



The effect of vapor pressure deficit on maize transpiration response to a drying soil

Jeffery D. Ray^{1,4}, Russ W. Gesch², Thomas R. Sinclair³ & L. Hartwell Allen³

¹USDA-ARS, Crop Genetics and Production, Stoneville, MS 38776, USA; ²USDA-ARS, North Central Soil Conservation Research Laboratory, Morris, MN, USA; ³USDA-ARS, Agronomy Physiology Lab., University of Florida, Gainesville, FL 32611-0840, USA; ⁴Corresponding author*

Received 26 April 2001. Accepted in revised form 9 November 2001

Key words: FTSW, maize, soil water, transpiration, vapor pressure deficit

Abstract

A decline in plant transpiration has been widely observed to occur within a fairly stable range of threshold values of fraction transpirable soil water (FTSW), usually 0.3–0.4. However, the stability of this function has not been compared at various levels of atmospheric vapor pressure deficit (VPD). Soil hydraulic conductivity is likely to be involved in determining the threshold where water supply is limiting. Thus, it was hypothesized that at a high VPD resulting in increased transpiration rates, the FTSW threshold for the decline of transpiration rates as a result of drying soil would be increased. This study was undertaken in controlled environment chambers with two maize (*Zea mays* L.) hybrids (Pioneer Brand Hybrids '3165' and '3737') so as to subject plants to four VPD levels (1.1, 2.0, 2.9 and 3.6 kPa) during a soil drying experiment. In contrast to the original hypothesis, there was little (≤ 0.05 FTSW) change in the threshold FTSW in response to increased VPD for either hybrid. In fact, over the narrow 0.31–0.38 FTSW range observed, the two hybrids showed opposite trends in FTSW threshold as VPD increased. These results supported the view that the FTSW threshold for the decline in transpiration with drying soil is stable, showing little sensitivity to changes in VPD.

Abbreviations: FTSW – fraction of transpirable soil water; NTR – normalized transpiration ratio; VPD – vapor pressure deficit

Introduction

Transpiration responses to a drying soil are well documented (Sadras and Milroy, 1996; Weisz et al., 1994). In general, as the soil dries under constant environmental conditions, transpiration rate remains constant until a threshold soil-water content is reached, and thereafter, it declines linearly. With few exceptions, the threshold at which transpiration begins to decline occurs when 0.3–0.4 of the transpirable soil water remains in the soil. This general relationship was fairly stable in a number of experimental conditions and species (Ray and Sinclair, 1998; Sadras and Milroy, 1996; Weisz et al., 1994).

However, there was some indication of variation in the threshold among maize genotypes (Ray and Sinclair, 1997). The basis for the observed widespread consistency in the response of transpiration to drying soil may result from a need for plants to balance water loss to the atmosphere and the water supply from the soil. As the soil dries and conductivity in the soil becomes limiting to water transport to the roots (Cowan, 1965), the decreased water supply rate must be balanced by an inhibition of shoot transpiration rate or the plant rapidly desiccates. Therefore, a decrease in stomata conductance appears to be a necessity at that soil-water content where water cannot be supplied to match the transpiration rate allowed with uninhibited stomata conductance. This mechanism offers a

* FAX No: 662-686-5218. E-mail: jray@ars.usda.gov

possible explanation for the observed stability in the volumetric soil-water content for a particular soil at which transpiration rate declines (Sinclair et al., 1998).

Assuming that the threshold volumetric soil-water content at which transpiration rate declines is a result of balancing plant water content, then factors influencing the water demand of the plant could influence the threshold for the decline in transpiration. That is, the threshold at which soil-water content begins to limit water flux into the plant is hypothetically dependent on the value of the water flux (Cowan, 1965; Tardieu et al., 1992). A higher potential transpiration rate, and hence a greater water flux demand from the soil, will cause the limitation of water movement in the soil to be reached at a higher soil-water content. This logic results in the hypothesis that atmospheric vapor pressure deficit (VPD) should influence the threshold volumetric soil-water content at which transpiration declines. Higher VPD values are hypothesized to result in higher soil-water content thresholds at which transpiration rate is observed to decline.

Denmead and Shaw (1962), working with *Zea mays* (maize) grown in containers buried in the field, found a wide range of soil-water content at which transpiration declined in response to potential evaporation as determined by the Penman equation (Penman, 1956). Their results are often interpreted as indicating that the threshold at which transpiration begins to decline is dependent upon evaporative demand of which VPD is a large component. However, they did not directly measure or control VPD. In contrast, in controlled environment studies done by Turner et al. (1985) with sunflower (*Helianthus annuus*) and by Gollan et al. (1985) with *Nerium oleander*, no difference in the soil-water content threshold of transpiration decline with VPD was observed. Differences between these studies may lie in potential differences in root systems or possibly in that Denmead and Shaw (1962) did not specifically measure or control VPD. Therefore, this study was undertaken to measure possible changes in the threshold soil-water content at which transpiration declines in maize over a range of VPD in a highly controlled environment.

