

ALTERATION OF WATER RELATIONS AND YIELD OF CORN GENOTYPES IN RESPONSE TO DROUGHT STRESS

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Summary. The influence of drought stress on internal water status and the final grain yield of three Egyptian corn (*Zea mays* L.) genotypes; GIZA2, TWC310 and TWC320 at different developmental stages was investigated. Plants grown in pots were subjected to four levels of water stress at vegetative and tassel emergence stages. Exposure of plants to drought led to noticeable decreases in leaf water potential (Ψ_w), relative water content (RWC) and osmotic potential (Ψ_π). Water stress changed the relation between leaf water potential and relative water content of all genotypes so that stressed plants had lower water potentials than control at the same leaf RWC. In all genotypes, stressed plants maintained osmotic potentials approximately -0.47 MPa lower than controls. The declining Ψ_w and RWC were associated with lower stomatal conductance and photosynthetic rate. Data showed that tassel emergence stage was more sensitive to drought than vegetative stage where its corresponding grain yield was dramatically reduced. Genotype GIZA2 was the most drought-tolerant, among the tested corn genotypes, expressed in its high productivity under the simulated drought conditions.

Key words: Corn, drought, internal water status, stomatal conductance, photosynthetic rate, yield.

Abbreviations: RWC – relative water content, Ψ_w – water potential, Ψ_π – osmotic potential, FW – fresh weight, DW – dry weight, TW –turgid weight

Introduction

Selection of plant species/crop cultivars with considerable resistance to drought stress has been considered an economic and efficient means of utilizing drought-prone areas

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when appropriate management practices to reduce water losses (Turner 1991). Therefore, improved drought resistance is one of the major objectives in plant breeding programmes for crops grown in dry areas (Matin et al., 1989).

It is now evident that drought occurs widely in arid and semiarid regions of the world where salinity is also prevalent because of rapid evapotranspiration of subsoil water. The best option for crop production, yield improvement and yield stability under soil moisture deficient conditions is to develop drought tolerant crop varieties. A physiological approach would be the most attractive way to develop new varieties rapidly, but breeding for specific, sub-optimal environments involves a deeper understanding of the yield-determining process (Blum, 1985). This is where knowledge of crop responses to water deficits may be best put to use.

Water potential (Ψ_w) is considered to be a reliable parameter for measuring plant water stress response. It varies greatly, depending on the type of plant and on environmental conditions. Hsiao et al. (1976) outlined a number of plant responses to water stress, which occur before desiccation becomes lethal. Most responses (e.g. cell growth, wall and protein synthesis, enzymes activity, etc.) are affected by Ψ_w reductions of less than -1.5 MPa. Passive plant control of desiccation itself occurs when stomatal closure results from reduced Ψ_w .

The effect of drought is usually perceived as a decrease in photosynthesis and growth (Mwanamwenge et al., 1999). The rate of CO_2 assimilation in the leaves is reduced at moderate drought (Sharkey and Seemann, 1989; Yordanov et al., 1997) or even before leaf water status is changed in response to a drop in air humidity (Bunce, 1981), or in soil water potential (Socias et al. 1997). Several lines of evidence indicate that a decrease in photosynthesis due to drought has been attributed to both stomatal and non-stomatal limitations (Graan and Boyer, 1990; Shanguan et al., 1999). Stomatal closure is the first line of defense against desiccation, since it is much quicker than changes in roots growth, leaf area, chloroplast ultrastructure and pigment proteins. In many cases the more drought tolerant species control stomatal function to allow some carbon fixation at stress, thus improving water use efficiency or open stomata rapidly when drought is relieved. The relative part of stomatal limitation of photosynthesis depends on severity of drought. At long-term drought the non-stomatal limitation predominates. Except by increased diffusive resistance (Faver et al., 1996; Herpich and Peckmann, 1997), photosynthesis may also be controlled by the chloroplast's capacity to fix CO_2 .

In maize, grain yield reduction caused by drought ranges from 10% to 76% depending on the severity and stage of occurrence (Bolaños et al., 1993). Drought stress coinciding with flowering delays silking and results in an increase in the anthesis-silking interval (Bolaños and Edmeades, 1993); this usually associates with reductions in grain number and yield (Edmeades et al., 1993).

The objective of this study was to determine and compare the variation in the internal water status of three Egyptian corn genotypes due to drought imposition at different developmental stages and its consequences on the final yield.

