

Effects of Salicylic Acid and Glycine Betaine on Gas Exchanges, Proline content and Yield of Potato Cultivars under Water Stress Conditions

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Received November 24, 2022

This investigation was aimed to study the response of potato plants to water deficit and exogenous application of salicylic acid (SA) and glycine betaine (GB). Potato cultivars, Spirit, Born, Arinda and Banba were experienced under two irrigation regimes, 30 and 60 % depletion of available soil water, and two concentrations of both SA (0.5 and 1.0 mM) and GB (1.0 and 2.0 mM) additionally the control (0.0 mM SA and GB). Gas exchanges, proline content (Pro), root volume (RV), root/shoot ratio (R/S), plant dry mass (PDM), number tuber (NT) and yield of potato cultivars were measured. With the exception of R/S, water deficit led to notable decreases in gas exchanges, RV, PDM, NT and yield of potato cultivars and increases in Pro content. Foliar application of SA and GB resulted in significant increases in photosynthesis (Photo), carbon dioxide concentration in the sub-stomatal chamber (Ci), stomatal conductance (Gs), Pro, PDM and yield in some levels of SA and GB; the level of the increases appeared more when potato plants were grown under water deficit conditions. All the overhead effects supported PDM and yield of potato cultivars to increase by exogenous application of SA and GB and directed to the assumption that water deficit converted harmful effects on potato cultivars could be released by exogenous applied SA and GB.

Key words: *Water deficit, Potato cultivars, Gas exchanges, Yield*

Abbreviations: *Photo photosynthesis, E transpiration, Ci carbon dioxide concentration in the sub-stomatal chamber, Gs stomatal conductance, A/E water use efficiency, Pro proline, RV root volume, R/S root/shoot ratio, NT number tuber, PDM plant dry mass*

Potatoes are the fourth important food crop after wheat, maize and rice (Vreugdenhil *et al.*, 2007) and actually have more related wild species than any other crop. On the other hand, potato was likely domesticated at least 7,000 years ago near Lake Titicaca (Singh and Kaur, 2009) on the border of what is now Peru and Bolivia (Glave, 2001). Conversely, water plays an essential role in the life of plant and its accessibility is a main factor that regulates the plant population in the environment (Placide *et al.*, 2013) and the content of water was estimated at 80 to 95% in masses of growing tissues, 85 to 95% in vegetative tissues, 35 to 75% in wood with dead cells, and at 5 to 15% in dried seeds (Placide *et al.*, 2013).

Conversely, Monneveux *et al.*, (2014) revealed and expected that the frequency of drought events in many regions will be increased due to the climate change. So, the loss in potato yield was estimated to range between 18 and 32% during the first three decades of this century (Monneveux *et al.*, 2014). Also, environmental stresses for example, cold, salinity and drought (Bohnert *et al.*, 1995) are well known to harmfully affect crop productivity; these stresses can decrease average yields of major crop plants by more than 50% (Wang *et al.*, 2003). Moreover, drought stress is a major abiotic factor that restricts agricultural crops production (Stiller, 2008) compared to other isolated biotic or abiotic stress factors (Placide *et al.*, 2013) and potato (*Solanum tuberosum* L.) is well known as a crop which is highly sensitive to soil drought (Heuer and Nadler 1998; Martinez-Gutiérrez *et al.*, 2012). As well as, water deficit results in stomatal closure, photosynthetic efficacy, transpiration rates decreases (Yordanov *et al.*, 2003) and CO₂ assimilation is significantly reduced in susceptible genotypes. In addition to, photosynthesis and respiration depends on the kind and timing of water deficit. So, resistant genotypes can continue with photosynthesis for weeks after water deficit onset (Watkinson *et al.*, 2006; Schafleitner, 2009). Furthermore, a decrease in the water potential of plant tissues, gathers of abscisic acid (ABA), mannitol, sorbitol, formation of radical scavenging compounds (ascorbate, glutathione, α -tocopherol (Yordanov *et al.*,

2003) and also induces gathering of compatible solutes such as glycerol, sugars and Betaines (Anosheh, 2012). The same, stomatal closure is very sensitive to increasing levels of water deficit as confirmed by decreasing transpiration rates when the water potential of leaf was lower than -0.1 MPa. This state can develop quickly when soil moisture reductions or on days of high potential evaporation (Harris, 1992). Meanwhile, slight decreases in stomatal conductance can affect water loss by transpiration more than carbon assimilation. (Levy *et al.*, 2013). Also, drought shortens plant growth cycle (Kumar *et al.*, 2007; Yordanov *et al.*, 2003), reductions fresh weight and stolon expansion (Heuer and Nadler, 1998; Martinez-Gutiérrez *et al.*, 2012), dry matter (Araus *et al.*, 2002; Stiller, 2008) and chlorophyll content (Sarani *et al.*, 2014).

However, foliar application of growth regulators such as salicylic acid (SA) has presented to reduce the effects of salinity stress. SA is a biomolecule that may be involved in several cell processes under regular and stress circumstances. Under biotic and abiotic stress situations, increasing evidence shows that SA “a phytohormone that acts at low concentrations” is produced and gathers inside cells to function as a signaling molecule in plants (Choi *et al.*, 2012). As well as, SA, which belongs to a group of phenolic compounds, plays critical roles in regulating various physiological processes such as germination, ion absorption, photosynthesis, and growth of plants (Vicente *et al.*, 2011). Moreover, it is an antioxidant compound which plays an important role in plant response to abiotic stresses (Vicent and Plasencia, 2011). Other than, Glycine betaine (GB) is a fully N-methylsubstituted derivative of glycine. This quaternary ammonium compound is existing in bacteria, animals, and higher plants, and functions by stabilizing the quaternary structure of intricate proteins, membrane systems, enzymes, and photosynthetic machinery, such as PSII complexes and RuBisCo (Sakamoto and Murata, 2000). Additionally, GB is gathered in many plant species at elevated levels in reaction to various kinds of abiotic stress, resulting in their enhanced tolerance (Rhodes and Hanson, 1993). Therefore, this research was conducted to study the influence of foliar application of salicylic acid and glycine betaine on gas

exchanges, yield and biomass of four potato cultivars in response to water stress under greenhouse conditions.

MATERIALS AND METHODS

Plant material, growing settings and experimental design

This pot investigate was accompanied from September to December 2017 in the greenhouse of agriculture college, Isfahan University of Technology located in Esfahan (51° 28' E, 42° 33' N and 1626.2 m above the mean sea level) to study the effects of aerial spraying salicylic acid (0.0, 0.5, and 1.0 mM) and glycine betaine (0.0, 1.0, and 2.0 mM) for three times. However, applying SA and GB treatments were done after two weeks of starting water deficit treatments (30 and 60 % depletion of available soil water) and every five days on four potato cultivars (Spirit, Born, Arinda and Banba). This investigate was based on a randomized complete block design with three replications. As well, before planting, tubers (about 50-60 g) were preserved for two weeks at room temperature (25°C) to germinate and cultivated in the culture medium of pots (35×25 cm dimensions) which was consisted of sand, garden soil and rotten animal manure with the ratio of 4: 1: 1, respectively. Moreover, culture medium was sterilized with the metam sodium ($C_2H_4NNaS_2$) to prevent the spread of diseases (insects, nematods, fungus etc.). All potato plants were irrigated normally and fertilized with a complete floral fertilizer of 20-20-20 (a product of CIFO S.P.A., Bologna, Italy). Thus, treatment of drought stress was applied at the period of forming eight and ten leaves. In addition, the instrument for measuring and recording the moisture and soil temperature (IDRG SMS-T1) was used to determine the time irrigation. At the end of this investigate (i.e., 120 days), samples from the upper expand and mature leaves were collected and directly immersed in liquid nitrogen (-196 C°) for analysis of physiological characteristics. The available soil water and the volume of irrigation water were calculated based on Askari and Ehsanzadeh (2015a).

Measurement of growth parameters

Plant dry mass and yield measurement

Aerial parts of potato plants in each replicate were dehydrated individually in an oven at 80 °C for 72 h to

specify a fixed dry weight and weighted on the basis of g/plant. Also, tubers were counted and weighted on the basis of g/plant.