Materials and methods

Cultural practices

Maize (*Zea mays* L.) hybrids Pioneer '3165' and '3737' were used in this study because previous eval-

uations showed that they had differing soil-water content thresholds for the initial transpiration decline in response to a drying soil (Ray and Sinclair, 1997). Seed of the hybrids were sown on 6 January 1999 into 140 pots (70 for each hybrid) containing a commercially available sandy loam top soil (Sunniland Corporation, Sanford, FL). The pots were made of plastic and were 16 cm tall and 16 cm in diameter at the top tapering to an 11-cm diameter at the bottom. The pots held approximately 2.2 L of soil. Four seeds were sown per pot and thinned to one plant per pot approximately 12 d after sowing. All plants were initially grown in a greenhouse maintained at a temperature of 18/28 °C (minimum/maximum) in Gainesville, FL. Plants were watered regularly to maintain well-watered conditions and fertilized twice a week with a commercially available fertilizer (Scotts Miracle-Gro Products, Inc., Port Washington, NY).

At 26 d after sowing, the 64 most uniform plants of each genotype were individually placed in plastic bags, sealed around the base of the plant and weighed. The result of sealing the pots in plastic bags was that virtually all water loss was through transpiration. The bagged plants were transferred into eight outdoor controlled-environment chambers. The chambers were controlled so as to give four VPD treatments with two replications. Eight plants of each hybrid were placed in each of the eight chambers. Plants were arranged such that the eight plants of each hybrid were in two rows by four plants with one hybrid on each side of the chamber. For each genotype, in each chamber, three plants were randomly chosen as well-watered controls and the remaining five plants were used for the dry-down treatment.

At the beginning and end of the experiment, maximum plant height and number of expanded leaves were measured. Maximum plant height was measured from the base of the plant to the tip of the longest leaf when held vertically above the plant. The number of expanded leaves was counted by defining a leaf as being fully expanded when the edges of blade had completely separated at the leaf base. The plants were harvested at the end of the experiment and separated into shoot and root components. Dry weight for each component was determined by drying in forced-air ovens at 90 °C for at least 3 d. Individual plants in the dry-down treatment were harvested as soon as the FTSW value dropped below 0.10. Averaged over all VPD treatments, hybrid 3165 plants were harvested 11.3 (\pm SD 0.66) days after the experiment began and for hybrid 3737 at 12.1 (\pm SD 0.69) days. There were

no significant differences among VPD treatments for either hybrid in the number of days the dry-down lasted. In the well-watered treatment, all plants of all VPD treatments and both hybrids were held until the last plant was harvested in the dry-down treatment. All well-watered plants were harvested 14 d after the experiment began.

Outdoor controlled-environment chambers

The design and operation of the air handling, environment control, and data logging systems of the outdoor controlled-environment chambers are described in detail elsewhere (Baker et al., 1997; Jones et al., 1984; Pickering et al., 1994). Direct measurements of the ambient air temperature, exterior irradiance, chamber dew point and dry bulb temperature, relative humidity, and CO₂ concentration were made every 2 s and 5 min averages were computed and recorded. The air handling, environment control, and data logging systems worked together to maintain programmed chamber settings.

Each chamber was controlled by a Campbell Scientific, Inc. (Logan, Utah) CR-10T controller/data logger. These units were programmed using a host PC connected by addressable coaxial cable and operated using Campbell Scientific Inc., Real-Time Monitoring System (RTMS).

The canopy component of the chambers consisted of a transparent polyethylene terephthalate (Sixlight, Taiyo Kogyo Co., Tokyo, Japan) covered aluminum frame 2 m long, 1.5 m wide, and 1.5 m tall at the rear sloping to a 1.2-m height at the front. The volume of the canopy component was about 4 m³ and the air exchange rate was 2.7 chamber volumes per minute.

The canopy component was sealed to a 2-m long × 1-m wide × 0.6-m deep aluminum soil compartment. The extra width of the canopy component created a 0.5-m overhang at the front of the chamber. The overhang was hinged at the top and could be opened to allow full access to the inside of the chamber. However, opening the entire overhang caused a loss of the controlled atmosphere within the chamber. To protect the controlled atmosphere of the chamber, a trap door fitted with a body glove was constructed in the bottom of the overhang. Once the experiment started, plants were accessed inside the chambers only through the trap door. To protect against abrupt changes in the internal atmospheric conditions (especially CO₂ concentrations) of the chamber, a respirator connected

