Genotypic Variation in Peanut for Transpiration Response to Vapor Pressure Deficit

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ABSTRACT

Conservation of soil water resulting from decreases in stomata conductance under atmospheric high vapor pressure deficit (VPD) conditions is a possible approach for enhanced tolerance of water deficit by crops. Water deficit is usually a concern in peanut (*Arachis hypogea* L.) since it is frequently grown on sandy soils with low water-holding capacity. Seventeen peanut genotypes were studied to determine the response of their transpiration rates (TR) to VPD. The results of this study demonstrated variation among peanut genotypes with nine genotypes exhibiting a breakpoint in their VPD response at about 2.2 kPa, above which there was little or no further increase in TR. Therefore, these genotypes with a breakpoint have the possibility of soil water conservation when VPD exceeded 2.2 kPa. The remaining eight genotypes had a linear response in TR over the whole range of tested VPD. Also, the 17 genotypes could be separated into groups with differing rates of increasing TR at low VPD. The change in TR with increasing VPD may be important in determining the rate at which soil water is used under field conditions.

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Abbreviations: BP, breakpoint; PVC, polyvinyl chloride; TR, transpiration rate; VPD, vapor pressure deficit.

Peanut (*Arachis hypogea* L.) is a major rain-fed grain legume crop and is a rich source of edible oil (0.43 to 0.55 g g^{-1}) and protein (0.25 to 0.28 g g^{-1}) content. It is native to South America and primarily cultivated in Asia and Africa. It is extensively grown in the semiarid tropics by resource-poor farmers where many biotic and abiotic factors limit its productivity and seed quality (Sharma and Lavanya, 2002). However, water deficits commonly limit the productivity of peanut due its production on soils with low water-holding capacity and in environments with erratic rainfall patterns. Drought contributes to over 6.7 million metric tons loss in annual world peanut production (Subbarao et al., 1995).

Various efforts have been made to enhance the efficiency of selection for drought-tolerant genotypes based on yield and specific physiological traits. Unfortunately, most of these attempts have failed because of large genotype × environment interactions for yield and/or lack of precise screening techniques for trait selection (Branch and Hilderbrand, 1989; Cooper and Hammer, 1996; Mitra, 2001). Hence, the selection of a physiological trait to screen water-deficit tolerance requires a comprehensive understanding of the nature of the trait and its contribution to yield and the trait's responsiveness to the environment (Ludlow and Muchow, 1990; Sheshshayee et al., 2003).

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One possibility to improve performance of peanut under water-limited conditions is to develop genotypes that have low canopy gas exchange during periods of high vapor pressure deficit (VPD). Since high VPD is likely during the midday in many environments in which peanut is grown, this response could be expressed as midday stomata closure. Limitation on canopy gas exchange under high VPD could result in conservation of soil water, leaving more water in the soil to support plant growth later in the season in the event drought conditions develop. Under these circumstances, the decrease in water loss under high VPD would result in somewhat higher transpiration efficiency. Of course, the negative impact of this trait would be an immediate decrease in CO_2 assimilation rate that would need to be compensated by assimilation activity later in the season if a water deficit developed.

It has been observed in soybean [*Glycine max* (L.) Merr.] that when atmospheric VPD was greater than about 2 kPa, there was stability in transpiration rate by genotype PI 416937, which expressed a slow-wilting phenotype in the field (Fletcher et al., 2007; Sinclair et al., 2008). Recently, Sadok and Sinclair (2009) confirmed little or no change in transpiration rate (TR) when VPD was greater than approximately 2 kPa. There are, however, no comparable studies that include several peanut genotypes in which TR in response to VPD is fully documented. There is evidence that individual genotypes exhibit limited TR at atmospheric VPD greater than about 2 kPa (Bunce, 1981; Turner et al., 1984; Salih et al., 1999; Isoda and Wang, 2002). However, the results are limited and the specific response of transpiration over a range of VPD has not been documented for a number of genotypes. In this paper, therefore, we report observations on the response of transpiration to VPD in 17 peanut genotypes. These genotypes represented a diversity of germplasm that were originally identified for differing transpiration efficiency in drying soil (Jyostna Devi et al., 2009).

