



Improvement of drought tolerance of soybean plants by using methyl jasmonate

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Abstract Methyl jasmonate (MeJA) is a naturally occurring plant growth regulator and play vital roles in plant defense and many developmental processes such as root growth and seed germination. This study was undertaken to study the possible role of using methyl jasmonate to alleviate the adverse effect of water stress on soybean genotypes (Giza 22 and 35). The results showed that water stress reduced shoot length, fresh and dry weights of shoot and root, photosynthetic pigments, relative water content and oil content in the shoots of all soybean genotypes. On the other hand, there was a considerable increase in cell wall fractionation, saturated and unsaturated fatty acids, flavonoids, phenolic acid and sugar fraction content in the shoots of the soybean genotypes in response to the water stress. Foliar spray with methyl jasmonate increased all the above parameters as compared to stressed plants. The results investigate the important role of MeJA in alleviation of water stress in soybean plants and suggest that MeJA could be used for improving plant growth under water stress as a potential growth regulator. The soybean genotypes Giza 22 was found to be more resistant to water stress than Giza 35.

Keywords Fatty acid · Flavonoids · Phenolic · Photosynthetic pigments · Relative water content · Sugars fractions

Introduction

Water stress is one of the most important environmental factors causing reduction in plant growth and photosynthesis (Abass and Mohamed 2011). It is one of the major causes of crop loss in the world and has the ability to decrease 50% of yield for the most major crop plants (Wang et al. 2003). Plants can acclimate to water stress through various physiological and biochemical changes (Mohamed and Akladios 2014).

Plants can tolerate water stress by maintaining adequate cell turgor by minimizing metabolic disruptions. There are two ways that contribute to tolerance are, (1) changes in tissue flexibility and (2) osmotic adjustment involving carbohydrates, inorganic ions and compatible solutes (Munns and Tester 2008).

Osmotic adjustment includes the accumulation of compatible solutes in a cell, this accumulation caused the lowered in the osmotic potential of the cell, which in turn attracts water into the cell and tends to maintain turgor pressure. In addition, the accumulation of sugar alcohols is considered an important approach to increasing crop drought resistance by genetic engineering (Bohnert et al. 1995).

Methyl jasmonate (MeJA) is considered as natural plant growth regulators (Walia et al. 2007). The jasmonates are derived from the metabolism of membrane fatty acids (Avanci et al. 2010). The MeJA is synthesized through the octadecanoic pathway that represents a series of metabolic steps following the oxidation of linolenic acid (Ketabchi and Shahrtash 2011). MeJA application may cause enhancement in the resistance of plants against abiotic stresses (Karami et al. 2013). Also, MeJA has a strong influence on regulation of secondary metabolism by stimulating the accumulation of alkaloids, flavonoids, phenols and coumarins (Yan et al. 2013).

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Soybean is considered one of the main leguminous crops in the world because of its importance in human nutrition as good source for protein and oil (Maltas et al. 2011). This crop was introduced and newly cultivated in Egypt as a summer crop. It is valuable as a source of protein. Soybean seed protein ranges from 34 to 57% of total seed weight and oil content ranges from 8.3 to 28% (Wilson 2004).

The aim of the present study was to check the interactive effect of methyl jasmonate and water stress on growth, photosynthesis, total oils, fatty acid composition, relative water content, cell wall fractionation, sugar fraction, phenolic acid and flavonoid compounds of the shoots of the two soybean genotypes in increasing resistance to water stress.

Materials and methods

Plant material and growth conditions

A pot experiment was conducted in a wire house at the Faculty of Education, Ain Shams University, Egypt from 5 June to 30 July 2014. During this period, day time temperatures ranged from 30.5° to 35.5 °C with an average of 33.5° ± 2.0 °C. Night temperatures ranged from 18.9° to 25.5 °C with an average of 23.1° ± 1.4 °C. Soybean seeds (*Glycine max* L. Giza 22 and Giza 35) were obtained from the Agricultural Research Center, Ministry of Agriculture, Egypt. Healthy seeds were selected and were washed in distilled water and sterilized in 1% (v/v) sodium hypochlorite for approx. 2 min, then washed again in distilled water and left to dry at room temperature (25 °C) for approx. 1 h. Ten, uniform, air-dried soybean seeds were sown in pots 35 cm diameter and 40 cm depth containing about 7.0 kg of clay soil. Soil characteristics were: sandy loam in texture, sand 82.2%, silt 13.9%, clay 3.9%, pH 7.1, EC 0.4 dSm⁻¹ and organic matter 1.2%. Rhizobial inoculants were applied as peat slurry containing 10⁷ *Rhizobium* l g.

Seven seeds were sown per pot and were thinned to four after 2 weeks from planting. Five pots for each treatment were used as replicates. Soybean plants were grown with normal water supply until 25th day from sowing, and then were divided into four sets: (1) set at 80% maximum hold capacity (well-watered) receiving distilled water, (2) set at 80% maximum hold capacity and foliar sprayed with 20 µM MeJA (3) set at 40% of maximum hold capacity (drought) (4) set at 40% of maximum hold capacity and after 35 days from sowing the plants were sprayed every 4 days two times with MeJA (20 µM).

The soil water-holding capacity was measured by saturating the soil in each pot with water and weighing it after

it had drained for 48 h. Soil water contents were maintained at approx. 80% (w/v) of the soil water-holding capacity.

Plant sampling

After 55 days from sowing, ten plants were randomly chosen from each treatment and the following parameters were studied: shoot and root length (cm), fresh and dry weights of shoots and roots and leaf relative water content.

Determination of leaf relative water content

The fresh leaf from each treatment were weighed (FW) and immediately immersed on double-distilled water in Petri dishes for 24 h, in the dark, to saturate them with water. Any adhering water was blotted-off and the turgid weight (TW) was measured. The DW was recorded after dehydrating the leaves to constant weight at 70 °C. RWC values were then calculated using the formula (Hayat et al. 2007).

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

Biochemical analyses

Determination of photosynthetic pigments

Chlorophyll a, Chlorophyll b, and carotenoids were determined in soybean leaves by using the spectrophotometric method as described by Vernon and Seely (1966) was used. The pigment contents were calculated as mg g⁻¹ fresh weight of leaves.

Determination of cell wall fraction

Cell wall fraction was conducted according to Dever et al. (1968) and Galbraith and Shields (1981). Dry shoots were extracted twice in distilled water, twice in 80% ethanol to remove soluble metabolites. The residue was then extracted in 17.5% NaOH for hemicellulose and in 72% H₂SO₄ (with 15 min autoclaving) for cellulose extraction. After that, the remaining residue was ascribed to the lignin fraction.

Determination of peroxidase (POD, EC 1.11.1.7)

Two hundred mg of the shoots fresh tissues were homogenized in 10 mL of 0.1 M potassium phosphate buffer, pH 6.8, containing 0.1 mM EDTA. The homogenate was centrifuged at 12,000 g for 20 min and the supernatant was used as source of crude enzyme. All steps to obtain enzyme preparation were carried out at 4 °C. The activity of

peroxidases was determined according to Kar and Mishra (1976).