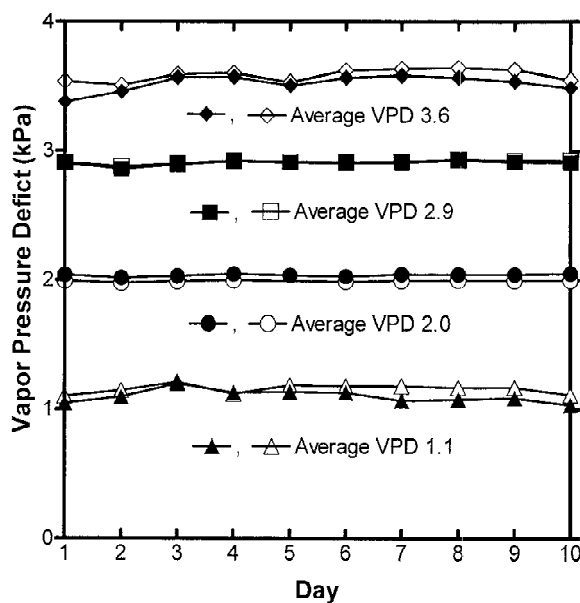


Figure 1. Daily vapor pressure deficit (VPD) values maintained by outdoor chambers between 0900 and 1500 hrs. Each line represents one of the eight chambers. The average values are the VPD averaged over 10 days and both chambers assigned to that treatment level. Note that symbols mask error bars.

to a vacuum pump was worn by the observer while measurements were made inside the chambers.

The controls of the chambers were set to give four atmospheric VPD values of 1, 2, 3 and 4 kPa (2 chambers for each VPD setting) during the daylight hours. The VPD treatments were imposed by maintaining a constant dry bulb temperature at 33 °C in all chambers and varying the dew point temperature among treatments to achieve the desired VPD. At the conclusion of the experiment, the results showed that the chambers actually maintained average daytime (0900–1500 hrs) VPD of 1.1, 2.0, 2.9 and 3.6 kPa (Figure 1). The average nighttime VPDs were 1.4, 1.9, 2.7 and 3.2 kPa which were only slightly different than the VPD calculated for the daytime values for each treatment. During the daytime, control of CO₂ concentration was set to 360 ppm and the chambers maintained an average value of 359.6 ppm.

Over the course of the experiment, daytime (0900–1500) photosynthetically active radiation (PAR) averaged 1,024 $\mu\text{mol photon m}^{-2} \text{s}^{-2}$ as measured by external sensors on each chamber. However, two independent measurements comparing external and internal measurements showed that the Mylar covering of the chambers decreased internal irradiance by an average of 16% in all chambers except for the

two chambers with the 1.1 kPa VPD treatment. In this treatment, there was heavy condensation on the interior walls and top of the chamber almost continuously. The condensation had the effect of further reducing the irradiance in the chamber to 34% less than the exterior irradiance. In order to maintain the high humidity levels in the chambers for this treatment, supplemental humidifiers (Vicks Cool Mist Humidifier, Model V400, Proctor & Gamble Co., Cincinnati, Ohio) were placed in the chambers.

Soil–water content calculations

On the evening of the day before the plants were transferred from the greenhouse to the controlled-environment chambers, all pots were watered to soaking. The pots were allowed to drain overnight and the next morning, the pots were placed in plastic bags, sealed around the base of the plant, and weighed. This initial weight was used as the upper limit of soil–water content in the calculation of fraction of transpirable soil water (FTSW). The plants of each hybrid were randomly assigned to chambers. The plants were maintained under well-watered conditions (re-watered to 200 g below the initial pot weight) for 2 d before initiating the soil-drying treatment.

Pots were weighed every afternoon at approximately 1430 h EST. Water was added to the well-watered pots each day to achieve a weight of 200 g below the initial pot weight. The water was added to the pots at two times during the day to maintain well-watered conditions: 100 g was added at approximately 1000 h EST and the balance of the daily transpired water was added at approximately 1500 h EST. For pots in the soil-drying treatment, the net daily decrease in soil–water content was held to no more than 70 g by adding to each pot the amount of transpiration water lost in excess of 70 g. This was necessary to readjust the soil water to the same level in the VPD treatments so that the rate and duration of soil drying was equalized among VPD treatments. This approach slowed the rate of soil drying so that the experiment lasted about two weeks, or more nearly what might be expected under field situations. The daily transpiration of each pot was calculated as the weight change on subsequent days, taking into account the water added to the pots.

The procedures used to analyze the transpiration data are described in detail elsewhere (Ray and Sinclair, 1997, 1998; Sinclair and Ludlow, 1986). Briefly, the data were subjected to two daily normalizations.

The first normalization was performed by dividing the transpiration rate on each day of each stress plant by the average of the well-watered plants for that VPD treatment. This normalization served to eliminate the variations in transpiration rates among days as a result of weather variations (e.g. cloudy days). The second normalization was performed for each plant subjected to drying soil by dividing the daily value of the first normalization of each plant by the average of the first normalization value of that plant over the first 3 d of the experiment (when the plants in the drying soil were still under well-watered conditions). The result of the second normalization was called the Normalized Transpiration Ratio (NTR) and served to eliminate variations in plant size as well as to center the initial well-watered condition of all plants around a value of 1.0. Values of NTR below 1.0 indicated decreases in transpiration rate compared to the well-watered plants.