MATERIALS AND METHODS

Seventeen peanut genotypes (Table 1) that had been found to express a range of transpiration efficiencies when subjected to soil drying (Jyostna Devi et al., 2009) were selected for this investigation. Seeds of these genotypes were obtained from the U.S. peanut germplasm bank. Before the measurement of VPD response, the plants were grown in pots in a greenhouse at the University of Florida, Gainesville, FL (29°38' N, 82°22' W). Polyvinyl chloride (PVC) pots (100 mm diam., 180 mm tall) fitted with a flat end cap on the bottom were constructed for this experiment. A small hole was drilled in the end cap to allow drainage of any excess water.

The pots were filled with garden soil (Miracle-Gro Lawn Products, Inc., Marysville, OH) that included 15–5–10 N–P–K fertilizer. The pots were inoculated with peanut rhizobia (Southern States Cooperative, Richmond, VA) using a liquid inoculation (Brockwell, 1982). Seeds were treated with 2% ethrel to break dormancy, if any, before sowing. Two seeds were sown per pot; after 1 wk, each pot was thinned to one plant. The plants were grown under well-watered conditions, and the air temperature in the greenhouse was regulated at 27°C/21°C (day/night).

Transpiration response to VPD was measured in a system similar to that described by Fletcher et al. (2007). The pots in which the plants were grown were originally fitted with toilet flanges at the top of the pot. When the VPD response was to be measured, a 254-mm-diameter lid of a food container (Rubbermaid Commercial Products, Winchester, VA) was attached to the toilet flange on the pot. A hole 100 mm in diameter had been cut in the lid to match the pot diameter. The soil surface was covered with aluminum foil to minimize soil evaporation during the measurements of plant water loss. Finally, a 5.45-L translucent plastic container (Rubbermaid Commercial Products) was placed over the plant in an inverted position and sealed to the lid. The chamber was fitted with a 12-V, 76-mm-diameter computer box fan (Northern Tool and Equipment, Burnsville, MN) to continuously stir the air inside the chamber. A pocket humidity-temperature pen (Extech Instruments, League City, TX) was placed through a slit in the side wall of the container to measure the chamber environment.

Different humidity levels were obtained around the plants in the chamber by flowing air through the chambers at various rates and from different sources. Three humidity levels were tested each day to measure TR in three ranges of VPD: low (0–1.5 kPa), medium (1.5–2.5 kPa), and high (2.5–4 kPa). The low VPD

Table 1. List of peanut genotypes included in each set, date of sowing, date of experiment conducted, and recorded minimum and maximum vapor pressure deficit (VPD) of each experiment.

Set	Genotypes	Date of Sowing	Date of Exp.	VPD	
				Min.	Max.
				kPa	
Set 1, Exp. 1	ICGV 86031, ICGV 87141, & TAG 24	11 Oct. 2007	16 and 19 Nov. 2007	1.10	3.24
Set 1, Exp. 2	ICGV 86031, ICGV 87141, & TAG 24	11 Oct. 2007	20 and 21 Nov. 2007	0.99	3.28
Set 2, Exp. 1	ICG S44, ICG 3179, ICGV 86388, & Kopergagon 3	5 Nov. 2007	6 and 7 Dec. 2007	0.98	3.48
Set 2, Exp. 2	ICGS 44, ICG 3179, ICGV 86388, & Kopergagon 3	5 Nov. 2007	11 and 12 Dec. 2007	0.96	3.62
Set 3, Exp. 1	ICGV 91284 & ICGV 86015	12 Dec. 2007	23 and 24 Jan. 2008	0.91	4.12
Set 3, Exp. 2	ICGV 91284 & ICGV 86015	12 Dec. 2007	27 and 28 Jan. 2008	0.76	4.20
Set 4, Exp. 1	TMV 2, ICGV 86564, PI 259747, & PI 544346	14 Dec. 2007	4 and 5 Feb. 2008	0.94	3.9
Set 4, Exp. 2	TMV 2, ICGV 86564, PI 259747, & PI 544346	14 Dec. 2007	6 and 7 Feb. 2008	0.85	4.20
Set 5, Exp. 1	Gajah, ICG 11376, ICGV 86699, & ICGV 87128	31 Mar. 2008	5 and 6 May 2008	0.91	3.80
Set 5, Exp. 2	Gajah, ICG 11376, ICGV 86699, & ICGV 87128	31 Mar. 2008	7 and 8 May 2008	0.98	3.97

