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Peanut genotypic variation in transpiration efficiency and decreased transpiration during progressive soil drying

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ABSTRACT

Peanut (*Arachis hypogaea* L.) is commonly grown on sandy soils in warm climates where water-deficit can impose a limitation on yield. Identification of plant traits related to increased productivity under water-deficit conditions could be used to increase yields in these water-limited environments. Two traits were examined among 17 peanut genotypes. Transpiration efficiency (TE), ratio of mass increase to water transpired, was the first trait examined. TE was measured both under well-watered conditions (greenhouse) and soil drying (outdoors in pots) conditions. Virtually no difference was observed in TE among genotypes under well-watered conditions indicating the gas exchange properties were similar. However, under soil drying conditions there were substantial differences among genotypes. These results indicated that TE with drying soil might interact with traits associated with water loss on drying soils. Therefore, the second trait examined in this study was the fraction transpirable soil water (FTSW) content at which the decline in transpiration with soil drying was observed. This greenhouse experiment showed large variability among the 17 genotypes. A second-order polynomial described the relationship between TE under soil drying conditions and the threshold for the decline in transpiration. The FTSW for maximum TE was 0.55, but this value is expected to depend on the environmental conditions to which the plants influence TE.

1. Introduction

Water-deficit causes enormous decreases in yield in many crops grown in drought-prone areas. Peanut (*Arachis hypogaea* L.) is an important oil-seed legume that is especially vulnerable to water-deficit limitations because it is usually grown on sandy soils. An annual peanut yield loss due to drought world wide has been estimated at US $520 million (Sharma and Lavanya, 2002). In Asia and Africa, peanut is grown under rainfed conditions during the rainy season and suffers intermittent drought spells due to gaps in rainfall that can occur at any time during the crop cycle.

Under conditions of intermittent drought, genotypes that perform better under these water-deficit conditions are likely those achieving high transpiration efficiency (TE), the ratio of plant mass produced to amount of water transpired. In peanut, various studies have revealed genotypic variation for TE (Krishnamurthy et al., 2007; Rao and Wright, 1994; Rao and Nigam, 2001; Rao et al., 1993; Sheshshayee et al., 2003, 2006; Wright et al., 1994, 1996). An important question to resolve is whether the genotypic variation in TE is an inherent consequence of basic physiological activity of a genotype regardless of soil moisture conditions. That is, do major genotypic variations exist both under well-water and water-deficit conditions, and is there consistency in such variation between the two levels of soil moisture? The first objective of this research was to measure the TE of the same set of peanut genotypes subjected both to well-watered and water-deficit treatments.

High TE may be particularly important for crop improvement as soil water deficits develop. Soil drying strongly influences a number of physiological processes that could influence TE including stomatal conductance, photosynthesis rate, and leaf area development (Nobel, 1999; Salih et al., 1999). Decreases in both stomatal conductance and leaf expansion have been considered the main mechanisms in which plants respond to soil water-deficit (Jones, 1992; Turner, 1997). The point during the soil drying cycle at which stomata conductance starts declining in response to soil water-deficit could be a key trait explaining genotypic differences in TE. Early decreases in stomata conductance during the midday period will decrease canopy gas exchange at times of the day with high vapor pressure deficit, and as a consequence TE is increased.

Ritchie (1981) proposed that the characterization of plant response to soil water content could result in consistent relationships across crops and soils. Indeed, when expressing plant water

Abbreviations: FTSW, fraction transpirable soil water; NTR, normalized transpiration rate; TE, transpiration efficiency.

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loss rate as a function of normalized available soil water, he found that transpiration rate of plants on drying soil relative to well-watered plants was unchanged until about one-third of the available water remained in the soil. After reaching that threshold, soil water content transpiration rate decreased linearly with further soil drying. Subsequently, a number of studies with a wide range of crop species and environmental conditions have confirmed this general response (Sadras and Milroy, 1996). Sinclair and Ludlow (1986) refined the definition of the lower limit of the available soil moisture by identifying this limit as the point where transpiration, and hence gas exchange supporting crop growth, became negligible. In practice, this lower limit was defined as the soil water content at which transpiration of plants on drying soil decreased to 10% or less of the well-watered plants. Studies that have normalized plant response to fraction of transpirable soil water (FTSW) reported that the threshold for the decrease in transpiration rate with most plant species and under many experimental conditions is in the FTSW range of 0.3–0.4 (Gollan et al., 1986; Kuppers et al., 1988; Meyer and Green, 1981; Ray and Sinclair, 1998; Rosenthal et al., 1987; Sadras and Milroy, 1996; Sinclair and Ludlow, 1986; Weisz et al., 1994). The second objective of this research was to determine if there are variations in plant response to drying soil, i.e. the FTSW threshold for decline in transpiration, which might explain variation of TE under water-deficit conditions.

