

Response of Maize (*Zea mays* L.) Hybrids to Diurnal Variation of Vapor Pressure Deficit (VPD) and Progressive Soil Moisture Depletion

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Abstract: This study investigated the transpiration (TR) response to (i) diurnal changes of vapor pressure deficit (VPD) and (ii) soil dry down in four maize hybrids contrasting for yield performance under drought stress in the field. These four hybrids included a popular local variety P3K and a commercial check SC303 that were found to be drought susceptible. The experiment was carried out in pots at early vegetative stage (8-leaf stage). Results showed an increase of TR with increasing VPD but with significant variations between the hybrids tested. The two susceptible hybrids P3K and SC303 had higher TR over nearly the whole range of VPD values than the two other hybrids, with the largest variation recorded at VPD values above 6 kPa. Regarding the TR response to soil moisture depletion, normalized TR (NTR) of all genotypes reduced with soil moisture depletion for all treatments. In addition, NTR showed a significant reduction for plants that were irrigated at 3 days intervals before the experiment as compared to those irrigated daily. There was a trend of higher water extraction, as evaluated with the fraction of transpirable soil water (FTSW) threshold, in the tolerant hybrids relative to the susceptible ones for the two irrigation treatments. In addition, prior exposure to water deficit tends to lower the FTSW threshold which leads to increased water extraction capacity at lower soil moisture level. These results demonstrate that control of TR under high VPD conditions coupled with high water extraction capacity from progressively drying soil can contribute to drought tolerance in maize hybrids.

Keywords: Maize, Transpiration, VPD, Drought

1. Introduction

Maize (*Zea mays* L.), is the third most important cereal grain crop after wheat and rice, accounting for approximately 4.8% of the total cropped area and 3.5% of the value of agricultural output [1]. It can be used as a source of energy in human's diets in the form of carbohydrates, raw material to agro-based industries, livestock feed and a source of income

[2]. World maize production is estimated at 785 million tons. In Sub-Saharan Africa (SSA), maize yields have stagnated at approximately less than 25% of potentially attainable yields while the per capita food production has continued to decrease over the last five decades [3]. In many parts of SSA, maize yields are estimated at less than 1.5 tons ha⁻¹ while the

actual potential is more than 5 tons ha⁻¹ [3]. The low yields are attributed to adverse climatic conditions, poor soil fertility, poor crop management and limited access to inputs. These adverse climatic conditions are the consequences of seasonal variations that occur very often causing various constraints to agricultural production. Crop response to stresses associated with these constraints depends on the intensity and duration of these stresses and the phenological stage of the crop at which they occur. Many breeding efforts have been made to improve crop resistance to drought. These efforts can be more successful if they integrate genotype × environment interactions and more accurate line screening approach [4, 5]. Thus, selection of a physiological trait for water deficit tolerance requires a comprehensive understanding of the nature of the trait and its contribution to yield as well as its response to the environment [6, 7].

Vapor pressure deficit (VPD) is a climatic variable related to the ambient temperature and relative humidity. This variable is important for maintaining the water status of crops. The rise in VPD induces an increase in transpiration, thus accelerating the dehydration of crops. The limitation of gaseous exchange of canopy under high VPD could allow soil water conservation, which can be used later in the season to support crop reproductive phase in case of drought occurrence. Therefore, knowledge of morpho-physiological mechanisms involved in response to VPD changes and soil moisture depletion may contribute to a better selection of varieties adapted to different agro-climatic conditions. This study aimed to assess characteristics related to plant water use in maize hybrids genotypes contrasting for yield performance under drought stress in the field. Specifically, the work aimed at: (i) assessing the transpiration response to diurnal variation of VPD and (ii) investigating how soil moisture depletion affects the transpiration of these hybrids.

2. Material and Methods

2.1. Plant Material and Growth Conditions

Four maize (*Zea mays* L.) hybrids contrasting for seed yield under drought stress in the field (Table 1) were selected for characterization of traits related to water use. The plants were grown in pots of 6.25 cm diameter and 7 cm height filled with 2 kg of a locally collected sandy soil under outdoor conditions (max: min temperature: 36.1–27.7°C: 16.8–13.8°C; max: min relative humidity: 87.4–94.3%: 29.8–42.8%) at the University of Maradi (Niger) (13°49'N; 7°12'W; altitude 385 m) within a period of 2 months during the rain free period starting from early November 2017. Two sets were prepared with four replicates per hybrid. Prior to planting, seeds were treated with fungicide to protect against fungus. Two seeds were sown per pot and after emergence; each pot was thinned to a single plant. One set was kept well-watered (daily), the second, was irrigated once every 3 days; all until 8-leaf stage.