condition was obtained by flowing air through an atomizing humidifier (Herrmidifier, Sanford, NC) and then into each VPD chamber at 0.4 L min^{-1}. The medium VPD was obtained by flowing ambient greenhouse air through each chamber at 2.0 to 2.5 L min^{-1}. The highest VPD treatment was achieved by first flowing air through a PVC column (100 mm diam., 380-mm length) filled with drierite (W.A. Hammond Drierite Co., Xenia, OH). The flow of dried air into each chamber was varied between 1.0 to 2.5 L min^{-1} to achieve the desired range of VPD in the plant chamber. The air flow rate into the chambers was monitored with flow meters (Model FL-2043, Omega, Stamford, CT).

Transpiration rate was measured by the change in pot weight that occurred during exposure to each VPD treatment. Measurements were first begun with the low VPD treatment, then the medium VPD treatment, and finally the high VPD treatment. This sequence was selected to avoid any recovery that might be needed if stomata closure was induced by exposure to the high VPD treatment. Chambers were allowed to stabilize for 30 min after introducing each humidity treatment. Following this stabilization period, the initial weight of the pot was measured on a balance with a resolution of 0.1 g (Model SI-8001, Denver Instrument, Denver, CO). The plants were exposed to each humidity treatment for 1 h and then reweighed. The difference in initial and final weights and the duration of exposure to the VPD treatment were used to calculate water-loss rate. Relative humidity and temperature were recorded three times during each humidity treatment: at the beginning, middle, and end of exposure. The VPD for each chamber was calculated on the basis of temperature and relative humidity at each observation and averaged. The standard error in the averaged VPD among the three readings at each treatment was commonly in the range of 0.05 to 0.12 kPa at the lowest VPD treatment and 0.10 to 0.34 kPa for the highest VPD treatment.

Twelve plants, i.e., chambers, were monitored simultaneously. In all cases, a set of measurements usually consisted of three replicate chambers for each of four peanut genotypes. The evening before making measurements, the selected plants were watered until the pots were dripping. The pots were left overnight for drainage of the excess water. For each set of 12 plants, measurements were made on two consecutive days. Between the 2 d, the pots were rewatered. After completing measurements on the second day, the plants were harvested. Leaves were separated from the stem and leaf area was measured using a leaf area meter (LI-1300, Licor, Lincoln, NE). Transpiration rate was expressed as water-loss rate divided by plant leaf area.

The individual data for each plant at each VPD treatment and each day of measurement were used in the regression analysis of transpiration response to VPD. All the data of each genotype were first examined by attempting to fit the data to a two-segment linear regression using GraphPad Prism 2.01 (GraphPad Software Inc., San Diego, CA). The output of a successful regression fit to the two-segment model were the coefficients defining two intersecting linear regressions:

$$\text{If VPD} < \text{BP, TR} = \text{intercept 1} + \text{slope 1 (VPD)} \quad [1]$$

$$\text{If VPD} \geq \text{BP, TR} = \text{intercept 2} + \text{slope 2 (VPD)} \quad [2]$$

The value of BP is the breakpoint between the two linear segments, which also is an output of the GraphPad analysis along with an estimate of the standard error for BP. The two slopes were statistically compared within GraphPad for significant difference ($p \leq 0.05$). If there was significant difference, the results for that genotype were concluded to be represented by the two-segment model. If two slopes were not found to be significantly different, all data for a genotype were assumed to fit a single linear regression model, and this result is reported.

RESULTS

Ultimately, the 17 peanut genotypes were studied in five sets of experiments (Table 1). Two experiments on consecutive days were conducted with each set to obtain a complete set of data to characterize their transpiration response to VPD. Across all experiments, the distribution of temperature and relative humidity during the experiments was in the range of 29 to 35°C and 25 to 84%, respectively. The average temperature in all the experiments and chambers was 32.8°C (±1.98 SD). The range of VPD treatments including all genotypes was between 0.76 ± 0.08 and 4.20 ± 0.11 kPa. The variation in VPD was mainly due to variation in the humidity levels established in the chambers as a result of differing air sources and flow rates. The desired levels of VPD were obtained in each experiment. In some experiments such as Set 3 (Exp. 1 and 2) and Set 4 (Exp. 2), the high VPD treatment exceeded 4 kPa (Table 1).