2. Materials and methods

A preliminary screen of peanut germplasm was undertaken at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) to identify potential genotypic variability among a broad base of peanut germplasm (unpublished). Genotypes were selected from this preliminary study of 440 genotypes that expressed possible variation in TE. Also, it was necessary that seed was available in the U.S. of the selected genotypes. Eventually, 17 genotypes were selected for study (Table 1).

2.1. Transpiration efficiency under well-watered conditions

Measurement of TE of the genotypes was done in an experiment established in a greenhouse in Gainesville, FL [29°38′N, 82°22′W]. Pots (16.5-cm diameter × 16.5-cm tall) were filled with approximately 2 kg of silty loam soil (Miracle-Gro Lawn Products, Inc., Marysville, OH). Seeds were treated with 2% ethrel to break dormancy and inoculated with a rhizobia mixture (peanut bacteria, Southern States Cooperative, Richmond, Virginia). Twelve pots were sown with two seeds in each pot for each genotype on 9 May 2008. After a week, the pots were thinned to a single plant per pot. All pots were maintained in a well-watered condition until the start of the TE measurements. From the 12 pots of each genotype, 10 plants were selected for the experiments.

Measurements for determination of TE were begun on 11 June 2008. The plants of all genotypes were flowering but not yet pegging. The minimum temperature in the greenhouse during the experiment averaged 24 °C and the maximum temperature was 30 °C. The midday vapor pressure deficit in the greenhouse on nearly all days was in the range of 2.2–2.6 kPa. One set of four replicate pots of each genotype were harvested on this date to estimate initial plant mass. Both the shoots and roots were harvested, dried at 60 °C in an oven, and weighed to obtain plant mass. The remaining six replicate pots of each genotype were over watered and allowed to drain overnight. The following morning pots were placed in polythene bags and the bags were sealed at the base of the plant stem to prevent soil evaporation. Immediately after bagging the initial weights of the pots were recorded. All pots were weighed every day beginning at 08:00 (Eastern Standard Time). Each pot was watered each day to return pot weight to 100 g less than the initial weight. The experiment was terminated after 2 weeks and the shoots and roots of each plant were harvested separately. The plant samples were dried at 60 °C in an oven and the dry weights were recorded. Transpiration efficiency was calculated as the difference in total plant weight between the final and initial harvest, divided by the total amount of water transpired during the experimental period. Statistical analysis of differences among genotypes in TE was done using analysis of variance (ANOVA). Tukey's method was used for the comparison of mean TE among genotypes.

2.2. Transpiration efficiency under water-deficit conditions

Transpiration efficiency under progressive exposure to water-deficit was measured at ICRISAT on plants grown in pots under continuously drying soil. The experiment was carried out under outdoor conditions, during the post-rainy season, between mid-February and mid-April 2006. Pots (25-cm diameter × 20-cm tall) were filled with 9 kg of a soil mixture. The soil mixture consisted of a sandy clay loam Alfisol collected on the ICRISAT farm to which farm manure was added (50:1, v/v). In addition, 2.25 g of single

Table 1
Seventeen genotypes compared for their transpiration efficiency and response of transpiration to drying soil. The four experiments identified in this table are those used to resolve the response of transpiration rate to drying soil.

