Soil Environ. 35(2): 216-223, 2016
www.se.org.pk
Online ISSN: 2075-1141
Print ISSN: 2074-9546

A comparison of the effects of soil water deficit on root and shoot traits of maize genotypes

Qurat ul Ain[1], Saad Imran Malik[1*] and Muhammad Irshad Ul Haq[2]
[1]Department of Plant Breeding & Genetics, PMAS-Arid Agriculture University, Rawalpindi
[2]Millets Research Station, Shamsabad, Muree Road, Rawalpindi

Abstract

Drought is one of the major environmental constraints limiting crop productivity especially in dryland regions. Fifteen maize genotypes suitable for cultivation in rain-fed regions of Pakistan were evaluated for their response under drought conditions. The parameters questioned were relative water content (RWC), osmotic potential (Ψπ), root length (RL), shoot length (SL) and root-shoot ratio (RS-ratio). A comparison for these parameters was made between drought exposed plants and well-watered control plants. A highly significant difference (P≤0.01) between genotypes was recorded for RWC, Ψπ, RL and shoot length. Genotypes NP-3 and EV-77 showed highest retention of water contents (79% and 78%, respectively) after seven days of drought stress, while I. Gold and Rakaposhi had the lowest RWC of 59% and 61%, respectively. A significant overall increase in Ψπ was observed in all genotypes after drought stress, yet genotypes EV-77 and NP3 showed the highest Ψπ of –1.13 and –1.03 MPa, respectively under water deficit conditions. RS-ratio did not differ significantly in all genotypes before as well as after drought stress. NARC-2704 and NP-3 exhibited the longest root lengths of 23.3 cm and 23 cm, respectively in control plants without water stress but increase in their RL after drought stress was not remarkable. Comparisons showed that NP-4 had the highest increase (21.3%) in RL while EV-77 showed 16.3% increase after drought stress. As expected, relative shoot lengths significantly decreased in nearly half of the genotypes after drought treatment, nevertheless, this decrease remained non-significant in the remaining genotypes compared to control well-watered plants. This decrease was more evident in EV-77 (17%) followed by Soan-3 (15%). Collectively, our findings suggest that NP-3 and EV-77 are superior genotypes for the traits investigated under both drought and well-watered conditions, especially, for having high RWC and Ψπ.

Keywords: Maize, drought tolerance, root traits, shoot traits, osmotic potential

Introduction

Drought tends to reduce up to 60-70% crop yields in different regions of the world (Ana-Kulkarni *et al*., 2008) and in Pakistan (Rashid and Rasool, 2010). Scarcity of irrigation water and precipitation coupled with global climate change are increasing the risks of drought and, consequently casing yield losses (Chaves and Davies, 2010).

Maize (*Zea mays* L.) is a very diverse crop and is the highest yielding cereal grain per unit area of an arable land. Soil water deficit disrupts plant-water relations and severe drought conditions may cause irreversible damage to the cellular components of plants (Beck *et al.*, 2007; Farooq *et al.*, 2009; Avramova *et al*., 2016). The capacity of maize plant to uptake ample amount of available soil moisture and to simultaneously reduce water losses, collectively known as "plant hydraulic machinery" (Blum, 2011) is largely dependent on its physiological features and morphological traits which vary in different genotypes.

Maize is a warm season crop which can't thrive below 15 °C mean daily temperature even in the temperate zones and is sensitive to frost (FAO, 2015). Temperate germplasm grows well in low temperature environments while tropical material can tolerate up to 45 °C day temperature (Birch *et al*., 2003; FAO, 2015). Maize needs plenty of sunshine throughout its growing season and an ample amount of water either by irrigation or precipitation. These features make this crop even more prone to soil water deficit, which leads to low seed set and compromised yield (Bohnert *et al*., 1995). Among cereals, with the exception of rice, maize is most susceptible to drought stress (Banziger and Araus, 2007).

Plants possess certain innate physiological, morphological or molecular defense mechanisms to tackle drought conditions (Zhou *et al*., 2007). Traits like osmotic adjustment, leaf rolling, stomatal closure, root length and biomass, rate of cell division and cell size help reduce plant water loss (Agbicado *et al*., 2009; Chimungu *et al*., 2014; Avramova *et al*., 2016). Phenotypic screening for such traits in maize seedlings has been an attractive, low-input and quick method of evaluating maize germplasm (Meeks *et al*., 2013; Pace *et al.*, 2014). These approaches have been

*Email: saad.malik@uaar.edu.pk

© 2016, Soil Science Society of Pakistan (http://www.sss-pakistan.org)

very successfully employed in many crops for drought tolerance screening.