The initial pot weight and the pot weight when NTR dropped below 0.10 were used as the upper and lower endpoints of transpirable soil water (Sinclair and Ludlow, 1986). The difference between these endpoints defined the total transpirable soil water held by each pot. The fraction of transpirable soil water (FTSW) for each pot was calculated by dividing the pot weight on a given day minus the final pot weight, by the total transpirable soil water for that pot.

Statistical procedures

Data were analyzed using the first order linear regression procedures of GraphPad Prism (GraphPad Software, Inc., San Diego, CA). Linear regression was performed on the mean of the subsamples (5 subsamples for the water deficit treatment and 3 for the well-watered treatment) of each replication (thus each regression was over eight means). The data was further analyzed using the ANOVA procedures of SAS (Cary, NC). For the ANOVA, the experimental design was a split-plot design with VPD as the main-plot factor and genotype (hybrid) as the subplot factor. Well-watered plants and plants subjected to the water deficit were analyzed independently. A plateau regression procedure was used in SAS to determine the point at which transpiration began to decline relative to soil–water content for each plant in the water deficit treatment. This point was defined as the FTSW threshold.

Results

Plant growth and development

At the time of transfer of plants from the greenhouse to the controlled-environment chambers, plants of hybrid 3165 were 81.4 cm (\pm SD 3.9) tall and those of hybrid 3737 were 81.1 cm (\pm SD 5.2). Both hybrids had 4.9 (\pm SD 0.3) fully expanded leaves. By the end of the experiment, average plant height in the well-watered treatment had increased to 120.0 cm (\pm SD 5.8) for hybrid 3165 and to 115.5 cm (\pm SD 5.5) for hybrid 3737. The number of fully expanded leaves had increased to an average of 6.5 (\pm SD 0.12) for hybrid 3165 and 7.3 (\pm SD 0.09) for hybrid 3737, but for neither hybrid was there any significant ($P > 0.05$) effect of VPD. In the water-deficit treatment, plant height also increased but to a lesser extent. Final plant height was 104.4 cm (\pm SD 5.6) for hybrid 3165 and 100.7 cm (\pm SD 5.9) for hybrid 3737. The number of fully expanded leaves showed a small increase (hybrid 3165, $5.8 \pm$ SD 0.07; hybrid 3737, $5.9 \pm$ SD 0.06) and as with plant height, VPD showed no significant ($P > 0.05$) effect.

The effect of VPD on the growth of the plants is shown by examining final plant dry weight (Figure 2). In the well-watered treatment, the linear relationship between VPD and shoot dry weight, root dry weight and total dry weight was not significant ($P > 0.05$) for hybrid 3165, although in each case there was a negative trend. For hybrid 3737, there was a significant ($P < 0.05$) negative linear trend for all three variables (Figure 2). In the water-deficit treatment, for both hybrids and for all three variables (shoot, root, and total dry weight) there were significant ($P < 0.05$) negative linear trends with increasing VPD. For both hybrids and all VPD treatments, the roots were visibly apparent throughout the soil volume in the pots. However, they appeared more dense in the well-watered treatment compared to the water stressed treatment.

Transpiration

A considerable range in transpiration was measured among treatments. In the well-watered treatment, the total water transpired over the duration of the experiment ranged from 2472 g under a VPD of 1.1 kPa to 3746 g under a VPD of 3.6 kPa. In the water-deficit treatment, cumulative transpiration ranged from 993 g under 1.1 kPa to 1362 g under 3.6 kPa. In both water management treatments and for both hybrids, the total