Experiment	Genotype	Date of sowing	Dates of experiment
Experiment 1	ICG 3179 ICGV 86015 ICGV 86388 ICGV 91284 Kopergagon 3	22 November 2007	4 January 2008 to 22 January 2008
Experiment 2	ICGV 86564 ICGV 86699 PI 544346	12 February 2008	4 April 2008 to 19 April 2008
Experiment 3	ICG 11376 ICGV 87128 PI 259747 Gajah TMV 2	18 February 2008	29 April 2008 to 15 May 2008
Experiment 4	ICGS 44 ICGV 86031 TAG 24 ICGV 87141	23 May 2008	10 July 2008 to 23 July 2008

super phosphate was added to each pot (di-ammonium phosphate). The pots were inoculated with rhizobium strain NC-29 (IC 7001) by liquid inoculation method (Brockwell, 1982). Four replicate blocks were established in which two pots of each genotype were sown. Each pot was sown with two seeds per pot, and later thinned to one seedling per pot after plant emergence. The experiment was sown between 21 and 24 February 2006. Since the genotypes reported here were part of a large evaluation of many genotypes (440 entries), it was possible to sow only one replicate block each day.

The first harvest of the experiment to obtain initial shoot mass of the plants was started on 27 March. One replicate block of the four replicates was harvested per day over the period from 27 to 30 March. To determine dry mass, the shoots were dried at 60 °C in an oven. The remaining pot of each genotype in each replicate was watered to saturation and allowed to drain overnight. The next morning, the drained pots were bagged with plastic bags around the stem of the plant to avoid any further soil evaporation and pot weight was recorded. Plants of each replication were weighed every 4 days (one block per day). For the first 4-day period between consecutive weighing, the pots were allowed to lose no more than 600 g of water. In subsequent 4-day periods, pots were allowed to lose no more than 400 g of water. This meant that any transpiration water in excess of these values was added back to each respective pot. This was done to ensure that all entries were following a relatively similar kinetics of water stress imposition. Even though there was little probability of rain during the experimental period, a 33.6-mm rain fell on 13 April. Consequently, the experiment was terminated on that day and only the shoots were harvested and dried at 60 °C in an oven. For the period from 27 March to 13 April the average ambient temperature during this period was 29.4 °C, minimum relative humidity was 50%, and average solar radiation was 21.5 MJ m^{-2} day^{-1}.

Transpiration efficiency (g kg^{-1}) was calculated for each pot in this drying experiment as the difference in shoot mass in the individual pot minus average initial shoot mass for that genotype, divided by the total water transpired for that pot during experimental period. Statistical analysis of differences among genotypes in TE was done using analysis of variance (ANOVA). Tukey's method was used for the comparison of mean TE among genotypes and to estimate significance level.

2.3. FTSW threshold on drying soil

Due to limited greenhouse space, the determination of the FTSW threshold for decrease in transpiration rate on drying soil required several experiments to evaluate all 17 genotypes (Table 1). These experiments were done by growing a single plant of each genotype in nine replicate polyvinyl chloride pots (10-cm diameter × 30-cm tall). The pots were filled with a sandy loam top soil (Robin Hood Timber Co., Adel, GA) that was sieved through a 0.5-mm and later 0.2-mm sieve to remove large pieces of organic matter. Prior to sowing, pots were inoculated with rhizobia (Peanut bacteria, Southern States Cooperative, Richmond, Virginia). Seeds were treated with 2% ethrel to break any dormancy that might have existed. All plants were grown under well-watered conditions until the start of the experiments. The plants were grown in the same greenhouse in Gainesville, FL in which the TE experiment was performed. The temperature in the greenhouse for all experiments was regulated at 27 °C day and 21 °C night.

Each dry-down experiment was initiated when the plants within an experiment had reached a height of about 8–9 cm and the plants were at least 6-weeks old. All genotypes were flowering at this stage but had not yet formed pegs. The evening before the experiment was initiated all pots were fully watered and left overnight to drain excess water. The following morning the top of each pot was sealed with a two-piece lid to prevent soil evaporation. All pots were weighed to obtain the initial weight of the fully watered pot. Four pots were assigned to the well-watered treatment (WW) and five pots were assigned to the drought-stressed treatment (DS). All pots were weighed daily in the afternoon around 14:00 (Eastern Standard Time) and transpiration rate was calculated as the difference in weight between successive days. Water was added to each well-watered pot each afternoon to return its weight to 100 g less than the initial weight. The 100-g deficit was maintained to avoid saturated water conditions in the WW pots. Water was also added to the DS pots on days when the water loss amount was greater than 70 g. Watering to limit daily net water loss to 70 g avoided rapid imposition of stress and allowed progressive development of water-deficit stress over approximately 2 weeks.