Determination of phenolic and flavonoids compounds using HPLC

The phenolic acid and flavonoid compounds of the shoots of soybean plants were extracted according to the method described by Goupy et al. (1999) and Mattila et al. (2000) respectively. The supernatant was collected in a vial for injection into a HPLC instrument (Hewlett packed, series 1050) composed of a C18 hypersil BDS column with a particle size 5 μm . Separation was carried out with methanol and acetonitrile as the mobile phase, using a flow rate of 1 mL min^{-1} . Quantification was carried out using a calibration with phenolic acid and flavonoid as standards.

Determination of total oils and fatty acid composition

Oil content was determined according to the methods of AOAC (2000). Fatty acids determination of soybean oil was extracted by hexane and were analyzed by Agilent HP 6890 capillary gas chromatography and reported in relative area percentages. The methyl esters of fatty acids were prepared according to the method of Glass (1971). The fatty acid methyl esters were identified using a gas chromatograph equipped with dual flame ionization detector was used. The fatty acid methyl esters were identified by comparison their retention times with known fatty acid standard mixture. Peak areas were automatically computed by an integrator. The fatty acid composition was expressed as percentage of total fatty acids.

Determination of sugar fraction

Soluble sugars were extracted according to the method described by Bartolozzi et al. (1997). Briefly, the soluble sugars from dry shoots of soybean were extracted twice in 80% ethanol at 70 °C. Extracts were dried and converted into trimethylsilyl ethers with a silylation mixture made up of pyridine, hexamethyldisilazane and trimethylchlorosilane. Soluble sugars were analysed using a gas chromatograph mass spectrometer (Hewlett-Packard 5890 series II, Calif). Derivatives of standard monosaccharides and sugar alcohols (ribose, xylose, glucose, mannose, galactose, fructose, mannitol, sorbitol and galacturonic acid) were injected into the GC to ensure the retention time of each sugar.

Statistical analysis

All data were subjected to the analysis of variance (ANOVA) for a completely randomized design, after

testing the homogeneity of error variances according to the procedure outlined by Gomez and Gomez (1984). Statistically significant differences between means were compared at $P \leq 0.05$ using Fisher's Least Significant Difference (LSD) test.

Results and discussion

Effect of water stress and MeJA on growth parameters

Data in Table 1 showed that shoot length, fresh and dry weights of shoots were significantly decreased in stressed plants as compared to well watered plants in all soybean genotypes. The maximum decrease was observed in Giza 35 than Giza 22. These results are in agreement with those obtained by Mohamed and Akladios (2014) who found that drought stress caused significantly decreased in growth parameters of the two genotypes of soybean plants (Giza 22 and 111) and the genotype Giza 22 was found to be more resistant to drought stress than Giza 111.

Water stress causes losses in water content in tissues and decreased turgor pressure in cell, thereby inhibiting cell division and enlargement causing a reduction in plant growth and dry weight (Delfine et al. 2002).

Results also showed that root length, fresh and dry weights of roots was significantly increased in all soybean genotypes under water stress. The increase was much pronounced in soybean genotypes Giza 22 than Giza 35. These results are in accordance with Jaleel et al. (2008) who found that root growth of *Catharanthus roseus* was increased due to water stress. Moreover, the roots send a signal to the shoots via xylem and to leaves via the xylem vessels through the transpiration stream causing physiological changes and stomatal closure under water stress conditions which help in the adaptation to limited water supply in the field (Anjum et al. 2011).

The results showed that the genotype (Giza 22) was differ in their response to water stress than the other genotype (Giza 35) and a rapid recovery from wilting was observed. These observations are in agreement with those of Shimshi et al. (1982) who found that the resistant plants have morphological and metabolic properties that helped them to maintain a high degree of tissue hydration under drought stress.

Foliar spray with MeJA alone or in combination with stressed plants was significantly increased all growth parameters as compared with stressed plants. This result was in harmony with the findings by Abdelgawad et al. (2014) who found that all growth parameters of maize plants increased under water stress after pre-soaking grains with 50 μM MeJA. Moreover, the cell division may

Table 1 Effect of water stress and foliar spray with methyl jasmonate on growth parameters of soybean genotypes

Genotypes	Treatment	Shoot length (cm)	Root length (cm)	Fresh weight of shoots (g)	Dry weight of shoots (g)	Fresh weight of roots (g)	Dry weight of roots (g)	Relative water content %
Giza 22	Control	36.3c [†]	14.7d	5.16b	0.93c	0.64d	0.09e	52.1b
	MeJA	40.3a	17.0c	6.23a	1.36a	0.94a	0.12d	55.0a
	Drought	32.0e	21.2b	4.83c	0.77e	0.85b	0.17b	40.7d
	Drought + jasmonic	37.8b	27.0a	5.64b	1.21b	0.92a	0.19a	47.8c
Giza 35	Control	31.3f	11.5e	3.02e	0.72e	0.38f	0.08e	46.4c
	MeJA	37.7b	16.7c	3.33e	0.75e	0.82b	0.12d	52.4b
	Drought	27.7g	12.0e	2.74f	0.67f	0.53e	0.11d	33.6f
	Drought + jasmonic	33.7d	13.8d	4.18d	0.84d	0.75c	0.14c	38.0e

[†] Mean values (n = 10) in the same column for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

increase and the permeability of plasma membrane may alter after treatment with Jasmonic acid (Kaur et al. 2013).

Effect of water stress and MeJA on relative water contents (RWC)

The progressive drought stress caused subsequent reduction in leaf RWC of soybean genotypes as compared to well watered plants (Table 1). The RWC of leaf was significantly decreased in the two soybean genotypes. The most reduction was reported in Giza 35. This decrease in RWC may be due to the lower availability of water under stress conditions (Shalhevet 1993), or to a root system that was not able to compensate the water loss via transpiration through a reduction in its water absorbing surface (Gadallah 2000). RWC has been reported as an important indicator of water stress in leaves which is directly related to soil water content (Katerji et al. 1997).

Exogenous application of MeJA alone or in combination with stressed plants caused significantly increased in RWC of soybean genotypes (Giza 35 and Giza 22) as compared to stressed plants. These results are in agreement with the results of Pazirandeh et al. (2015) who showed that MeJA application improved the barley performance under drought by modulating the tissue water contents.

Effect of water stress and MeJA on photosynthetic pigments

Water stress caused significant decrease in Chl a, Chl b, carotenoid and total photosynthetic pigments as compared with well watered plants in all soybean genotypes (Table 2). These results are in harmony with those obtained by Abass and Mohamed (2011) who reported the increase in the level of drought stress caused reduction in the photosynthetic pigments content in leaves of common bean

plants. Carotenoids are responsible for scavenging of singlet oxygen (Knox and Dodge 1985) and the decrease in carotenoid under water stress might also have contributed to the increased ROS, which further oxidized the photosynthetic pigments.

