (5.94-mm x 19.05-mm (15/64 x 3/4 inch) slots) in Oklahoma and Virginia.

Table 2. Data collection times for traits associated with drought tolerance.

| | Weeks After Planting[a] | | | | | |
| | Oklahoma | | Texas | | Virginia | |
Trait[b]	2018	2019	2018	2019	2018	2019
SCMR	7, 9, 11, 15	8, 9, 11, 13	9, 11, 13, 15	10, 13, 16	9 (D), 10(W), 13	—
Flower Counts	7, 9, 11	8, 9, 11, 13	9, 11, 13, 15	10, 13, 16	—	—
Canopy Temperature	—	—	9, 11, 13, 15	10, 13, 16	—	—
CTD	—	—	—	—	4, 5, 7, 10 (D)	6, 7, 9, 13, 14, 15, 16
NDVI	—	—	13, 15	10, 13, 16	4, 5, 6, 7, 9 (W), 10, 13 (W), 15 (D), 16 (D)	4, 6, 7, 9, 13, 14, 15, 16
Paraheliotropism	7, 9, 10, 15	9, 11, 13	9, 11, 13, 15	10, 13, 16	—	—
Wilting	7, 9, 10, 15	9, 11, 13	11, 13	16	5,7, 9 (D), 10 (D), 13, 14, 15 (D), 16(D)	9, 13, 14, 15, 16
Yield/Seed[c]	134, 148	141 (W), 172 (D)			116 (W), 126 (D)	134

[a] In Virginia and Oklahoma, drought-treatment plots (D) or irrigated plots (W) only.

[b] SCMR, soil plant analysis development chlorophyll meter reading; CTD, canopy temperature depression; NDVI, normalized difference vegetation index.

Table 2. Data collection times for traits associated with drought tolerance.

	Weeks After Planting[a]					
	Oklahoma		Texas		Virginia	
Trait[b]	2018	2019	2018	2019	2018	2019

[c] Days after planting (digging date) for yield and seed traits (% total sound mature kernels and grams per 100 seed).

Temperature and rainfall were monitored using the Fort Cobb Oklahoma Mesonet station at the Caddo Research Station (McPherson *et al.*, 2007), the Plant Stress & Water Conservation Meteorological Tower at ARS-Lubbock (https://www.ars.usda.gov/plains-area/lubbock-tx/cropping-systems-research-laboratory/wind-erosion-and-water-conservation-research/docs/pswc-met-tower-data/), and the WeatherStem system at TAREC (http://vt-arec.weatherstem.com/arec115). Degree day heat units were calculated using the West Texas method 1 formula for peanut (Rowland *et al.*, 2006)(Figure 1):
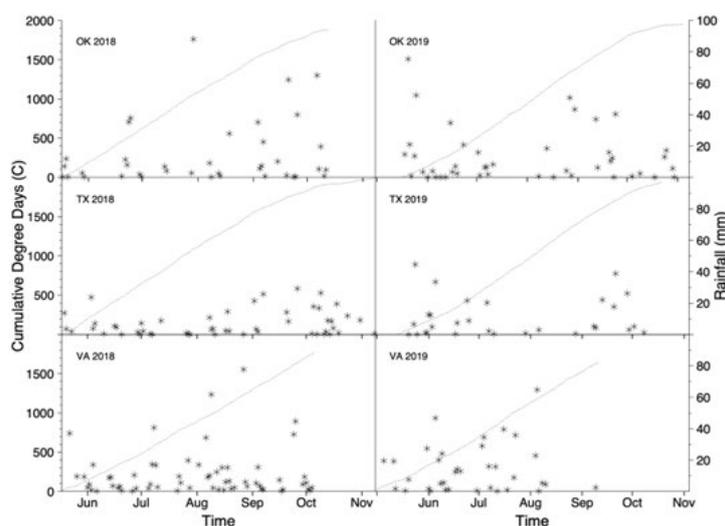

Figure 1. Rainfall events (asterisks)(supplemental irrigation not included) and cumulative degree days (dotted line) between planting and digging in Oklahoma, Texas, and Virginia in 2018 and 2019. Rainout shelters were used only in Virginia for the water-restricted plots.

Degree Day = $(AT_{max35} + AT_{min12.8})/2 - 12.8$

where AT_{max35} and $AT_{min12.8}$ are the maximum and minimum air temperatures capped at 35C and 12.8C, respectively.

Data were analyzed with SAS version 9.4 (SAS Institute, Cary, NC). To account for environmental differences between years and among states (environments), cumulative degree day was tested as a covariate in all analyses. Differences among genotypes and environments for drought-associated traits were estimated using mixed-model ANOVA with PROC MIXED. Fixed effects included state, genotype, year, and block; year*block was used as the random effect. The SLICE option was used to examine the effects of state and genotype. For flower count data, the sum of flowers counted each season per plot was used for the analyses to minimize the effect of genetic differences in flowering times among genotypes. Similarly, differences among genotypes and water treatments (irrigated and water-deficit) in Oklahoma and Virginia were also examined with PROC MIXED. Pearson's correlations among traits collected from the water-restricted plots in all states and years were calculated using the raw data with PROC CORR.

RESULTS AND DISCUSSION

Since rainout shelters were not available in Oklahoma and Texas, water-restricted plots were exposed to rain. However, rainfall events greater than 20 mm were relatively rare between 40 and 105 DAP in both years, when deficit irrigation was imposed (Figure 1). The following range of cumulative degree days between 40 and 105 DAP were observed: 561-1493 and 429-1374 in Oklahoma, 582-1529 and 420-1384 in Texas, and 426-1269 and 428-1277 in Virginia in 2018 and 2019, respectively (Figure 1). In 2018 in Virginia, irrigated plots were harvested early (116 DAP) due to severe disease outbreaks of late leaf spot, southern blight, and Sclerotinia blight (caused by *Nothopassalora personata*, *Athelia rolfsii*, and *Sclerotinia*

minor, respectively). In 2019, plants in the water-restricted plots in Oklahoma were killed by an early freeze (22 October) 13 days before digging.

