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Morpho-Physiological Changes in Maize Seedlings under Osmotic Stress

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Summary: Drought is a major abiotic stress factor limiting crop growth, development and production worldwide. The objective of this study was to evaluate tolerance to osmotic stress of maize seedlings. More than 6,000 accessions from the Maize Research Institute gene bank were tested under controlled drought (at flowering) in Egypt, and afterwards in temperate climate (Serbia and Macedonia). Out of 41 drought tolerant accessions in the field, five inbred lines were chosen for laboratory testing, as well as one drought sensitive line. These genotypes were exposed to 4% polyethylene glycol-PEG (Mr 10000) for 24 h and 48 h. Nine-day-old seedlings compared to control conditions were analyzed in root and shoot length, fresh and dry weight and proline content. Results showed reduction in all parameters under stress, while only proline content increased in all PEG treated genotypes compared to control.
Key words: drought, dry weight, fresh weight, maize, osmotic stress, proline, root length, seedlings, shoot length, stresses

Introduction

Drought tolerance is a complex quantitative trait involving many morphological, anatomical and physiological characteristics controlled by several small effects genes (Barnabas et al., 2008). The high variability factors make it difficult to define plant traits required for improved performance under all possible drought situations (Rao & Cramer, 2003). With the unpredictability of drought, geographical and seasonal, including ongoing climate changes, the destructive impact of drought is likely to further increase (Bänziger & Araus, 2007).

Plants have many adaptive mechanisms in response to abiotic stress, being morphological modifications (increase in root size and reduction in leaf area) or changes in physiological and biochemical processes (Yordanov et al., 2000). These adaptive mechanisms include traits which promote the maintenance of high tissue water content, as well as those for promoting tolerance to low water availability. Thus, osmotic adjustment plays an important role in sustaining growth under water deficit conditions and represents the decrease in osmotic potential by the active accumulation of organic solutes like sugars, polyols, betaines and proline, as well as inorganic solutes within the cells. All compatible solutes may be classified into two categories: one is nitrogen containing compounds such as proline and other amino acids, quaternary ammonium compounds and polyamines, and the other is hydroxy compounds, such as sucrose, polyhydric alcohols and oligosaccharides. In response to drought stress, they are accumulated in high concentrations in the cytoplasm, without perturbing the normal physiological functions (Ashraf & Foolad, 2007).

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Accumulation of proline, as an osmoticum, is a widespread plant response to abiotic and biotic stresses. This accumulation is associated with protective functions, as stabilization of macromolecules, osmotic adjustment (Oliveira-Neto et al., 2009), radical detoxification and regulation of cellular redox status (Sharma & Dietz, 2006).

One of the well known mechanisms for beneficial crop yield responses to osmolyte accumulation is the maintenance of root development in order to reach water that may be available in the deeper soil profiles (Serraj & Sinclair, 2002). The examination of profiles of water uptake of rice (Yadav et al., 1997) and lettuce (Johnson et al., 2000) demonstrate that root depth is a relevant determinant of the ability of plants to extract water from deep soil layers. In several crop species including maize, the growth of roots and shoots is inhibited during water deficit, although roots continue growing at low water potentials that are completely inhibitory to shoot growth (Spollen et al., 1993). Verslues & Sharp (1999) showed that proline concentration increases greatly in the growing region of maize primary roots at low water potentials, largely as a result of an increased net rate of the proline deposition.

Numerous physiological and morphological traits are proposed in breeding for drought tolerant genotypes as additional tools for selection on the basis of yield (Blum, 1988).

In maize, grain yield is highly affected by drought, especially when the stress occurs during flowering and grain filling (Grant et al., 1989). However, selection of genotypes with tolerance to drought in the field and stable yield is very difficult to obtain due to fluctuation of agroecological and climatic conditions. Another reason could be a lack of diversity in the conventional breeding programs, although a huge number of maize accessions are stored within gene banks worldwide (FAOSTAT, 2010). Usually the size of germplasm collections limits their utilization in plant breeding research.

The necessity of higher maize production, alongside global warming, has made investigation of biochemical and physiological mechanisms during drought stress more important (Ashraf & Foolad, 2007). Plant response to complex trait could be changed according to the developmental stage and the results of screening in the early growth are not representative for final yield according to Dickin et al. (2009). However, in other studies on maize (Ruta, 2010) co-location of QTLs was detected for seedling root traits with traits of adult plants under stress in the field, indicating that adaptive mechanism with preferable root over shoot development could give more stable yield under drought conditions.

The aim of this study was to evaluate the changes in maize seedlings of root and shoot traits that confer drought tolerance and to study influence of osmotic stress imposed through application of polyethylene glycol (PEG). This experiment was undertaken to evaluate whether variability in drought tolerance among maize inbreds in the field also exists in seedlings under laboratory conditions.