It has been established that cell membrane stability, osmotic adjustment, stem reserve mobilization and epicuticular wax are important traits for drought tolerance in maize (Montes *et al*., 2011; Oraki *et al*. 2012). Long-term exposure to water stress leads to reduction in plant height, leaf size, net photosynthesis rate and carbon assimilation (Porro and Cassel, 1986; Avramova *et al*., 2016) along with oxidative injury caused by increasing reactive oxygen species (ROS) production (Mittler, 2002; Neill *et al*., 2002). Water deficit also reshapes the whole plant transcriptome - the expression of genes, and production of osmoprotectant proteins (Zeng, 2010; Lei, 2015; Voothuluru *et al*., 2016).

Root and shoot lengths and root surface area are considered as effective parameters for drought tolerant germplasm screening (Li *et al*., 2015). Roots are the first to perceive drought in the soil and tend to grow deeper under water deficit conditions to acquire more water, hence increasing the overall root-shoot ratio (Lambers *et al*., 2002). Nevertheless, the root biomass and shoot length as well as biomass decrease (Wu and Cosgrove, 2000; Rauf *et al*., 2009; Fenta *et al*., 2014). Genotypes with an extensive and deep root system are more tolerant to soil water deficit with relatively better plant water status (Hund *et al*., 2009; Zhu *et al*., 2010; Jaramillo *et al*., 2013). However, the soil water use efficiency is linked with these features as deep-rooted genotypes may exhibit inefficient photosynthesis (Hund *et al*., 2009). Plant relative water contents (RWC) is a reliable indicator of water status in plants and is an important determinant of water assimilation capacity (Chimungu *et al*., 2014). RWC reduce significantly in drought susceptible varieties when exposed to low water regimes (Siddique *et al*., 2000) due to injury in the cell membrane structure, hence the function is disrupted due to water loss from tissues. This water loss results in the accumulation of solutes in cells. The osmotic potential becomes lower which attract water into the cell maintaining the turgor pressure (Sassi *et al*., 2010).

A comparative study on young maize plants was undertaken to monitor the change in different morphological and physiological plant character under well-watered and water deficit conditions. We used fifteen maize genotypes suitable for cultivation in the arid and semi-arid region of Pakistan with the aim to identify those with higher root growth after drought, more water retention capacity and least effects on plant growth under water stress conditions. Comparisons were made for the potential of these genotypes to thrive under drought stress conditions and those having better morpho-physiological traits to combat drought were identified.

Materials and Methods

Plant material and growth conditions

The plant material comprised of 15 maize genotypes for which the seed was obtained from the National Agricultural Research Centre, Islamabad. The experiments were performed during 2015-16 in the Department of Plant Breeding and Genetics, PMAS Arid Agriculture University Rawalpindi. Seeds of fifteen maize genotypes were sown in pots filled with a mixture of soil, sand and farmyard manure (2:1:1). For root and shoot length experiments, the plants were grown in 40 cm long polythene tubes. Drought-stress conditions were imposed on 20 days old seedlings of uniform size by withholding water supply for six days while control plants were watered normally. The experiments were replicated three times and the samples were collected from three independent plants in each replication.

Determination of relative water content (RWC)

Leaf samples were weighed for their fresh weights, hydrated at room temperature for 4 h and weighed again to obtain fully turgid tissue weight (TW). The samples were oven dried for 24 h at 80 °C and weighed again to get dry weights (DW). Percent relative water contents (RWC) were measured as (FW–DW) / (TW–DW) x 100 (Weatherly and Slatyer, 1957).

Determination of leaf osmotic potential ($\Psi\pi$)

Leaf samples from both control and drought treated plants were placed in microtubes and dipped in liquid nitrogen for 5 min. The samples were placed at -80 °C for 2 days. The samples were crushed with micro-pestles and centrifuged for 10 min at 12,000g for cell-sap extraction. For each sample, 50 µl of cell-sap was used to measure osmotic potential (OP) with the aid of an osmometer (Make model). The readings were recorded in mmol/kg unit and expressed as –Mega Pascal (–MPa) according to Vant's Hoff equation (Reference).

$$OP\ (-MPa) = R \times T \times \text{Osmometer reading}$$

Where, R is Gas constant (0.008314) and T is lab temperature.

Seedling root and shoot length measurement

Twenty days old plants grown in the 40 cm plastic tubes were uprooted and the roots were carefully washed without any damage. Root-length (RL) was measured from

the coleoptile to primary root tip. Similarly, shoot-length (SL) was measure from the coleoptile to the ligule of fully developed youngest leaf. The root-shoot ratio (RS-ratio) was obtained by dividing root length by shoot length.

Measurement of seedling dry mass

Seedling dry mass (SDM) was measured by drying 20 days old maize seedlings at 80 °C in a hot-air oven for up to 2 days and weighing on a top loading digital balance.

Data analysis

The data for replicated trials were subjected to the analyses of variance (ANOVA) separately and means were compared by Fisher's least significant difference (LSD). Minitab15 and Statistix 8.1 data analysis packages were used to all statistical analyses.