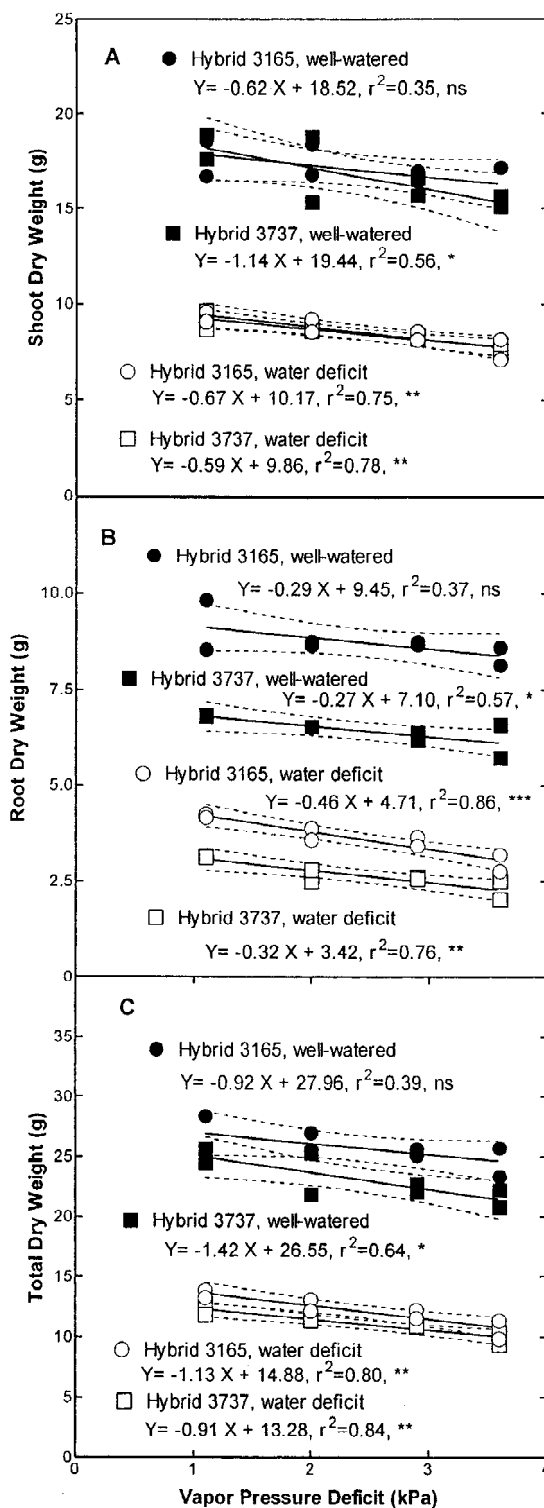


Figure 2. Shoot, root and total dry weight of maize hybrids Pioneer 3165 and 3737 over four VPD levels and two water management treatments. For shoot dry weight in the water deficit treatment, there was no significant difference in the slope or elevation of the regression lines for individual hybrids. Therefore, one regression line is presented for both hybrids. Asterisks indicate that the slope was significantly non-zero (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$), 'ns' indicates that the slope was not significantly non-zero, and dashed lines indicate the 95% confidence interval of the regression lines.

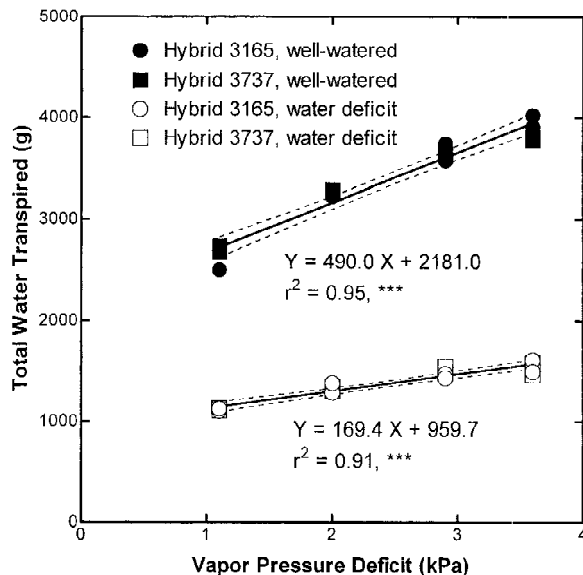


Figure 3. Total water transpired over four vapor pressure deficits in two water management treatments for two maize hybrids. Regression analysis indicated a significant linear trend of increasing total water transpired with increasing VPD. Within treatments there were no significant differences in slope or elevation of the regression lines between hybrids. Therefore, one regression line is presented for each treatment. The slope of the regression lines between water management treatments were significantly different ($P < 0.0001$). Asterisks indicate that the slope was significantly non-zero (*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$), and dashed lines indicate the 95% confidence interval of the regression lines.

water transpired increased with increasing VPD (Figure 3). Since there was no difference between hybrids, the data for the hybrids within a water management treatment were combined for statistical analysis. The total water transpired over this period showed a significant ($P < 0.001$) linear trend of increasing water transpired with increasing VPD in both watering treatments (Figure 3). Between watering treatments, the slopes of the regression lines for each water management treatment were significantly ($P < 0.0001$) different.

Although more water was transpired with increasing VPD, the available soil water within pots was not affected by VPD. For each hybrid there were no significant available soil water differences ($P > 0.05$) between VPD levels and no significant linear trend across increasing VPD levels (for hybrid 3165, $r^2 = 0.15$, $P = 0.61$ and for hybrid 3737, $r^2 = 0.75$, $P = 0.13$). Averaged over all VPD treatments, for hybrid 3165 the available soil water was 695 g (SD \pm 24.9) and for hybrid 3737 it was 739 g (SD \pm 34.3). The av-