Materials and Methods

Experimental design

Grains of the studied corn genotypes GIZA2, TWC310 and TWC320 were obtained from the Cereal Crops Dept., Agricultural Research Center, Egypt. Sterilized grains, similar in size and weight, of each genotype were germinated in a great number on wet filter paper in plastic trays. Then after two weeks the seedlings of uniform growth rate were selected. They were transplanted in plastic pots of diameter 40 cm. These pots were filled with a mixture of clay and sand in proportion of 1:3, respectively. Each pot is provided with a small outlet near its base as a means of drainage. The transplanted seedlings of all the used genotypes were arranged in well-distributed rows in the same pot. Each pot contained six seedlings (two seedlings per genotype). Total number of pots was 100 (25 pots per treatment).

The plants were subjected to four water treatments:

(T₁) Control: pots were regularly irrigated.

(T₂) Vegetative drought: stress was imposed by withholding irrigation for one week at early vegetative stage.

(T₃) Tassel emergence drought: water was withheld for one week at the beginning of tassel emergence stage.

(T₄) Both vegetative and tasselling drought: drought stress was imposed by withholding water for one week at early vegetative as well as tassel emergence stages.

Measurements

Water potential Ψ_w was measured once on flag leaves 7 days after imposing drought stress at vegetative and tassel emergence stages. It was measured between 11:00 AM and 01:00 PM because Fischer et al., (1977) showed that Ψ_w was reasonably stable during this period. Measurements of Ψ_w were made by the spanner type thermocouple psychrometers as described by Morgan, (1980).

RWC was measured using flag leaves after imposing drought conditions. Immediately after cutting at the base of lamina, leaves were sealed within plastic bags and quickly transferred to the lab. Fresh weight (FW) was determined within 2 h after excision. Turgid weight (TW) was obtained after soaking leaves in distilled water in test tubes for 16 to 18 h at room temperature. After soaking, leaves were quickly and carefully blotted dry with tissue paper in preparation for determining turgid weight. Dry weight (DW) was obtained after oven drying the leaf samples for 72 h at 70°C. RWC was calculated from the formula:

$$\text{RWC}(\%) = 100 \times (\text{FW} - \text{DW}) / (\text{TW} - \text{DW})$$

Osmotic potential Ψ_π of the cell sap was measured in a Wescor Model 5100 Osmometer. Stomatal conductance and photosynthetic rates were measured on young

fully-expanded leaves of seedlings and on flag leaves of full grown stressed and non-stressed plants following the procedure of Mishra et al. (1999).

Statistical analysis

Analysis of variance of data for all the parameters was computed using COSTAT computer package (CoHort Software, Berkeley, CA). The least significant differences between the mean values were calculated following Snedecor and Cochran (1980).

Results

Relative water content

RWC measurement characterizes the internal water status of plant tissues and is also a convenient method for following changes in tissue water content without errors caused by continually changing tissue dry weight (Erickson et al., 1991).

GIZA2 maintained the highest RWC values at tassel emergence, whereas TWC310 had the lowest (Table 1).

Overall, plants suffered from drought at tasselling stage had significantly ($P < 0.05$) lower RWC values relative to those stressed at vegetative stage (69.5% versus 76.3%).

Leaf water potential

Ψ_w measured under water stress conditions was significantly ($P < 0.05$) lower in GIZA2 (Table 1). Water deficit reduced the mean Ψ_w from -0.85 MPa in control plants to -1.52 MPa in stressed plants. A comparison of the Ψ_w between the studied genotypes revealed that GIZA2 actually maintained higher Ψ_w than the TWC310 and TWC320 genotypes prior to tassel emergence. However, during the time of tasselling, GIZA2 had mean Ψ_w of -0.58 and -0.44 MPa lower than TWC310 and TWC320, respectively.

Osmotic potential

When plants were allowed to dehydrate at the beginning of vegetative and tasselling stages, Ψ_π declined as the soil dried (Table 1). Stressed plants of GIZA2 showed significantly lower osmotic potentials than TWC310 and TWC320 by an average of -0.28 and -0.26 MPa, respectively.

Relation between RWC and Ψ_w

The relationship between RWC and Ψ_w of the three genotypes is shown in Fig. 1. Stressed plants had lower water potentials than the control at all values below 85%

Table 1. Effect of drought at vegetative and tassel emergence stages on RWC (%), Ψ_w (MPa) and Ψ_π (MPa) of the tested corn genotypes.