Water stress caused reduction in the chlorophyll may be due to one or more of the following reasons: (1) the chlorophyll degradation by the formation of chlorophyllase enzymes, (Sabater and Rodriguez 1978), (2) damaging to the photosynthetic apparatus (Yasseen et al. 1987), (3) the suppression of the enzymes that are responsible for the synthesis of photosynthetic pigments (Murkute et al. 2006), (4) reduction of chloroplast stoma volume and regeneration of reactive oxygen species (Allen 1995), (5) the reduction in the uptake of Mg mineral which needed in the chlorophyll biosynthesis (Sheng et al. 2008), (6) or membrane deterioration (Ashraf and Harris 2013).

In addition, foliar spray with MeJA alone or in combination with stressed plants caused significant increases in photosynthetic pigments as compared to stressed plants in all soybean genotype. These results are in accordance with Asma and Lingakumar (2015) who found that jasmonic acid has been shown to stimulate the accumulation of plant pigment. Additionally, enhancement in the chlorophyll pigments synthesis may be due to treatment with jasmonic acid that resulted in an increase of active cytokinin concentration (Kovac and Ravnkar 1994).

Effect of water stress and MeJA on cell wall composition and peroxidase activity

Data in Table 3 showed that the lignin, cellulose content and peroxidase activity in shoots of the two soybean genotypes increased significantly under water stress. The increment was more pronounced in Giza 22 than Giza 83. The secondary cell wall can be strengthened by the

Table 2 Effect of water stress and foliar spray with methyl jasmonate on photosynthetic pigments in leaves of soybean genotypes

Genotypes	Treatment	Chl a mg g ⁻¹	Chl b mg g ⁻¹	Carotenoid mg g ⁻¹	Total photosynthetic pigments mg g ⁻¹
Giza 22	Control	0.46b [†]	0.25b	0.18b	0.89b
	MeJA	0.56a	0.28a	0.23a	1.07a
	Drought	0.42c	0.20d	0.15c	0.76d
	Drought + jasmonic	0.43c	0.22c	0.16c	0.81c
Giza 35	Control	0.37d	0.23c	0.12d	0.72e
	MeJA	0.44c	0.25b	0.22a	0.91b
	Drought	0.32e	0.17e	0.09e	0.58g
	Drought + jasmonic	0.35d	0.19d	0.11d	0.65f

[†] Mean values (n = 3) in the same column for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

incorporation of lignin. Lignification is a complex process include participation between different phenolic compounds and enzymes (Wang et al. 2013). It helps the plants to avoid cell wall damage when exposed to a long water stress conditions (Moura et al. 2010). Also, water stress enhanced the activation of guaiacol peroxidase and peroxidase in white clover leaf which was correlated with an increase in lignin content (Lee et al. 2007).

In addition, under water stress, the cellulose synthesis increased and the cell wall integrity and cell turgor pressure are maintained, thus allowing continuous cell growth (Ricardi et al. 2014). Moreover, POD activity increased in *Camptotheca acuminata* in response to drought stress (Ying et al. 2015).

The results also showed that lignin, cellulose and peroxidase contents were significantly increased in all soybean genotypes treated with MeJA alone or in combination with stressed plants as compared to stressed plants. Additionally, previous research reported that cell wall composition and lignin production changed after treatment with MeJA during different biotic and abiotic stresses (Denness et al. 2011). In addition, MeJA application caused the changes in the cell wall strengthening of eggplant roots due to lignin deposition and induction of several defense enzymes such

as CAT, PPO, POD and PAL (Mandal 2010). In addition, Abdelgawad et al. (2014) found that the antioxidant defense activity in plants increased after treatment with MeJA and helps the plants to remove the toxic effects of free radicals and become more resistant to water stress.

Effect of water stress and MeJA on oil content and fatty acid composition

Plants can adapt to water stress by the alteration of fatty acid composition in membrane lipids (Yordanov et al. 2000). In the present study, soybean genotypes showed differences in the concentration of oil and fatty acids composition and these differences were bigger under water stress conditions (Table 4). Oil content was significantly decreased in stressed plants as compared to well watered plants. Similar results by Al-Palsan et al. (2001) showed that water stress reduced oil percentage of sesame crops.

Oleic, linoleic and linolenic acids were significantly increased under water stress in all soybean genotypes. Palmitic and stearic acids (saturated fatty acids) were the least sensitive to water stress. In addition, palmitic acid was significantly increased but stearic acid was significantly decreased in all soybean genotypes under water stress.

Table 3 Effect of water stress and foliar spray with methyl jasmonate on cell wall composition and peroxidase activity in shoots of soybean genotypes

Genotypes	Treatment	Lignin %	Cellulose %	Peroxidase Units g ⁻¹ FW
Giza 22	Control	4.83f [†]	46.2d	26.6e
	MeJA	5.93a	50.5b	34.9a
	Drought	5.21d	50.2b	29.6c
	Drought + jasmonic	5.61b	60.5a	31.0b
Giza 35	Control	4.42g	32.2g	27.0e
	MeJA	5.16d	44.7d	29.6c
	Drought	4.99e	42.6e	28.8d
	Drought + jasmonic	5.33c	48.2c	29.7c

[†] Mean values (n = 3) in the same column for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

These results are similar to Petcu et al. (2001) who found that drought stress caused stimulation in the palmitic acid concentration in sunflower seeds while stearic acid concentration decreased under the same conditions. Laribi et al. (2009) also suggested that palmitic acid content increased under water stress. The increase in oleic acid may be due to an enzyme D–12 desaturase, which catalyses the second desaturation of oleic acid in linoleic acid (Stymne and Appelqvist 1978).

Eicosapentaenoic acid (C20:5) and Arachidi acid (C20:0) significantly increased in soybean plants under water stress. Similar results reported by Zhong et al. (2011) who found that drought stress caused significant increase in Eicosapentaenoic and Arachidic acid in bermudagrass. It could reflect an adaptive response to drought stress in bermudagrass, which may reduce water loss from the leaf surface and protect leaves from desiccation. The Arachidi acid is a component of the long-chain fatty acid complex in the epicuticular wax present on the leaf surface (Rhee et al.

1998). Epicuticular wax accumulation on leaves has been associated with reduction in transpiration and improved drought tolerance (González and Ayerbe 2010).

Polyunsaturation of fatty acids has proven to be correlated to adaptation when plants are challenged in responses to biotic and a biotic stresses (Goldhaber-Pasillas et al. 2014). Several investigators such as Bellaloui et al. (2013) and Gao et al. (2009) found that the increase of unsaturated fatty acids (oleic, linoleic and linolenic acid) concentrations may be due to water stress altering the rate of oil and fatty acids accumulation by affecting fatty acid desaturases enzymes. It can thus be concluded that drought stress decreases total oil altering fatty acid composition.