Comparisons Among Water-restricted Plots in Oklahoma, Texas, and Virginia

For all analyses comparing drought-associated traits within the water-restricted plots, the effect of cumulative degree day was highly significant (P < 0.01), validating its use as a covariate. In the analyses of SCMR readings (Table 3), states and genotypes differed in SCMR (P < 0.01), as well as the genotype*environment interaction (F = 1.77, P < 0.01), which indicated that mean SCMR values for genotype varied with state. For all genotypes, SCMR readings were highest in Texas and lowest in Virginia, perhaps due to differences in SCMR

meter models (Huang and Peng, 2004), the time of day the data were collected (Arunyanark *et al.*, 2008), or plant water status (Martínez and Guiamet, 2004). Despite the significant genotype*environment interaction, common genotypes occupied the top five lowest and highest SCMR in all states: CC546, CC080, and New Mexico Valencia C had low SCMR; Tamrun OL11, CC678, and CC529 had high SCMR. In the wilt analyses, genotype (F = 4.04, P < 0.01) had a significant effect on wilting across states, but the effects of state (P = 0.7) and genotype*environment interaction (P = 0.1) were not significant. While genotype had a significant effect across states, no significant differences in wilting among genotypes were observed in Texas, contributing to the near-statistically significant genotype*environment interaction. CC053 had the highest wilt scores in all states, and CC535 and Walton were among the least wilted genotypes in Oklahoma and Virginia.

Table 3. SCMR and plant wilting data from water-restricted plots in Oklahoma, Texas, and Virginia in 2018 and 2019.

Genotype[a]	SCMR[b]					Plant Wilting[d]					
	OK		TX		VA		P[c]	OK		TX	VA
C76-16	47.5	a-b	51.0	a-c	43.3	a-b	0.42	1.4	g-j	1.9 a	1.4 e-f
NMValC	42.5	h-i	45.3	f-g	31.4	h-k	0.53	2.0	a-f	2.0 a	2.2 a
TROL11	48.4	a	51.5	a	42.0	a-c	0.21	1.6	d-j	2.1 a	2.1 a-b
TS90	46.7	a-c	48.7	c-e	39.5	b-e	0.16	1.7	c-j	1.6 a	2.0 a-c
TVOL14	45.1	c-f	48.7	c-e	35.4	e-i	0.75	1.8	c-i	1.8 a	1.8 a-e
Walton	45.0	c-f	49.8	a-d	42.0	a-c	0.28	1.4	h-j	1.9 a	1.3 f
Wynne	45.1	c-f	50.4	a-d	42.2	a-c	0.39	1.4	h-j	2.0 a	1.6 c-e
CC053	43.6	e-i	45.5	f-g	30.4	j-k	0.48	2.5	a	2.5 a	2.2 a
CC068	45.0	c-f	46.4	e-f	35.2	e-j	0.59	2.0	a-g	1.8 a	1.8 a-e
CC075	43.6	e-i	45.6	f-g	32.7	g-k	0.46	2.0	a-e	1.8 a	2.0 a-c
CC080	42.1	i	44.8	f-g	31.4	h-k	0.74	2.0	a-e	1.9 a	2.0 a-c
CC112	43.0	f-i	44.9	f-g	32.4	g-k	0.69	2.2	a-c	2.2 a	2.1 a-b
CC157	41.8	i	44.5	f-g	36.6	d-g	0.20	2.0 a-e		1.6 a	1.9 a-d
CC189	42.6	g-i	45.5	f-g	36.1	d-h	0.03	2.4	a-b	1.8 a	2.1 a-b
CC208	48.4	a	50.4	a-d	39.2	b-e	0.05	1.5	e-j	1.7 a	2.1 a-b
CC230	45.1	c-f	50.8	a-c	35.6	d-h	0.18	1.9	b-h	1.6 a	2.1 a-b
CC246	45.3	b-e	50.0	a-d	36.4	d-g	0.04	1.7	d-j	2.4 a	1.5 d-f
CC342	45.4	b-e	51.2	a-b	40.0	a-e	0.96	1.7	c-j	1.8 a	1.7 b-e
CC388	44.4	d-h	48.1	d-e	33.8	f-k	0.23	2.1	a-d	2.4 a	1.8 a-e
CC458	44.7	c-g	50.2	a-d	41.6	a-c	0.64	1.2	j	1.6 a	1.5 c-e
CC529	48.4	a	51.3	a	42.5	a-c	0.02	1.4	h-j	1.4 a	2.0 a-c
CC535	45.7	b-e	48.9	b-d	39.8	a-e	0.72	1.3	i-j	1.8 a	1.4 e-f
CC546	41.6	i	44.0	g	29.1	k	0.34	2.1	a-e	2.3 a	1.8 a-e

Table 3. SCMR and plant wilting data from water-restricted plots in Oklahoma, Texas, and Virginia in 2018 and 2019.

Genotype[a]	SCMR[b]					Plant Wilting[d]					
	OK		TX		VA		P[c]	OK		TX		VA
CC553	48.1	a	49.6	a-d	37.9	c-f	0.14	1.5	f-j	1.7	a	1.1	f
CC588	42.3	h-i	45.6	f-g	30.7	i-k	0.76	2.0	a-f	2.1	a	2.2	a-b
CC650	45.4	b-e	50.4	a-d	38.3	c-f	0.75	1.5	e-j	1.8	a	1.5	d-f
CC678	48.4	a	51.7	a	44.4	a	0.40	1.6	d-j	2.0	a	1.5	d-f
CC812	46.7	a-d	50.9	a-c	40.3	a-d	0.57	1.5	f-j	1.8	a	1.8	a-e
No. Obs.	784		687		168			784		328		1007

[a] NMValC, New Mexico Valencia C; TROL11, Tamrun OL11; TS90, Tamspan 90; TVOL14, TamVal OL14. Genotypes with the same lowercase letter within columns are not significantly different ($P < 0.05$).

[b] SCMR, soil plant analysis development chlorophyll meter reading. Virginia SCMR data collected in 2018 only.

[c] P-values for wilting scores for genotypes among states. For SCMR, all genotypes signfiicant ($P < 0.01$).