Genotype	Parameter	Treatment	Growth stage	
			Vegetative	Tasselling
GIZA2	RWC	Control	86.6	81.4
		Stressed	69.6	63.0
	Ψ_w	Control	- 0.65	- 1.25
		Stressed	- 0.77	- 2.88
	Ψ_π	Control	- 0.87	- 1.89
		Stressed	- 1.15	- 2.05
TWC310	RWC	Control	87.1	77.3
		Stressed	64.7	57.4
	Ψ_w	Control	- 0.59	- 0.96
		Stressed	- 0.61	- 2.00
	Ψ_π	Control	- 0.79	- 1.28
		Stressed	- 1.17	- 1.43
TWC320	RWC	Control	85.2	77.8
		Stressed	64.8	60.3
	Ψ_w	Control	- 0.63	- 1.03
		Stressed	- 0.66	- 2.22
	Ψ_π	Control	- 0.84	- 1.34
		Stressed	- 1.07	- 1.60
LSD (P<0.05)			0.38	0.44

RWC. When compared to the other genotypes, GIZA2 exhibited higher dehydration avoidance that has been defined as having a higher RWC at certain Ψ_w (Ludlow, 1976). At 85% RWC, the stressed GIZA2, TWC310 and TWC320 had water potentials values of - 0.77, - 0.61, and - 0.66 MPa while at 60% RWC, they had leaf water potentials of values - 2.88, - 2.00 and -2.22 MPa, respectively.

Relation between RWC and Y_p

When comparing Ψ_π with RWC (Fig. 2), stressed plants had significantly lower Ψ_π ($P < 0.05$) than controls. All the stressed genotypes had Ψ_π of about 0.47 – lower than their respective controls. GIZA2, however, was uniquely different from the other two genotypes in that it reached lower Ψ_π at RWC values below 85%. For example, at 60% RWC, the GIZA2 control had Ψ_π of 1.31 – whereas TWC310 and TWC320 were at 0.98 and 1.02 MPa, respectively. Stressed GIZA2 was at 2.05 MPa, while TWC310 and TWC320 were at 1.63 and 1.55 MPa, respectively.