The treatment with MeJA caused significant increase in unsaturated fatty acids in all soybean genotypes especially C18:3 (linolenic acid) as compared with well watered plants. These results are similar to the results obtained by Czapski et al. (1992) who found that the content of linolenic acid in tomato plants increased after treatment with

Table 4 Effect of water stress and foliar spray with methyl jasmonate on oil content and fatty acid composition in shoots of soybean genotypes

Fatty acids fraction (%)		Giza 22				Giza 35			
		Control	MeJA	Drought	Drought + jasmonic	Control	MeJA	Drought	Drought + jasmonic
C6	Caproic	0.16d	0.20d	0.39b	0.43a	0.05f	0.13e	0.10e	0.19d
C8	Caprylic	0.51c	0.52c	0.86b	1.27a	0.22e	0.41d	0.40d	0.85b
C10	Capric	0.41f	0.93d	1.40b	1.69a	0.67e	0.65e	0.82d	1.19c
C11	Undecnoic	0	4.42a	3.50b	4.56a	0	0	2.75c	3.90b
C13	Tridecanoic	1.60d	1.63e	2.18c	3.66a	1.00f	1.30f	1.82d	2.29c
C14:0	myristic	0.43d	0.69c	0.80b	1.05a	0.33e	0.47d	0.51d	0.63c
C14:1	Myristoleic	0.48f	0.70b	0.66c	0.68b	0.44f	0.35g	0.53e	0.59d
C15:0	Pentadecanoic	0.41e	0.35f	0.59d	1.12a	0.56d	0.29g	0.66c	0.93b
C16:0	Palmetic	0.79d	1.12c	1.06c	3.10a	0.49e	0.72d	0.66d	0.91c
C16:1	Palmitoleic	3.80b	0	0	0	1.70c	4.05b	0	2.09c
C17:1	Cis 10 heptadecenoic	1.03b	0	0	1.61a	0	0	0.58c	0
C18:0	Stearic	0.42d	0.13 g	0.20f	0.66a	0.33e	0.45d	0.19f	0.56c
C18:1,2	Oleic Linoleic	16.50e	18.59d	26.40b	29.40a	11.80f	15.83e	17.80d	27.23b
C18:3	linolenic	9.16c	13.3b	12.0b	23.9a	6.06d	7.5d	11.3b	19.19b
C20:0	Arachidic	0.45e	1.23c	1.11d	1.25c	0.37e	0.50e	1.76a	1.66a
C20:5	Eicosapentaenoic	0	0.61d	1.10b	1.28a	0	0	0.97b	1.09b
C21:0	Heneicosanoic	5.64c	0	6.41b	8.03a	0	0	0	8.68a
C22:0	Behenic	1.79d	0.49e	2.80b	3.10a	0.44e	0	1.71d	2.21c
C22:1	Erucic	2.60e	0.95f	5.95d	6.75c	0.84f	0.45f	7.62b	10.15a
C24:1	Nervonic	0.40d	0.53c	0.59c	1.74a	0.35d	0.40d	0.42d	0.59c
Total amount of saturated		12.61d	11.71d	21.30c	29.92b	4.46e	4.92e	11.38d	24.00c
Total amount of unsaturated		33.97d	34.68d	46.7c	65.36a	21.19f	28.58e	39.22d	60.93b
Total fatty acids		46.58d	46.39d	68.00c	95.28a	25.65f	33.5e	50.60d	84.93b
% of oil		6.68c	7.54a	6.28d	6.94b	6.82b	7.67a	5.02e	6.16d

Mean values in the same row for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

MeJA. The differences in oil and fatty acids could be due to genotype/cultivar differences (Maestri et al. 1998), and/or irrigation management (Bellaloui et al. 2012).

Effect of water stress and MeJA on flavonoid fractions

Results showed that all treatments significantly increased the total flavonoids content in all soybean genotypes under water stress (Table 5). The maximum amount of total flavonoid was detected in Giza 35 which is considered susceptible genotype under water stress alone or in combination with MeJA. This result confirms the findings by Caldwell et al. (2005) who showed that the level of isoflavones increases in soybean seeds under drought stress. This suggests that an abiotic stress may increase flavonoid compound biosynthesis under the oxidative stress. The flavonoids are generated by the formation of reactive oxygen species (ROS) under the environmental stress (Navarro et al. 2006).

Water stress and MeJA application caused stimulation of rutin and quercetin acids in all soybean genotypes. These results are similar to Bâatour et al. (2012) who showed that salt stress caused the accumulation of flavonoids content and the improvement of quercetin biosynthesis. The accumulation of flavonoids helps in the plant's defense mechanisms (Dixon and Paiva 1995). In addition, Salem et al. (2014) found that drought caused enhancement in the biosynthesis of a new flavonoid; rutin trihydrate in two *Carthamus tinctorius* varieties.

The tolerant genotypes (Giza 22) have lower amount of flavonoid and smaller amounts of free radicals so that they produced small amount of antioxidant compounds than the susceptible one (Giza 35). The less production of flavonoids as well as total antioxidants by soybean genotypes may be due to higher repair mechanism of free radical damage, which is a well studied feature of drought tolerant genotype (Kumar et al. 2011).

There was a significant increase in total flavonoids at all genotypes treated with MeJA in combination with water stress as compared to water stressed plants. This result indicated that total flavonoids may be modulated and controlled by the MeJA.

Effect of water stress and MeJA on phenolic fraction

Data in Table 6 showed that there were significant differences in total phenolic compounds among all treatments. All genotypes under water stress and treated with MeJA showed significant increase in phenolic compounds. The maximum amount of phenolic compounds were obtained in Giza 35 under water stress and MeJA treatment. The increase of phenolic acids content may be linked to the lignifications of cell walls and the synthesis of certain amino acids which regulate the osmotic adjustment in cell (Ayaz et al. 1999). Many authors demonstrated that the production of phenols in plant tissues rises under a biotic stress conditions (Weidner et al. 2009). Phenolic compounds play an important role in scavenging free radicals

Table 5 Effect of water stress and foliar spray with methyl jasmonate on flavonoid fractions in shoots of soybean genotypes

Flavonoids mg 100 g ⁻¹	Giza 22				Giza 35			
	Control	MeJA	Drought	Drought + jasmonic	Control	MeJA	Drought	Drought + jasmonic
Narengin	0.17g	1.29d	1.74c	1.93b	1.84b	0.38f	0.88e	2.61a
Rutin	0.74f	1.31d	1.03e	1.38d	2.81b	2.34c	2.84b	3.50a
Hesperidin	0.60d	1.21c	1.15c	1.20c	2.83b	6.34a	6.84a	6.46a
Rosmarinic	0.18f	0.30e	0.19f	1.05a	0.38d	0.23f	0.73b	0.42d
Quercetrin	0.88e	1.75d	0.85e	1.34d	2.58c	5.96b	6.46a	5.98a
Quercetin	0.04f	0.10d	0.08e	0.12c	0.15b	0.08e	0.13c	0.17a
Narenginin	0.06d	0.08c	0.02f	0.09c	0.08c	0.12b	0.17a	0.16a
Kaempferol	0.03e	0.05d	0.03e	0.11b	0.05d	0.08c	0.13a	0.11b
Hesperitin	2.80e	3.16c	4.61a	2.90d	3.35c	3.24c	3.74b	3.01d
Apegnin	0.09d	0.13c	0.08d	0.17b	0.08d	0.12c	0.16b	0.25a
OH Flavone	0.07c	0.08b	0.10a	0.07c	0.03d	0.02d	0.07c	0.03d
Total amount	5.66f	9.46d	9.88d	10.36d	14.18c	19.0b	22.15a	22.70a