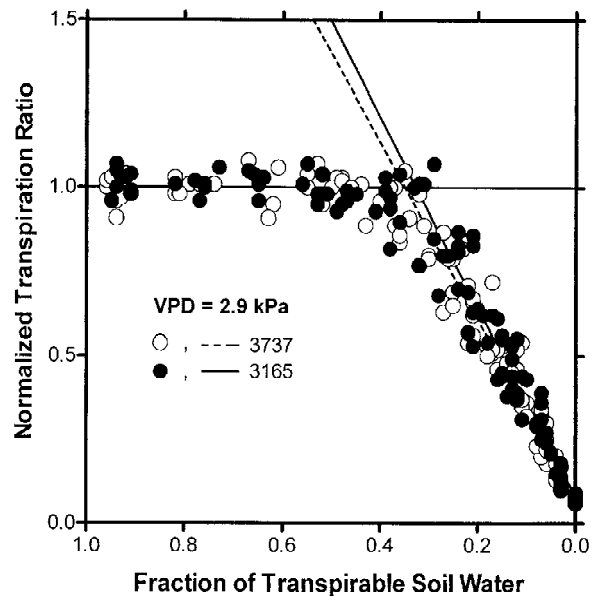


Figure 4. NTR-FTSW response curve of maize hybrids Pioneer 3165 and 3737 at a VPD level of 2.9 kPa. The slanted solid and dashed lines indicate the plateau regression line. The intersection of these lines with the horizontal line at 1.0 indicates the point at which transpiration begins to decline. The data from the other three VPD levels (1.1, 2.0 and 3.6 kPa) were very similar.

erage available soil water difference between hybrids was significant ($P < 0.05$).

Fraction of transpirable soil water (FTSW)

In this experiment, NTR was calculated to reflect daily transpiration rate and FTSW was calculated to reflect soil-water content. Figure 4 shows the relationship between NTR and FTSW for hybrids 3165 and 3737 at a VPD of 2.9 kPa. The threshold for the decrease in transpiration (NTR) occurred when FTSW values of about 0.30–0.35 were reached. Both hybrids and all four VPD treatments showed the same relationship between NTR and FTSW as that shown in Figure 4.

Using a plateau regression procedure, the FTSW threshold at which transpiration rates began to decline was determined for each hybrid at each VPD level. FTSW threshold values ranged from 0.31 at 3.6 kPa to 0.37 at 1.1 kPa for hybrid 3165, and from 0.33 at 1.1 kPa to 0.38 at 3.6 kPa for hybrid 3737 (Table 1). No significant trend in a change of the FTSW threshold for transpiration rate decrease with VPD was observed in hybrid 3737. For hybrid 3165, however, there was a significant ($P = 0.03$) linear ($r^2 = 0.93$) decline of FTSW threshold with increasing VPD level, although the range of the change in the threshold was narrow.

Table 1. Fraction of transpirable soil water (FTSW) thresholds as determined by plateau regression for maize hybrids Pioneer 3165 and 3737 over four vapor pressure deficits in a controlled environment chamber

VPD (kPa)	Hybrid 3165			Hybrid 3737		
	FTSW Threshold	±SEM	# of Observations	FRSW Threshold	±SEM	# of Observations
3.6	0.31	0.0073	10	0.38	0.0378	10
2.9	0.33	0.0109	10	0.35	0.0148	10
2.0	0.36	0.0308	10	0.38	0.0209	9
1.1	0.37	0.0122	10	0.33	0.0221	10

Discussion

The overall increases in transpiration with increasing VPD observed for the maize plants in this study were consistent with those in the literature (Hirasawa and Hsiao, 1999; Hsiao, 1990; Turner et al., 1984; Zou and Kahnt, 1988). Greater VPD resulted in greater amounts of water transpired regardless of water management treatment (Figure 3). At the same time, there was a consistent decrease in plant dry weight with increasing VPD across both hybrids and both water management treatments (Figure 2). Previous studies have shown that carbon exchange rates decrease at high VPD (Dai et al., 1992; El-Sharkawy et al., 1985; Kawamitsu et al., 1993) and that stomata conductance decreases in response to high VPD (Farquhar et al., 1980; Lange, 1971; Maroco et al., 1997; Meinzer et al., 1997; Turner et al., 1985). A decreased stomata conductance, and an associated decrease in carbon exchange rate, could account for the decrease in dry weight with increasing VPD (Figure 2).

The specific objective of this study was to examine the transpiration response to a drying soil of two maize hybrids (Pioneer hybrids 3165 and 3737) under differing atmospheric VPD (1.1, 2.0, 2.9 and 3.6 kPa). Numerous studies have shown that transpiration rate does not begin to decline from well-watered rates until the soil–water content reaches FTSW values of between 0.3 and 0.4, and that this response is consistent across species and treatments (Ray and Sinclair, 1998; Sadras and Milroy, 1996; Weisz et al., 1994). Additionally, Sinclair et al. (1998) looked at a range of soil types, including a sandy loam, and found that soil type had little effect on FTSW thresholds except for soils that were very high in sand or in clay content. However, the hypothesis for this study was that increased atmospheric VPD may cause the threshold

FTSW for the initiation of the decline in transpiration rate to be shifted to higher than anticipated values.