Table 1. Yield performance of four maize genotypes grown under drought conditions in the field.

Genotype	Trait	Yield (Kg ha ⁻¹)	
		Optimum	Drought
CZH131001	DT	1046.77	912.39
P3K	DS	568.46	334.89
CZH142013	DT	954.40	732.71
SC303	DS	572.80	139.31

2.2. Assessment of Leaf Transpiration Under Diurnal Changes in VPD

A measurement of leaf transpiration rate (g h⁻¹) was done when the plants were at early vegetative stage (8-leaf stage), in outdoor conditions over the course on an entire clear day and under natural changes in atmospheric VPD conditions. This was performed by sequentially weighing potted plants at regular time intervals, starting in the morning when the VPD was low and until the afternoon when the VPD decreased following the midday peak [8]. For all four treatments, plants were saturated one days before starting the experiment and allowed to drain overnight. They were bagged the following day with a plastic bag wrapped around the stem to avoid soil evaporation. Plant transpiration was estimated from the loss in weight of each pot. Pots were weighed with a 0.1 g precision scale HCB 6001 (Adam Equipment Inc, Fox Hollow Road, Oxford, USA) every hour from 07:30 hours to 18:30 hours. To calculate atmospheric VPD, temperature and relative humidity were recorded every 15 min using a temperature and relative humidity recorder (Gemini Tinytag Ultra 2 TGU-4500 Dataloggers (UK) Ltd, Chichester, UK), which was positioned near the plants. Measurements were made in four homogenous plants of each genotype.

2.3. Assessment of Leaf Transpiration Under Dry Down Conditions

One day before the start of the experiment, all pots were watered to saturation in the evening and left overnight to drain. The following morning, they were bagged with a plastic bag wrapped around the stem to avoid soil evaporation, then weighed to obtain initial weight. Subsequently, all pots were weighed each morning at the same time (9 am). Each well-watered pot received water daily as necessary to return its weight to about 50 g less than the initial weight. Water was also added, if needed, to the drying pots so that their net daily water loss was no more than about 70 g.

2.4. Normalization of Transpiration

Normalization was made for the purpose of comparing the transpiration rate of the plants exposed to water deficit to those under optimal irrigation (controls). It was performed in two steps [9]:

- For the water deficit treatment, the daily transpiration ratio of each plant was calculated as: TR = transpiration of the plant /mean transpiration of controls;
- Then to minimize the differences in plant size within a genotype, the transpiration ratios of each day, for each

individual plant was divided by the mean TR of the first 2 days, i.e. before there was any stress. The normalized transpiration ratio, NTR for day_n, was then:

$$\text{NTR} = \text{TR}_{\text{day}_n} / \text{mean TR}_{\text{days}_{1-2}}$$

2.5. Estimation of Fraction of Transpirable Soil Water (FTSW)

The fraction of transpirable soil water (FTSW) is the fraction of water available in the soil for plant transpiration between the stage when the soil is at field capacity and that when transpiration has become negligible and when it was considered there was no longer any water available for transpiration, i.e. when the NTR was below 0.1 [10]. Therefore the FTSW is set at 1 when the soil is at field capacity (100%) and 0 when NTR falls below 0.1. The total transpirable soil water (TTSW) of the pot was calculated as the difference in pot weight between field capacity (the first weighing of pots) and FTSW = 0 (the pot weight when NTR reaches 0.1). TTSW was then used to calculate daily FTSW on any day 'n' such as:

$$\text{FTSW}_n = 1 - (\text{weight}_{\text{FC}} - \text{weight}_{\text{day}_n}) / \text{TTSW};$$

where $\text{weight}_{\text{FC}}$ and $\text{weight}_{\text{day}_n}$ are the pot weight at field capacity and on every single day 'n', respectively.

For each plant of a genotype, the daily NTR values were plotted as a function of FTSW value. A segmental linear regression procedure was used to determine the FTSW threshold (t) when NTR began to decrease for each genotype. Segmental linear regression was set to fit one linear regression line ($y=1$) to the first part of the data (when X is less than some value X_0), and a second linear regression line to the rest (when X is greater than X_0). The FTSW threshold (with confidence interval) at which NTR began to decrease was taken as the intersection between the plateau ($y=1$) and

the linear decline equation.