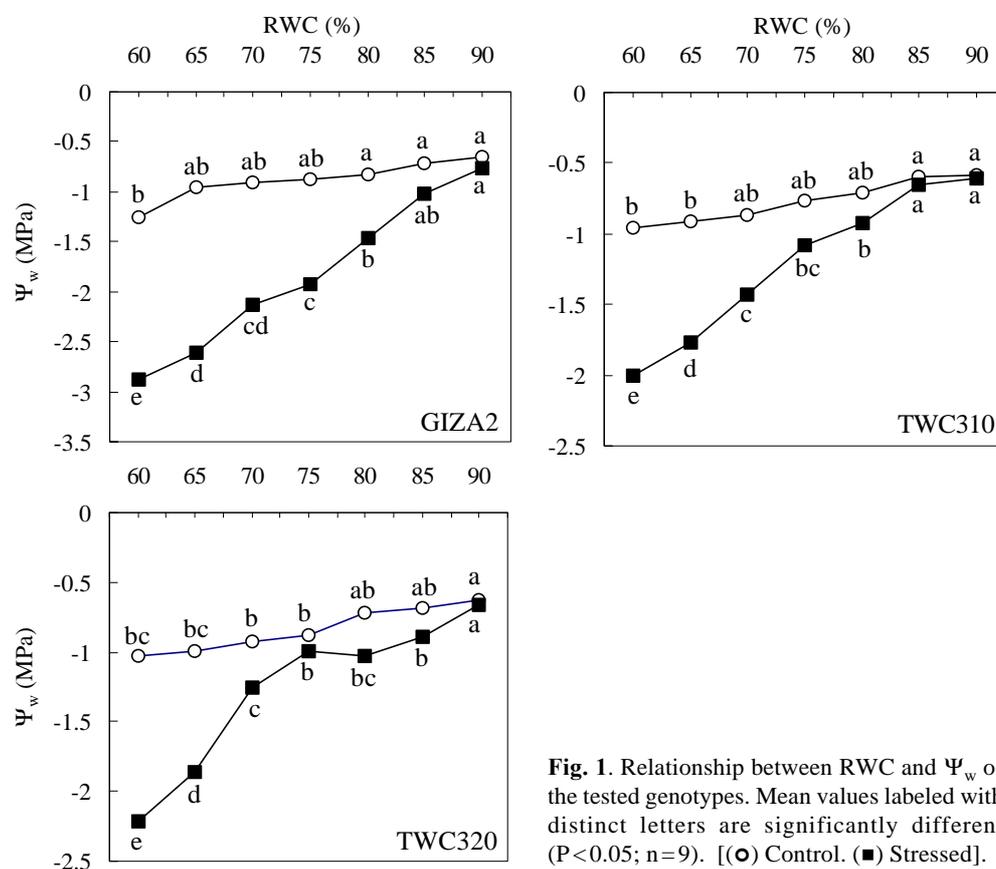


Fig. 1. Relationship between RWC and Ψ_w of the tested genotypes. Mean values labeled with distinct letters are significantly different ($P < 0.05$; $n=9$). [(○) Control. (■) Stressed].

Stomatal conductance

Stomata were highly sensitive to changes in soil water deficit. Stomatal conductance decreased very quickly as the soil dried and before there was much if any loss of Ψ_w . Genotypic difference in stomatal conductance at the vegetative stage was not significant, but it was significant ($P < 0.05$) at tasselling (Fig. 3). GIZA2 had higher stomatal conductance at tassel emergence stage than TWC310 and TWC320. Withholding water at both vegetative and tassel emergence (T_4) reduced stomatal conductance by 75.2% in comparison with the control. Although, there were significant differences ($p < 0.05$) in stomatal conductance among the genotypes, the interaction between genotype and drought treatment was not significant.

Photosynthetic rate

A particularly significant and striking difference among the genotypes was observed with respect to net photosynthetic rate in response to drought stress (Fig. 3). Water

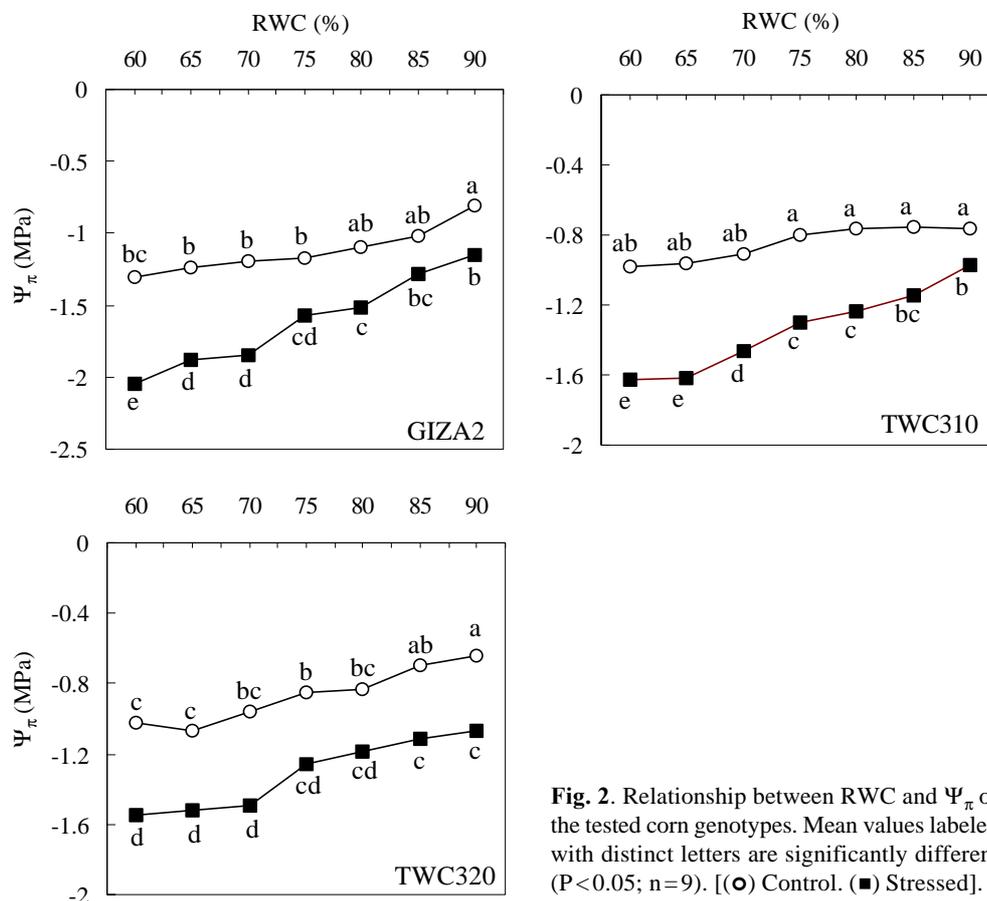


Fig. 2. Relationship between RWC and Ψ_{π} of the tested corn genotypes. Mean values labeled with distinct letters are significantly different ($P < 0.05$; $n = 9$). [(○) Control. (■) Stressed].