Proline content

The method of Bates *et al.*, (1973) was used to measure proline content. The absorbance of the samples was measured via a spectrophotometer U-1800 (Hitachi, Japan) at 520 nm. Proline content was determined according to the normal chart and expressed using the following formula in terms of $\mu\text{mol/g}$ of fresh weight of plant leaves:

$$\text{Proline} = [(\Delta\text{abc} \times 4 \text{ ml toluene})/115.5] \times [\text{sample weight}/5]$$

Where Δabs is the absorption of samples.

Gas exchanges

The youngest adult leaves of potato plants were used to measure gas exchanges, i.e., photosynthesis, stomatal conductance, transpiration, carbon dioxide concentration in the sub-stomatal chamber, by using a portable apparatus model (L.C.I. Software version 1:10 UK), on. All measurements were done between 10 AM and 13 PM hours.

Root volume

The following formula described by Askari and Ehsanzadeh (2015b) was used to measure this trait:

$$\text{Volume roots (cm}^3\text{)} = V_0 - V_1$$

Where V_0 , volume water and V_1 , volume water and roots.

Harmonic mean productivity (HAR)

HAR index was used to select the susceptible cultivars. Lower HAR corresponds to higher drought tolerance and this index was calculated according to the relationship of Baheri *et al.*, (2003).

$$\text{Formula: HAR} = [2 \times (Y_{pi} - Y_{si})] / [(Y_{pi} + Y_{si})]$$

Where in the above formula, Y_{pi} and Y_{si} = yield of cultivars under control and water deficit, respectively.

Statistical analysis

Data of this investigate were tested and subjected to analysis of difference (ANOVA) by using SAS and MSTATC programs to define the variance in both treatments and cultivars and based on a randomized

complete block design. Assessment of means was achieved by using LSD test ($p < 0.05$) and the correlation coefficients between the characters were done by using PROC CORR of SAS.

RESULTS

Analysis of variance for photosynthesis (Photo), transpiration (E), carbon dioxide concentration in the sub-stomatal chamber (Ci), stomatal conductance (Gs), water use efficiency (A/E), proline (Pro), root volume (RV), plant dry mass (PDM), number tuber (NT) and potato cultivars yield revealed significant differences ($p < 0.01$) between all interactions (drought \times cultivar, drought \times treatment, cultivar \times treatment and drought \times cultivar \times treatment) with the exception of root/shoot ratio (R/S) at drought \times cultivar and drought \times cultivar \times treatment, PDM at drought \times treatment and E at drought \times cultivar \times treatment interactions (Table 2).

Plant dry mass, root/shoot ratio, yield and number tuber

In this investigate, results of PDM, yield and NT except (R/S) of potato cultivars revealed significant influence between, drought \times cultivar \times treatment interactions and these traits were affected by SA and GB treatments (Table 2, 7).

Water insufficiency was connected with reduced PDM, yield and NT by about 47, 67 and 14%, respectively (Table 3). Yet, between cultivars, the maximum PDM was observed in Spirit and Arinda, yield in Arinda and NT in Spirit, but the minimum value of R/S was showed in Arinda (Table 4). But foliar spraying of SA and GB in all concentrations increased PDM, yield and NT, with the exception of yield and NT in the treatment 2.0 mM of GB and R/S in the treatment (1.0 mM SA and 2.0 mM of GB) (Table 5). The highest PDM under control circumstances was detected in Arinda at (0.5 mM SA and 2.0 GB) and under drought conditions at (1.0 mM SA) in Spirit cultivar (Table 7). The maximum yield under control circumstances was observed in Arinda at (1.0, 2.0 mM GB) and Banba and Arinda at (0.5 mM SA), respectively. Also, the maximum yield under drought conditions was watched in Born at (0.5

and 1.0 mM SA). As well, the maximum NT under control situations was perceived in Spirit at (0.5 and 1.0 mM SA), but the maximum NT under water stress conditions was observed in Spirit at (1.0 mM GB) (Table 2, 7). The harmonic mean productivity (HAR) index was calculated (data not shown) to estimate the level of water deficit tolerance of potato cultivars; the consequences showed differences between cultivars, ranging from 0.779 (Spirit) to 0.819 (Born), 1.14 (Arinda) and 1.19 (Banba).

Root volume

In our study, RV of potato cultivars displayed statistically significant influence between interactions (drought \times cultivar \times treatment) and was affected by SA and GB concentrations (Table 2, 7). Water deficit was related with decreased RV by about 44% (Table 3). The maximum RV was observed in Spirit and Born (Table 4) and between treatments at the level 0.5 mM of SA (Table 5). Under control situations, the highest value of RV was achieved in Arinda and Banba at 0.5 mM of SA. In the contrary, the maximum value of RV under drought conditions was observed in Spirit at the treatment 1.0 mM of SA (Table 7).

Leaf proline content

In our investigate, Pro content in the leaves of potato cultivars revealed statistically significant effect between drought \times cultivar \times treatment interactions, and was influenced by drought, SA and GB levels (Table 2, 7). Water deficit was connected with increased Pro content by about 410% (Table 3). The maximum Pro content was observed in Spirit (Table 4) and between treatments at the level 1.0 mM of SA (Table 5). Under drought conditions, our results showed that exogenous SA and GB in all levels, improved Pro content in all cultivars as compared with their controls. However, the maximum values of Pro content under drought conditions, were observed in Spirit cultivar at (1.0 mM GB) and Born at (1.0 mM SA) treatment, respectively. In the contrary, the minimum values of proline content were obtained in Arinda and Banba cultivars at (0.0 mM SA and GB) treatments (Table 6).

Table 1. Physical and chemical properties of the experimental soil.

pH	Electric conductivity (dSm ⁻¹)	Organic carbon %	Available K (mg kg ⁻¹)	Available P (mg kg ⁻¹)	Total N (mg kg ⁻¹)	Type of soil	Organic content %
7.75	1.1	0.76	381.5	55.1	342	sandy	1.33

Table 2. Analysis of variance for photosynthesis (Photo), transpiration (E), carbon dioxide concentration in the sub-stomatal chamber (Ci), stomatal conductance (Gs), water use efficiency (A/E), proline (Pro), root volume (RV), root/shoot ratio (R/S), plant dry mass (PDM), number tuber (NT) and yield of potato cultivars (Cult) evaluated at two levels, 30% (control), 60% (drought) soil moisture depletion and treatment (Treat) three levels of salicylic acid and glycine betaine in the pots. degree of freedom (df).

	Mean square											df	Source of variation
	Yield	NT	PDM	R/S	RV	Pro	A/E	Gs	Ci	E	Photo		
**	1078255.2**	97.20**	762.55**	0.0001 ^{ns}	6177.67**	284.96**	11.67**	1.17**	216580.03**	390.93**	4082.1**	1	Drought
Significant at P < 0.01,	36228.54**	1638.91**	15.65**	0.0045**	63.49**	10.71**	1.55**	0.007**	11998.98**	2.66**	8.18**	3	Cult
* Significant	1995.52**	80.96**	7.15**	0.005**	28.69**	4.86**	4.83**	0.048**	2657.6**	33.17**	184.84**	4	Treat
at P < 0.05,	33329.1**	240.82**	28.54**	0.002 ^{ns}	351.61**	6.09**	4.03**	0.019**	3997.4**	9.44**	25.9**	3	Drought*Cult
ns; non-significant,	1831.77**	62.28**	0.807 ^{ns}	0.004**	89.82**	6.09**	1.33**	0.018**	19894.2**	11.70**	13.44**	4	Drought*Treat
respectively.	2082.19**	58.42**	3.475**	0.002**	94.29**	1.18**	1.52**	0.0005**	2250.9**	1.11**	4.36**	12	Cult*Treat
	1993.16**	73.68**	1.280**	0.001 ^{ns}	33.09**	0.821**	1.45**	0.001**	996.2**	0.507 ^{ns}	5.57**	12	Drought*Cult*Treat
	238.54	2.57	0.455	0.001	4.72	0.049	0.28	0.00024	152.0	0.289	1.20	80	Error
	8.20	13.75	8.33	23.32	8.59	9.69	12.25	8.93	7.19	11.33	5.85	-	C.V

Table 3. Means of Photo, E, Ci, Gs, A/E, Pro, RV, PDM, NT and yield of potato cultivars evaluated at two levels, 30% (control), 60% (drought) soil moisture depletion in pots under greenhouse conditions.