Results

Mean square values from the analyses of variance and their significance using F-statistics, grand means and coefficient of variation (CV) is shown in Table 1. The statistical analysis indicated a highly significant difference among genotypes ($P \leq 0.01$) for leaf relative water contents (RWC) in drought treated plants, osmotic potential ($\Psi\pi$), root length (RL), shoot length (SL). However, the difference for RWC in control plants and for root-shoot ratio (RS-ratio) in both control and drought-stressed plants was recorded as non-significant at $P \leq 0.05$ (Table 1). Mean (μ) values for individual genotypes along with standard deviation (SD) for shoot and root traits and ranking based on $LSD_{\alpha=0.05}$ and represented by small letters is also summarized in Table 2.

(79%) after drought stress followed by EV-77 (78%) and Rustam (77%), while, I. Gold, Rakaposhi and Soan-3 had 59%, 61% and 63% RWC which were the least amounts of water retained among the subject genotypes after drought stress (Figure 1).

Leaf osmotic potential ($\Psi\pi$)

Drought tolerant genotypes are known to accumulate osmotically active substances in the cells in order to maintain vacuolar turgor for a longer time and mitigate the harmful effects of water deficit for normal cellular functions. The leaf $\Psi\pi$ for all genotypes showed significant difference for well-watered ($F_{2,14}$=2.58, $P \leq 0.01$) as well as drought-stressed plants ($F_{2,14}$=13.94, $P \leq 0.001$) (Table 1). The measurement of $\Psi\pi$ established a range of –0.31 to –0.49 MPa in the well-watered plants (control) while the drought exposed plants showed a range of –1.13 to –0.51 MPa in all genotypes evaluated (Table 2). The highest values for $\Psi\pi$ in drought-exposed plants were recorded in EV-77 (–1.13 MPa), NP-3 (–1.03 MPa) and NARC-2704 (–1.03 MPa) ranked as "a" using LSD while MT-2, IG-1 and NP-4 showed the least $\Psi\pi$ values of –0.47, –0.51 and –0.53 MPa, respectively (Table 2).

Collectively, these data suggest that genotypes EV-77 and NP-3 are more capable of retaining high RWC when compared to control plants and exhibit high $\Psi\pi$ in order to keep with soil water deficit. Hence, these genotypes are marked as relatively drought tolerant in comparison to rest of the genotypes investigated in this study regarding RWC and $\Psi\pi$ (Figure 1 and 2).

Table 1: Mean squares from the ANOVA, grand means and CV(%) for different parameters under well-watered (control) and water deficit (drought) conditions

		R/water content		Osmotic Potential		Root Length		Shoot Length		Root-Shoot ratio	
	DF	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
Genotypes	14	12.04^{NS}	125.05**	0.009**	0.108**	11.07**	17.01**	13.09**	11.66**	0.0196^{NS}	0.029^{NS}
Replications	2	20.28^{NS}	11.22^{NS}	0.018^{NS}	0.020^{NS}	0.04^{NS}	2.61^{NS}	0.12^{NS}	0.02^{NS}	0.007^{NS}	0.006^{NS}
Grand mean		84.99	70.72	0.389	0.730	19.61	21.18	20.50	19.10	1.06	1.02
CV (%)		3.35	4.15	14.47	12.07	9.14	9.43	6.71	6.45	12.58	14.48

** Significant at $p \leq 0.01$; ^{NS} Non-significant

Leaf relative water content

The RWC for 15 genotypes did not differ significantly for well-watered plants without drought stress ($F_{2,14}$=1.49, $P \leq 0.01$) designated as control. The drought stress for six days resulted in a varying and highly significant decline in RWC in genotypes tested ($F_{2,14}$=14.53, $P \leq 0.01$). The genotype NP-3 showed highest retention of water contents

Root and shoot characteristics

A comparison of RL showed highly significant difference for this parameter both in control ($F_{2,14}$=3.45, $P \leq 0.01$) and drought treated plants ($F_{2,14}$=4.26, $P \leq 0.01$) (Table 1). The means were ranked using $LSD_{\alpha=0.05}$ which showed NARC-2704 with highest RL (23.3 cm) under control conditions followed by NP-3 (23 cm), while Rustam

Table 2: Means ($\bar{x}$) ± St. Dev. (SD) and ranking of genotypes based on Fisher's LSD (α = 0.05) in control and drought treated maize genotypes