The daily transpiration ratio was calculated for each DS pot as the ratio for the transpiration rate for the DS pot divided by the mean transpiration rate for the four WW plants of that genotype. This normalization allowed large day-to-day environmental variations to be minimized in the results. A second normalization was done on these data to remove variation mainly as a result of differences in plant size among DS plants within a genotype. This second normalization was done so that the normalized transpiration rate of each DS plant was centered on a value of 1.0 during the well-watered stage before water-deficit developed in the soil. Therefore, an average transpiration ratio obtained on the first 3 days of the experiment for each DS pot was used to calculate the normalized transpiration rate (NTR).

Changes in NTR during the soil drying cycle were expressed as a function of FTSW. To calculate FTSW, total transpirable soil water available to the plant in each pot was calculated as the difference between the initial and final pot weight. The final pot weight was defined as the pot weight on the day when transpiration of the drought stress plant was <10% of the well-watered plant, NTR of 0.10 (Sinclair and Ludlow, 1986). Second, daily FTSW was calculated as the amount of transpirable soil water remaining in the soil divided by the total transpirable soil water.

$$\mathrm{FTSW} = \frac{\text{daily weight} - \text{final weight}}{\text{initial weight} - \text{final weight}} \quad (1)$$

Total transpirable soil water was compared among genotypes by using analysis of variance (ANOVA). Tukey's method was followed for the comparison of means to estimate significance level using Genstat 8.0.

Plots of NTR against FTSW were generated for each genotype including individual replicated data on each day from all plants. Non-linear regression analysis was done using Prism 2.0. (Graph Pad, Software, Inc., San Diego, CA) to fit the exponential model presented by Muchow and Sinclair (1991).

$$\mathrm{NTR} = \frac{1}{1 + A \times \exp(B \times \mathrm{FTSW})} \quad (2)$$

Regression results obtained using Eq. (2) were compared among genotypes based on 95% confidence intervals of coefficients A and B.

A plateau regression procedure of SAS (SAS Institute, Inc., Michigan) was employed to estimate a specific FTSW threshold value where NTR begins to decline (Ray and Sinclair, 1997). The plateau regression attempts to fit two linear segments where one segment is a plateau at $y = 1$ and the second regression is a linear change in y with respect to x. A key output from this analysis is the FTSW threshold for the two segments and the confidence intervals for this threshold. In this analysis, the regression analysis was performed on each replicate plant and a mean calculated for the genotype. The mean threshold values for all genotypes were

compared using Tukey's method (Genstat 8.0, VSN International, Hemel Hempstead, UK).

3. Results and discussion

There were significant differences among genotypes in the growth of the peanut plants during the well-watered TE experiment. The growth of the shoots during this period was on the order of eight times greater than the roots, but there were no significant differences among genotypes in root growth (data not shown). In spite of the differences in total plant growth, there was very little difference in TE among genotypes in the experiment where the plants were maintained in well-watered conditions (Table 2). In this experiment, the only significant difference among genotypes was between ICGV 91284 with a TE of 6.14 g kg^{-1}, and ICGV 87128 and Tag 24 with TE of 4.30 and 4.27 g kg^{-1}, respectively. The limited variation in TE among these 17 genotypes under well-watered conditions is consistent with the theoretical derivation for TE presented by Sinclair et al. (1984). Their analysis showed that the two critical variables accounting for variation in TE would be differences (1) in the composition of the plant products and/or (2) the CO_2 concentration maintained in the leaves. In the well-watered experiment neither of these conditions would vary greatly among genotypes resulting in the stability in TE.

In contrast to the lack of variation in TE under well-watered conditions, there was more that a fourfold range in TE based on shoot mass when plants were subjected to a drying soil (Table 2). The lowest TE was 0.59 g kg^{-1} for ICGV 86388 and the highest was 2.53 g kg^{-1} for PI 259747 (Table 2). While there were several genotypes with low TE, an important result of this experiment was that several genotypes had significantly high TE. In addition to PI 259747, high TE was observed for PI 544346, ICGV 86015, ICGV 91284, ICGS 44, and Kopergagon 3. There was no correlation between the size of the plants at the beginning of the experiment and TE. Of course, there was no correlation in TE among the two experiments because of the lack variation in TE for the well-watered experiment.