Irrigation regime	Photo (μmol CO ₂ /m ² s)	E (mmol H ₂ O/m ² s)	Ci (μmol/mol)	Gs (mol CO ₂ /m ² s)	A/E (μmol CO ₂ /mmol H ₂ O)	Pro (μmol/g F.W)	RV (cm ³)	PDM (g)	NT	Yield (g)
Control	24.59 ^a	6.55 ^a	213.9 ^a	0.270 ^a	3.98 ^b	0.752 ^b	32.43 ^a	10.62 ^a	12.57 ^a	283.08 ^a
Drought stress	12.93 ^b	2.94 ^b	128.93 ^b	0.073 ^b	4.61 ^a	3.83 ^a	18.08 ^b	5.57 ^b	10.77 ^b	93.5 ^b
Variances %	-47	-55	-40	-73	+16	+410	-44	-47	-14	-67
LSD %	0.399	0.196	4.48	0.006	0.191	0.081	0.789	0.245	0.583	5.61

Mean followed by the same letter in each column are not significant different according LSD test (probability level of 5 %). Values in the parentheses are percent decrease (-) or increase (+) as compared with the control (30%).

Table 4. Means of Photo, E, Ci, Gs, A/E, Pro, RV, R/S, PDM, NT and yield of four potato cultivars in pots under greenhouse conditions.

Cult	Photo ($\mu\text{mol CO}_2/\text{m}^2 \text{ s}$)	E ($\text{mmol H}_2\text{O}/\text{m}^2 \text{ s}$)	Ci ($\mu\text{mol}/\text{mol}$)	Gs ($\text{mol CO}_2/\text{m}^2 \text{ s}$)	A/E ($\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$)	Pro ($\mu\text{mol}/\text{g F.W}$)	RV (cm^3)	R/S	PDM (g)	NT	Yield (g)
Spirit	19.13 ^a	4.49 ^b	199.03 ^a	0.165 ^b	4.39 ^{ab}	2.97 ^a	26.83 ^a	0.136 ^a	8.61 ^a	22.70 ^a	138.83 ^c
Born	19.29 ^a	5.03 ^a	171.07 ^b	0.184 ^a	4.02 ^c	2.61 ^b	25.97 ^a	0.134 ^a	7.82 ^b	7.33 ^c	195.33 ^b
Arinda	18.29 ^b	4.49 ^b	152.07 ^d	0.154 ^c	4.55 ^a	1.71 ^d	24.73 ^b	0.115 ^b	8.75 ^a	9.00 ^b	220.16 ^a
Banba	18.34 ^b	4.99 ^a	163.5 ^c	0.185 ^a	4.23 ^{bc}	1.88 ^c	23.50 ^c	0.144 ^a	7.20 ^c	7.63 ^c	198.83 ^b
LSD %	0.564	0.277	6.33	0.008	0.271	0.114	1.12	0.016	0.346	0.825	7.94

Mean followed by the same letter in each column are not significant different according LSD test (probability level of 5 %).

Table 5. Means of Photo, E, Ci, Gs, A/E, Pro, RV, R/S, PDM, NT and yield of potato cultivars evaluated at three levels of salicylic acid and glycine betaine in pots under greenhouse conditions.

Treatments (mM)	Photo ($\mu\text{mol CO}_2/\text{m}^2 \text{ s}$)	E ($\text{mmol H}_2\text{O}/\text{m}^2 \text{ s}$)	Ci ($\mu\text{mol}/\text{mol}$)	Gs ($\text{mol CO}_2/\text{m}^2 \text{ s}$)	A/E ($\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$)	Pro ($\mu\text{mol}/\text{g F.W}$)	RV (cm^3)	R/S	PDM (g)	NT	Yield (g)
0.0	14.07 ^d	3.08 ^e	186.71 ^a	0.104 ^d	4.83 ^a	1.63 ^e	25.50 ^b	0.15 ^a	7.31 ^d	11.21 ^b	187.92 ^b
0.5 SA	18.82 ^c	4.24 ^d	166.75 ^c	0.162 ^c	4.63 ^{ab}	2.60 ^b	26.83 ^a	0.135 ^{ab}	8.19 ^{bc}	13.04 ^a	201.46 ^a
1.0 SA	20.25 ^b	5.51 ^b	169.12 ^c	0.205 ^b	3.91 ^c	2.76 ^a	25.46 ^b	0.116 ^c	8.73 ^a	13.04 ^a	183.12 ^{bc}
1.0 GB	19.40 ^c	4.78 ^c	158.67 ^d	0.170 ^c	4.33 ^b	2.39 ^c	23.95 ^c	0.137 ^a	8.42 ^{ab}	12.37 ^a	191.67 ^b
2.0 GB	21.25 ^a	6.13 ^a	175.83 ^b	0.218 ^a	3.78 ^c	2.07 ^d	24.54 ^{bc}	0.119 ^{bc}	7.83 ^c	8.67 ^c	177.29 ^c
LSD %	0.631	0.309	7.08	0.009	0.303	0.128	1.25	0.02	0.387	0.922	8.87

Mean followed by the same letter in each column are not significant different according LSD test (probability level of 5 %).

Table 6. Interactions between drought, cultivar, treatment of salicylic acid and glycine betaine on Photo, Ci, Gs, A/E and Pro of potato cultivars evaluated at two levels, 30 and 60% of soil moisture depletion in the pots under greenhouse conditions.