[d] Plant wilting rated using the following scale in Oklahoma and Texas: 1, no wilting; 2, 25% of plants wilted; 3, 50% wilted; 4, 75% wilted; and 5, 100% leaves wilted and ca. 50% leaves brown for >90% plants within plot. In Virginia, wilting was rated on a scale from 0 to 5 (Sarkar et al., 2021).

Paraheliotropism and flower count data were collected from Oklahoma and Texas (Table 4). State ($F = 136.13$, $P < 0.01$) and genotype ($F = 23.68$, $P < 0.01$) had significant effects on paraheliotropism scores, but the interaction between the two effects was not significant ($P = 0.65$). Paraheliotropism scores were generally higher in Texas than in Oklahoma. Leaf folding in alfalfa was shown to vary depending on ambient vapor pressure deficit (Reed and Travis, 1987), and the lower humidity in West Texas despite similar daily maximum temperatures to Oklahoma may have resulted in more paraheliotropism. In both states, the least paraheliotropism was observed in CC189, and genotypes exhibiting the most leaf folding included CC678, CC342, and Walton. For flower counts, state ($F = 312.7$), genotype ($F = 10.3$), and the genotype*environment interaction ($F = 2.45$) had highly significant effects ($P < 0.01$) on the total number of flowers counted. More flowers were counted in Oklahoma than in Texas for 21 of the 28 genotypes (Table 4). In Texas, large numbers of flowers were observed following rainfall or irrigation in 2019 (data not shown), but few were observed on

Table 4. Paraheliotropism scores and flower counts from water-restricted plots in Oklahoma and Texas in 2018 and 2019

Genotype[a]	Paraheliotropism[c]					Total Flowers/m[d]				
	P[b]	OK		TX		P	OK		TX	
C76-16	0.03	3.8	a-e	4.8	a-b	<0.01	40.9	b-f	26.9	d-i
NMValC	<0.01	2.1	i-l	3.6	d-e	<0.01	32.7	e-i	15.7	j-l
TROL11	0.03	3.4	c-f	4.5	b-c	<0.01	43.5	b-e	39.8	a-c
TS90	0.36	3.2	e-g	3.9	c-e	<0.01	47.7	b-c	25.5	d-i
TVOL14	<0.01	2.3	i-k	3.6	d-e	<0.01	32.9	e-i	18.3	h-l
Walton	0.25	4.2	a-b	4.9	a-b	<0.01	23.1	h-j	16.2	i-l
Wynne	<0.01	3.8	a-e	5.2	a	<0.01	22.9	h-j	22.4	f-k
CC053	<0.01	1.9	k-l	3.3	e-g	<0.01	22.3	i-j	13.8	k-l
CC068	0.20	2.2	i-l	2.9	f-g	<0.01	24.9	g-j	9.4	l
CC075	<0.01	2.4	h-k	3.9	c-d	<0.01	50.2	b	33.1	b-f
CC080	0.04	2.7	g-i	3.7	d-e	<0.01	69.4	a	47.8	a
CC112	0.01	2.2	i-k	3.4	d-f	<0.01	29.9	f-i	21.4	f-k
CC157	0.14	2.9	f-h	3.8	d-e	<0.01	30.5	f-i	39.0	a-c
CC189	0.03	1.6	l	2.6	g	<0.01	15.0	j	9.3	l
CC208	0.13	3.9	a-d	4.8	a-b	<0.01	28.2	g-i	20.1	g-k
CC230	0.01	3.4	c-f	4.7	a-b	<0.01	33.8	e-i	43.3	a-b

Table 4. Paraheliotropism scores and flower counts from water-restricted plots in Oklahoma and Texas in 2018 and 2019

Genotype[a]	Paraheliotropism[c]					Total Flowers/m[d]				
	P[b]	OK		TX		P	OK		TX	
CC246	0.04	3.4	c-f	4.4	b-c	<0.01	27.4	g-i	30.4	c-g
CC342	0.03	4.0	a-c	5.1	a	<0.01	34.3	d-h	36.7	a-d
CC388	<0.01	2.3	i-k	3.9	c-e	<0.01	49.2	b	31.3	c-g
CC458	0.03	3.7	b-e	4.8	a-b	<0.01	28.5	g-i	35.7	b-e
CC529	0.15	3.9	a-d	4.7	a-b	<0.01	36.2	c-g	29.0	c-h
CC535	0.01	3.6	c-e	4.8	a-b	<0.01	34.0	d-i	32.5	b-g
CC546	<0.01	2.0	j-l	3.6	d-e	<0.01	35.2	d-g	31.5	c-g
CC553	<0.01	2.2	i-l	3.7	d-e	<0.01	45.9	b-d	37.1	a-d
CC588	<0.01	2.4	h-k	3.7	d-e	<0.01	32.3	e-i	23.5	e-j
CC650	0.02	3.3	d-g	4.4	b-c	<0.01	34.2	d-h	27.9	c-h
CC678	0.45	4.4	a	5.0	a-b	<0.01	23.0	h-j	29.5	c-g
CC812	<0.01	3.4	c-f	4.8	a-b	<0.01	26.0	g-j	30.3	c-g
No. Obs.		700		768			700		768	

[a] NMValC, New Mexico Valencia C; TROL11, Tamrun OL11; TS90, Tamspan 90; TVOL14, TamVal OL14. Genotypes with the same lowercase letter within columns are not significantly different (P < 0.05).

[b] P-values for comparisons between states within entry.

[c] Paraheliotropism scored using the following scale: 0, no folding; 1, 10% leaves folded; 2, 30% leaves folded; 3, 50% leaves folded; 4, 70% folded; 5, 90% folded; and 6, 90% folded but with leaves closed tightly and puckered around leaf margins. OK/TX,

[d] Total number of flowers counted per meter over four collection dates each year in Oklahoma and four and three dates in 2018 and 2019 in Texas, respectively.

actual data collection dates in Texas. Nonetheless, both states shared genotypes with the highest (CC80) and fewest (CC189) flower counts when grown under drought stress.