Soil water status differences between the two experiments in which TE was measured had a large impact on discrimination for TE among the genotypes. The large differences in TE among genotypes when subjected to water-deficit as compared to the well-watered condition indicate that the dynamics of soil drying has a major influence on TE. One possibility is that plants that have a high threshold for decline in NTR on drying soil is likely associated with midday stomata closure. Stomata closure during midday would diminish the relative proportion of plant gas exchange occurring under high vapor pressure deficit conditions so that the effective vapor pressure deficit driving overall transpiration would be decreased and result in a higher TE. Therefore, those genotypes that had a high threshold for the NTR decline are hypothesized to have a higher TE in the ICRISAT experiment than genotypes with a decline in NTR at a lower FTSW.

The above hypothesis for explaining the observed variation in TE under soil drying conditions when no variation occurred under well-watered conditions was examined directly by determining soil water content, i.e. FTSW, at which restricted NTR was observed. To study the 17 genotypes, measurements had to be done in four experiments. However, there was no apparent bias in the results from the four since the mean thresholds for the decline in NTR were not statistically different. Further, there was no difference in the amount of transpirable water extracted from the pots among all genotypes. The same overall pattern of decline in NTR to decreasing FTSW was observed across all genotypes in all experiments.

A consistent pattern in the NTR response to drying soil was observed among the five plants in each genotype (Fig. 1). When the soil was still comparatively wet, the value of NTR across all genotypes was equivalent in that there was initially a constant value centered by definition on a NTR value of 1.0. At lower FTSW there was a gradual decrease in NTR until it reached a value of less than 0.1 at zero FTSW. The inverse exponential model described well the change in NTR as the soil dried. While there was a range among genotypes for the values of the A and B coefficients, the r^2 was 0.90 or better for all genotypes (Table 3).

To compare genotypes, the two-segment plateau regression was used to extrapolate a breakpoint as the FTSW threshold where NTR began to decline. The two-segment linear regression also fit the data very well ($p < 0.001$). These results (Table 4) confirmed the general pattern of the two-segment response to soil drying that has been widely reported for crop plants (Sadras and Milroy, 1996), and specifically for peanut (Sinclair et al., 1995). However, there were substantial differences in the FTSW value for the threshold in NTR decline among genotypes as illustrated in Fig. 1. Across all genotypes, the estimated threshold varied greatly from 0.22 for ICGV 86388 to 0.71 for ICG 11376.

The variation in the threshold for NTR decline is substantially greater than previously reported for any single species. In peanut, Bhatnagar-Mathur et al. (2007) reported variation in the threshold decline in NTR among transgenic lines derived from cultivar JL 24. Although reanalysis of their data shows the range of difference may not be as large as originally presented, the wild-type genotype JL 24 still had a higher threshold than transgenic RD 2. Our results and those of Bhatnagar-Mathur et al. (2007) indicate that the threshold for NTR decline for some peanut genotypes is substantially greater than that predicted by the theoretical analysis based on water transport in drying soil (Sinclair, 2005). It appears that some genotypes of peanut have the capability to respond to soil drying and decrease transpiration rate well in advance of hydraulic limitations in the soil. The basis for such genotypic variation is unknown.

While not explored here, the screening of a large number of genotypes for differences in the threshold for NTR decline might be possible under field conditions. In such a screen, all genotypes would be simultaneously subjected to a water-deficit once they had achieved canopy closure. Those genotypes that displayed wilting at a later date than others were likely either accessing more water or conserving the available soil water. Of course, a NTR threshold at high soil water content would result in conservation of

Table 2
Transpiration efficiency (TE) of 17 genotypes with drying conducted at ICRISAT and with well-watered plants conducted at the University of Florida. Values identified with the same letter are not statistically different from each other based on Tukey's method ($p < 0.05$).

Genotype	Transpiration efficiency (g kg^{-1} water transpired)	
	Well watered	Drought stressed
ICGV 86388	5.23 ab	0.59 g
ICG 3179	4.54 ab	0.78 fg
TMV 2	4.61 ab	0.84 fg
ICGV 86699	4.69 ab	0.94 fg
ICG 11376	4.55 ab	0.95 fg
ICGV 86564	5.21 ab	0.99 fg
ICGV 87128	4.30 b	1.166 ef
ICGV 86031	5.02 ab	1.26 def
Gajah	5.71 ab	1.27 def
ICGV 87141	4.88 ab	1.59 cde
TAG 24	4.27 b	1.75 cd
Kopergagon 3	4.77 ab	1.79 bc
ICGS 44	4.64 ab	1.87 bc
ICGV 91284	6.14 a	2.03 bc
ICGV 86015	5.18 ab	2.05 bc
PI 544346	4.77 ab	2.27 ab
PI 259747	4.76 ab	2.53 a