	R/water contents (%)		Osmotic Potential		Root Length		Shoot Length	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought
Genotypes	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD
IG-1	83±4.1 na	65±3.5 ghi	0.31±0.08 e	0.51±0.10 d	21.3±2.1 abc	21.0±1.0 bcde	20.0±1.3 cdefg	19.7±1.53 cde
Rustam	83±4.4 na	77±2.4 abc	0.35±0.07 cde	0.69±0.10 bc	17.0±1.0 e	19.8±3.0 cde	16.7±2.4 defg	17.8±1.53 cdef
EV-77	84±3.7 na	78±1.2 ab	0.41±0.05abc	1.13±0.05 a	18.0±1.0 de	21.5±1.3 bcd	15.7±2.6 bcd	19.7±1.00 def
MT-2	87±2.5 na	76±3.3 abcd	0.31±0.04 de	0.47±0.11 b	18.8±1.7 cde	18.7±2.1 e	18.7±0.6 cdef	20.3±1.53 cdef
NP-4	83±3.4 na	76±2.5 abcd	0.35±0.03 cde	0.53±0.10 d	17.7±2.1 de	22.5±3.0 bcd	19.3±0.6 bc	22.7±1.15 cde
EV-7004	86±1.5 na	72±2.8 def	0.36±0.06 cde	0.71±0.11 b	20.4±0.6 abcd	19.7±0.6 de	21.7±1.0 b	22.0±1.53 b
NP-3	86±4.2na	79±1.3 a	0.42±0.04 abc	1.03±0.04 a	23.0±2.6 ab	23.3±2.1 bc	22.0±0.6 cde	20.7±0.58 cdef
RK-1	86±2.1 na	74±2.0 bcde	0.46±0.04 ab	0.74±0.03 b	17.7±1.2 de	20.0±1.0 cde	18.5±0.6 efg	18.0±0.50 ef
I. White	82±2.0 na	69±5.6 efg	0.41±0.04 abc	0.69±0.09 bc	20.3±1.2 bcd	18.7±1.5 de	20.3±1.0 g	15.0±1.53 ef
Azam	87±2.4 na	68±1.9 fgh	0.49±0.06 a	0.54±0.17 bcd	19.3±2.1 cde	21.2±2.0 cde	22.3±1.0 bcd	21.7±0.58 bc
Rakaposhi	86±3.7 na	61±2.0 ij	0.42±0.02 abc	0.69±0.16 bc	17.7±2.1 de	18.2±2.6 e	18.3±1.0 defg	18.0±1.53 def
Soan-3	84±3.2 na	63±4.6 hij	0.41±0.12 abcd	0.62±0.07 bcd	20.0±2.0 cd	24.0±1.7 ab	20.0±1.7 b	23.0±1.00 bcd
NARC-2704	86±1.5 na	72±3.1 cdef	0.46±0.03 ab	1.03±0.08 a	23.3±0.6 a	27.3±2.1 a	25.3±1.2 a	24.3±0.58 a
I. Gold	82±2.2 na	59±1.5 j	0.42± 0.04 abc	0.68±0.04 bc	19.3±2.5 cde	19.8±2.6 de	17.7±1.5 efg	17.0±0.58 f
Agati-2002	89±1.2 na	74±2.9abcde	0.39±0.14 bcde	0.55±0.04 cd	20.3±1.5 bcd	20.3±0.6 cde	16.7±0.6 fg	18.3±1.53 ef
St. Error	2.322	2.395	0.047	0.072	1.463	1.632	1.123	1.006
t(α=0.05)	4.757	4.906	0.096	0.147	2.996	3.342	2.300	2.060

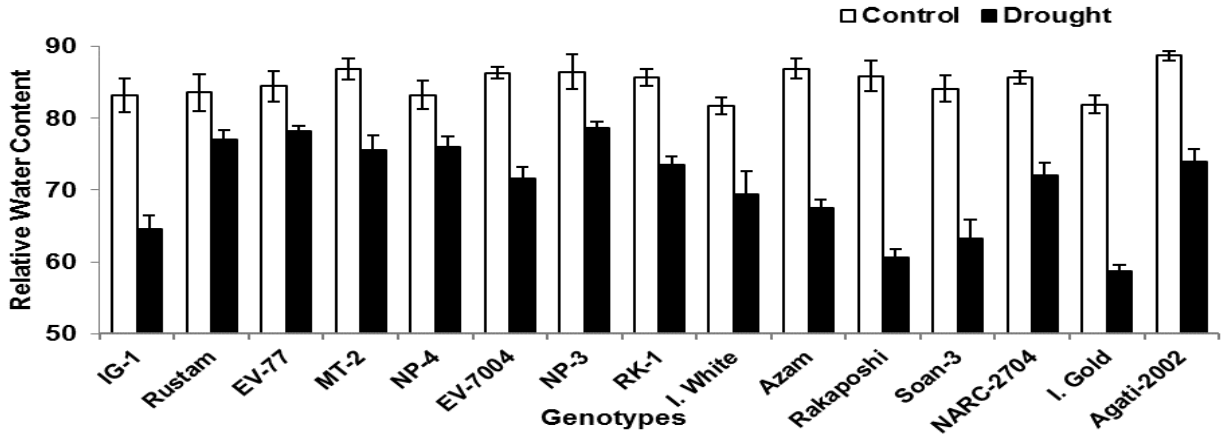

Figure 1: Relative water contents in well-watered (control) and drought exposed plants