Cult	Treat	Photo ($\mu\text{mol CO}_2/\text{m}^2 \cdot \text{s}$)						Ci ($\mu\text{mol}/\text{mol}$)						Gs ($\text{mol CO}_2/\text{m}^2 \cdot \text{s}$)						A/E ($\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$)						Pro ($\mu\text{mol/g F.W}$)					
		30%		60%		30%		60%		30%		60%		30%		60%		30%		60%		30%		60%							
Spint	0.0	11.21 ^{op}	19.60 ^{hi}	92.00 ^{rs}	350.66 ^a	0.057 ^{kl}	0.177 ^f	0.057 ^{kl}	0.177 ^f	4.91 ^{cg}	4.91 ^{cg}	4.02 ^{h-n}	4.02 ^{h-n}	3.03 ^h	3.03 ^h	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l	1.16 ^l			
		(-43)	(-43)	(-74)	(-74)	(-66)	(-66)	(-66)	(-66)	(-66)	(-66)	(-66)	(-18)	(-18)	(161)	(161)															
	0.5	15.41 ^{jk}	21.26 ^{gh}	168.33 ^{ik}	300.00 ^b	0.087 ^{hij}	0.216 ^e	0.087 ^{hij}	0.216 ^e	4.42 ^{ei}	4.42 ^{ei}	6.19 ^{ab}	6.19 ^{ab}	5.58 ^b	5.58 ^b	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}	1.09 ^{lmn}			
		(-27)	(-27)	(-44)	(-44)	(-60)	(-60)	(-60)	(-60)	(-60)	(-60)	(40)	(40)	(412)	(412)																
	1	14.51 ^{kl}	25.94 ^{def}	137.33 ^{mmo}	218.33 ^{de}	0.127 ^g	0.263 ^d	0.127 ^g	0.263 ^d	4.91 ^{cg}	4.91 ^{cg}	3.96 ^{h-n}	3.96 ^{h-n}	5.13 ^c	5.13 ^c	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}	0.703 ^{o-s}		
		(-44)	(-44)	(-37)	(-37)	(-52)	(-52)	(-52)	(-52)	(-52)	(-52)	(-19)	(-19)	(630)	(630)																
Born	1	15.53 ^{jk}	22.61 ^g	152.33 ^{klm}	182.66 ^{hij}	0.093 ^{hi}	0.223 ^e	0.093 ^{hi}	0.223 ^e	3.89 ^{cg}	3.89 ^{cg}	4.22 ^{e-k}	4.22 ^{e-k}	6.41 ^a	6.41 ^a	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p	0.990 ^p			
		(-31)	(-31)	(-17)	(-17)	(-58)	(-58)	(-58)	(-58)	(-58)	(-58)	(+8)	(+8)	(547)	(547)																
	2	15.68 ^j	29.51 ^a	151.33 ^{klm}	237.33 ^d	0.107 ^{gh}	0.300 ^c	0.107 ^{gh}	0.300 ^c	3.95 ^{h-n}	3.95 ^{h-n}	4.23 ^{e-k}	4.23 ^{e-k}	4.49 ^d	4.49 ^d	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}	1.12 ^{lm}		
		(-47)	(-47)	(-36)	(-36)	(-64)	(-64)	(-64)	(-64)	(-64)	(-64)	(+7)	(+7)	(+301)	(+301)																
	Banba	0.0	8.44 ^{qr}	19.65 ^{hi}	111.33 ^{pqr}	282.66 ^{bc}	0.053 ^{lm}	0.160 ^f	0.053 ^{lm}	0.160 ^f	5.06 ^{cde}	5.06 ^{cde}	3.45 ^{k-p}	3.45 ^{k-p}	2.55 ^l	2.55 ^l	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}	1.01 ^{l-o}		
			(-57)	(-57)	(-61)	(-61)	(-67)	(-67)	(-67)	(-67)	(-67)	(-67)	(-32)	(-32)	(+152)	(+152)															
0.5		12.90 ^{lo}	25.96 ^{def}	106.00 ^{qrs}	171.33 ^{ijk}	0.080 ^{jk}	0.257 ^d	0.080 ^{jk}	0.257 ^d	4.76 ^{ci}	4.76 ^{ci}	3.91 ^{l-o}	3.91 ^{l-o}	5.79 ^b	5.79 ^b	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}	0.840 ^{lr}		
		(-50)	(-50)	(-38)	(-38)	(-69)	(-69)	(-69)	(-69)	(-69)	(-69)	(-18)	(-18)	(+889)	(+889)																
1		15.67 ^j	27.01 ^{b-f}	140.00 ^{nno}	196.00 ^{gh}	0.097 ^{hi}	0.350 ^b	0.097 ^{hi}	0.350 ^b	3.09 ^{op}	3.09 ^{op}	3.97 ^{h-n}	3.97 ^{h-n}	6.63 ^a	6.63 ^a	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}	0.763 ^{m-s}		
		(-42)	(-42)	(-29)	(-29)	(-72)	(-72)	(-72)	(-72)	(-72)	(-72)	(+28)	(+28)	(+769)	(+769)																
Arinda	1	13.82 ^{k-n}	26.17 ^{c-f}	137.66 ^{nno}	178.66 ^{hij}	0.107 ^{gh}	0.257 ^d	0.107 ^{gh}	0.257 ^d	4.68 ^{cj}	4.68 ^{cj}	4.12 ^{g-m}	4.12 ^{g-m}	3.72 ^{ef}	3.72 ^{ef}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}	0.650 ^{p-s}			
		(-47)	(-47)	(-23)	(-23)	(-58)	(-58)	(-58)	(-58)	(-58)	(-58)	(-12)	(-12)	(+472)	(+472)																
	2	15.95 ^j	27.33 ^{b-e}	163.66 ^{kl}	223.33 ^{de}	0.093 ^{hi}	0.383 ^a	0.093 ^{hi}	0.383 ^a	3.00 ^p	3.00 ^p	4.15 ^{g-m}	4.15 ^{g-m}	3.74 ^{ef}	3.74 ^{ef}	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s	0.433 ^s			
		(-42)	(-42)	(-27)	(-27)	(-76)	(-76)	(-76)	(-76)	(-76)	(-76)	(+38)	(+38)	(+764)	(+764)																
	Photo	0.0	9.71 ^{pq}	18.43 ⁱ	86.66 ^s	214.00 ^{ef}	0.123 ^g	0.123 ^g	0.123 ^g	0.123 ^g	5.52 ^{bc}	5.52 ^{bc}	6.55 ^a	6.55 ^a	1.82 ^k	1.82 ^k	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}	0.747 ^{n-s}		
			(-47)	(-47)	(-59)	(-59)	(-76)	(-76)	(-76)	(-76)	(-76)	(-76)	(-19)	(-19)	(+144)	(+144)															
0.5		12.26 ^{no}	22.91 ^g	112.33 ^{pq}	166.00 ^{jk}	0.060 ^{kl}	0.223 ^e	0.060 ^{kl}	0.223 ^e	4.17 ^{g-m}	4.17 ^{g-m}	5.29 ^{cd}	5.29 ^{cd}	3.05 ^h	3.05 ^h	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}	0.607 ^{qrs}			
		(-46)	(-46)	(-32)	(-32)	(-73)	(-73)	(-73)	(-73)	(-73)	(-73)	(+402)	(+402)	(+402)	(+402)																
1		14.21 ^{lm}	25.58 ^{ef}	124.33 ^{opq}	204.00 ^{efg}	0.067 ^{kl}	0.317 ^c	0.067 ^{kl}	0.317 ^c	3.41 ^{k-p}	3.41 ^{k-p}	4.56 ^{dj}	4.56 ^{dj}	4.05 ^e	4.05 ^e	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}	0.917 ^{l-q}			
		(-44)	(-44)	(-39)	(-39)	(-79)	(-79)	(-79)	(-79)	(-79)	(-79)	(+34)	(+34)	(+342)	(+342)																
Banba	1	12.93 ^{lo}	25.48 ^f	134.66 ^{nno}	171.33 ^{ijk}	0.067 ^{kl}	0.250 ^d	0.067 ^{kl}	0.250 ^d	3.87 ^{l-o}	3.87 ^{l-o}	4.08 ^{g-m}	4.08 ^{g-m}	2.37 ^{ll}	2.37 ^{ll}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}	0.517 ^{rs}			
		(-49)	(-49)	(-21)	(-21)	(-73)	(-73)	(-73)	(-73)	(-73)	(-73)	(+5)	(+5)	(+358)	(+358)																
	2	13.28 ^{lmn}	28.09 ^{ab}	144.66 ^{lmm}	162.66 ^{kl}	0.080 ^{jk}	0.320 ^c	0.080 ^{jk}	0.320 ^c	3.26 ^{nop}	3.26 ^{nop}	4.74 ^{c-i}	4.74 ^{c-i}	2.36 ^{ll}	2.36 ^{ll}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}	0.680 ^{o-s}			
		(-53)	(-53)	(-11)	(-11)	(-75)	(-75)	(-75)	(-75)	(-75)	(-75)	(+45)	(+45)	(+247)	(+247)																
	Banba	0.0	7.37 ^f	18.17 ⁱ	87.66 ^s	288.66 ^c	0.027 ⁿ	0.203 ^e	0.027 ⁿ	0.203 ^e	4.10 ^{g-m}	4.10 ^{g-m}	5.03 ^{c-f}	5.03 ^{c-f}	2.19 ^j	2.19 ^j	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}	0.560 ^{qrs}		
			(-59)	(-59)	(-67)	(-67)	(-87)	(-87)	(-87)	(-87)	(-87)	(-87)	(+23)	(+23)	(+291)	(+291)															
0.5		12.28 ^{no}	27.61 ^{bcd}	123.66 ^{opq}	186.33 ^{ghi}	0.057 ^{kl}	0.313 ^c	0.057 ^{kl}	0.313 ^c	4.08 ^{g-m}	4.08 ^{g-m}	4.20 ^{h-i}	4.20 ^{h-i}	3.36 ^{gh}	3.36 ^{gh}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}	0.483 ^{rs}		
		(-55)	(-55)	(-34)	(-34)	(-82)	(-82)	(-82)	(-82)	(-82)	(-82)	(+3)	(+3)	(+596)	(+596)																
1		12.39 ^{no} </																													

Table 7. Interactions between drought, cultivar, treatment of salicylic acid and glycine betaine on RV, PDM, NT and yield of potato cultivars evaluated at two levels, 30 and 60% of soil moisture depletion in the pots under greenhouse conditions.