2.6. Plant Biomass Determination

At the end of the water stress treatment period, the plant of each pot was cut at the base of the stem. The stem and roots were then separated and then dried at 70°C in an oven for 72h. They were weighted using a 0.1g precision scale HCB 6001 (Adam Equipment Inc, Fox Hollow Road, Oxford, USA).

2.7. Statistical Analysis

FTSW threshold was determined and the data were plotted and linear regressions were fitted using Graphpad Prism 7 software (GraphPad Software, Inc., California, USA). Differences between mean values of treatments were evaluated using the least significant difference (l.s.d.) at a 0.05 significance level.

3. Results

3.1. Effect of Water Deficit on Growth Parameters

Shoot and root biomass as well as plant height were reduced by water deficit in all genotypes but the effect varied with genotype (Table 2). The average reduction was 42.26% and 32.18% for shoot and root biomass, respectively while plant height decreased by 11.8% as compared to controls. CHZ131001 presented the highest shoot biomass reduction (45.4%) followed by CZH142013 (37.09%). Regarding root biomass, the lowest reduction was recorded with CZH142013 (27.5%) while the P3K genotype exhibited the largest reduction (38.67%). In addition, CZH131001 presented the highest reduction in plant height (25.25%) whereas P3K showed the smallest reduction (7.85%) (Table 2).

Table 2. Plant growth parameters in four maize genotypes grown in pots outdoor under two irrigation regimes.

Genotype	Irrigation	Plant height (g)	Root biomass (g)	Shoot biomass (g)
CZH131001	Daily	18	34.29	12.2
P3K	Daily	11.12	13.48	12.5
CZH142013	Daily	15.33	9.84	8.3
SC303	Daily	11.75	9.45	11.45
P3K	After 3 days	10.62	18.73	8.35
CZH131001	After 3 days	15.62	19.35	10.45
SC303	After 3 days	9.25	10.20	7.78
CZH142013	After 3 days	14.5	8.79	9.48

3.2. Leaf Transpiration Under Diurnal Changes in VPD

The VPD values varied largely during the course of the day (Figure 1a). The VPD increased gradually between 7:30 and 15:30 hours and rapidly decreased after. The values ranged between 0.87 and 8.5 kPa, with the highest recorded at around 15:30 hours (Figure 1a). There was genotypic variation in TR across all the VPD conditions (Figure 1b). In the early morning (around 7:30 hours) and late evening

(around 18:10 hours), the transpiration was the lowest and similar across all genotypes (ranging between 140 and 160g per plant). Overall, the two sensitive genotypes had significantly higher TR with SC303 exhibiting the highest level of transpiration. The transpiration of these two genotypes was significantly higher than that of the two tolerant genotypes as early as 8:50 up to 16h50 hours (Figure 1b). From the two tolerant genotypes, CHZ142013 presented the lowest TR values.