and NP-4 had smaller roots (Table 2). After six days of drought stress, NARC-2704 exhibited the highest RL of 27.3 cm followed by Soan-3 (24 cm) and NP-3 (23.3 cm). This is important to note that NARC-2704 showed 15% relative increase in the root length after drought stress, however, NP3 showed a negligible increase (1%). Comparison highlights that NP-4 showed the highest increase in the RL (21.3%) after drought stress when compared to well-watered plants (Figure 5). This was followed by Soan-3 (16.7%), EV-77 (16.3%) and NARC-2704 (14.7%) which showed a significant root elongation after drought stress (Figure 3 and 5). Notably, the relative shoot length in drought treated plants when compared to well-watered control plants decreased in most genotypes (Figure 4). However, this decrease remained significant in nearly half of the genotypes tested. In contrast, the RL increase after drought stress in all genotypes except a decrease by 8.5% in I. white (shown as negative value in Figure 5) and slight decrease in EV-7004 (3.6%). RS-ratio didn't change significantly after drought stress ($F_{2,14}$=1.34, P≤0.01).

Discussion

Drought is known to affect plant morphology and physiology in several different ways. A reduction in the cell division and elongation, diminished photosynthetic rate and

stem elongation, and modified root architecture are the characteristic outcomes of water deficit in plants. A varying response of different maize genotypes for all the parameters studied was observed and no single genotype was regarded as the best collectively for all traits.

However, our results indicate that NP-3 and EV-77 are better performing genotypes under water deficit conditions considering these genotypes assimilate more water contents by keeping high osmotic potential under drought stress. Nevertheless, only EV-77 exhibited a significant increase in

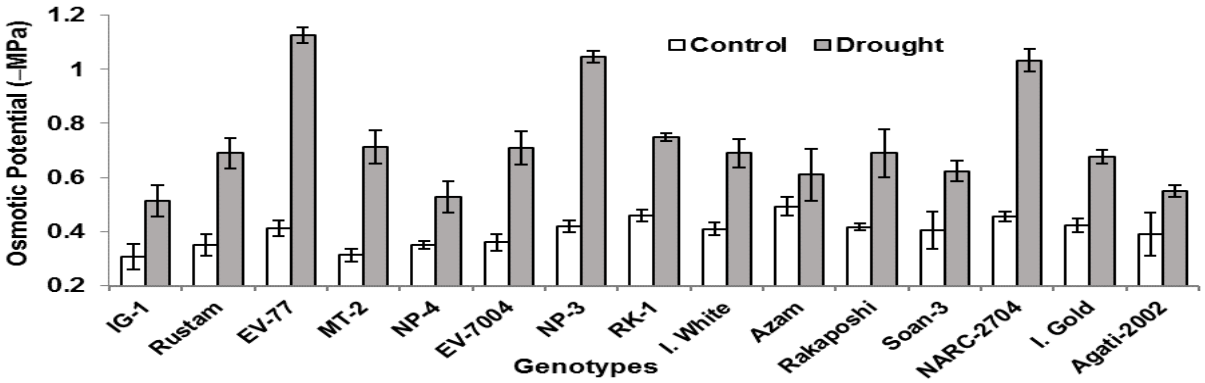

Figure 2: Changes in osmotic potential of well-watered (control) and drought exposed plants

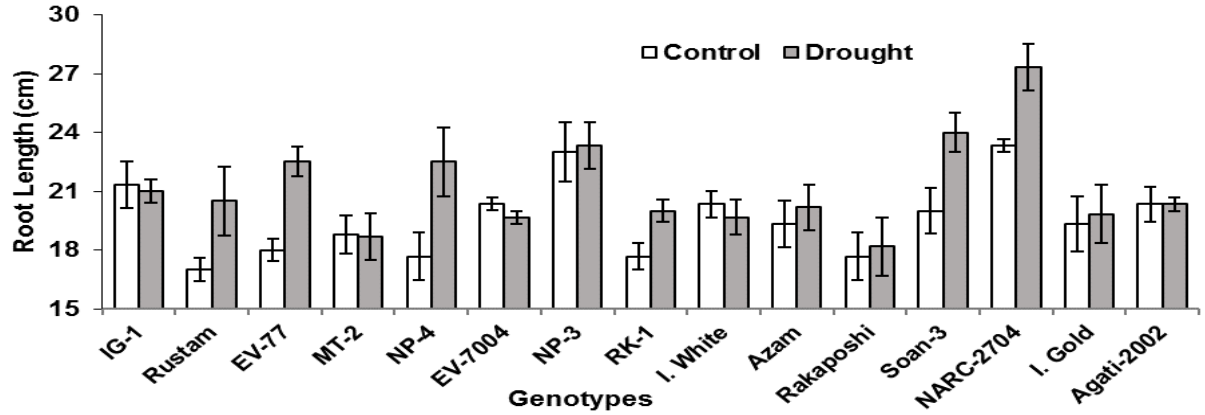

Figure 3: A comparison of root length in well-watered (control) and drought exposed plants