Cult	Treat	RV (cm ³)			PDM (g)			NT			Yield (g)										
		30%	60%	30%	60%	30%	60%	30%	60%	30%	60%	30%	60%								
Spirit	SA (mM)	0.0	34.33 ^{b-e}	23.66 ^{ijk} (-31)	9.04 ^{ghi}	6.44 ^{klj} (-29)	13.67 ^{fg}	26.00 ^{cd} (+90)	190.00 ^h	90.00 ^{mn} (-53)	SA (mM)	0.0	34.33 ^{b-e}	23.66 ^{ijk} (-31)	9.04 ^{ghi}	6.44 ^{klj} (-29)	13.67 ^{fg}	26.00 ^{cd} (+90)	190.00 ^h	90.00 ^{mn} (-53)	
		0.5	28.00 ^{gh}	19.67 ^{lm} (-30)	9.09 ^{ghi}	7.34 ^j (-19)	24.67 ^d	26.33 ^{cd} (+7)	170.00 ^{hi}	88.33 ^{mno} (-48)		0.5	28.00 ^{gh}	19.67 ^{lm} (-30)	9.09 ^{ghi}	7.34 ^j (-19)	24.67 ^d	26.33 ^{cd} (+7)	170.00 ^{hi}	88.33 ^{mno} (-48)	
	GB (mM)	1	37.33 ^b	26.67 ^{hij} (-28)	12.58 ^{abc}	9.16 ^{ghi} (-27)	28.33 ^c	32.33 ^b (+14)	186.67 ^h	95.00 ^{k-n} (-49)	GB (mM)	1	37.33 ^b	26.67 ^{hij} (-28)	12.58 ^{abc}	9.16 ^{ghi} (-27)	28.33 ^c	32.33 ^b (+14)	186.67 ^h	95.00 ^{k-n} (-49)	
		2	31.00 ^{efg}	17.33 ^{m-q} (-13)	10.33 ^{ef}	6.73 ^{jk} (-35)	11.67 ^{gh}	8.00 ^l (+211)	260.00 ^{ef}	88.33 ^{mno} (-66)		2	31.00 ^{efg}	17.33 ^{m-q} (-13)	10.33 ^{ef}	6.73 ^{jk} (-35)	11.67 ^{gh}	8.00 ^l (+211)	260.00 ^{ef}	88.33 ^{mno} (-66)	
	Born	SA (mM)	0.0	32.33 ^{def}	18.33 ^{mno} (-43)	8.75 ⁱ	4.49 ^{pqr} (-49)	8.33 ^{ijk}	6.33 ^{k-n} (-24)	301.66 ^{bcd}	100.00 ^{l-n} (-67)	SA (mM)	0.0	32.33 ^{def}	18.33 ^{mno} (-43)	8.75 ⁱ	4.49 ^{pqr} (-49)	8.33 ^{ijk}	6.33 ^{k-n} (-24)	301.66 ^{bcd}	100.00 ^{l-n} (-67)
			0.5	32.33 ^{def}	23.66 ^{ijk} (-27)	9.99 ^{fg}	5.34 ^{n-p} (-46)	11.66 ^{gh}	6.66 ^{klm} (-43)	313.33 ^{bc}	123.33 ^j (-60)		0.5	32.33 ^{def}	23.66 ^{ijk} (-27)	9.99 ^{fg}	5.34 ^{n-p} (-46)	11.66 ^{gh}	6.66 ^{klm} (-43)	313.33 ^{bc}	123.33 ^j (-60)
GB (mM)		1	22.67 ^{kl}	18.33 ^{mno} (-19)	9.87 ^{fgh}	6.12 ^{k-n} (-38)	8.33 ^{ijk}	5.00 ^{mn} (-40)	248.33 ^{fg}	120.00 ^{jk} (-52)	GB (mM)	1	22.67 ^{kl}	18.33 ^{mno} (-19)	9.87 ^{fgh}	6.12 ^{k-n} (-38)	8.33 ^{ijk}	5.00 ^{mn} (-40)	248.33 ^{fg}	120.00 ^{jk} (-52)	
		2	31.67 ^{def}	19.33 ^{lmn} (-39)	11.70 ^{cd}	6.41 ^{l-m} (-45)	7.66 ^{jkl}	8.00 ^l (+4)	228.33 ^g	111.66 ^{l-m} (-51)		2	31.67 ^{def}	19.33 ^{lmn} (-39)	11.70 ^{cd}	6.41 ^{l-m} (-45)	7.66 ^{jkl}	8.00 ^l (+4)	228.33 ^g	111.66 ^{l-m} (-51)	
Arinda		SA (mM)	0.0	36.00 ^{bc}	14.33 ^{p-t} (-60)	11.17 ^{de}	4.67 ^{pqr} (-58)	12.00 ^{gh}	7.00 ^{klm} (-41)	315.00 ^b	106.66 ^{l-m} (-66)	SA (mM)	0.0	36.00 ^{bc}	14.33 ^{p-t} (-60)	11.17 ^{de}	4.67 ^{pqr} (-58)	12.00 ^{gh}	7.00 ^{klm} (-41)	315.00 ^b	106.66 ^{l-m} (-66)
			0.5	43.00 ^a	13.00 ^{rst} (-70)	13.46 ^a	6.62 ^{jk} (-51)	12.00 ^{gh}	6.00 ^{k-n} (-50)	351.66 ^a	108.33 ^{l-m} (-69)		0.5	43.00 ^a	13.00 ^{rst} (-70)	13.46 ^a	6.62 ^{jk} (-51)	12.00 ^{gh}	6.00 ^{k-n} (-50)	351.66 ^a	108.33 ^{l-m} (-69)
	GB (mM)	1	34.00 ^{b-e}	17.67 ^{m-p} (-48)	12.35 ^{bc}	5.96 ^{k-o} (-52)	12.33 ^{gh}	5.00 ^{mn} (-59)	316.66 ^b	105.00 ^{l-m} (-67)	GB (mM)	1	34.00 ^{b-e}	17.67 ^{m-p} (-48)	12.35 ^{bc}	5.96 ^{k-o} (-52)	12.33 ^{gh}	5.00 ^{mn} (-59)	316.66 ^b	105.00 ^{l-m} (-67)	
		2	24.00 ^{ijk}	14.33 ^{p-t} (-40)	11.83 ^{cd}	5.36 ^{l-p} (-55)	15.00 ^f	6.33 ^{k-n} (-58)	375.00 ^a	75.00 ^{nop} (-80)		2	24.00 ^{ijk}	14.33 ^{p-t} (-40)	11.83 ^{cd}	5.36 ^{l-p} (-55)	15.00 ^f	6.33 ^{k-n} (-58)	375.00 ^a	75.00 ^{nop} (-80)	
	Banba	SA (mM)	0.0	32.67 ^{c-f}	12.33 st (-62)	9.80 ^{fi}	4.16 ^{qr} (-57)	10.33 ^{hi}	6.00 ^{k-n} (-42)	323.33 ^b	76.66 ^{nop} (-76)	SA (mM)	0.0	32.67 ^{c-f}	12.33 st (-62)	9.80 ^{fi}	4.16 ^{qr} (-57)	10.33 ^{hi}	6.00 ^{k-n} (-42)	323.33 ^b	76.66 ^{nop} (-76)
			0.5	43.67 ^a	11.33 ^t (-74)	11.49 ^{cd}	4.18 ^{qr} (-64)	11.33 ^{gh}	5.66 ^{lmn} (-50)	363.33 ^a	93.33 ^{lmn} (-74)		0.5	43.67 ^a	11.33 ^t (-74)	11.49 ^{cd}	4.18 ^{qr} (-64)	11.33 ^{gh}	5.66 ^{lmn} (-50)	363.33 ^a	93.33 ^{lmn} (-74)
GB (mM)		1	33.00 ^{cde}	14.00 ^{q-t} (-58)	9.59 ^{fi}	4.16 ^{qr} (-57)	8.33 ^{ijk}	4.66 ^{mn} (-44)	301.66 ^{bcd}	91.66 ^{mn} (-70)	GB (mM)	1	33.00 ^{cde}	14.00 ^{q-t} (-58)	9.59 ^{fi}	4.16 ^{qr} (-57)	8.33 ^{ijk}	4.66 ^{mn} (-44)	301.66 ^{bcd}	91.66 ^{mn} (-70)	
		2	29.33 ^{fi}	15.00 ^s (-49)	10.02 ^{fg}	4.92 ^{opq} (-51)	10.00 ^{hij}	4.00 ⁿ (-60)	316.66 ^b	78.33 ^{nop} (-75)		2	29.33 ^{fi}	15.00 ^s (-49)	10.02 ^{fg}	4.92 ^{opq} (-51)	10.00 ^{hij}	4.00 ⁿ (-60)	316.66 ^b	78.33 ^{nop} (-75)	
LSD%		3.53	1.1	2.60	25.1																

Mean followed by the same letter in each column are not significant different according LSD test (probability level of 5 %).

Table 8. Correlation coefficients of different traits under 60 % soil moisture depletion in the greenhouse conditions.