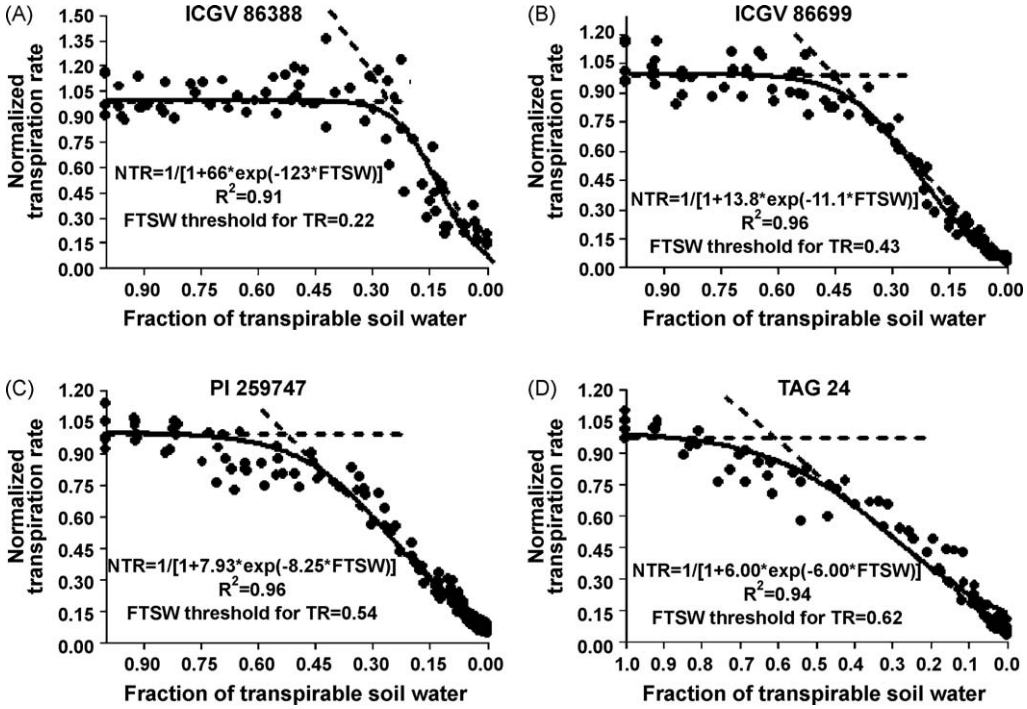

Fig. 1. Normalized transpiration rate vs. fraction of transpirable soil water of four peanut genotypes (A) ICG 86388, (B) ICGV 86699, (C) PI 259747 and (D) TAG 24. The solid line in each figure is the regression fit using the inverse exponential model. The dotted lines are the results from the two-segment plateau regression.

water. Therefore, those genotypes with delayed wilting would be candidates for expressing the high threshold for NTR decrease. We are now testing this screening approach in the field using the 17 genotypes in the current study.

The hypothesis that high TE under water-deficit conditions might be associated with a high threshold for NTR decrease was examined by plotting these two variables for the 17 genotypes (Fig. 2). Indeed there was a strong correlation between these two traits but the relationship was better described by a second-order polynomial regression ($r^2 = 0.62$, $p < 0.01$) than a linear regression. At very high threshold values for NTR, TE was decreased. The regression results indicated that maximum TE under soil drying conditions in the experiment at ICRISAT was achieved with a NTR threshold at an FTSW equal to 0.55. Due to the demonstrated sensitivity of TE to environmental conditions, it is anticipated that the coefficients obtained in the polynomial regression are likely to be environmentally dependent. However, the relative shape of an optimum FTSW threshold for TE is expected to exist under a range of conditions.