deficit led to a significant ($P < 0.05$) inhibition in photosynthetic rate. A 55.1% reduction in photosynthetic rate was found in stressed plants at tasselling stage, as compared to the vegetative stage in all genotypes. This reduction was corresponding to 61.8% of that of the control treatment. Photosynthetic rate of stressed genotype GIZA2 plants was superior in comparison with stressed plants of TWC310 and TWC320 throughout the entire experiment.

Grain yield

Water stress significantly ($p < 0.05$) reduced the final grain yield irrespective of the stage at which drought was experienced (Fig. 4). Data showed that withholding of water at tassel emergence resulted in a great yield loss. The final grain yield of the plants subjected to drought at the tassel emergence stage was dramatically lower than those subjected to drought at vegetative stage or those of control.

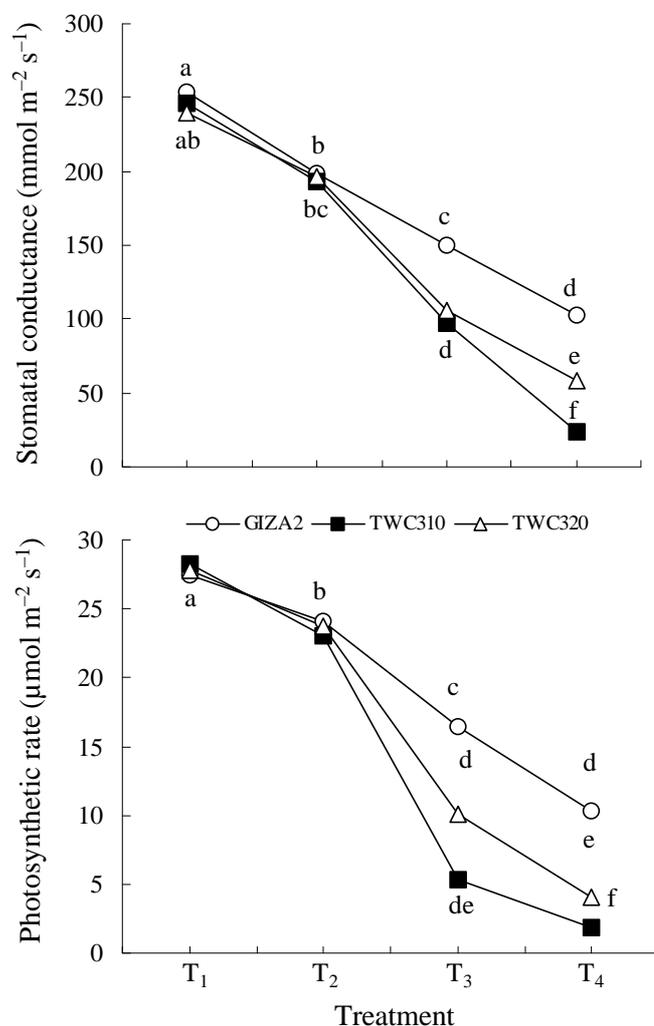


Fig. 3. Effect of drought stress on stomatal conductance and photosynthetic rate of the tested corn genotypes. Mean values labeled with distinct letters are significantly different ($P < 0.05$; $n = 9$). T₁ – Control; T₂ – Stressed vegetative stage; T₃ – Stressed tasselling stage; T₄ – Stressed at both vegetative and tasselling stages

Repeated drought at vegetative and tassel emergence stages was the most detrimental to grain yield. Differences in grain yield amongst genotypes were significant ($p < 0.05$). The magnitude of yield reduction due to water stress was variable in all genotypes and at the different growth stages. The highest reduction in grain yield (72.1%), as compared to its control, was found in genotype TWC310 under repeated