Materials and methods

Plant material and growing conditions. All accessions from Maize Research Institute gene bank collection (about 6,000) were screened under controlled water stress in Egypt, at Sids Agricultural Research Station (150 km south of Cairo). After two-year testing for drought related secondary traits and yield characteristics under field conditions, subset of 41 genotypes (landraces, introduced populations and inbred lines) were chosen (Babić et al., 2011). Out of them, five drought tolerant inbred lines (L_1-L_5) and one drought sensitive (L_6) maize inbred line were used in the present study.

Seeds were germinated for three days on moistened filter paper and then transferred into plastic pots containing ¼ strength Knopp solution with modified nitrogen content (Hadži-Tašković Šukalović et al., 2005). The initial pH of the solution was adjusted to 5.6. Plants were grown for the following six days in a growth chamber under 12 h photoperiod at 22/18°C, with the irradiance of 40 W m^{-2} and relative humidity of 70%. For the terminal 24 h and 48 h of the growing period, one half of the plants (treatment) were grown on the aerated nutrient solution supplemented with 4% polyethylene glycol (PEG, Mr 10 000), parallel to control plants grown on the nutrient solution without PEG. Roots and shoots of each plant were sampled and used for further analyses.

Free proline determination. Free proline was determined according to Bates et al. (1973). Roots and shoots were homogenized with

3% sulfosalicylic acid (1:10 w/v). The filtered homogenate was mixed with acid ninhydrin solution and boiled for 15 min. After extraction with toluene, absorbance of reaction product was determined at 520 nm. The proline content in the sample was calculated from the proline standard curve and expressed in mg g^{-1} FW.

Statistical analysis. All statistical analyses are performed in four replicates and the results were presented as means ± standard error (SE). Simple correlation analysis was used to determine the relationships between traits.

Results and Discussion

Essential biochemical processes including photosynthesis, respiration, protein synthesis and assimilation of organic nitrogen are seriously affected by drought in agricultural production areas. Root systems are important for taking up water and nutrients from the soil, to communicate with shoots and to maintain total plant growth (Girdthai et al., 2010). The root system is usually less inhibited than shoot under drought (Sharp et al., 2004) and continuous root growing under water deficit is advantage for plants. Water deficiency caused inhibition in root and shoot growth in all maize genotypes, after 24 h and particularly after longer exposure to stress (Figure 1). At low water potential caused by PEG, maize primary root growth is inhibited, causing shorter and thinner roots compared to the roots grown under normal conditions (Sharp et al., 1988). In fact, even under mild drought stress, shoots may stop growing completely, while roots continue to grow and help seedling establishment.

Reduction in length ranged from 9.92% up to 40.65% and from 13.11% to 45.31% in root and shoot, respectively, being the most pronounced in genotype L1. According to Tuberosa et al. (2002) root QTLs from unstressed seedlings in hydroponics were related to QTLs of field grown maize under drought stress, indicating constitutive trait expressions. In another QTLs study of maize seedlings under water stress, drought tolerant parent contributed to larger root lengths (Ruta, 2010). Moussa & Abdel-Aziz (2008) concluded that biochemical mechanisms of drought tolerance are already active in maize seedlings.

Information about seedlings responses (root and shoot growth, fresh and dry weight, etc.) to abiotic stress are limited and varied among different crops. In maize seedlings reduction in available water and increasing salt intensity resulted in decreasing root and shoot fresh weight (Bilgin et al., 2008). A common adverse effect of water stress on crop plants is the reduction in fresh biomass production (Farooq et al., 2009). Reduction in root fresh weight varied from 11.25% up to 62.14% and from 22.9% to 63.93% in shoot, with increase of osmotic stress (Table 1). A significant decrease in FW of root and shoot was observed in sorghum seedlings under four abiotic stresses (Gill et al., 2001).

The dry weight of root and shoot decreased with increased stress compared to control. Only in genotype L_1 shoot dry weight increased at 24 h stress and decrease at more severe deficit (48 h). Similar

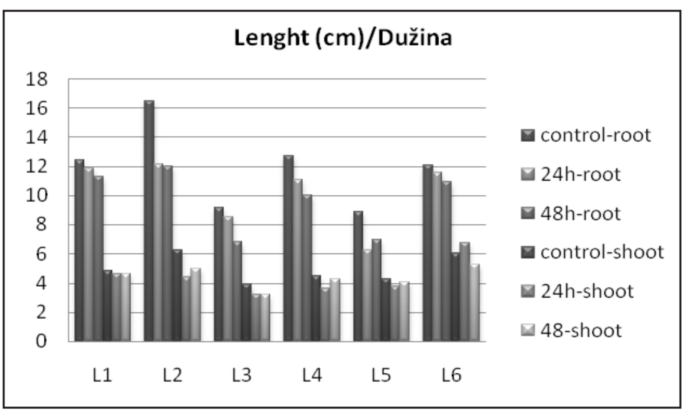

Figure 1. Effect of PEG treatment on changes in root and shoot growth
Grafik 1. Efekat PEG-a na porast korena i izdanka