There were clear distinctions among genotypes in the response of transpiration rate to VPD. Some genotypes were well represented by the two-segment model with a BP, whereas others showed a linear increase in transpiration rate over the entire tested range of VPD (Fig. 1). Among the 17 genotypes, 9 were found to exhibit a BP in the increase in transpiration rate as VPD was increased (Table 2). The R^2 for all data of each of these nine genotypes based on the two-segment regression ranged from 0.58 to 0.91. The value for the BP ± SE ranged from 1.98 ± 0.22 to 2.56 ± 0.12 kPa, with an average of 2.20 ± 0.06 kPa for the nine genotypes. Except for 'Kopergagon 3' with a BP of 2.56 kPa, the values of the BP were not different among all other genotypes based on significance of their confidence limits. The slope of the regressions of these nine genotypes above the BP ranged from −6.27 to +6.34 mg H_2O m^{-2} s^{-1} kPa^{-1} with an average slope near zero (−0.37 mg H_2O m^{-2} s^{-1} kPa^{-1}). The distribution between negative and positive slopes for these nine genotypes was six negative slopes and three positive slopes.

Data for eight genotypes were found not to fit the two-segment model, and hence, a single linear regression model was used (Table 3). The linear regression generally fit these data well with the R^2 ranging from 0.76 to 0.92. An interesting segregation occurred among these eight genotypes based on their slopes. The genotypes fell into two groups with slopes of approximately 11.9 to 12.7 and 23.4 to 25.4 mg H_2O m^{-2} s^{-1} $kPa^{-1.}$ This compares to the slope below the BP for the nine genotypes exhibiting a BP. For the nine genotypes with a BP, their slopes below the