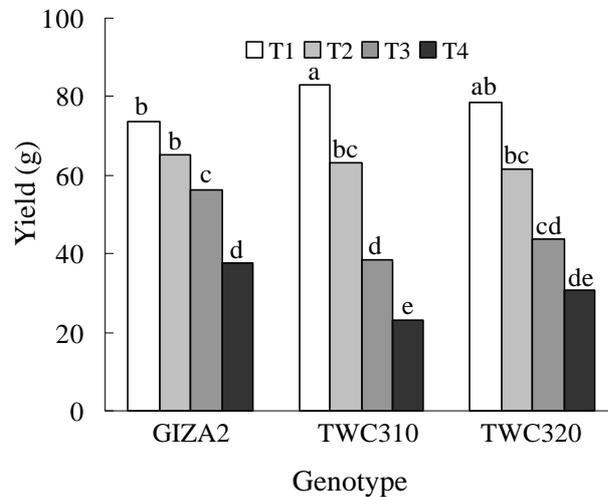


Fig. 4. Mean yield of the studied corn genotypes. Mean values labeled with distinct letters are significantly different ($P < 0.05$; $n = 9$).

drought at both vegetative and tassel emergence. GIZA2 displayed the highest drought tolerance, as the reduction in grain yield was only 11.4%, 23.3% and 48.9% at stressed vegetative, tassel emergence and both stages, in comparison with its corresponding control plants, respectively. Whereas TWC310 exhibited the highest sensitivity to the imposed drought through a reduction in its yield by about 23.6%, 53.6% and 72.1%, relative to the control, at the above mentioned stages, respectively.

The yield of GIZA2 was about 1.5-fold that of TWC310 at the stressed tassel emergence stage (T_3). However, under the control conditions of regular water supply, the yield of TWC310 was the highest.

Discussion

Corn genotypes showed differential sensitivity to drought. The results provide clear evidence of differences between the tested genotypes in plant water relations and their response to the imposing stress. Plants subjected to water stress at the vegetative stage showed RWC values as high as control plants at tassel emergence, suggesting that re-watering after the release of stress at the vegetative stage enabled full recovery of plant vigor. By the time plants attained the reproductive stage, the effects of water stress imposed at the preceding growth stage had diminished. Maintenance of high RWC has been considered to be a drought-resistance rather than drought-escape mechanism, and it is a consequence of adaptive characteristics such as osmotic adjustment and/or bulk modulus of elasticity (Grashoff and Ververke, 1991).

Current results revealed that Ψ_w is dramatically decreased with the increasing water deficit. These results are in agreement with those of Pennypacker et al., (1990) who find similar decrease of Ψ_w in alfalfa as a result of drought stress. The changes in plant water potential might be attributed to a change in osmotic potential. Although, there were significant differences ($p < 0.05$) in Ψ_w among the genotypes, the interaction between genotype and drought treatment were not significant.

Figure 1 indicated that stressed plants had significantly lower water potentials at RWC values below 85 %. Therefore, desiccation-resistant plants demonstrate a large decrease in $\Psi_{\pi w}$ for a given decrease in RWC than less resistant plants (Parsons and Howe, 1984). Using this correlation, it can be suggested that GIZA2 is more resistant than TWC310 or TWC320.

All stressed genotypes showed a decrease in osmotic potential of approximately 0.47 MPa . Cutler et al. (1980) tested several rice cultivars and noted that the capacity for turgor maintenance was similar among the varieties tested. Both stressed and control GIZA2 had lower osmotic potential values than TWC310 or TWC320 at RWC values below 85% (Fig. 2). The lower osmotic potential in GIZA2 could occur for several possible reasons: lower water content, which would cause greater solute concentration, greater tissue elasticity, and/or active accumulation of solutes.

Perhaps the most critical plant response under drought conditions is stomatal regulation of water loss. The classical control system involves stomatal closure as a result of guard cell turgor under water deficits. This negative “feed back” response (Yao et al., 2001) protects the physiologically active mesophyll cells from further injury. Differences in stomatal response to water stress help determine the relative ability of species to cope with drought conditions. Reduction in stomatal conductance might be attributed to the lower Ψ_w and a reduction in RWC, which resulted in loss of turgor. This agrees with the findings of Kramer and Boyer, (1995) and Atteya, (2002). The reduction in water loss by stomatal behavior, represented here in genotype GIZA2, is one of the adaptive responses that prevented more serious loss of foliar hydration and maintained high water use efficiency as the drought develops. This, to an extent, ameliorates the stress onset and helps to maintain photosynthesis. Davies and Kozlowski (1977) observe that stomata of two maple species close at high water potentials, whereas stomata of black walnut stayed open until lower water potentials is reached.