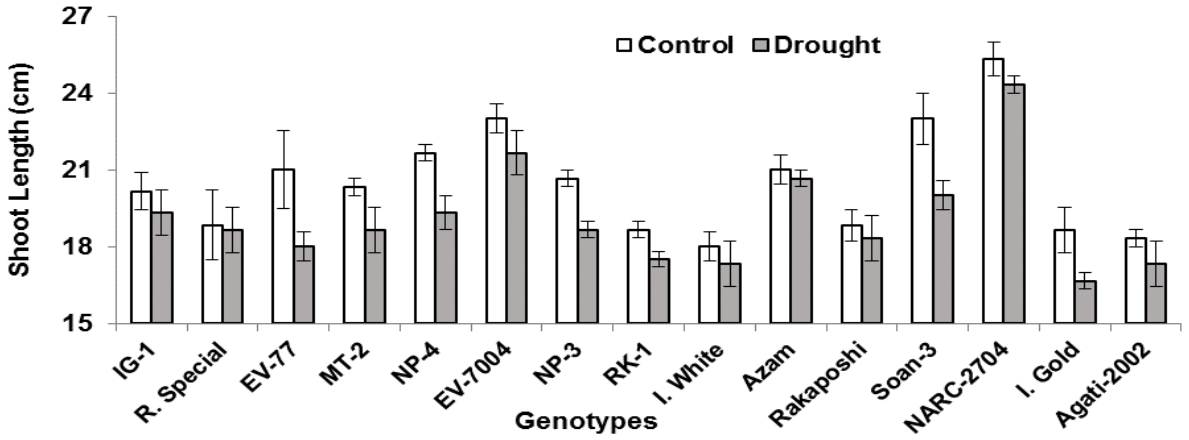

Figure 4: A comparison of shoot length in well-watered (control) and drought exposed plant

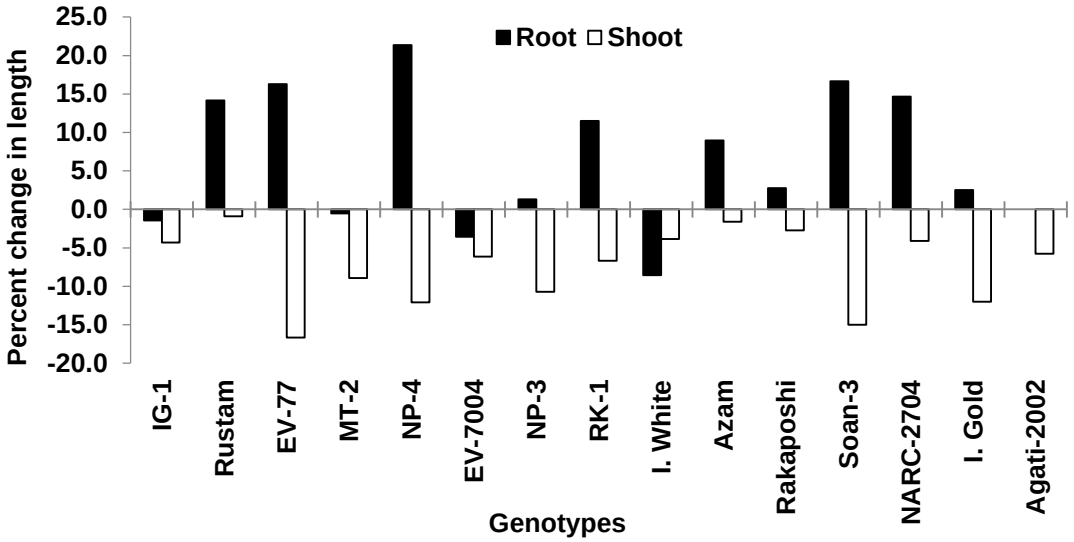

Figure 5: Percent increase/decrease in root length vs. shoot length after six days of drought stress

the root length after drought stress. Non-significant change in the RS-ratio under water deficit conditions suggests that maize roots tend to penetrate in deeper soil layers to extract more water which is a characteristic feature of drought tolerant genotypes. However, this tendency varies with genotypes. Plants under drought stress reduce or shutdown aerial growth. Consequently, a decrease in the stem elongation is expected to observe which was more evident in drought susceptible genotypes.

References

Agbicodo, E.M., C.A. Fatokun, S. Muranaka, R. G.F. Visser and C.G. Linden-van-der. 2009. Breeding drought tolerant cowpea: constraints, accomplishment and future prospectus. *Euphytica* 167: 353-370.