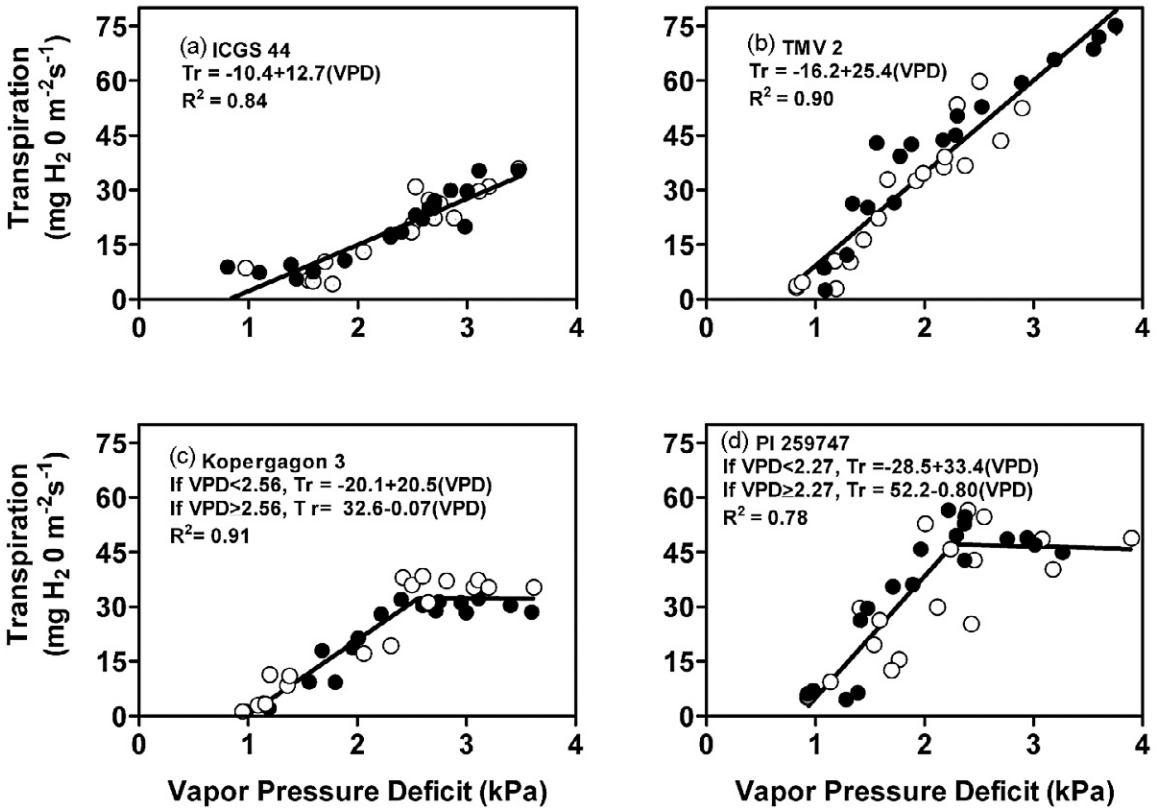

Figure 1. Transpiration rate (mg H_2O m^{-2} s^{-1}) response of four peanut genotypes to different levels of vapor pressure deficit (kPa). Results from the two sets of experiments for each genotype are distinguished by the open and closed circles. Data in panels (a) and (b) were fitted with a single linear regression, whereas the data in panels (c) and (d) were fitted with a two-segment linear regression. The slopes and R^2 values are presented in the figure.

BP were clustered into groups with those having a slope of approximately 18 to 20 mg H_2O m^{-2} s^{-1} kPa^{-1} and those with a slope between 25 and 33 mg H_2O m^{-2} s^{-1} kPa^{-1}.

DISCUSSION

In contrast to the usual model of transpiration rate increasing linearly with increasing VPD (e.g., Sinclair and Bennett, 1998), this study with 17 peanut genotypes showed variation in this response. While approximately half the studied lines had continuously increasing transpiration rate with increasing VPD, half had a clear BP in transpiration rate when VPD reached about 2.2 kPa. The BP observed in nine of the genotypes is similar to the VPD for the BP of genotypes in other species in which a BP has been reported (Turner et al., 1984; Comstock and Ehleringer, 1993; Fletcher et al., 2007; Sinclair et al., 2008).

The existence of a BP in the transpiration rate at elevated VPD offers the opportunity to directly influence crop transpiration use efficiency under field conditions. The VPD during the midday on many days during the growing season will likely exceed 2.2 kPa. For those genotypes with a BP, transpiration rate would be constrained during the

Table 2. Results from two-segment linear regression for those peanut genotypes that were found to fit this model. Genotypes are arranged in ascending order corresponding to slope 1 value. The table contains slope 1, breakpoint (± SE), confidence limit of the breakpoint, slope 2 (± SE), *X*-intercept and their R^2. *X*-Intercept was calculated as a ratio of *Y*-intercept and slope 1.

Genotype	*n*†	Slope 1 ± SE	Breakpoint X_0 ± SE	Confidence limit of X_0	Slope 2 ± SE	*X*-intercept	R^2
ICGV 91284	35	18.4 ± 3.45	2.22 ± 0.15 ab‡	1.71 to 2.27	2.42 ± 1.82	18.4 ± 3.45	0.76
ICGV 87141	36	18.8 ± 2.55	2.12 ± 0.09 bc	1.93 to 2.31	–6.27 ± 3.02	18.8 ± 2.55	0.71
Kopergagon 3	36	20.5 ± 1.70	2.56 ± 0.12 c	2.32 to 2.69	–0.07 ± 3.20	20.5 ± 1.70	0.91
ICGV 86031	36	25.2 ± 5.94	2.00 ± 0.08 ab	1.82 to 2.17	–4.72 ± 2.21	25.2 ± 5.94	0.58
PI 544346	36	27.6 ± 7.61	2.13 ± 0.18 bc	1.96 to 2.20	–2.95 ± 4.50	27.6 ± 7.61	0.69
ICGV 86564	35	28.4 ± 5.48	2.17 ± 0.19 bc	1.96 to 2.38	5.93 ± 4.23	28.4 ± 5.48	0.81
ICGV 86015	34	28.9 ± 4.95	1.98 ± 0.22 ab	1.77 to 2.18	–3.18 ± 1.84	28.9 ± 4.95	0.67
Gajah	35	30.1 ± 4.26	2.39 ± 0.56 bc	2.02 to 2.27	6.34 ± 4.92	30.1 ± 4.26	0.59
PI 259747	36	33.4 ± 4.55	2.27 ± 0.15 bc	1.97 to 2.46	–0.80 ± 4.03	33.4 ± 4.55	0.78

†*n* = number of data points used to draw a segmental regression of each genotype.