NDVI and canopy temperature data were collected in Texas and Virginia (Table 5). State ($F = 20.0$, P < 0.01) had a significant effect on NDVI, but no differences among genotypes or a genotype*environment interaction were observed (P ≥ 0.93). In addition, no differences among genotypes were observed for canopy temperatures collected in Texas ($F = 0.81$, P = 0.74) or CTD collected in Virginia ($F = 1.38$, P = 0.10). Canopy temperature meters focused on relatively narrow sections of plots, and considerable variability was observed within plots in Texas (data not shown). Thus, imaging systems capable of obtaining mean temperatures from entire plots might be more useful.

Table 5. Normalized difference vegetation index (NDVI), canopy temperature (CT; TX), and canopy temperature differential (CTD; VA) from water-restricted plots in Texas and rainout-shelter plots Virginia in 2018 and 2019.

Genotype[a]	NDVI					CT (°C)		CTD	
	P[b]	TX		VA		TX		VA	
C76-16	0.09	0.801	a	0.672	a	44.0	a	-0.67	a
NMValC	0.02	0.790	a	0.635	a	44.5	a	-0.23	a
TROL11	0.01	0.803	a	0.643	a	44.6	a	0.35	a
TS90	0.61	0.780	a	0.695	a	43.1	a	-0.93	a
TVOL14	0.86	0.776	a	0.716	a	43.5	a	-1.01	a
Walton	0.10	0.806	a	0.679	a	44.3	a	-0.43	a
Wynne	0.15	0.807	a	0.688	a	44.4	a	-0.27	a
CC053	0.12	0.796	a	0.673	a	44.2	a	-0.59	a
CC068	0.34	0.812	a	0.710	a	43.7	a	-0.96	a
CC075	0.85	0.768	a	0.709	a	43.9	a	-1.15	a
CC080	0.17	0.811	a	0.694	a	43.3	a	-0.76	a

Table 5. Normalized difference vegetation index (NDVI), canopy temperature (CT; TX), and canopy temperature differential (CTD; VA) from water-restricted plots in Texas and rainout-shelter plots Virginia in 2018 and 2019.

Genotype[a]	NDVI					CT (°C)		CTD	
	P[b]	TX		VA		TX		VA	
CC112	0.29	0.788	a	0.683	a	44.0	a	-1.03	a
CC157	0.83	0.787	a	0.713	a	43.8	a	-1.21	a
CC189	0.13	0.795	a	0.672	a	43.7	a	-0.83	a
CC208	0.69	0.788	a	0.694	a	44.3	a	-0.54	a
CC230	0.04	0.805	a	0.662	a	43.9	a	-0.01	a
CC246	0.34	0.794	a	0.693	a	44.4	a	-0.59	a
CC342	0.31	0.785	a	0.681	a	44.8	a	-0.54	a
CC388	0.52	0.754	a	0.664	a	44.5	a	-0.36	a
CC458	0.87	0.792	a	0.720	a	45.0	a	-0.58	a
CC529	0.79	0.774	a	0.698	a	43.5	a	-0.73	a
CC535	0.22	0.811	a	0.699	a	43.0	a	-0.77	a
CC546	0.72	0.750	a	0.670	a	43.5	a	-0.51	a
CC553	0.40	0.787	a	0.689	a	43.1	a	-0.38	a
CC588	0.14	0.799	a	0.678	a	44.0	a	-0.33	a
CC650	1.00	0.776	a	0.710	a	44.0	a	-0.84	a
CC678	0.28	0.814	a	0.708	a	44.1	a	-0.76	a
CC812	0.34	0.821	a	0.720	a	44.0	a	-0.40	a
No. Obs.		552		1260		739		1092	

[a] NMValC, New Mexico Valencia C; TROL11, Tamrun OL11; TS90, Tamspan 90; TVOL14, TamVal OL14. Genotypes with the same lowercase letter within columns are not significantly different (P < 0.05).

[b] P-values for NDVI comparisons between states within entry.

Yield, grade, and seed weights were collected from plots in Oklahoma and Virginia (Table 6). Under water-limited conditions, the effects of state and genotype on yield and seed weights were highly significant (P < 0.01). For TSMK, the effect of state was not significant (P = 0.18) though genotype was significant (P < 0.01). However, the genotype*environment interactions were also significant for all traits (P < 0.01). Maximum yields under drought conditions were similar in both Oklahoma and Virginia, ca. 3200-3300 kg/ha. Yields from C76-16 and Walton were among the top five numerically, but the lowest yields were produced by different genotypes in each state (Table 6). The states also had few genotypes in common for the highest and lowest total sound mature kernels. Seed weight was more consistent between the two locations: Wynne, Walton, C76-16, and CC342 were among the heaviest seed, and CC075, CC080, and CC112 were among the lightest.

Table 6. Yield, total sound mature kernels (TSMK), and seed weights from water-restricted plots in Oklahoma and rainout-shelter plots in Virginia in 2018 and 2019.

Genotype[a]	Yield (kg/ha)				TSMK[c]				g/100 seeds				
	P[b]	OK		VA		P[b]	OK		VA		P[b]	OK	VA
C76-16	<0.01	3309	a	3205	a	0.17	60.5	h	63.0	a-d	<0.01	62.5	a-b	73.4	b-c
NMValC	<0.01	1906	g-k	1714	f-m	0.86	56.9	a-e	64.0	a-d	0.08	49.7	e-j	46.8	h-k
TROL11	<0.01	2685	a-e	2125	d-k	0.59	60.3	a-e	68.8	a-b	0.00	54.9	b-g	58.9	e-g
TS90	0.39	1728	h-k	2398	c-g	0.27	55.6	a-d	67.4	a-b	0.10	49.9	e-j	46.4	h-k
TVOL14	0.05	2247	d-j	2487	a-e	0.09	58.5	a-c	59.8	c-f	0.01	50.2	e-j	50.7	g-i

Table 6. Yield, total sound mature kernels (TSMK), and seed weights from water-restricted plots in Oklahoma and rainout-shelter plots in Virginia in 2018 and 2019.