Aldesuquy, H.S., A.Z. Baka, O.M. El-Shehaby, and H.E. Ghanem. 2012. Efficacy of seawater salinity on osmotic adjustment and solutes allocation in wheat (*Triticum aestivum*) flag leaf during grain filling. *International Journal of Plant Physiology and Biochemistry* 4(3): 33-45.

Ali, Q., M. Ashraf and H.U.R. Ather. 2007. Exogenously applied proline at different growth stages enhances growth of two maize cultivars grown under water deficit conditions. *Pakistan Journal of Botany* 39(4): 1133-44.

Ana-Kulkarni, M., T. Borse and S. Chaphalkar. 2008. Mining Anatomical Traits. A Novel Modeling Approach for increased water use efficiency under drought conditions in plant. *Czech Journal of Genetics and Plant Breeding* 44(1): 11-21.

Avramova, V., K.A. Nagel, H. Abd-El-Gawad, D. Bustos, M. DuPlessis, F. Fiorani and G.T. Beemster. 2016. Screening for drought tolerance of maize hybrids by multi-scale analysis of root and shoot traits at the seedling stage. *Journal of Experimental Botany* 67: 2453-66.

Bajji, M., J.M. Kinet and S. Lottus. 2001. The use of electrolyte leakage method for assessing cell membrane stability as a water stress tolerance test in durum wheat. *Plant Growth Regulation* 36(1): 61-71.

Banziger, M and J, Araus. 2007. p. 587-601. In: Advances in molecular breeding towards drought and salt tolerant crops. M. A. Jenks *et al*. (eds.). Springer, USA.

Beck, E.H., S. Fettig, C, Knake, K. Hartig, and T. Bhattarai. 2007. Specific and unspecific responses of plants to cold and drought stress. *Journal of Biosciences* 32: 501-510.

Birch, C.J., M.J. Robertson, E. Humphreys, N. Huntchins. 2003. Agronomy of maize in Australia: Review and Prospectus. *In*: Versatile Maize - Golden Opportunities. C.J. Birch and S.R. Wilson, (*Eds*.), *5th Australian Maize Conference. Australia*.

Bohnert, H.J., D.E. Nelson and R.G. Jensen. 1995. Adaptations to environmental stresses. *Plant Cell* 7: 1099-1111.

Chaves, M. and B. Davies. 2010. Drought effects and water use efficiency: improving crop production in dry environments. *Functional Plant Biology* 37(3): iii-iv.

Chen, H. and J. Jang. 2010. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. *Environmental Reviews* 18: 309-319.

Chimungu, J.G., K.M. Brown and J.P. Lynch. 2014. Large root cortical cell size improves drought tolerance in maize. *Plant Physiology* 166: 2166-78.

FAO. 2015. Land and water division. Food and Agriculture Organization of the United Nations. FAO online: http://www.fao.org/nr/water/cropinfo_maize.html [Accessed: 25/08/2016]

Farooq, M., A. Wahid, N. Kobayashi, D. Fujita and S.M.A. Basra. 2009. Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development* 29: 185-212.

Fenta, B. A., Beebe, S. E., Kunert, K. J., Burridge, J. D., Barlow, K. M., Lynch, J. P., and C. H. Foyer. 2014. Field phenotyping of soybean roots for drought stress tolerance. *Agronomy* 4: 418-435.

Hund A, S. Trachsel, and P. Stamp. 2009. Growth of axile and lateral roots of maize: I development of a phenotying platform. *Plant and Soil* 325: 335-349

Kaufmann, I., T. Schulze-Till, H.U. Schneider, U. Zimmermann, P. Jakob and L.H. Wegner. 2009. Functional repair of embolized vessels in maize roots after temporal drought stress, as demonstrated by magnetic resonance imaging. *New Phytologist* 184: 245-56.

Killi, D., F. Bussotti, A. Raschi, and M. Haworth. 2016. Adaptation to high temperature mitigates the impact of water deficit during combined heat and drought stress in C3 sunflower and C4 maize varieties with contrasting drought tolerance. *Physiologia Plantarum* (Accepted Manuscript), doi: 10.1111/ppl.12490.

Lambers, H., O.K. Atkin and F.F. Millenaar. 2002. p. 521-552. Respiratory patterns in roots in relation to their functioning. In: Y. Waisel, A. Eshel, K. Kafkaki, (eds.), Plant Roots: Hidden Half, 3rd Ed. Marcel Dekker, CRC press, New York.

Lei, L., J. Shi, J. Chen, M. Zhang, S. Sun, S. Xie, X. Li, B. Zeng, L. Peng, A. Hauck, H. Zhao, W. Song, Z. Fan, and J. Lai. 2015. Ribosome profiling reveals dynamic translational landscape in maize seedlings under drought stress. *Plant Journal* 84(6): 1206-18.