Traits	Photo	Gs	A/E	Pro	RV	PDM	NT	Yield	HAR
Photo	1	-	-	-	-	-	-	-	-
gs	0.82**	1	-	-	-	-	-	-	-
A/E	-0.14 ^{ns}	-0.42**	1	-	-	-	-	-	-
Pro	0.71**	0.67**	-0.19 ^{ns}	1	-	-	-	-	-
RV	0.49*	0.63**	-0.36**	0.57**	1	-	-	-	-
PDM	0.60**	0.75 ^{ns}	-0.10 ^{ns}	0.55**	0.67 ^{ns}	1	-	-	-
NT	0.29 ^{ns}	0.41**	-0.07**	0.47*	0.64**	0.69 ^{ns}	1	-	-
Yield	0.11 ^{ns}	0.14 ^{ns}	-0.13 ^{ns}	0.29 ^{ns}	0.39**	0.20**	-0.07 ^{ns}	1	-
HAR	-0.42 ^{ns}	-0.59**	0.14 ^{ns}	-0.59**	-0.67**	-0.72**	-0.51*	-0.53**	1

photosynthesis (Photo), stomatal conductance (Gs), water use efficiency (A/E), proline (Pro), root volume (RV), plant dry mass (PDM), number tuber (NT) and harmonic mean productivity (HAR).

Gas Exchanges

The effects between interactions (drought × cultivar × treatment) were statistically significant ($p < 0.01$) on photo (CO₂ absorbance), Ci, Gs, water use efficiency (A/E), except transpiration, and affected by salicylic acid and glycine betaine concentrations (Table 2, 7). Water stress was associated with reduced photo, E, Ci, Gs, by about 47, 55, 40 and 73%, respectively, and improved A/E by about 16% (Table 3). The maximum rate of photo was obtained in Spirit and Born, E in Born and Banba, Ci in Spirit, Gs in Born and Banba, and A/E in Arinda (Table 4) and between treatments, the maximum rate of photo, E and Gs were obtained at the level 2.0 mM of GB. But the maximum rate of Ci and A/E were achieved at the level 0.0 mM of SA and GB (Table 5). Under control and water insufficiency conditions, our outcomes revealed that exogenous SA and GB increased the rate of photo and Gs in all cultivars and in all levels as compared with their controls. But, our results revealed decreasing in the rate of Ci at the irrigation level 30% in all cultivars and in all concentrations of SA and GB as associated with their controls, and increasing rate of Ci was obtained at the irrigation level 60% (Table 6). However, under water stress conditions, the maximum rate of photo was detected in Spirit and Born at (0.5 and 1.0 mM SA) respectively, and in Spirit at (1.0 and 2.0 mM GB), and Born at (2.0 mM GB), Ci in Spirit at (0.5 mM SA), Gs in Spirit at (1.0 mM SA) and A/E in Spirit at (0.5 mM SA), Arinda at (0.0 mM SA and GB) and Banba at (1.0 mM GB) (Table 6).

Relationships between the traits

Correlation coefficients between different characters were calculated and achieved in Table 8. Under water deficit circumstances, photo was positively correlated with Pro and PDM. Also, Pro was positively interrelated with Gs, RV and PDM. Moreover, a positive correlation was obtained between yield, RV and NT. In the contrary, HAR showed negative correlation with yield and PDM, this means that increasing in HAR values leads to decreasing in yield and PDM.

DISCUSSION

In general, a great challenge in the future rises demand for nutrition products and for fresh water resources as a result of increasing an expected world people of 9 billion by 2050 and altered food behaviors (Levy *et al.*, 2013; Lobell *et al.*, 2008). Drought, salinity, low and high temperature are the most significant limiting factors among different environmental limitations which induce and reduce crop productivity of plants in many parts of the world (Lawlor, 2002). However, Monakhova and Chernyadev, (2002) showed that water stress causes variations in the content of photosynthetic pigments, degrades the photosynthetic device and decreases the activity of the Calvin cycle enzymes, and all of which are the main reasons of reduced yield and biomass of plants. Moreover, many researchers (Cheng *et al.*, 2013) presented that under stress conditions photo-damage for photosynthetic system happened and the higher carbon dioxide concentration in the substomatal chamber (Ci) was directly connected to CO₂ absorbance and stomatal conductance (Gs). On the other hand, under biotic and abiotic stresses many of

growth regulators materials in very low concentrations effect and control an wide range of physiological procedures i.e. opening and closing of stomata, photosynthesis, absorption and transfer ions in plants (Morgan, 1990). In the present study, similar to the results of Cheng *et al.*, (2013), our outcomes indicated that water deficit decreased gas exchanges i.e., Photo, Ci, Gs. But, exogenous application of SA and GB in most levels improved them (Table 6). under water deficit (60% depletion of available soil water) and treatments of SA and GB, the maximum values of photo were detected in Born ($15.95 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 2.0 mM GB and $15.67 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 0.5 mM of SA followed by Spirit (15.68 and $15.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 2.0 and 1.0 mM of GB and $15.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 0.5 mM of SA, respectively, also, Ci in Spirit ($168.33 \mu\text{mol/mol}$) at 0.5 mM of SA, Gs in Spirit ($0.127 \text{ mol CO}_2/\text{m}^2 \text{ s}$) at 0.5 mM of SA. Moreover, water deficit was decreased water use efficiency (A/E) in tolerant cultivars and increased it in sensitive ones (Table 6). the maximum values of A/E were obtained in Arinda ($6.55 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$) at the treatment 0.0 mM of SA and GB, followed by $6.46 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$ in Banba at 1.0 mM of GB and Spirit ($6.19 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$) at 0.5 mM of SA. However, results of Cheng *et al.*, (2013) on the plants of potato showed that exogenous application of SA and GB increased photo, transpiration, Ci, Gs and water use efficiency. Conversely, the rate of photorespiration in ambient air depends on the CO_2 concentration in the intercellular spaces (Ci), which is regulated by the stomata, the closure of which decreases the CO_2 concentration at the site of carboxylation, thus increasing photorespiration (Evans and Loreto, 2000). The increased rates of photorespiration during drought may be caused by stomatal closure, which although decreasing water loss and/else reductions carbon dioxide concentration in the sub-stomatal chamber (Wingler *et al.*, 1999).

Conversely, proline is one of the widespread osmolytes that are commonly found in high levels when plants are subjected to different stresses. As well as,

proline accumulation in the cells of plant might be due to an increase in proteolysis or a decrease in protein synthesis (Ashraf and Harris, 2004). So, in the current study, alike to the findings of Al-Mahmud *et al.*, (2015), Martinez *et al.*, (1995), our consequences shown increasing proline content in the leaves of potato plants under water deficit (60% depletion of available soil water) and/also, exogenous application of SA and GB in all levels and cultivars increased it as compared to their controls conditions. As well, the maximum increasing of proline content (Table 6) was obtained in the cultivars that have the less values of harmonic mean productivity (HAR). Then again, under water deficit circumstances, the higher values of proline contents were detected in Born ($6.6 \mu\text{mol g}^{-1}$ leaf) at 1.0 mM level of SA and Spirit ($6.4 \mu\text{mol g}^{-1}$ leaf) at 1.0 mM level of GB (Table 6). In addition to, under the same conditions, positive relationship were detected between proline content, Photo and PDM and a negative relationship was found between proline content and HAR, this suggests that the higher content of proline could have a relative increase in PDM and tolerance of potato cultivars under water deficit conditions (Table 8). Yet, Pro gathering is supposed to play adaptive roles in the stress tolerance of plant. Else, it has been recommended to act as a compatible osmolyte and to be a way to store carbon and nitrogen (Hare and Cress, 1997).

In this study, similar to discoveries of Stalham and Allen, (2001), Lahlou and lendent, (2005), our outcomes revealed that root volume (RV) was significantly reduced at 60% depletion of soil available water as related to the non-stress conditions (Table 7). However, under control irrigation regime (30% depletion of available soil water), the highest values of RV were obtained in Arinda and Banba (43.00 and 43.67 cm^3 respectively) at 0.5 mM of SA. Also, under water deficit (60% depletion of available soil water), the maximum values of RV were obtained in Born (27.66 cm^3) and Spirit (27.00 cm^3) at 2.0 and 1.0 mM GB respectively, (Table 7). Though, Farooq *et al.*, (2009) reported that the rate of root development, density, distribution and size are widely affected by water deficit conditions.