Genotype[a]	Yield (kg/ha)			TSMK[c]			g/100 seeds		
	P[b]	OK	VA	P[b]	OK	VA	P[b]	OK	VA
Walton	0.03	2999 a-c	3165 a-b	0.69	61.4 a-b	67.7 a-b	<0.01	58.1 a-d	86.9 a
Wynne	0.01	2674 a-e	2730 a-d	0.01	66.1 a	63.3 a-d	<0.01	64.0 a	87.9 a
CC053	<0.01	1713 h-k	1550 h-m	0.41	57.2 h	61.8 b-e	0.22	48.4 f-k	43.2 i-k
CC068	0.40	1472 k	2792 a-d	0.64	54.5 g-h	64.0 a-d	0.02	44.9 i-k	44.4 h-k
CC075	0.21	1697 h-k	2212 c-j	0.37	53.3 g-h	64.3 a-d	0.01	42.0 k	42.6 i-l
CC080	<0.01	2596 b-g	1939 e-m	0.33	54.2 f-h	65.5 a-d	0.83	46.0 h-k	34.9 l
CC112	0.66	1488 k	2318 c-g	0.90	55.7 e-h	63.9 a-d	0.01	42.9 j-k	43.1 i-k
CC157	0.27	1720 h-k	2294 c-h	0.17	51.8 d-h	54.4 f	<0.01	47.0 h-k	49.9 h-j
CC189	0.01	1496 k	1491 i-m	0.88	51.9 d-h	59.1 d-f	0.03	50.5 d-i	49.2 h-j
CC208	<0.01	1961 f-k	1258 m	0.36	54.8 c-h	59.1 d-f	<0.01	49.9 e-j	52.2 f-h
CC230	<0.01	3038 a-b	1427 k-m	0.90	56.8 c-h	64.1 a-d	0.07	53.1 c-h	50.5 h-i
CC246	<0.01	2993 a-d	1470 j-m	<0.01	66.3 c-h	58.8 d-f	<0.01	56.1 a-e	76.7 b
CC342	<0.01	3340 a	1770 e-m	<0.01	60.2 c-h	53.6 f	<0.01	60.3 a-c	68.9 b-d
CC388	<0.01	2131 e-k	1660 g-m	0.16	56.6 c-h	69.5 a	0.01	47.9 g-k	48.9 h-k
CC458	<0.01	2317 c-i	1329 l-m	0.22	55.5 c-h	58.6 d-f	0.29	52.8 c-h	46.9 h-k
CC529	<0.01	2069 e-k	1390 k-m	0.14	52.6 c-h	65.8 a-d	0.19	46.8 h-k	41.9 j-l
CC535	<0.01	2650 a-f	1739 e-m	0.09	61.1 c-h	62.5 a-e	<0.01	60.1 a-c	66.7 c-e
CC546	0.12	1441 k	1839 e-m	0.22	54.4 c-h	66.7 a-c	0.01	46.3 h-k	47.4 h-k
CC553	0.16	1612 j-k	2066 d-l	0.18	56.2 c-h	68.9 a-b	<0.01	47.6 g-k	49.9 h-j
CC588	<0.01	1782 h-k	1470 j-m	0.41	53.5 b-h	64.6 a-d	0.35	46.6 h-k	40.0 k-l
CC650	0.63	1620 i-k	2432 b-f	0.71	58.6 b-h	67.7 a-b	<0.01	56.2 a-e	63.6 d-e
CC678	0.22	2379 b-h	2912 a-c	0.15	55.4 a-g	68.5 a-b	<0.01	55.1 b-f	59.1 e-f
CC812	<0.01	3301 a	2230 c-i	<0.01	61.0 a-f	55.3 e-f	<0.01	56.7 a-e	62.3 d-e

[a] NMValC, New Mexico Valencia C; TROL11, Tamrun OL11; TS90, Tamspan 90; TVOL14, TamVal OL14. Genotypes with the same lowercase letter within columns are not significantly different (P < 0.05). Number of observations: n = 196, Oklahoma; n = 168, Virginia.

[b] P-values for comparisons between states within entry.

[c] Total sound mature kernels (TSMK) determined using the smallest screen for Spanish/Valencia kernel s(5.94-mm x 19.05-mm slots).

Correlation analyses revealed few strong associations among drought-associated traits (Table 7). While genotypes did not differ in canopy temperature, the strongest correlation observed was between canopy temperature and total flower counts in Texas (r = -0.8). NDVI (r = 0.6) and paraheliotropism (r = -0.4) were also moderately correlated with flower counts. Paraheliotropism and SCMR were also moderately associated (r = 0.5). Several traits were significantly, albeit moderately,

Table 7. Pearson's correlations among traits associated with drought resistance from Oklahoma, Texas, and Virginia in 2018 and 2019.

Traits[a]	NDVI	CTD	CT	Wilt	Parahelio	SCMR	Flowers	Yield	TSMK	g/100 sd
NDVI	1	0.01	0.30**	0.04	-0.35**	0	0.64**	0.20*	-0.07	0.13
N[b]	1820	1008	560	1077	560	560	206	168	167	167
CTD		1	—	0.23**	—	—	—	-0.29*	0.10	-0.30**
N		1092	—	756	—	—	—	84	84	84
CT			1	0.11*	0.25**	0.32**	-0.80**	—	—	—
N			792	438	792	734	235	—	—	—
Wilt				1	-0.16**	0.02	0.15**	0.11	-0.01	-0.30**
N				2174	1167	1165	431	277	276	276
Parahelio					1	0.52**	-0.40**	0.31**	0.00	0.35**
N					1521	1322	431	194	194	194
SCMR						1	-0.24**	0.48**	0.48**	-0.28**
N						1686	431	194	194	194
Flowers							1	-0.02	-0.15*	-0.01
N							628	194	194	194
Yield								1	0.37**	0.08
N								361	361	361
TSMK									1	-0.25**
N									361	361
g/100 sd										1
N										361

[a] NDVI, normalized difference vegetation index (TX, VA); CTD, canopy temperature depression (VA); CT, canopy temperature (TX); plant wilting (OK, TX, VA); parahelio, paraheliotropism (OK, TX); SCMR, soil plant analysis development chlorophyll meter reading (OK, TX, VA); sum of flowers counted per season (OK, TX); yield, total sound mature kernels (TSMK), and grams per 100 seeds (OK, VA); —, no data.

[b] Number of observations

* Significant at *P ≤ 0.05, ** P ≤ 0.01

correlated with yield and seed-quality traits, the strongest of which was between yield and TSMK with SCMR (r = 0.48).