The existence of an optimum threshold for maximum TE may be a consequence of growing the plants on a fixed amount of water in pots, which is not unlike what plants would experience under field drought conditions when soil water is not replenished. Those genotypes with a threshold for NTR decline near the optimum would have had early stomata closure in the soil drying cycle resulting in conservation of soil water. As a consequence of both conserved soil water due to lowered NTR and the midday stomata closure, a high NTR would allow a high TE for a greater fraction of time during the soil drying cycle. Hence, the observation of a high TE and the optimum NTR for water use in this particular

Table 3
Results of the non-linear regression analysis of transpiration rate vs. vapor pressure deficits. Values were obtained for the *A* and *B* coefficients in the inverse exponential model proposed by Muchow and Sinclair (1991).

Genotype	*A*	*B*	r^2
ICGV 86388	6.6	−12.3	0.91
ICG 3179	16.6	−13.2	0.98
TMV 2	5.16	−5.19	0.95
ICGV 86699	13.8	−11.1	0.96
ICG 11376	5.01	−5.41	0.91
ICGV 86564	5.21	−5.66	0.92
ICGV 87128	3.98	−6.66	0.91
ICGV 86031	8.38	−8.13	0.98
Gajah	6.77	−10.1	0.92
ICGV 87141	10.9	−11.8	0.90
TAG 24	6.00	−6.00	0.94
Kopergagon 3	6.65	−7.19	0.95
ICGS 44	8.27	−8.19	0.97
ICGV 91284	7.57	−7.81	0.94
ICGV 86015	5.44	−5.88	0.96
PI 544346	8.59	−8.26	0.94
PI 259747	7.93	−8.25	0.96

Table 4
FTSW threshold values for the 17 genotypes calculated using the two-segment plateau regression procedure with ±standard error and confidence limit. Threshold values identified with the same letter are not statistically varied from each other based on Tukey's method at significance level 0.05.

Genotype	FTSW for TR threshold	S.E. (±)	Confidence limit
ICGV 86388	0.22 d	0.03	0.20–0.26
ICG 3179	0.38 cd	0.04	0.33–0.40
TMV 2	0.42 c	0.03	0.38–0.45
ICGV 86699	0.43 c	0.03	0.37–0.48
ICG 11376	0.71 a	0.05	0.69–0.73
ICGV 86564	0.69 ab	0.03	0.67–0.72
ICGV 87128	0.57 bc	0.08	0.56–0.60
ICGV 86031	0.57 bc	0.05	0.56–0.59
Gajah	0.41 c	0.03	0.37–0.44
ICGV 87141	0.65 abc	0.04	0.62–0.69
TAG 24	0.62 abc	0.02	0.57–0.65
Kopergagon 3	0.57 abc	0.04	0.51–0.58
ICGS 44	0.53 c	0.02	0.99–0.57
ICGV 91284	0.58 abc	0.03	0.52–0.59
ICGV 86015	0.58 abc	0.02	0.56–0.61
PI 544346	0.54 c	0.06	0.43–0.59
PI 259747	0.54 c	0.05	0.49–0.57

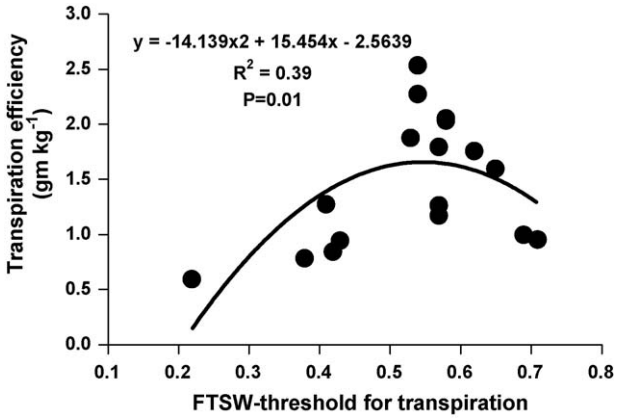

Fig. 2. Graph for each of the 17 genotypes of transpiration efficiency on drying soil plotted against their FTSW threshold with drying soil. The data were regressed with a second-order polynomial model ($p = 0.01$).

experiment. For those genotypes with very high thresholds, the plants may not have had an opportunity to fully use the conserved soil water and maximize growth before the experiment was terminated. Such an interpretation suggests that the NTR threshold for optimum TE is very much dependent on the environment and the course of the soil drying for any particular situation as indicated by the difference in the optimum between the results presented here and those of Bhatnagar-Mathur et al. (2007). A long-term environmental assessment will be required to determine what NTR threshold will be most desirable in any given location and stress conditions to maximize TE and yield.

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