Li, R., Y. Zeng, J. Xu, Q. Wang, F. Wu, M. Cao, H. Lan, Y. Liu and Y. Lu. 2015. Genetic variation for maize root architecture in response to drought stress at the seedling stage. *Breeding Science* 65: 298-307.

Mattioli, R., P. Costantino and M. Trovato. 2009. Proline accumulation in plants not only stress. *Plant Signaling and Behaviour* 4(11): 1016-18

Mittler, R. 2002. Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Science* 7:405-410.

Molaei, P., A. Ebadi, A. Namvari and T.K. Bejandi. 2012. Water relation, solute accumulation and cell membrane injury in sesame (*Sesamum indicum* L.) cultivars subjected to water stress. *Annals of Biological Research* 3 (4):1833-1838.

Moinuddin, R.A. and R. Khannu-Chopra. 2004. Osmotic adjustment in chickpea in relation to seed yield and yield parameters. *Crop Science* 44: 449-455.

Montes, J.M., F. Technow, B.S. Dhillon, F. Mauch and A.E. Melchinger. 2011. High-throughput non-destructive biomass determination during early plant development in maize under field conditions. *Field Crop Research* 121(2): 268-273.

Neill, S., R. Desikan and J. Hancock. 2002. Hydrogen peroxide signalling. *Current Opinion in Plant Biology* 5: 388-395

Oraki, H., F.P. Khajani and M. Aghaalikhana. 2012. Effect of water deficit stress on proline contents, soluble sugars, chlorophyll and grain yield of sunflower (*Helianthus annuus* L.) hybrids. *Journal of African Biotechnology* 11(1): 164-168

Pace, J., N. Lee, H.S. Naik, B. Ganapathy-subramanian and T. Lubberstedt. 2014. Analysis of maize (*Zea mays* L.) seedling roots with the high-throughput image analysis tool ARIA (Automatic Root Image Analysis). *PLoS One* 9(9): e108255.

Porro, I. and D.K. Cassel. 1986. Response of maize to tillage and delayed irrigation. *Field Crop Abstracts* 40(2): 637.

Rashid, K and G. Rasul. 2010. Rainfall Variability and Maize Production over the Potohar Plateau of Pakistan. *Pakistan Journal of Meterology* 8(15): 63-74.

Rauf, S., H.A. Sadaqat, I.A. Khan, R. Ahmed. 2009. Genetic analysis of leaf hydraulics in sunflower (*Helianthus annuus* L.) under drought stress. *Plant Soil and Environment* 55: 62-69.

Sassi. S., S. Aydi, K. Hessini, E.M. Gonzalez, C. Arrese-lgor and C. Abdelly. 2010. Long Term mannitol-induced osmatic stress leads to stomatal closure, carbohydrate accumulation and changes in leaf elasticity in *Phaselous vulgaris* leaves. *African Journal of Biotechnology* 9(37): 61-69.

Siddique, M.R.B., A. Hamid and M.S. Islam. 2000. Drought stress effects on water relations of wheat. *Botanical Bulletin of Academia Sinica* 41: 35-39.

Lu, Y., Hao, Z., Xie, C., Crossa, J., Araus, J.L., Gao, S., Vivek, B.S., Magorokosho, C., Mugo, S., Makumbi, D. and S. Taba. 2011. Large-scale screening for maize drought resistance using multiple selection criteria evaluated under water-stressed and well-watered environments. *Field Crops Research* 124: 37-45.

Voothuluru, P., J.C. Anderson, R.E. Sharp and S.C. Peck. 2016. Plasma membrane proteomics in the maize primary root growth zone: novel insights into root growth adaptation to water stress. *Plant Cell and Environment* 39(9): 2043-54.

Wu, Y. and D.J. Cosgrove. 2000. Adaptation of roots to low water potentials by changes in cell wall extensibility and cell wall proteins. *Journal of Experimental Botany* 51: 1543-53.

Zheng, J, J. Fu, M. Gou, J. Huai, Y. Liu, M. Jian, Q. Huang, X. Guo, Z. Dong, H. Wang and G. Wang. 2010. Genome-wide transcriptome analysis of two maize inbred lines under drought stress. *Plant Molecular Biology* 72:407-421.

Zhou, J., Wang, X., Jiao, Y., Qin, Y., Liu, X., He, K., Chen, C., Ma, L., Wang, J., Xiong, L. and Q. Zhang. 2007. Global genome expression analysis of rice in response to drought and high salinity stresses in shoot, flag leaf and panicle. *Plant Molecular Biology* 63: 591-608.

Zhu J, K.M. Brown, J.P. Lynch. 2010. Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). *Plant Cell and Environment* 33: 740-49

Zhu, R.E., E.A. Nord, J.G. Chimungu, K.M. Brown and J.P. Lynch. 2013. Root cortical burden influences drought tolerance in maize. *Annals of Botany* 112: 429-37.