Comparisons Among Water-restricted and Irrigated Plots in Oklahoma and Virginia

To assess genotype responses to limited water in comparison to normal irrigation, analyses were conducted between water-restricted and irrigated plots in 2019 in Oklahoma and in both years in Virginia (Tables 8 and 9). In Oklahoma, no paraheliotropism and wilting data were collected from the irrigated plots because little leaf folding or wilting were observed under irrigation. The effect of cumulative degree day was significant only in the SCMR analysis (P < 0.01), so analysis of covariance was used only for this trait in Oklahoma. For SCMR, irrigation (F = 253.3) and genotype (F = 9.3) had significant effects (P < 0.01), and the irrigation*genotype interaction was not significant (P = 0.48). All genotypes had significantly higher SCMR values when grown under drought conditions than with normal irrigation. For flower counts, the water treatments did not have a significant effect (F = 2.1, P = 0.19), but both genotype and the genotype*water treatment interaction were significant (P < 0.01; Table 7). Seven genotypes (C76-16, CC157, CC208, CC458, CC553, CC650) produced significantly more flowers under irrigation

than when drought stressed. Conversely, New Mexico Valencia C, CC068, and CC112 produced more flowers under drought stress, and CC080 produced an equally high number of flowers under both water treatments. Meisner and Karnok (1992), taking daily flower counts, observed that flowering in Florunner could recover after being suppressed by drought. In our experiment, flower counts were taken on 3 d in 2018 and 4 d in 2019, so it is unclear if the three genotypes consistently produced many flowers over the duration of their flowering period. Unfortunately, the Oklahoma yield, TSMK, and seed weight data are confounded by a 31-d difference between harvest dates for the irrigated (141 DAP) and water-restricted plots (172 DAP), due in part to inclement weather. The early hard freeze in combination with the late harvest of the water-restricted plots likely had detrimental effects on yield and seed quality, particularly in early-maturing genotypes. Yield in Oklahoma was influenced by genotype (F = 11.4, P < 0.01) and genotype*water treatment (F = 3.3, P < 0.01), but the effect of the water treatment bordered on being significant (F = 4.8, P = 0.08). Yields from water-restricted plots ranged from 24% (CC553) to 91% (Wynne) of the irrigated plots (Table 8). For TSMK and seed weight, water treatment and genotype had significant effects (P < 0.05), but their interaction was not significant (P = 0.27 and 0.34, respectively; data not shown).

Table 8. Oklahoma total flower counts, SCMR, and yield in water-restricted (drought) and irrigated plots in 2019.

Genotype[a]	SCMR[b] Drought		Irrigated		P[c]	Total Flowers/m[d] Drought		Irrigated		P[c]	Yield (kg/ha)[e] Drought		Irrigated		%
C76-16	47.5	a-b	37.4	b-f	0.04	44.3	b-d	61.5	a-c	<0.01	3074	a	4774	a	64
New Mexico Valencia C	42.5	h-j	36.2	e-g	0.01	29.9	d-g	10.4	f	0.02	1320	f-h	2089	b-e	63
Tamrun OL11	48.4	a	42.4	a	0.62	46.8	a-e	52.2	a-d	<0.01	2062	b-g	3906	ab	53
Tamspan 90	46.7	a-c	39.4	a-e	0.02	42.5	b-f	61.5	a-c	<0.01	976	h	3689	a-d	26
TamVal OL14	45.1	c-f	36.7	d-f	0.63	29.7	d-g	35.0	a-f	<0.01	1664	c-h	3445	a-d	48
Walton	45.0	c-f	37.1	b-f	0.10	19.1	fg	33.4	a-f	0.13	2441	a-c	2957	a-e	83
Wynne	45.1	c-f	37.4	b-f	0.40	22.6	e-g	30.6	c-d	0.52	2206	b-e	2414	b-e	91
CC053	43.6	e-h	36.2	e-g	0.61	18.6	fg	24.1	c-f	0.01	850	h	1709	de	50
CC068	45.0	c-f	37.0	b-f	0.02	29.2	d-g	13.4	ef	0.28	940	h	1302	e	72
CC075	43.6	f-i	36.5	d-f	0.03	57.1	ab	42.4	a-f	<0.01	1013	h	2929	a-e	35
CC080	42.1	h-j	34.3	f-g	0.83	70.0	a	70.0	a	0.06	2080	b-f	2712	a-e	77
CC112	43.0	g-j	36.7	c-f	0.18	26.4	d-g	17.8	d-f	0.01	868	h	1790	c-e	48
CC157	41.8	i-j	33.0	g	0.04	29.3	d-g	46.7	a-f	<0.01	1284	f-h	3119	a-e	41
CC189	42.6	h-j	35.9	f-g	0.20	18.6	fg	10.4	f	0.07	1157	gh	1763	c-e	66
CC208	48.4	a	39.6	a-d	0.05	34.5	b-g	50.9	a-e	<0.01	1302	a-d	2441	b-e	53
CC230	45.1	c-f	36.4	d-g	0.43	32.1	c-g	39.6	a-f	0.03	2260	ab	2984	a-e	76
CC246	45.3	c-f	40.2	a-b	0.91	31.2	c-g	32.0	a-f	0.12	2740	ab	3309	a-e	83
CC342	45.4	c-e	39.3	a-e	0.55	37.9	b-g	35.0	a-f	0.00	2604	f-h	3689	a-d	71
CC388	44.4	d-g	37.5	b-f	0.13	47.9	a-d	61.2	a-c	<0.01	1320	f-h	3255	a-e	41
CC458	44.7	d-g	37.3	b-f	0.00	30.3	d-g	53.9	a-d	<0.01	1501	d-h	2604	b-e	58
CC529	48.4	a	36.7	c-f	0.89	43.0	b-f	45.7	a-f	<0.01	1429	e-h	3282	a-e	44
CC535	45.7	b-d	37.0	b-f	0.61	33.9	b-g	39.4	a-f	0.02	2080	c-f	2875	a-e	72
CC546	41.6	j	34.2	f-g	0.17	48.7	a-d	39.9	a-f	<0.01	995	h	2034	b-e	49
CC553	48.1	a	41.0	a	0.11	55.8	a-c	69.4	ab	<0.01	868	h	3553	a-d	24
CC588	42.3	h-j	35.6	f-g	0.56	34.3	b-g	31.4	b-f	<0.01	1483	d-h	2631	b-e	56
CC650	45.4	c-f	39.6	a-e	0.45	44.3	b-e	51.7	a-d	<0.01	1175	gh	3499	a-d	34
CC678	48.4	a	41.7	a	0.02	14.4	g	33.9	a-f	<0.01	1573	d-h	3635	a-d	43
CC812	46.7	a-c	40.1	a-c	0.53	27.2	d-g	24.1	c-f	<0.01	2622	ab	3797	a-c	69
No. Obs.	336		224			336		224			84		56		

[a] Genotypes with the same lowercase letter within columns are not significantly different (P < 0.05).