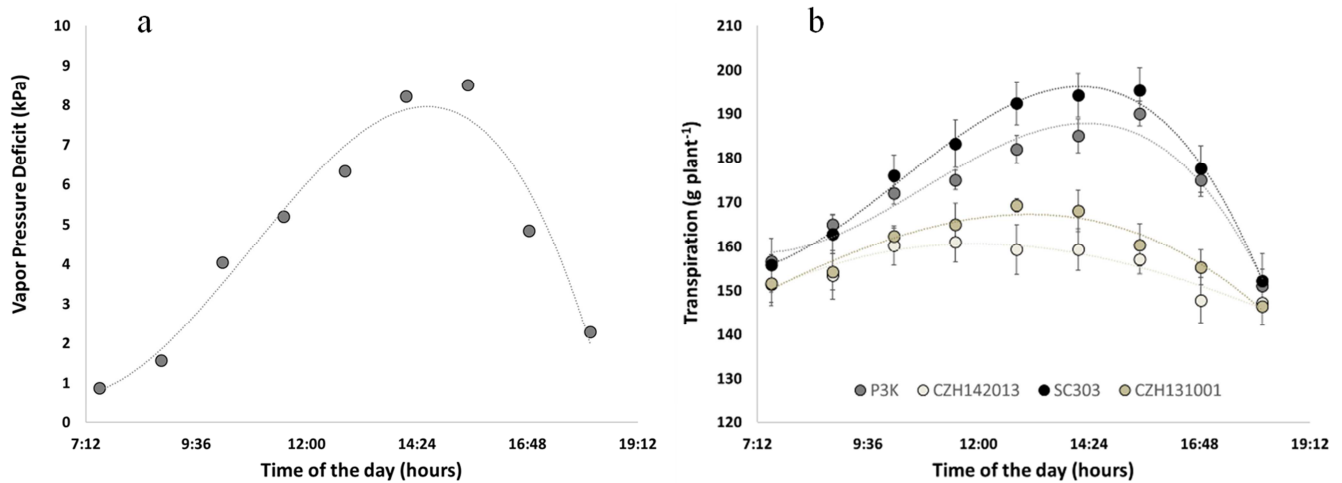


Figure 1. (a) Diurnal variation of vapor pressure deficit (VPD) and (b) transpiration rate under diurnal VPD variation of four maize genotypes contrasting for yield performance under drought stress in the field.

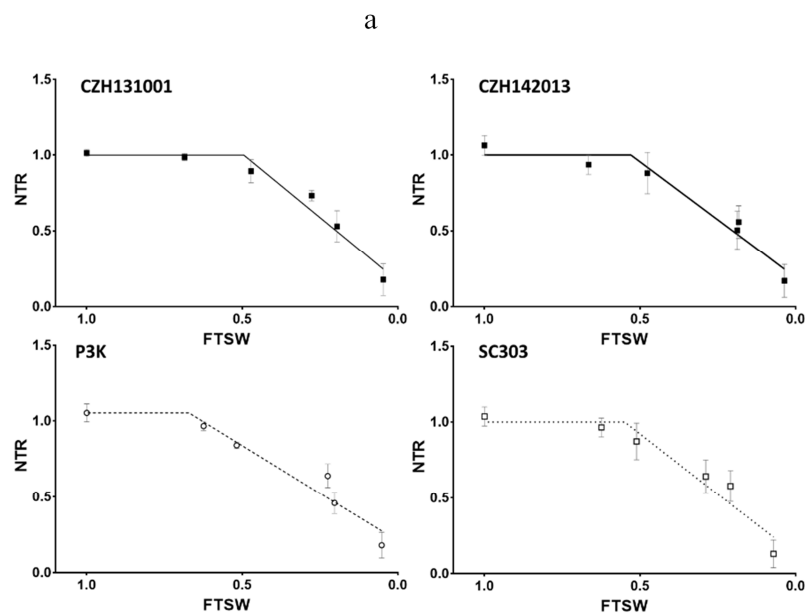
3.3. Transpiration Response to Soil Drying

For the plants that were irrigated daily prior to the dry down experiment, the transpiration started declining at FTSW values ranging between 0.67 and 0.49 (Figure 2a, Table 3). The FTSW threshold values were higher for sensitive P3K and to a lesser extent SC303 than for the two tolerant genotypes. Regarding the plants exposed to water

deficit before the dry down experiment, the FTSW threshold values varied between 0.55 and 0.26. Similar to the plants that received optimal irrigation, there was a trend of lower thresholds in drought tolerant genotypes relative to the susceptible ones (Figure 2b) for the plants exposed to water deficit. CHZ131001 presented the lowest threshold under both irrigation regimes.

Table 3. Fraction of transpirable soil water (FTSW) threshold value for transpiration decline in four maize genotypes contrasting for drought tolerance in the field (The s.e. and 95% confidence limits of FTSW are provided).

Genotype	Irrigation regime before dry down	FTSW Threshold value	Estimate s.e.	95% Confidence limits
CZH131001	Daily	0.495	0.0285	0.30-0.56
P3K	Daily	0.671	0.0451	0.53-0.77
CZH142013	Daily	0.512	0.0362	0.44-0.62
SC303	Daily	0.549	0.0421	0.42-0.62
CZH131001	After 3 days	0.265	0.0130	0.24-0.29
P3K	After 3 days	0.550	0.0421	0.49-0.70
CZH142013	After 3 days	0.447	0.0413	0.38-0.59
SC303	After 3 days	0.457	0.0315	0.38-0.61