‡Breakpoint values followed by the same letter are not significant from each other based on their confidence limits.

midday period, resulting in soil water conservation. While the decrease in stomata closure associated with the decreased transpiration rate would also constrain photosynthetic rate, this loss may be offset by water savings in the soil for use later in the season. If there is a late-season water deficit, genotypes with a BP have the possibility of using the conserved soil water to generate a greater yield than genotypes without the BP. In fact, Sinclair et al. (2005) showed in a simulation study of sorghum [*Sorghum bicolor* (L.) Moench] production in four locations in Australia that there was a yield increase in about 75% of the seasons as a result of the BP trait. There is also some evidence in peanut that it has the ability to maintain high photosynthetic activity while minimizing the water loss without showing impact on carbon assimilation and yield (Wright et al., 1994).

On the other hand, if there is late-season rainfall or the crop is irrigated through seed fill, the benefit of conserved water would not be obtained. Under the conditions of adequate late-season water, the limitation on leaf gas exchange earlier in the season will not be rewarded and there will likely be a decrease in yield compared with genotypes without the VPD response. Sinclair et al. (2009) performed a simulation analysis of soybean yield for genotypes that were assumed to express the VPD response trait. Simulation results for 50 yr across the United States showed a yield gain in about 70% of the years in most locations, but this meant that in 30% of the years, there was a neutral or negative yield change as a result of the VPD response. However, in those years in which yields were simulated to decrease, the yield loss was generally small.

The results of this study also indicated a range in the response of transpiration rates at elevated VPD for those genotypes with a BP. While several of the genotypes exhibited a fairly stable transpiration rate at VPD greater than the BP, one genotype ('Gajah') exhibited an increasing transpiration rate, although at a lower rate than at low VPD. These results indicate that it may be possible to tailor the transpiration response at elevated VPD to suit local environmental conditions. That is, the extent of water conservation to be expressed by genotypes can in principle be genetically developed to match the severity of drought expected at the end of the season. The possibility of breeding for this trait will, of course, require extensive investigation of the heritability of the VPD-response trait.

The results of these experiments do not offer any insights about the mechanism(s) resulting in the BP in the VPD response. In their study with soybean PI 416937, Sinclair et al. (2008) isolated the cause of the BP as a limiting hydraulic conductance in the leaves. Since the transpiration slope above the BP differed over a fairly wide range among these peanut genotypes, it is unlikely that a single explanation will apply to all of these genotypes. This conclusion is supported by the fact that several genotypes had a negative slope in transpiration rate at high VPD. For those genotypes with a negative slope, an adjustment in plant hydraulics would be needed so that there is a decrease in conductance less than that at the BP. Clearly, detailed investigations exploiting the genotypic diversity identified in this study are warranted.

Table 3. Results for those peanut genotypes found to be described by a single linear regression. The genotypes are listed in ascending order based on their slope values. The table includes *n*, slope with standard error, *X*-intercept and R^2 values. *X*-intercept was calculated as a ratio of *Y*-intercept and slope value.

Genotype	$n^{\dagger}$	Slope ± SE	*X*-intercept	R^2
ICGV 87128	35	11.9 ± 1.67	0.42	0.86
ICGS 44	36	12.7 ± 0.97	0.82	0.84
ICGV 86699	35	23.4 ± 1.63	0.76	0.76
ICG 3179	36	23.8 ± 2.18	0.75	0.78
TAG 24	36	24.4 ± 2.19	0.57	0.79
ICGV 86388	36	24.5 ± 1.29	1.11	0.92
TMV 2	36	25.4 ± 1.49	0.64	0.9
ICG 11376	36	28.5 ± 2.16	1.08	0.85

$^{\dagger}n$ = number of data points used to draw a single linear regression.

The linear increase in transpiration rate with VPD at low VPD for those genotypes with a BP and overall VPD for those without a BP indicates a constant stomata conductance. This stomata conductance could be viewed as the maximum conductance for the conditions of this experiment. A surprise in these results is that there is a wide range in these slopes, indicating substantial difference in their maximum stomata conductance. The basis for these differences is unknown. The clustering of transpiration slopes into only a few groups indicates that there may be dominating controlling factors on the conductance—whether anatomical or physiological—that are resulting in these maximum transpiration rates.

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