[b] SCMR, soil analysis plant development chlorophyll meter reading.

[c] P-values for comparisons between water-restricted and irrigated plots within entry. All comparisons for SCMR significant at P ≤ 0.05.

[d] Total number of flowers/m counted per year.

Table 8. Oklahoma total flower counts, SCMR, and yield in water-restricted (drought) and irrigated plots in 2019.

Genotype[a]	SCMR[b]			Total Flowers/m[d]			Yield (kg/ha)[e]		
	Drought	Irrigated	P[c]	Drought	Irrigated	P[c]	Drought	Irrigated	%

[e] Irrigated and water-restricted plots dug 141 and 172 d after planting (DAP), respectively. An early freeze killed vegetation of water-restricted plants 13 d before digging. %, yield of water-restricted plots as percentage of irrigated plots.

In Virginia, cumulative degree day had significant effects on each trait (P < 0.01) and was therefore used as a covariate for all analyses between irrigated and water-restricted plots. For CTD, the effects of water treatment, genotype, and the interaction between the two were not significant (P>0.75). Water treatment significantly affected NDVI ratings ($F = 55.9$, P < 0.01), but genotype and the genotype*water treatment interaction were also not significant (P > 0.32). Overall, NDVI readings taken from irrigated plots were numerically greater than those from drought-stressed plots (data not shown), showing that NDVI is affected by water stress on peanuts (Rouse *et al.*, 1974; Vergara-Diaz *et al.*, 2015). Analyses of plant wilting showed significant effects of water treatment and genotype (P < 0.01), and a nonsignificant interaction (P = 0.84). As expected, plant wilting was greater in the water-restricted than irrigated treatments (Table 9). Wilt scores for CC553, CC189, and Walton did not differ statistically between the two water treatments. For yield and seed weights, both water treatment and genotype were significant (P < 0.01), and the interaction between the two were nonsignificant (P > 0.56). Yields from the water-restricted plots ranged from 30% (CC230) to 66% (CC678) of the irrigated treatments (Table 9). Numerically, the five highest-yielding genotypes under drought conditions in Virginia were C76-16, Walton, CC678, CC068, and Wynne. For most genotypes, 100-seed weights between the two water treatments did not differ, except for Wynne, CC342, CC535, and Walton, where seed weights were significantly larger from the irrigated plots. For TSMK, all effects of water treatment, genotype, and their interaction were significant (P < 0.04). When TSMK significantly differed between water treatments within genotypes, shell-out in irrigated plots was greater than under water restriction. Genotypes with similar TSMK (P ≥ 0.43) regardless of water treatment included CC529, Tamspan 90, CC588, CC678, New Mexico Valencia C, and CC553.

Table 9. Virginia plant wilting, yield, total sound mature kernels (TSMK), and seed weight in water-restricted (drought) and irrigated plots in 2018 and 2019.