In contrast to the original conclusion based on the study of Denmead and Shaw (1962), the threshold FTSW for the decline in transpiration rate observed in our study with maize was not greatly influenced by VPD. The results we obtained were similar to the observations previously reported for sunflower (Turner et al., 1985) and *N. oleander* (Gollan et al., 1985). The differences between our study and the one of Denmead and Shaw (1962) likely resulted from the fact that VPD was not measured or controlled by Denmead and Shaw. Also, on the higher potential evaporation days in their study, the soil–water content of the containers may have decreased so rapidly that it was not possible to accurately determine a threshold for decreased transpiration rate. In our study, hybrid 3737 showed no significant sensitivity in the threshold for transpiration rate decline across the four tested VPDs. The results for hybrid 3165 were opposite to what was hypothesized in that there was a decreasing FTSW threshold for transpiration rate decline in response to increasing VPD. These analyses are, however, based on a narrow variation in the FTSW thresholds within each hybrid (Table 1). In fact, when the data were analyzed using a split-plot ANOVA, no significant ($P < 0.05$) difference between hybrids or between VPD treatments was detected.

These results appear to conflict with the physical arguments describing the transport of water in the soil as a function of soil–water content. That is, it is clear that the hydraulic conductivity of the soil decreases as the soil dries and this limitation would be encountered at higher soil–water contents when the demand for water transport is greater (Cowan, 1965; Tardieu et al., 1992). That the anticipated increase in the FTSW threshold was not observed in this experiment may

have resulted from the fact that the shift of FTSW would occur within a very narrow range of soil–water content. The hydraulic conductivity of soils is exponentially dependent on volumetric soil–water content (Arya et al., 1999), so only a very small change in soil–water content would account for the hypothetical influence of soil hydraulic conductivity. An increased transpiration rate resulting from an increased VPD could encounter a limitation of soil hydraulic conductivity at a higher volumetric water content, but the limitation occurred only at a very slightly higher volumetric water content that was not discernible in the analysis of the FTSW threshold.

The data indicates that hybrid 3737 was able to extract about 5% more water from the soil than was hybrid 3165. The difference between hybrids in soil water extraction may indicate a difference in plant hydraulic conductivity. However, this difference between cultivars did not result in a measurable effect on the FTSW threshold in this experiment. Averaged across both genotypes and all VPD treatments, the FTSW threshold for hybrid 3165 was 0.34 (SD \pm 0.06) and for hybrid 3737 it was 0.36 (SD \pm 0.08).

A confounding aspect of the hypothetical prediction of increased FTSW threshold for the decline in transpiration rate with increased VPD may result from the possibility of a change in hydraulic conductance within the plant in response to the VPD treatments. The rate of water supply to the plant shoot is dependent on both the conductance of water in the soil and in the roots (Hogg and Hurdle, 1997; Meinzer and Grantz, 1990). There are a number of reports showing that plant hydraulic conductance increases with increasing transpiration rate (Ruggiero et al., 1999), including in maize (Hirasawa and Ishihara, 1991). Therefore, under high VPD with higher transpiration rates there is the possibility that plant hydraulic conductance increased to compensate for the early limitation that might be imposed by a decreased soil conductance. This possibility offers a potential explanation for the observed decrease in the FTSW threshold in hybrid 3165 with increased VPD. Of course, such a conclusion is speculative and requires direct measurements of root conductance for the two tested maize hybrids in response to transpiration rate.

Conclusions

This experiment supported the general observation that the FTSW threshold for the decline in transpir-

ation rate with soil drying is fairly stable within the FTSW range of 0.3–0.4. Little or no change in the FTSW threshold was detected in response to substantial changes in atmospheric VPD to which maize plants were subjected. These results indicated that the general description for a decline in transpiration rate can be assumed without a major concern for the VPD environment in which the plants are being grown.