Table 1. Effect of PEG treatment on changes of fresh (FW) and dry (DW) weight in root and shoot
Tabela 1. Efekat PEG-a na promenu sveže (FW) i suve (DW) mase korena i izdanka

Genotype Genotip	PEG	Root/Koren		Shoot/Izdanak	
		FW (mg)	DW (mg)	FW (mg)	DW (mg)
L1	0 h	142.7	8.3	160.4	14.7
	24h	81.9	6.9	145.2	15.7
	48h	67.2	6.5	144.4	15.3
L2	0 h	161.5	9.6	206.5	19.5
	24h	56.7	5.8	127.4	14.6
	48h	55.6	6.5	134.8	17.2
L3	0 h	84.3	4.9	131.5	11.3
	24h	42.1	3.7	89.4	9.5
	48h	30.0	3.3	78.2	9.9
L4	0 h	101.9	5.5	143.8	12.7
	24h	49.9	3.8	93.9	9.5
	48h	46.6	4.3	71.9	11.4
L5	0 h	80.2	5.7	158.2	14.0
	24h	47.8	4.3	113.5	12.2
	48h	49.6	4.8	121.9	12.5
L6	0 h	80.0	4.3	156.8	11.1
	24h	76.2	4.1	138.4	10.5
	48h	71.2	3.7	121.1	9.5

tendency was obtained in *Arabidiopsis* seedlings after exposure to dark stress (Van der Weele et al., 2000). Gain in dry weight was observed in root and shoot of sorghum seedlings, exposed to light and darkness, after application of different abiotic stress except in root growth exposed to PEG (Gill et al., 2001).

In our genotypes proline level increased in response to PEG from 28.5% up to 150% in root and from 9.5% to 110.7% in shoot, comparing to control (Figure 2) which is confirmed by previous experiments in maize seedlings (Valentovič et al., 2006; Vuletić et al., 2010).

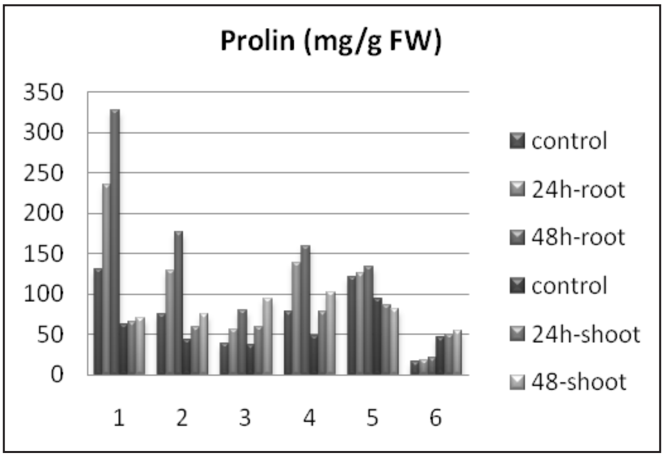

Figure 2. Effect of PEG treatment on changes in proline content in root and shoot
Grafik 2. Efekat PEG-a na promenu sadržaja prolina u korenu i izdanku

Proline accumulation increased under PEG treatment but its rate differs among accessions and organs. Genotypic variations in proline content have been observed in many studies and species, although it was difficult to correlate this trait with tolerance to stress. During the experiment we found significant differences in proline content among genotypes, not only between treatments. The lowest content was found in root and shoot of sensitive line (L_6). Proline content was higher in all treated seedlings being more significant in root. The similar tendency of proline content changes was found in wheat seedlings after exposure to high temperature stress compared to optimal conditions (Ahmed & Hasan, 2011). In maize primary root, the proline level increased a hundred fold under a low water potential (Voetberg & Sharp, 1991). No significant difference in proline accumulation was found among accessions of alfalfa seedlings in the absence of PEG, but proline content varied with changes in PEG concentrations (Safarnejad, 2008). Therefore, proline accumulation depends on duration and concentration of osmotic stress, the type of tissue, the developmental stage of the plant and the genotype (Ashraf & Foolad, 2007).

It could be expected that under more severe osmotic stress, genotypic differences will be more pronounced. In fact, proline accumulation is a result of two pathways: increased expression of proline synthetic enzymes and suppressed activity of proline degradation. Accumulation of proline is result of synthesis, catabolism and transport activities. According to Roy et al. (2009) high proline content is a good index for stress tolerance, under drought the protein degrades and consequently the proline content increases. Recent studies in transgenic plants indicate that the modified plants with higher proline amount were more tolerant to water deficit (Vendruscolo et al., 2007) and salt stress, compared to wild plants (Husaini & Abdin, 2008). It is important to point out that although accumulated proline does mediate osmotic adjustment, this trait alone is unlikely to be enough to ensure survival of plants under stress conditions.