Mean values in the same row for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

Table 6 Effect of water stress and foliar spray with methyl jasmonate on phenolic fractions in shoots of soybean genotypes

phenolic mg 100 g ⁻¹	Giza 22				Giza 35			
	Control	MeJA	Drought	Drought + jasmonic	Control	MeJA	Drought	Drought + jasmonic
Gallic	0.30g	0.87e	0.53f	0.92e	0.53f	1.15d	1.37c	3.25a
Pyrogallol	2.36e	2.59e	3.15d	5.77b	4.56c	3.35d	5.50b	7.11a
3-Hydroxy tyrosol	1.35f	0.76g	1.82e	1.96e	2.23d	1.24e	3.49b	4.18a
4-Amino-benzoic	0.22f	0.09f	0.48e	0.84c	0.56d	0.14f	1.51b	2.04a
Protocatchuic	0.38f	1.57e	0.46f	0.54f	2.59d	2.36d	3.39c	5.76a
Chlorogenic	0.90f	1.12e	1.75d	1.84d	0.70g	2.14c	2.71b	3.22a
Catechol	1.89d	1.19f	2.88b	2.99b	1.56e	2.21c	3.06b	3.44a
syringic	1.24d	1.60c	1.62c	2.16b	0.30g	2.20b	0.73f	0.92e
Catechein	3.31c	1.43e	3.77b	3.98b	1.31e	2.25d	3.09c	4.90a
Caffeine	0.58e	0.62e	0.84d	1.40b	0.44f	0.84d	1.30b	2.09a
P-OH-benzoic	0.06f	0.31e	0.45d	1.00b	0.30e	0.47d	0.82c	1.29a
Caffeic	0.30e	0.26e	0.66d	0.76d	1.33c	0.41d	3.43b	4.25a
Vanillic	0.16d	0.17d	0.20c	0.27c	0.27c	0.30c	1.62b	2.17a
Ferulic	0.75e	0.81e	0.85e	1.20d	0.74e	1.96c	1.88c	2.76b
Iso-Ferulic	0.44e	0.30f	0.75d	1.11c	0.60d	0.62d	1.56b	1.89a
E- vanillic	6.43d	6.17d	6.99d	6.73d	9.99c	9.68c	12.70b	18.99a
Revresetrol	0.14e	0.59d	0.17e	1.20c	0.38e	0.69d	2.09b	3.05a
Ellagic	1.89f	2.15e	2.31e	2.80d	2.26e	4.26c	4.09c	7.78a
Alpha-Coumaric	0.92g	2.45d	1.32f	1.84e	1.31f	3.77b	2.83c	3.65b
Benzoic	1.88e	2.68d	2.44d	2.06e	3.24c	6.15a	6.17a	4.03b
3,4,5-methoxy-cinnamic	0.12e	0.28d	0.18e	1.13a	0.00	0.46c	0.00	0.15e
Salicylic	0.51e	0.89c	0.78d	1.48b	0.70d	1.54b	1.04c	3.01a
coumarin	0.09e	0.25e	0.52d	1.23b	0.26e	0.92c	1.40b	2.20a
P-Coumaric	0.22e	0.58d	0.68d	1.31b	0.32e	1.15b	0.93c	1.25b
Cinnamic	0.07d	0.17d	0.10d	0.18d	0.26d	1.09c	1.47b	1.67b
Total	26.51f	29.90f	35.70e	46.71d	36.74e	51.35d	66.18c	99.33a

Mean values in the same row for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

and protect plants against the damaging effects of increased ROS levels due to water stress (Petridis et al. 2012).

Data showed that under water stress and MeJA treatment, ferulic acid and vanillic acid increased in all soybean genotypes as compared to well watered plants. These results are similar to Hura et al. (2009) who found that in the resistant genotype of spring triticale (CHD 247) significant increase in the ferulic acid content and total phenolic compounds content under weak hydration of leaf tissues which could be an indicator of the resistance to drought stress. Also, the appearance of ferulic acid under water stress could be correlated to the strengthening of the plant wall, the decrease of cell wall plasticity and to cell elongation (Wakabayashi et al. 1997). Gumerova et al. (2015) showed an increase in free ferulic acid in MeJA treated cells of buckwheat on the 4th day of cultivation as compared with control cultures.

Syringic acid was accumulated in soybean plants under water stress especially (Giza 22). Similar results reported by Sampietro et al. (2006) indicated that syringic promoted cell division. In addition, benzoic acid was significantly increased under water stress in all soybean genotype especially the susceptible genotypes (Giza 35). Similar results were obtained by Blum et al. (1999) who found that benzoic acid inhibit plant growth by affecting many physiological processes such as ion uptake and enhanced the accumulation of ABA.

Previous reports by Kim et al. (2007) reported an increase in phenolic compounds under MeJA treatments. The increased production of phenolic compounds may be part of the plant defense response system. In addition, salicylic acid was increased significantly in all soybean genotypes under water stress and treatment with MeJA as compared with well watered plants. Salicylic acid plays an

important role in biotic and abiotic stress responses and is related to several secondary defense metabolites (Wildermuth 2006).

Effect of water stress and MeJA on Sugar fraction

The effect of MeJA on the total soluble sugar of soybean genotypes under water stress was shown in Table 7. The results reported that water stress caused increase in the total soluble sugars as compared to well watered plants.

Carbohydrates play a very important role in the response to water stress. They can regulate the osmotic adjustment, or act as metabolic signaling molecules to activate some specific transduction pathways (Hirabayashi 1996). The most important soluble carbohydrates in soybean plants are glucose, sucrose, sorbitol and mannitol. The concentrations of these sugars varied under water stress.

Glucose and mannitol are the carbohydrates that caused the lowering of osmotic potential in soybean plants (Table 7). Mannitol especially maintains high concentrations in the more stressed treatments and also in plants after foliar spray with MeJA. Sugar alcohols such as mannitol, sorbitol, glucose etc., play an important role during osmotic adjustment because they accumulate during drought without disrupting metabolism (Yancey et al. 1982). Similar results obtained by Boussadia et al. (2013) who found that drought stress increased the sucrose fraction in olive cultivar (Meski) and the mannitol fraction in the leaves of ‘Meski’ and ‘Koroneiki’. This result supports the idea that sugars can play an active role in the process of osmotic adaptation under water stress (Chimenti et al. 2006).

The accumulation of mannitol is playing an important role in the growth and metabolism in tissue (Tattini et al. 1996). Mannitol also limits the peroxidation of lipids and protects cells from plasmolysis (Shen et al. 1997).

Also, sucrose and sorbitol increased under water stress and treatment with MeJA as compared with well watered plants in all soybean genotypes. These results are in accordance with Jie et al. (2010) who found that sorbitol and glucose concentrations in apple seedlings increased and were kept at a higher level during the drought stress period.