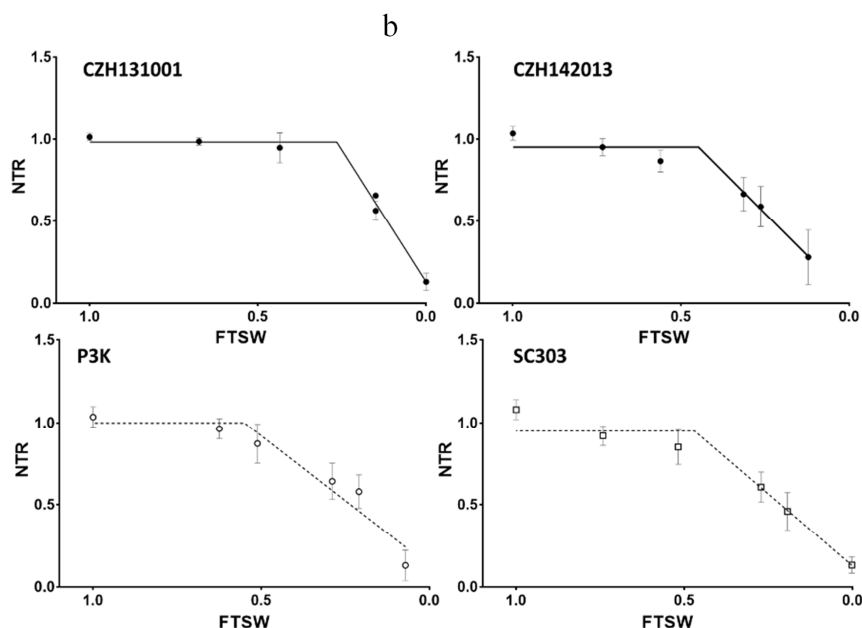


Figure 2. Relationship between the normalized transpiration ratio (NTR) and the fraction of transpirable soil water (FTSW) of four maize genotypes contrasting for yield performance under drought stress in the field. Plants were grown under (a) optimal irrigation (daily) and (b) water deficit (irrigation every 3 days).

4. Discussion

Crops adaptation to water stress involves matching their water requirements to supply, including ensuring that there is sufficient water available for the grain fill period [11]. Among crop water management strategies, the limited-transpiration trait is now well described across crop genotypes and species, including maize [12-19].

The response of transpiration to diurnal changes of VPD shows some genotypic variation (Figure 1). For all the genotypes, TR showed a significant increase with increasing VPD, which induced stomata opening. This ultimately leads to faster soil water depletion. Therefore, the restriction of transpiration under increasing VPD, at different thresholds of VPD, can be a means of adaptation to water limiting conditions. As shown in Figure 1, lower transpiration at high VPD is an important water conservation for which genotypic variation has been reported in other species such as pearl millet (*Pennisetum glaucum* L., [20]), sorghum (*Sorghum bicolor* L., [16]), soybean (*Glycine max* L, Merr, [21, 22]), peanut (*Arachis hypogaea* L., [15]), cowpea (*Vigna unguiculata* L., [23]) and recently on maize (*Zea mays* L., [19, 24]). Limited transpiration in response to high VPD will enable genotypes to conserve much more water which will be useful in case of drought later in the season. These results are in agreement with those of [15] on groundnuts, [23] on cowpea and [8, 25] on chickpea. This closure of the stomata may have consequences because it limits gas exchange (CO_2 / H_2O , O_2) and increases the dissipation of light energy in the form of heat [26]. According to [27], a reduction in transpiration following a closure of the stomata results in a heating of the leaf, often several degrees.

Reduction of transpiration during progressive soil drying

showed different pattern among the tested genotypes (Figure 2). Tolerant genotypes showed decreased transpiration in drier soils than sensitive genotypes. Similar results were reported by [20]. This could be attributed both to better root development in tolerant genotypes and differences in root hydraulic conductance.

Water stress significantly affected shoot and root biomass as well as plant height (Table 2). The relative reduction in shoot biomass was greater in CZH131001 and P3K (45.4% and 43.6%, respectively), while CZH142013 had the lowest reduction (37.09%). This is consistent with observations of other species (eg corn, soybean, cotton) where water stress has stimulated root growth and reduced shoot growth [28]. In addition, several authors [29-32] have reported that roots are the organs whose growth is the least affected compared to aerial parts under conditions of water deficit.

5. Conclusion

The results of this study showed that genotypes with contrasting yield performance under drought stress in the field differ significantly for their TR response to diurnal variation of VPD. Drought tolerant genotypes had lower TR, particularly at high VPD as compared to susceptible ones. In addition, the lower TR resulted in lower FTSW threshold where transpiration declines upon progressive exposure to water deficit. The tolerant genotypes were able to extract water from dryer soil better than the sensitive ones. This study suggests that TR can be considered as a selection criteria for drought tolerance screening in maize.

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