In the present study, water deficit (60% of soil moisture depletion) was complemented by significantly

decreased PDM, yield and NT (Table 3). But, used of SA and GB in most levels improved them (Table 5). However, under control irrigation (30% depletion of available soil water), we detected difference in production PDM, yield and NT of potato cultivars and applied of SA and GB in certain levels increased them (Table 7). The higher PDM was achieved in Arinda (13.46 and 13.01 g/plant) at (0.5 and 2.0 mM SA and GB), respectively followed by Spirit (12.58 g/plant) at 1.0 mM of SA treatment (Table 7).

Also, the higher yield was achieved in Arinda (375 and 371.7 g/plant at 1.0 and 2.0 mM of GB, respectively and 351.7 g/plant at 0.5 mM of SA), as well, Banba (363.3 g/plant at 0.5 mM SA). So, these cultivars could be appropriate for agriculture in areas where water is not limited for crop production. Else, the higher NT was achieved in Spirit (28.33 plant) at 1.0 mM of SA (Table 7).

In the contrary, similar to the outcomes Nouri *et al.*, (2016), Shi *et al.*, (2015), Eiasu *et al.*, (2007) and Monneveux *et al.*, (2014), our consequences revealed that PDM and yield were significantly reduced at 60% depletion of soil available water as associated to their controls conditions. But, NT at 60% depletion of soil available water was decreased in all cultivars and treatments except in cultivar Spirit, we detected increasing in NT at 0.0, 0.5, 1.0 mM SA and 1.0 mM GB. The higher PDM (9.16 g/plant) and NT (36.33) were attained in Spirit at 1.0 mM SA and 1.0 mM GB, and yield in Born (123.33 and 120.00 g/plant) at 0.5, 1.0 mM SA (Table 7). In fact, under drought conditions plant growth and biomass of plants were reduced (Kumar *et al.*, 2007; Stiller, 2008). Also, results of Spitters and Schapendonk, (1990) on potato plants under drought stress indicated that, reduction in leaf size was the first morphological effect. This effect is more obvious in reduced leaf area senescence than in leaf dry weight (Vreugdenhil *et al.*, 2007). As well, Hur, (1991) pointed out that the most important consequences of water deficit in agriculture is reduction of plant yield by reducing light absorption, leaf area, decreasing the efficiency of turning light-absorbed to dry matter and finally reducing photosynthesis by declining stomatal conductance and reducing the absorption of carbon dioxide which effects on the yield productivity. However,

Eiasu *et al.*, (2007), Martin *et al.*, (1992) and Monneveux *et al.*, (2014), revealed that under water deficit stress conditions the number and quality of potato tubers were decreased. In fact, the most two elements defining quality of potato tubers are dry matter concentration and tuber size distribution. Dry matter level continuously increases with the period of growth (Vreugdenhil *et al.*, 2007). As well, the tuber size distribution of potato crop determines by the yield and the number of tubers per square meter. Also, depends on the number of stems and the number of tubers per stem. However, numbers of stems are depending on water availability, variety, tuber size and the physiological stage of the seed tubers throughout the growing period (Vreugdenhil *et al.*, 2007).

In the other hand, many researchers indicated that salicylic acid and glycine betaine are described to be biosynthesized in plants in response to water deficit and other stresses and exogenous them lead to improve growth of plants and their tolerance to non-suitable conditions (Janda *et al.*, 2014; Askari and Ehsanzadeh, 2015b) by regulating some physiological and biochemical processes (Vicent and Plasencia, 2011). As well, many of physiological investigates have confirmed that GB most likely preserves the osmotic balance between intracellular and extracellular under drought and salt stress conditions (Chen and Murata, 2011).

CONCLUSION

From the data gathered in the current study, water deficit exerted negative effects on gas exchanges, plant dry mass and yield of potato plants. Also, this study provides evidence that potato cultivars are responsive to applying salicylic acid and glycine betaine. Also, used them are capable of partial counteracting the harmful effects of water insufficiency. Else, photo, proline accumulation and plant dry mass are presented to be correlated to stress tolerance of potato cultivars as the levels of increases in these traits were better in Spirit and Born cultivars. In addition to, foliar spraying with salicylic acid and glycine betaine significantly changed the activity of gas exchanges and proline content that all these characters supported potato plants to withstand water insufficiency.

ACKNOWLEDGMENT

This work was supported by the Isfahan University of Technology, Faculty of agriculture, and Department of Horticulture Science.

CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

REFERENCES

- Al-Mahmud A., Kadian M.S., Hossain M. and Hoque M.A. (2015) Physiological and biochemical changes in potato under water stress condition. *Ind. J. Plant Physiol.*, 20, 297-303. <https://doi:10.1007/s40502-015-0173-4>
- Anosheh H.P., Emam Y., Ashraf M. and Foolad M.R. (2012) Exogenous application of salicylic acid and chlormequat chloride alleviates negative effects of drought stress in wheat. *Advan. Stud. in Biol.*, 4, 501-520.
- Araus J.L., Slafer G.A., Reynolds M.P. and Royo C. (2002) Plant breeding and drought in C3 cereals: what should we breed for? *Ann. Bot.*, 89, 925-940.
- Ashraf M. and Harris P.J.C. (2004) Potential biochemical indicators of salinity tolerance in plants. *Plant Sci.*, 166, 3-16.
- Askari E. and Ehsanzadeh P. (2015a) Drought stress mitigation by foliar application of salicylic acid and their interactive effects on physiological characteristics of fennel (*Foeniculum vulgare* Mill.) genotypes. *Acta Physiol. Planta.*, 37, 1-14. <https://doi.10.1007/s11738-014-1762-y>
- Askari E. and Ehsanzadeh P. (2015b) Effectiveness of exogenous salicylic acid on root and shoot growth attributes, productivity and water use efficiency of water deprived fennel genotypes. *Hort. Environ. Biotech.*, 56, 687-696. <https://doi.10.1007/s13580-015-0038-9>
- Baheri S.F., Javanshir A., Kazemi H.A. and Aharizad S. (2003) Evaluation of different drought tolerance indices in some spring barley genotypes. *J. Agric. Sci.*, 13, 95-100.
- Bates L.S., Waldren P.R. and Teare D.I. (1973) Rapid determination of free proline for water stress studies, *Plant and Soil*, 39, 205-208.
- Bohnert H.J., Nelson D.E. and Jensen R.G. (1995) Adaptations to environmental stresses. *Plant Cell*, 7, 1099-1111.
- Chen T.H. and Murata N. (2011) Glycinebetaine protects plants against abiotic stress: mechanisms and biotechnological applications. *Plant Cell Environ.*, 34, 1-20. DOI:[10.1111/j.1365-3040.2010.02232.x](https://doi.org/10.1111/j.1365-3040.2010.02232.x)
- Cheng Y.J., Deng X.P., Kwak S.S., Chen W. and Eneji A.E. (2013) Enhanced tolerance of transgenic potato plants expressing choline oxidase in chloroplasts against water stress. *Bot. Stud.*, 54, 1-9.
- Choi S.M., Song H.R. and Han S.K., et al. (2012) HDA19 is required for the repression of salicylic acid biosynthesis and salicylic acid-mediated defense responses in Arabidopsis. *Plant J.* 71, 135-146. doi: 10.1111/j.1365-313X.2012.04977.x.
- Eiasu, B.K., Soundy, P., and Hammes, P.S. (2007). Response of potato (*Solanum tuberosum* L) tuber yield components to gelpolymer soil amendments and irrigation regimes. *J. of Crop Hort.*, 35, 25-31. DOI:[10.1080/01140670709510164](https://doi.org/10.1080/01140670709510164)
- Evans J.R. and Loreto F. (2000) Acquisition and diffusion of CO₂ in higher plant leaves. In: Leegood R.C., Sharkey T.D. and von Caemmerer S. (eds) *Photosynthesis: Physiology and Metabolism*, pp 321-351. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Farooq M., Wahid A., Kobayashi N., Fujita D. and Basra S.M.A. (2009) Plant drought stress, effects, mechanisms and management. *Agro. Sustain. Develop.*, 29, 185-212. <https://doi.org/10.1051/agro:2008021>
- Glave L.M. (2001) The conquest of highlands in the potato treasure of the Andes from agriculture to culture, Graves, C. Ed. Lima, Peru, *Inter. Potato Center*, 41, 42-51.
- Hare P.D. and Cress W.A. (1997) Metabolic implications of stress-induced proline accumulation in plants. *Plant growth regulat.*, 21, 79-102.
- Harris P.M. (1992) *The potato crop: The scientific basis for improvement*. London: Chapman and Hall.