The increment in mannitol content in leaves could be related to an increased activity of the enzymes involved in the biosynthesis and catabolism of this sugar (Tattini et al. 1996). Also Sickler et al. (2007) reported that mannitol can be considered not only as a compatible solute, but also as an antioxidant able to protect chloroplasts and allow higher photosynthetic rates under water and salt stress.

The results herein also revealed that foliar application of MeJA to all genotypes under stress stimulated the accumulation of total soluble sugars as compared to control plants. The increase in sugar concentration fraction may be a result from the degradation of starch (Fischer and Höll 1991).

Conclusion

Foliar application of MeJA modulated several physiological responses, leading to improved resistance against water stress on soybean genotypes. MeJA enabled soybean plants

Table 7 Effect of water stress and foliar spray with methyl jasmonate on sugar fractions in shoots of soybean genotypes

Sugar fraction %	Giza 22				Giza 35			
	Control	MeJA	Drought	Drought + jasmonic	Control	MeJA	Drought	Drought + jasmonic
Arabinose	4.92f	8.50a	5.40e	6.24d	3.50h	7.75b	4.00g	7.08c
Xylose	7.60e	11.98a	8.71d	9.26c	6.30f	10.32b	7.22e	12.30a
Ribose	0.31c	0.00	0.36b	0.28d	0.00	0.46a	0.20e	0.25d
Rhamnose	2.00e	2.22d	2.28c	2.41c	1.20g	3.28a	1.35g	2.73b
Galactose	4.70c	5.31b	4.32d	5.24b	2.00e	7.79a	3.48d	2.25e
Mannose	0.79f	1.98b	1.23d	1.40c	1.50c	0.00	2.02b	2.50a
Glucose	42.28e	39.18f	44.35d	47.17c	44.70d	43.81d	50.56b	63.17a
Sucrose	12.16e	14.48d	15.39c	15.55c	10.80f	16.30b	12.20e	17.28a
Sorbitol	14.57d	14.37d	16.24b	16.29b	13.88e	14.78d	15.70c	16.60a
Fructose	0	0.38b	0	0	0	0.19c	0.17c	0.44a
Mannitol	28.0e	32.0d	32.2d	36.0c	23.4h	42.5a	30.0e	40.2b
Total Sugars	117.33e	130.40d	130.48d	139.84c	107.28f	147.18b	126.90d	164.80a

Mean values in the same row for each trait followed by a different lower-case letter are significantly different according to Fisher's Least Significant Difference (LSD) test at $P \leq 0.05$

to tolerate water stress by increasing secondary metabolites (phenolic and flavonoids compounds) and solutes (sugars). Our study therefore recommended using MeJA at the level of 20 μM to alleviate water stress in soybean plants. MeJA could be used as a potential growth regulator for improving plant growth under water stress. The soybean genotypes Giza 22 are found to be more resistant to water stress than Giza 35.

References

- Abass SM, Mohamed HI (2011) Alleviation of adverse effects of drought stress on common bean (*Phaseolus vulgaris* L.) by exogenous application of hydrogen peroxide. *Bangladesh J Bot* 41:75–83
- Abdelgawad ZA, Khalafaallah AA, Abdallah MM (2014) Impact of methyl jasmonate on antioxidant activity and some biochemical aspects of maize plant grown under water stress condition. *Agric Sci* 5:1077–1088
- Allen RD (1995) Dissection of oxidative stress tolerance using transgenic plants. *Plant Physiol* 107:1049–1054
- Al-Palsan M, Boydak E, Hayta M, Gercek S, Simsek M (2001) Effect of row space and irrigation on seed composition of Turkish sesame. *J Crop Sci* 78:933–935
- Anjum SA, Xie X, Wang L, Saleem MF, Man C, Lei W (2011) Morphological, physiological and biochemical responses of plants to drought stress. *Afr J Agric Res* 6(9):2026–2032
- AOAC (2000) Official methods of analysis, vol I, 17th edn. Association of Official Analytical Chemists, Inc., Maryland
- Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. *Photosynthetica* 51(2):163–190
- Asma M, Lingakumar K (2015) Jasmonate foliar spray induced vegetative growth and pigment composition in *Vigna Radiata* L. WILCZEK. *Int J Adv Res* 3(1):664–669
- Avanci NC, Luche DD, Goldman GH, Goldman MHS (2010) Jasmonates are phytohormones with multiple functions, including plant defense and reproduction. *Genet Mol Res* 9:484–505
- Ayaz FA, Kadioglu AR, Turgut R (1999) Water stress effects on the content of low molecular weight carbohydrates and phenolic acids in *Ctenanthe setosa* (Rosc.) Eichler. *Can J Plant Sci* 80:373–378
- Bâatour O, Mahmoudi H, Tarchoun I, Nasri N, Kaddour R, Zaghoudi M, Wissal A, Hamdaoui G, Lachaâl M, Marzouk B (2012) Salt effect on phenolics and antioxidant activities of Tunisian and Canadian sweet marjoram (*Origanum majorana* L.) shoots. *J Sci Food Agric* 93(1):134–141
- Bartolozzi F, Bertazza G, Bassi D, Cristoferi G (1997) Simultaneous determination of soluble sugars and organic acids as their trimethylsilyl derivatives in apricot fruits by gas–liquid chromatography. *J Chromatogr A* 758:99–107
- Bellaloui N, Mengistu A, Fisher DK, Abel CA (2012) Soybean seed composition as affected by drought and phomopsis in phomopsis susceptible and resistant genotypes. *J Crop Improv* 26(3):428–453
- Bellaloui N, Mengistu A, Kassem A (2013) Effects of genetics and environment on fatty acid stability in soybean seed. *Food Nutr Sci* 4:165–175
- Blum U, Shafer SR, Lehman ME (1999) Evidence for inhibitory allelopathic interactions involving phenolic acids in field soils: concepts vs. an experimental model. *Crit Rev Plant Sci* 18:673–693
- Bohnert HJ, Nelson DE, Jensen RG (1995) Adaptations to environmental stresses. *Plant Cell* 7:1099–1111
- Boussadia O, Bchir A, Steppe K, Van Labeke MC, Lemeur R, Braham M (2013) Active and passive osmotic adjustment in olive tree leaves during drought stress. *Eur Sci J* 9(24):423–439
- Caldwell CR, Britz SJ, Mirecki RM (2005) Effect of temperature, elevated carbon dioxide, and drought during seed development on the isoflavone content of dwarf soybean [*Glycine max* (L.) Merrill] grown in controlled environments. *J Agric Food Chem* 53:1125–1129
- Chimenti CA, Marcantonio M, Hall AJ (2006) Divergent selection for osmotic adjustment results in improved drought tolerance in maize (*Zea mays* L.) in both early growth and flowering phases. *Field Crops Res* 95:305–315
- Czapski J, Horbowicz M, Saniewski M (1992) The effect of methyl jasmonate on free fatty acids content in ripening tomato fruits. *Biol Plant* 34:71–76
- Delfine S, Tognettir R, Loreto F, Alvino A (2002) Physiological and growth responses to water stress in field grown bell pepper (*Capsicum annuum* L.). *J Hortic Sci Biotechnol* 77(6):697–704
- Denness L, McKenna JF, Segonzac C, Wormit A, Madhou P, Bennett M, Mansfield J, Zipfel C, Hamann T (2011) Cell wall damage-induced lignin biosynthesis is regulated by a ROS and jasmonic acid dependent process in *Arabidopsis thaliana*. *Plant Physiol* 156:1364–1374
- Dever JE Jr, Bandurski RS, Kivilaan A (1968) Partial chemical characterization of corn root cell walls. *Plant Physiol* 43:50–56
- Dixon RA, Paiva NL (1995) Stress induced phenylpropanoid metabolism. *Plant Cell* 7:1085–1097
- Fischer C, Höll W (1991) Food reserves of Scots pine (*Pinus sylvestris* L.). I. Seasonal changes in the carbohydrate and fat reserves of pine needles. *Trees* 5:187–195
- Gadallah MAA (2000) Effects of indole-3-acetic acid and zinc on the growth, osmotic potential and soluble carbon and nitrogen components of soybean plants growing under water deficit. *J Arid Environ* 44:451–467
- Galbraith DW, Shields BA (1981) Analysis of the initial stages of plant protoplast development using 33258 Hoechst: re-activation of the cell cycle. *Physiol Plant* 51:380–386
- Gao W, Hillwig ML, Huang L, Cui G, Wang X, Kong J, Yang B, Peters RJ (2009) A functional genomics approach to tanshinone biosynthesis provides stereochemical insights. *Org Lett* 11:5170–5173
- Glass RL (1971) Alcoholysis, saponification and the preparation of fatty acid methyl esters. *Lipids* 6(12):919–925
- Goldhaber-Pasillas GD, Mustafa NR, Erpoorte RV (2014) Jasmonic acid effect on the fatty acid and terpenoid indole alkaloid accumulation in cell suspension cultures of *Catharanthus roseus*. *Molecules* 19:10242–10260
- Gomez KA, Gomez AA (1984) Statistical procedures for agricultural research. Wiley, Singapore, p 680
- González A, Ayerbe L (2010) Effect of terminal water stress on leaf epicuticular wax load, residual transpiration and grain yield in barley. *Euphytica* 172:341–349
- Goupy P, Hugues M, Biovin P, Amiot MJ (1999) Antioxidant composition and activity of barley (*Hordeum Vulgare*) and malt extracts and of isolated phenolic compounds. *J Sci Food Agric* 79:1625–1634
- Gumerova EA, Akulov AN, Romyantseva NI (2015) Effect of methyl jasmonate on growth characteristics and accumulation of phenolic compounds in suspension culture of Tartary Buckwheat. *Russ J Plant Physiol* 62(2):195–203
- Hayat S, Ali B, Hasan SA, Ahmad A (2007) Brassinosteroid enhanced the level of antioxidants under cadmium stress in *Brassica juncea*. *Environ Exp Bot* 60:33–41