Data presented here showed that under normal water supply the investigated genotypes were characterized by rather different rates of photosynthesis. As drought developed, photosynthetic rate decreased in all genotypes, although not to the same extent, due to decreasing stomatal conductance. The decrease of photosynthesis caused by water deficit has been attributed to both stomatal (restricted CO_2 availability) and non-stomatal limitations (Srivastava and Strasser, 1997, Shangguan et al., 1999). Although stomatal closure generally occurs when plants are exposed to drought, in some cases e.g. severe stress, photosynthesis may be controlled by the chloroplast capacity to fix

CO₂ (non-stomatal limitation) rather than by the increased diffusive resistance (Faver et al. 1996; Herpich and Peekmann, 1997). Plants subjected to drought at the vegetative stage apparently recovered quickly to show a greater rate of photosynthesis at tassel emergence. This might be due to the adaptive mechanism of drought-affected plants (Yordanov et al., 1997). Interaction between genotypes and water treatments was not significant.

Decreasing Ψ_w induced a decrease in photosynthetic rate and stomatal conductance, which led to a conclusion that stomatal closure, was the major cause of reduced photosynthetic rate under water stress. Stomatal closure during water stress without change in mesophyll capacity should result in lower intercellular CO₂ concentration (Ramanjulu et al., 1998).

During vegetative stage drought had small effect on grain yield, while application of drought at tassel emergence caused great loss in grain yield. Presumably the latter treatment did not permit sufficient recovery of growth after resumption of irrigation. The higher grain yield observed in plants subjected to drought at vegetative stage compared with those subjected to drought at tassel emergence stage were associated with more cobs/plant (6.15 versus 2.45), and remarkable increases in the number of grains/cob (113.98 versus 72.33) and average grains weight (20.92 versus 8.90 g/100 grain). Generally, variations in grain yield positively correlated with the number of cobs/plant (Table 2).

Henckel (1962) attributed the reduction in yield, under drought conditions, to reduced protoplasm productivity during flowering which leads to a fall in resistance to dehydration during this critical period. Abd El-Rahman and Marie (1972) attributed the reduction in yield of plants subjected to drought to the decreased in RWC. Fischer (1980), on the other hand, concluded that yield production may be related to limitations of transpiration due to inadequate water supply and to unfavorable effects on assimilate allocations resulting from and to reduced assimilate productions a result of lowered water potential (negative increase). The results of this experiment may draw attention to the most suitable genotype to be cultivated under the various conditions of drought. When irrigation water is available it is advisable to grow the genotype TWC310, whereas under shortage of irrigation water, GIZA2 is the most suitable with the highest productivity.

Conclusion

Results obtained in this experiment indicated that drought stress significantly altered the internal water status by decreasing osmotic potential, Ψ_w and RWC of corn that consequently inhibited photosynthetic rate and reduced the final yield. Imposition of drought especially at tassel emergence stage has a deleterious impact on the plant productivity. The genotype GIZA2 proved to be the most water economic genotype

Table 2: Effect of drought at vegetative and tassel emergence stages on yield components of the studied corn genotypes.

Genotype	Parameter	Treatment	Growth stage	
			Vegetative	Tasselling
GIZA2	No. of cobs plant ⁻¹	Control	6.52	6.55
		Stressed	6.23	3.01
	No. of grain cob ⁻¹	Control	145.75	157.33
		Stressed	129.16	84.11
	100-grains weight (g)	Control	27.56	27.66
		Stressed	22.55	10.94
TWC310	No. of cobs plant ⁻¹	Control	6.91	7.02
		Stressed	6.01	1.88
	No. of grain cob ⁻¹	Control	173.44	194.27
		Stressed	101.66	62.58
	100-grains weight (g)	Control	28.42	29.45
		Stressed	19.63	7.80
TWC320	No. of cobs plant ⁻¹	Control	6.37	6.51
		Stressed	6.22	2.48
	No. of grain cob ⁻¹	Control	141.26	167.55
		Stressed	111.13	70.30
	100-grains weight (g)	Control	24.09	25.19
		Stressed	20.58	7.97
LSD (P<0.05)			2.44	1.08

when subjected to drought stress evidenced by reservation of more water content in plant tissues, higher stomatal conductance and photosynthetic rate. All these characters account for its highest productivity under shortage of water supply. Overall, it is advisable to grow this genotype of corn in land areas with limited irrigation water.

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