Correlation analysis was performed between proline content, fresh and dry weight and length of six maize genotypes under optimal (control) and stress conditions (imposed to PEG) in root and shoot (Table 2). The analyses revealed that the changes in proline content are highly negatively correlated with observed morphological traits in root, but correlations were with no significance in shoot.

Although importance of seedling stage for final yield is usually underestimated, there is evidence for significant associations in maize between seedlings and plants in the field, regarding grain yield and root depth (Landi et al., 1998). As an example, significant associations were found in maize between traits of the seedlings grown under controlled conditions and traits of the plants in the field, especially related to grain yield (Tuberosa et al., 2002) and root (Landi et al., 1998; Sanguineti et al., 2006). Similar to maize, associations between root at seedlings and root traits of adult plant in the field or grain yield in the field under water stress were found in wheat (Richards 1996). Another study on wheat showed that the avoidance of water deficit by developing greater root depth resulted in an increase of grain yield (Kirkegaard et al., 2007). According

Table 2. Pearson's correlation coefficients among observed morphological and biochemical traits under stress

Tabela 2. Pirsonovi korelacioni koeficijenti između zapaženih morfoloških i biohemijskih osobina u uslovima stresa

	Root/Koren				**Shoot/Izdanak**			
	Pro	**FW**	**DW**	**Lenght**	**Pro**	**FW**	**DW**	**Lenght**
Pro/Prolin	1				1			
FW	-0.975***	1			-0.183ns	1		
DW	-0.875*	0.448 ns	1		-0.136 ns	0.659 ns	1	
Lenght/Dužina	-0.870*	0.928**	0.609 ns	1	-0.292ns	0.960**	0.364 ns	1

*** - significant at the 0.001 probability level; ** - significant at the 0.01 probability level; * - significant at the 0.05 probability level; ns – non-significant to Tuberosa et al. (2002) QTLs for seedlings in hydroponics were identical to QTLs for grain yield in the field grown maize under drought stress, indicating constitutive trait expressions.

Conclusions

Establishment of significant genetic diversity for physiological traits in germplasm collection is necessary for determination of the importance of specific traits. Breeding by utilization of physiological and morphological traits could be useful to improve selection efficiency for drought tolerance and to supplement selection on the basis of yield alone.

Our study showed that proline accumulation is closely associated with growth inhibition induced by PEG treatment in respect to root and shoot length, fresh and dry weight.

Considering root length, genotypes L_1 and L_6 were without differences and showed similar tendency of root reduction after exposure to stress.

Genotype L_1 exhibited the most pronounced level of root proline content compared to drought sensitive genotype L_6. These results, as well as grain yield (data not presented) indicated that genotypes possessing higher proline content under osmotic stress in early developmental stage are more tolerant to drought in the field. Accordingly, genotypes L_3 and L_6 had the lowest root proline content (under stress) and the lowest grain yield in the field.

Hence, knowing morpho-anatomical, physiological and biochemical changes during osmotic stress could be very useful for fast screening under laboratory conditions and further applications in breeding programs.

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Morfološko-fiziološke promene u klijancima kukuruza u uslovima osmotskog stresa

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Izvod: Suša je glavni abiotički stres koji ograničava porast, razvoj i produktivnost useva širom sveta. Cilj ovog rada bio je ocena tolerantnosti klijanaca kukuruza na osmotski stres. Više od 6.000 uzoraka banke gena Instituta za kukuruz testirano je u uslovima kontrolisanog stresa suše (faza cvetanja) u Egiptu, a posle toga u umerenom klimatu (Srbija i Makedonija). Od 41 uzorka tolerantnog na sušu u poljskim uslovima, odabrano je pet linija, kao i jedna osetljiva na sušu, za testiranje u laboratoriji. Ovi genotipovi su izloženi 4% polietilen glikolu (PEG, Mr 10000) u trajanju od 24 h i 48 h. Odgovor klijanaca izloženih stresu (starih 9 dana) u odnosu na kontrolu, analiziran je kroz porast korena i izdanka, svežu i suvu masu i sadržaj prolina. Rezultati su pokazali smanjenje svih parametara u uslovima stresa, dok je jedino sadržaj prolina bio u porastu kod svih ispitivanih genotipova pod uticajem PEG-a u odnosu na kontrolu.

Ključne reči: klijanac, kukuruz, osmotski stres, porast izdanka, porast korena, prolin, suša, stres, suva masa, sveža masa