Genotype[a]	Plant Wilting[c]			Yield (kg/ha)[d]				TSMK[e]			g/100 seed[f]	
	P[b]	Drought	Irrigated	Drought	Irrigated	%	P	Drought	Irrigated	P[b]	Drought	Irrigated
C76-16	0.01	1.4 h-j	0.7 e-f	3205 a	5476 b-c	59	0.02	63.0 c-h	68.3 d-h	0.67	73.4 b-c	66.8 D
NMValC	0.05	2.2 a	1.7 a-b	1714 d-h	4301 d-f	40	0.51	64.0 a-h	64.5 e-i	0.46	46.8 g-i	45.5 g-j
TROL11	<0.01	2.1 a	1.0 b-f	2125 a-h	3994 e-f	53	0.01	68.8 a-b	74.7 a-b	0.95	58.9 e-f	54.5 e-f
TS90	<0.01	2.0 a-e	1.1 b-f	2398 a-g	3753 f	64	0.72	67.4 a-e	67.1 d-i	0.86	46.4 g-i	42.6 h-j
TVOL14	<0.01	1.8 a-i	1.0 c-f	2487 a-f	4157 d-f	60	0.01	59.8 f-i	66.3 d-i	0.49	50.7 f-h	49.2 f-h
Walton	0.09	1.3 i-j	0.8 c-f	3165 a-b	6732 a	47	0.16	67.7 a-d	70.4 b-d	0.04	86.9 a	91.8 A
Wynne	<0.01	1.6 b-j	0.7 e-f	2730 a-e	6199 a-b	44	0.10	63.3 b-h	66.7 d-i	<0.01	87.9 a	99.3 a
CC053	<0.01	2.2 a	1.2 a-e	1550 f-h	4002 e-f	39	0.01	61.8 e-h	68.9 d-g	0.57	43.2 h-j	41.8 i-j
CC068	<0.01	1.8 a-i	0.9 c-f	2792 a-d	5048 c-e	55	0.07	64.0 a-h	67.9 d-h	0.45	44.4 g-i	43.2 g-j
CC075	0.03	2.0 a-e	1.4 a-c	2212 a-h	4549 c-f	49	0.11	64.3 a-g	67.7 d-i	0.86	42.6 h-j	38.8 i-j
CC080	<0.01	2.0 a-e	1.0 b-f	1939 c-h	3825 f	51	0.22	65.5 a-e	68.0 d-h	0.15	34.9 j	37.6 j
CC112	0.01	2.1 a	1.4 a-d	2318 a-h	5186 b-d	45	0.04	63.9 a-h	68.6 d-h	0.24	43.1 h-j	43.8 g-j
CC157	0.01	1.9 a-g	1.2 a-f	2294 a-h	4642 c-f	49	<0.01	54.4 i-j	61.6 i	0.18	49.9 g-h	51.4 f-h
CC189	0.20	2.1 a-c	1.7 a	1491 f-h	3882 f	38	0.07	59.1 f-j	63.0 g-i	0.56	49.2 g-i	47.3 f-i
CC208	<0.01	2.1 a-b	0.8 c-f	1258 h	3923 f	32	<0.01	59.1 f-j	66.4 d-i	0.10	52.2 f-g	55.3 e-f
CC230	<0.01	2.1 a-d	0.8 c-f	1427 f-h	4684 c-f	30	0.14	64.1 a-h	67.8 d-h	0.17	50.5 f-h	52.6 f-g
CC246	0.01	1.5 d-j	0.8 c-f	1470 f-h	4330 d-f	34	0.06	58.8 g-j	63.0 h-i	0.34	76.7 b	76.5 b
CC342	<0.01	1.7 a-i	0.6 e-f	1770 d-h	4502 c-f	39	<0.01	53.6 j	67.0 d-i	0.01	68.9 b-d	76.2 b-c
CC388	0.05	1.8 a-h	1.3 a-e	1660 e-h	3642 f	46	0.03	69.5 a	74.5 a-c	0.83	48.9 g-i	45.3 g-j
CC458	<0.01	1.5 c-j	0.5 f	1329 g-h	4236 d-f	31	<0.01	58.6 h-j	70.5 b-d	0.06	46.9 g-i	50.8 f-h
CC529	<0.01	2.0 a-f	0.9 c-f	1390 f-h	3814 f	36	0.99	65.8 a-e	64.5 e-i	0.34	41.9 h-j	41.7 i-j
CC535	0.01	1.4 g-j	0.7 e-f	1739 d-h	3906 f	45	<0.01	62.5 d-h	69.5 b-f	0.02	66.7 c-e	72.5 b-d
CC546	0.01	1.8 a-i	1.0 c-f	1839 c-h	4238 d-f	43	0.27	66.7 a-e	68.5 d-h	0.83	47.4 g-i	43.8 g-j
CC553	0.29	1.1 j	0.8 c-f	2066 b-h	3692 f	56	0.43	68.9 a	69.9 b-e	0.97	49.9 g-h	45.1 g-j
CC588	<0.01	2.2 a	1.3 a-e	1470 f-h	3702 f	40	0.62	64.6 a-f	65.0 d-i	0.29	40.0 i-j	40.9 i-j
CC650	0.03	1.5 e-j	0.9 c-f	2432 a-g	4415 c-f	55	<0.01	67.7 a-d	80.6 a	0.25	63.6 d-e	67.5 c-d

Table 9. Virginia plant wilting, yield, total sound mature kernels (TSMK), and seed weight in water-restricted (drought) and irrigated plots in 2018 and 2019.

Genotype[a]	P[b]	Plant Wilting[c]		Yield (kg/ha)[d]				TSMK[e]		P[b]	g/100 seed[f]	
		Drought	Irrigated	Drought	Irrigated	%	P	Drought	Irrigated		Drought	Irrigated
CC678	0.01	1.5 f-j	0.7 d-f	2912 a-c	4431 c-f	66	0.53	68.5 a-c	68.9 c-f	0.80	59.1 e-f	55.6 e-f
CC812	<0.01	1.8 a-i	0.6 e-f	2230 a-h	4615 c-f	48	<0.01	55.3 i-j	63.9 f-i	0.07	62.3 d-e	66.1 d-e
No. Obs.		1007	672	168	168			168	168		168	168

[a] NMValC, New Mexico Valencia C; TROL11, Tamrun OL11; TS90, Tamspan 90; TVOL14, TamVal OL14. Genotypes with the same lowercase letter within columns are not significantly different (P < 0.05).

[b] P-values for comparisons between water-restricted and irrigated plots within entry. All comparisons for yield significant at P ≤ 0.01.

[c] Plant wilting rated on a scale from 0 to 5, where 0 is no wilting and 5 is severely wilted and >50% leaves are brown.

[d] Irrigated plots and water-restricted plots dug 116 and 126 days after planting (DAP), respectively, in 2018. All plots dug 134 DAP in 2019. %, yield of water-restricted plots as a percentage of irrigated plots

[e] Total sound mature kernels, determined using the smallest screen for Spanish/Valencia kernels (5.94-mm x 19.05-mm slots).

[f] Seed weight in g/100 seed.

Outside the U.S., germplasm has been screened for multiple drought tolerance-associated traits in geographically and climatically diverse environments (Faye *et al.*, 2015; Pandey *et al.*, 2021). However, to date, just one study in the U.S. has evaluated drought tolerance in considerably different production environments—Georgia and Arizona (Holbrook *et al.*, 2000). Here, we identified mini-core accessions with divergent phenotypes for drought-associated traits that were consistent across three distinct environments. A significant genotype by environment interaction was observed for SCMR, but common genotypes occupied the extremes in all states. Similar to observations by Holbrook et al. (2009), a significant correlation was not observed between SCMR and visual drought stress/wilting, but moderate, significant correlations were observed with paraheliotropism, yield, and TSMK. Others have also observed correlations between SCMR and pod yield (Upadhyaya, 2005; Songsri *et al.*, 2008; Singh *et al.*, 2014). Genotypes were significantly different for plant wilting and paraheliotropism, and these traits appeared to be less affected by genotype by environment interactions. Thus, wilting and paraheliotropism may be particularly useful for breeding as surrogate traits for drought tolerance as previously suggested (Holbrook *et al.*, 2000; Luis *et al.*, 2016). While these visually-assessed traits are non-destructive and less time-consuming to collect than other physiological traits such as leaf water potential (O'Toole *et al.*, 1984), rating for wilt and paraheliotropism is still labor intensive. Remote sensing technologies may offer high-throughput solutions for phenotyping these traits (Sullivan and Holbrook, 2007; Sarkar *et al.*, 2021).

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