- Hirabayashi J (1996) On the origin of elementary hexoses. *Q Rev Biol* 71:365–380
- Hura T, Hura K, Grzesiak S (2009) Leaf dehydration induces different content of phenolics and ferulic acid in drought resistant and sensitive genotypes of spring triticale. *Zeitschrift für Naturforschung* 64c:85–95
- Jaleel CA, Gopi R, Sankar B, Gomathinayagam M, Panneerselvam R (2008) Differential responses in water use efficiency in two varieties of *Catharanthus roseus* under drought stress. *C R Biol* 331:42–47
- Jie Z, Yuncong Y, Streeter JG, Ferree DC (2010) Influence of soil drought stress on photosynthesis, carbohydrates and the nitrogen and phosphorus absorb in different section of leaves and stem of Fuji/M.9EML, a young apple seedling. *Afr J Biotechnol* 9:5320–5325
- Kar M, Mishra D (1976) Catalase, peroxidase, and polyphenoloxidase activities during rice leaf senescence. *Plant Physiol* 57:315–319
- Karami A, Shahbazi M, Niknam V, Shobbar Z, Tafreshi R, Abedini R, Mabood H (2013) Expression analysis of dehydrin multigene family across tolerant and susceptible barley (*Hordeum vulgare* L.) genotypes in response to terminal drought stress. *Acta Physiol Plant* 35(7):2289–2297
- Katerji N, Vanhoorn JW, Hamdy A, Mastrorilli M, Mou Karzel E (1997) Osmotic adjustment of sugar beets in response to soil salinity and its influence on stomatal conductance, growth and yield. *Agric Water Manag* 34:57–69
- Kaur H, Sharma P, Sirhindi G (2013) Sugar accumulation and its regulation by jasmonic acid in *Brassica napus* L. under salt stress. *J Stress Physiol Biochem* 9(4):53–64
- Ketabchi S, Shahrtash M (2011) Effects of methyl Jasmonate and cytokinin on biochemical responses of maize seedlings infected by *Fusarium moniliforme*. *Asian J Exp Biol Sci* 2:299–305
- Kim HJ, Fonseca JM, Choi JH, Kubota C (2007) Effect of methyl jasmonate on phenolic compounds and carotenoids of romaine lettuce (*Lactuca sativa* L.). *J Agric Food Chem* 55(25):10366–10372
- Knox JP, Dodge AD (1985) Singlet oxygen and plants. *Phytochemistry* 24:889–896
- Kovac M, Ravnikar M (1994) The effect of jasmonic acid on the photosynthetic pigments of potato plant grown *in vitro*. *Plant Sci* 103:11–17
- Kumar A, John MM, Gul MZ, Bimolata W, Ghazi IA (2011) International conference on food engineering and biotechnology. IPCBEE. IACSIT Press, Singapore; Differential responses of non-enzymatic antioxidative system under water deficit condition in Rice (*Oryza sativa* L.). pp 176–179
- Laribi B, Bettaieb I, Kouki K, Sahli A, Mougou A, Marzouk B (2009) Water deficit effects on caraway (*Carum carvi* L.) growth, essential oil and fatty acid composition. *Ind Crops Prod* 30:372–379
- Lee BR, Kim KY, Jung WJ, Avice JC, Ourry A, Kim TH (2007) Peroxidases and lignification in relation to the intensity of water-deficit stress in white clover (*Trifolium repens* L.). *J Exp Bot* 58(6):1271–1279
- Maestri DM, Labuckas DO, Guzman CA, Giorda LM (1998) Correlation between seed size, protein and oil contents and fatty acid composition in soybean genotypes. *Grasas Aceites* 49:450–453
- Maltas E, Dageri N, Vurrall C, Yildiz S (2011) Biochemical and molecular analysis of soybean seed from turkey. *J Med Plants Res* 5:1575–1581
- Mandal S (2010) Induction of phenolics, lignin and key defense enzymes in eggplant (*Solanum melongena* L.) roots in response to elicitors. *African. J Biotechnol* 9(47):8038–8047
- Mattila K, Asikainen S, Wolf J, Jousimies-Somer H, Valtonen V, Nieminen M (2000) Age, dental infections, and coronary heart disease. *J Dental Res* 79:756–760
- Mohamed HI, Akladios SA (2014) Influence of garlic extract on enzymatic and non enzymatic antioxidants in soybean plants (*Glycine max*) grown under drought stress. *Life Sci J* 11(3s):46–58
- Moura JC, Bonine MS, de Oliveira Fernandes Viana J, Dornelas MC, Mazzafera P (2010) Abiotic and biotic stresses and changes in the lignin content and composition in plants. *J Integr Plant Biol* 52:360–376
- Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annu Rev Plant Biol* 59:651–681
- Murkute AA, Sharma S, Singh SK (2006) Studies on salt stress tolerance of citrus rootstock genotypes with arbuscular mycorrhizal fungi. *Hortic Sci* 33:70–76
- Navarro JM, Flores P, Garrido C, Martinez V (2006) Changes in the contents of antioxidants compounds in pepper fruits at different ripening stages, as affected by salinity. *Food Chem* 96:66–73
- Pazirandeh MS, Hasanloo T, Shahbazi M, Niknam V, Moradi-Payam A (2015) Effect of methyl jasmonate in alleviating adversities of water stress in barley genotypes. *Int J Farm Allied Sci* 4(2):111–118
- Petcu E, Arsintescu A, Stanciu D (2001) The effect of drought stress on fatty acid composition in some romanian sunflower hybrids. *Rom Agri Res* 15:39–43
- Petridis A, Therios I, Samouris G, Tananaki C (2012) Salinity induced changes in phenolic compounds in leaves and roots of four olive cultivars (*Olea europaea* L.) and their relationship to antioxidant activity. *Environ Exp Bot* 79:37–43
- Rhee Y, Hlousek-Radojicic A, Ponsamuel J, Liu D, Beitenmiller D (1998) Epicuticular wax accumulation and fatty acids elongation activities are induced during leaf development. *Plant Physiol* 116:901–911
- Ricardi MM, Gonzalez RM, Zhong S, Dominguez PG, Duffy T, Turjanski PG, Salter JDS, Alleva K, Carrari F, Giovannoni JJ (2014) Genome-wide data (ChIP-seq) enabled identification of cell wall-related and aquaporin genes as targets of tomato ASR1, a drought stress-responsive transcription factor. *BMC Plant Biol* 14(29):1–14
- Sabater B, Rodriguez MI (1978) Control of chlorophyll degradation in detached leaves of barley and oat through effect of kinetin on chlorophyllase levels. *Physiol Plant* 43:274–276
- Salem N, Msaada K, Dhifi W, Sriti J, Mejri H, Limam F, Marzouk B (2014) Effect of drought on safflower natural dyes and their biological activities. *EXCLI J* 13:1–18
- Sampietro DA, Vattuone MA, Isla MI (2006) Plant growth inhibitors isolated from sugarcane (*Saccharum officinarum*) straw. *J Plant Physiol* 163:837–846
- Shalhevet J (1993) Plants under salt and water stress. In: Fowden L, Mansfield T, Stoddart J (eds) Plant adaptation to environmental stress. Chapman and Hall, London, pp 133–154
- Shen B, Jensen RG, Bohnert HJ (1997) Mannitol protects against oxidation by hydroxyl radicals. *Plant Physiol* 115:527–532
- Sheng M, Tang M, Chan H, Yang B, Zhang F, Huang Y (2008) Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. *Mycorrhiza* 18:287–296
- Shimshi D, Mayokal ML, Atsmon D (1982) Responses to water stress in wheat and related wild species. *Crop Sci* 22(123–1):28
- Sickler CM, Edwards GE, Kiirats O, Gao Z, Loescher W (2007) Response of mannitol-producing *Arabidopsis thaliana* to abiotic stress. *Funct Plant Biol* 34:382–391
- Stymne S, Appelqvist LA (1978) The biosynthesis of linoleate from oleoyl-coa via oleoylphosphatidylcholine in microsomes of developing safflower seeds. *Eur J Biochem* 90:223–229