References

- Arya L M, Leij F J, Shouse P J and Van Genuchten M T 1999 Relationship between the hydraulic conductivity function and the particle-size distribution. *Soil Sci. Soc. Am. J.* 63, 1063–1070.
- Baker J T, Allen Jr L H, Boote K J and Pickering N B 1997 Rice responses to drought under carbon dioxide enrichment. 1. Growth and yield. *Global Change Biol.* 3, 119–128.
- Cowan I R 1965 Transport of water in the soil-plant-atmosphere system. *J. Appl. Ecol.* 2, 221–239.
- Dai Z, Edwards G E and Ku M S B 1992 Control of photosynthesis and stomatal conductance in *Ricinus communis* L. (castor bean) by leaf to air vapor pressure deficit. *Plant Physiol.* 99, 1426–1434.
- Denmead O T and Shaw R H 1962 Availability of soil water to plants as affected by soil moisture content and meteorological conditions. *Agron. J.* 54: 385–390.
- El-Sharkawy M A, Cock J H and Held A A 1984 Water use efficiency of cassava. II. Differing sensitivity of stomata to air humidity in cassava and other warm-climate species. *Crop Sci.* 2, 503–507.
- Farquhar G D, Schulze E-D and Küppers M 1980 Responses to humidity by stomata of *Nicotiana glauca* (L.) and *Corylus avellana* (L.) are consistent with the optimization of CO₂ uptake with respect to H₂O loss. *Aus. J. Plant Physiol.* 7, 315–327.
- Gollan T, Turner N C and Schulze E-D 1985 The responses of stomata and leaf gas exchange to vapor pressure deficits and soil water content III. In the sclerophyllous woody species *Nerium oleander*. *Oecologia* 65, 356–362.
- Hirasawa T and Hsiao T C 1999 Some characteristics of reduced leaf photosynthesis at midday in maize growing in the field. *Field Crops Res.* 62, 53–62.
- Hirasawa T and Ishihara K 1991 On resistance to water transport in crop plants for estimating water uptake ability under intense transpiration. *Jap. J. Crop Sci.* 60, 174–183.
- Hogg E H and Hurdle P A 1997 Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. *Tree Physiol.* 17, 501–509.
- Hsiao T C 1990 Plant–atmosphere interactions, evapotranspiration, and irrigation scheduling. *Acta Hort.* 278, 55–56.
- Jones P, Jones J W, Allen Jr L H and Mishoe J W 1984 Dynamic computer control of closed environment plant growth chambers. Design and Verification. *Trans. Am. Soc. Agricul. Eng.* 27, 879–888.
- Kawamitsu Y, Yoda S and Agata W 1993 Humidity pretreatment affects the response of stomata and CO₂ assimilation to vapor pressure deficit difference in C₃ and C₄ plants. *Plant Cell Physiol.* 34, 113–119.
- Lange O L, Losch R, Schulze E-D and Kappen L 1971 Responses of stomata to changes in humidity. *Planta* 100, 76–86.

- Maroco J P, Pereira J S and Chaves M M 1997 Stomatal responses to leaf-to-air vapour pressure deficit in sahelian species. *Aus. J. Plant Physiol.* 24, 381–387.
- Meinzer F C and Grantz D A 1990 Stomatal and hydraulic conductance in growing sugarcane: Stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13, 383–388.
- Meinzer F C, Andrade J L, Goldstein G, Holbrook N M, Cavellair J and Jackson P 1997 Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. *Plant Cell and Environ.* 20, 1242–1252.
- Pickering N B, Allen Jr L H, Albrecht S L, Jones P, Jones J W and Baker J T 1994 Environmental plant chambers: Control and measurement using CR-10T dataloggers. *In Computers in Agriculture*. Eds. Watson D G, Zazueta F S and Harrison T V. pp 29–35. Proceedings of the 5th International Conference, Orlando, FL, Feb 5–9. Amer. Soc. Agric. Eng. St. Joseph, Michigan.
- Ray J D and Sinclair T R 1997 Stomatal closure of maize hybrids in response to drying soil. *Crop Sci.* 37, 803–807.
- Ray J D and Sinclair T R 1998 The effect of pot size on growth and transpiration of maize and soybean during water deficit stress. *J. Exp. Bot.* 49, 1381–1386.
- Ruggiero C, De Pascale S and Fagnano M 1999 Plant and soil resistance to water flow in faba bean (*Vicia faba* L. *major* Harz.). *Plant Soil* 210, 219–231.
- Sadras V O and Milroy S P 1996 Soil–water thresholds for the responses of leaf expansion and gas exchange: A review. *Field Crops Res.* 47, 253–266.
- Sinclair T R, Hammond L C and Harrison J 1998 Extractable soil water and transpiration rate of soybean on sandy soils. *Agron. J.* 90, 363–368.
- Sinclair T R and Ludlow M M 1986 Influence of soil water supply on the plant water balance of four tropical grain legumes. *Aus. J. Plant Physiol.* 13, 329–341.
- Tardieu F, Bruckler L and Lafolie F 1992 Root clumping may affect the root water potential and the resistance to soil–root water transport. *Plant Soil* 140, 291–301.
- Turner N C, Schulze E-D and Gollan T 1984 The response of stomata and leaf gas exchange to vapor pressure deficits and soil–water content. I. Species comparison at high soil water contents. *Oecologia* 63, 338–342.
- Turner N C, Schulze E-D and Gollan T 1985 The response of stomata and leaf gas exchange to vapor pressure deficits and soil water content. II. In the mesophytic herbaceous species *Helianthus annuus*. *Oecologia* 65, 348–355.
- Weisz R, Kaminski J and Smilowitz Z 1994 Water deficit effects on potato leaf growth and transpiration: Utilizing fraction extractable soil water for comparison with other crops. *Am. Potato J.* 71, 829–840.
- Zou D S and Kahnt G 1988 Effect of air humidity on photosynthesis and transpiration of soybean leaves. *J. Agron. Crop Sci.* 161, 190–194.

Section editor: H. Lambers