- Heuer B. and Nadler A. (1998) Physiological response of potato plants to soil salinity and water deficit. *Plant Sci. Letters*, 137, 43-51. DOI:[10.1016/S0168-9452\(98\)00133-2](https://doi.org/10.1016/S0168-9452(98)00133-2)
- Hur S.N. (1991) Effect of osmo-conditioning on the productivity of Italian ryegrass and sorghum under suboptimal conditions. *Korean, J. Animal. Sci.*, 33, 101-105.
- Janda T., Gondor O.K., Yordanova R., Szalai G. and Pal M. (2014) Salicylic acid and photosynthesis, signaling and effects. *Acta Physiol. Plant.*, 36, 2537-2546. <https://doi.org/10.1007/s11738-014-1620-y>
- Kumar S., Asrey R. and Mandal G. (2007) Effect of differential irrigation regimes on potato (*Solanum tuberosum* L) yield and post-harvest attributes. *Ind. J. of Agric. Sci.*, 77, 366-368.
- Lahlou O. and Ledent J.F. (2005) Root mass and depth, stolons and roots formed on stolons in four cultivars of potato under water stress. *Eur. J. Agron.*, 22, 159-173. DOI:[10.1016/j.eja.2004.02.004](https://doi.org/10.1016/j.eja.2004.02.004)
- Lawlor D.W. (2002) Limitation to photosynthesis in water-deficited leaves: stomata vs. metabolism and the role of ATP. *Ann. Bot.*, 89, 871-885.
- Levy D., Coleman W.K. and Veilleux R.E. (2013) Adaptation of potato to water shortage: irrigation management and enhancement of tolerance to drought and salinity. *Amer. J. Potato Res.*, 90, 186-206. <https://doi.org/10.1007/s12230-012-9291-y>
- Lobell D.B., Burke M.B., Tebaldi C., Mastrandrea M.D., Falcon W.P. and Naylor R.L. (2008) Prioritizing climate change adaptation needs for food security in 2030. *Sci.*, 319, 607-610. doi:[10.1126/science.1152339](https://doi.org/10.1126/science.1152339)
- Martin R.J., Jamieson P.D. and Wilson D.R. (1992) Effects of soil moisture deficits on yield and quality of 'Russet Burbank' potatoes. *New Zealand J. Crop Horticul. Sci.*, 20, 1-9. DOI: [10.1080/01140671.1992.10422319](https://doi.org/10.1080/01140671.1992.10422319)
- Martinez C.A., Guerrero C. and Moreno U. (1995) Diurnal fluctuations of carbon exchange rate, proline content, and osmotic potential in two water-stressed potato hybrids. *The Revis. Brasil. de Fisiol. Veget.*, 7, 27-33.
- Martinez-Gutiérrez R., Mora-Herrera M.E. and Lopez-Delgado H.A. (2012) Exogenous H₂O₂ in phytoplasma-infected potato plants promotes antioxidant activity and tuber production under drought conditions. *Amer. J. Potato Res.*, 89, 53-62.
- Monakhova O.F. and Chernyadev I.I. (2002) Protective role of kartolin-4 in wheat plants exposed to soil drought. *Appl. Biochem. Microbiol.*, 38, 373-380.
- Monneveux P., Ramirez D.A., Awais-Khan M., Raymundo R.M., Loayza H. and Quiroz R. (2014) Drought and Heat Tolerance Evaluation in Potato (*Solanum tuberosum* L.). *Potato Res.*, 57, 225-247. <https://doi.org/10.1007/s11540-014-9263-3>
- Morgan P.W. (1990) Effects of abiotic stresses on plant hormone systems. In: *Stress Responses in plants: adaptation and acclimation mechanisms*, Wiley-Liss. Inc. New York, USA.
- Nouri A., Nezami A., Kafi M. and Hassanpanah D. (2016) Growth and yield response of potato genotypes to deficit irrigation. *Inter. J. of Plant Prod.*, 10, 139-158.
- Placide R., Shimelis H., Laing M. and Gahakwa D. (2013) Physiological mechanisms and conventional breeding of sweet potato (*Ipomoea batatas* L. Lam.) to drought-tolerance. *Afr. J. Agri. Res.*, 8, 1837-1846.
- Rhodes D. and Hanson A. (1993) Quaternary ammonium and tertiary sulfonium compounds in higher plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 44, 357-384. DOI:[10.1146/ANNUREV.PP.44.060193.002041](https://doi.org/10.1146/ANNUREV.PP.44.060193.002041)
- Sakamoto A. and Murata N. (2000) Genetic engineering of GB synthesis in plants: current status and implications for enhancement of stress tolerance. *Exp. Bot.*, 51, 81-88.
- Sarani M., Namrudi M., Hashemi S.M. and Raofi M.M. (2014) The effect of drought stress on chlorophyll content, root growth, glucosinolate and proline in crop plants. *The Inter. J. of Farming and Allied Sci.*, 9, 994-997.
- Schafleitner R. (2009) Growing more potatoes with less water. *Tropical Plant Biology*, 2, 111-121. <https://doi.org/10.1007/s12230-009-9111-1>

- 10.1007/s12042-009-9033-6
- Shi S., Fan M., Iwama K., Li F., Zhang Z. and Jia L. (2015) Physiological basis of drought tolerance in potato grown under long term water deficiency. *Inter. J. of Plant Prod.*, 9, 305-320.
- Singh J. and Kaur L. (2009) Advances in potato chemistry and technology. In J. E. Bradshaw and G. Ramsay (Ed.), *Potato Origin and Production*. 67, pp. 1-26. Academic Press is an imprint of Elsevier. USA.
- Spitters C.J.T. and Schapendonk A.H.C.M. (1990) Evaluation of breeding strategies for drought tolerance in potato by means of crop growth simulation. *Plant and Soil*, 123, 193-203.
- Stalham M.A. and Allen E.J. (2001) Effect of variety, irrigation regime and planting date on depth, rate, duration and density of root growth in the potato (*Solanum tuberosum* L) crop. *J. Agric. Sci.*, 137, 251-270.
- Stiller I., Dulai S., Kondrak M., Tarnai R., Szabo L., Toldi O. and Banfalvi Z. (2008) Effects of drought on water content and photosynthetic parameters in potato plants expressing the trehalose-6-phosphate synthase gene of *Saccharomyces cerevisiae*. *Planta*, 227, 299-308. <https://doi.org/10.1007/s00425-007-0617-9>
- Vicent M.R.S. and Plasencia J. (2011) Salicylic acid beyond defence: its role in plant growth and development. *J. Exp. Bot.*, 62, 3321-3338.
- Vreugdenhil D., Bradshaw J., Gebhardt C., Govers F., Mackerron D.K.L., Taylor M. and Ross H.A. (2007) *Potato biology and biotechnology*. In Kirkman M.A., (ed.) *Global Markets for Processed Potato Products*. 2, Amsterdam, United Kingdom.
- Wang W., Vinocur B. and Altman A. (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta*, 218, 1-14.
- Watkinson J.I., Hendricks L. and Sioson A.A. (2006) Accessions of (*Solanum tuberosum* ssp.) andigena show differences in photosynthetic recovery after drought stress as reflected in gene expression profiles. *Plant Sci.*, 171, 745-758.
- Wegener C.B. and Jansen G. (2013) Antioxidants in different potato genotypes: effect of drought and wounding stress. *Agri.*, 3, 131-146.
- Wingler A, Quick W.P., Bungard R.A., Bailey K.J., Lea P.J. and Leegood R.C. (1999) The role of photorespiration during drought stress, an analysis utilizing barley mutants with reduced activities of photo-respiratory enzymes. *Plant Cell Environ.*, 22, 361-373.
- Yordanov I., Velikova V. and Tsonev T. (2003) Plant responses to drought and stress tolerance. *Bulg. J. Plant Physiol.*, Special Issue, 187-206.