- Tattini M, Gucci R, Romani A, Baldi A, Everaro JD (1996) Changes in non-structural carbohydrates in olive leaves (*Olea europaea*) during root zone salinity stress. *Physiol Plant* 98:117–124
- Vernon LP, Seely GR (1966) *The chlorophylls*. Academic Press, New York
- Wakabayashi K, Hoson T, Kamisaka S (1997) Osmotic stress suppresses cell wall stiffening and the increase in cell wall bound ferulic and diferulic acids in wheat coleoptiles. *Plant Physiol* 113:967–973
- Walia H, Wilson C, Condamine P, Liu X, Ismail AM, Close TJ (2007) Large-scale expression profiling and physiological characterization of jasmonic acid-mediated adaptation of barley to salinity stress. *Plant Cell Environ* 30:410–421
- Wang WX, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta* 218:1–14
- Wang Y, Chantreau M, Sibout R, Hawkins S (2013) Plant cell wall lignification and monolignol metabolism. *Front Plant Sci* 4(220):1–14
- Weidner S, Karolak M, Karamać M, Kosińska A, Amarowicz R (2009) Phenolic compounds and properties of antioxidants in grapevine roots (*Vitis vinifera* L.) under drought stress followed by recovery. *Acta Soc Bot Pol* 78:97–103
- Wildermuth MC (2006) Variations on a theme: synthesis and modification of plant benzoic acids. *Curr Opin Plant Biol* 9:288–296
- Wilson RF (2004) Seed composition. In: Boerma H, Specht JE (eds) *Soybeans: improvement, production, and uses*, 3rd edn. ASA, CSSA, and SSSA, Madison, pp 621–668
- Yan Y, Borrego E, Kolomiets MV (2013) Jasmonate biosynthesis, perception and function in plant development and stress responses, chap 16. In: Baez RV (ed) *Lipid metabolism*. In Tech, Rijeka, pp 393–442
- Yancey PH, Clark ME, Hand SC, Bowlus RD, Somero GN (1982) Living with water stress: evolution of osmolyte systems. *Science* 217(4566):1214–1222
- Yasseen BT, Jurjee JA, Sofajy SA (1987) Changes in some growth processes induced by NaCl in individual leaves of two barley cultivars. *Indian J Plant Physiol* 30:1–6
- Ying YQ, Song LL, Jacobs DF, Mei L, Liu P, Jin SH, Wu JS (2015) Physiological response to drought stress in *Camptotheca acuminata* seedlings from two provenances. *Front Plant Sci* 6(361):1–8
- Yordanov I, Velikova V, Tsonev T (2000) Plant responses to drought, acclimation and stress tolerance. *Photosynthetica* 38:171–186
- Zhong D, Du H, Wang Z (2011) Genotypic variation in fatty acid composition and unsaturation levels in bermudagrass associated with leaf dehydration tolerance. *J Am Soc Hortic Sci* 136(1):35–40