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Physiological and agro-morphological response of potato to drought stress and hormone application

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Abstract

Potato is considered as a drought sensitive plant. To study the effect of drought stress and hormone on agro-morphological and physiological traits of potato, an experiment was carried out as split plot design based on randomized complete blocks with three replications in 2015 and 2016. The irrigation levels were control (well-watered), mild stress, severe stress and extreme stress, which were arranged in main plots. The second factor included four spaying treatments that were arranged in sub-plots. The foliar applications were as follows: no foliar application (control), gibberellic acid, epibrassinolide and acetyl salicylic acid. Results showed that drought stress and hormones had significant effect on most of the agro-morphological and physiological traits of potato. Leaf dry weight, shoot dry weight, tuber dry weight, plant height, number of stolons, number of tubers, leaf area index (LAI), relative water content (RWC), net photosynthesis rate, transpiration rate, intercellular CO_2 concentration and stomatal conductance decreased, while amount of water saturation deficit (WSD) increased by the drought stress. It seems that the negative impact of drought stress on physiological traits, such as RWC, adversely affected the agro-morphological traits of potato. Except for chlorophyll index, hormones significantly affected agro-morphological and physiological traits of the potato plants. Epibrassinolide improved RWC, WUE, intercellular CO_2 concentration, tuber dry matter, plant height, number of stolons, leaf dry weight, shoot dry weight and tuber dry weight, while application of gibberellic acid had better effects on LAI, WSD, transpiration rate and number of tubers as compared to epibrassinolide. In fact, these hormones mitigated the negative effects of drought stress in potato.

Keywords: Growth hormones; Leaf area index; Photosynthesis; Relative water content; Stomatal conductance; Tuber weight

Abbreviation: PH: Plant Height, LAI: Leaf Area Index; LDW: Leaf Dry Weight; WSD: Water Saturation Deficit; NS: Number of Stolens; NT: Number of Tubers; SDW: Shoot Dry Weight; TDM: Tuber Dry Matter; TDW: Tuber Dry Weight; WUE: Water Use Efficiency; RWC: Relative Water Content; *Pn*: Net photosynthesis rate; *Gs*: Stomatal conductance; *Tr*: Transpiration rate; *Ci*: Intercellular CO_2 concentration.

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Introduction

Potato (*Solanum tuberosum* L.) is an important food crop, which produce high yields (Aliche *et al*. 2018). Global climate change in the form of extreme heat and drought negatively affects plant performance and crop yield (Dahal *et al.* 2019). As a fourth major food crop, enhancing potato yield is necessary to cope with the global population growth. However, potato is a drought-sensitive plant (Dahal *et al.* 2019). Losses in yield may reach 79% reduction under water stress conditions (Luitel *et al.* 2015). According to Monneveux *et al*. (2013), drought stress at the tuberization stage reduced tuber number and yield of potato. Other researchers have also reported the negative effect of drought on the tuber number (Xie *et al*. 2012; Yactayo *et al.* 2013). However, the information about the water status, growth and yield of potato under farm drip irrigation system is limited in Iran. Tuber formation in potato can be affected by plant growth regulators (PGR) (Stuart and Cathey 1961). The role of GA_3 on tuber elongation, growth (Alexopoulos *et al.* 2007), dry matter accumulation and yield (Javanmardi and Rasuli 2017) has been reported in the potato plant. Sánchez-Rojo *et al.* (2010) reported the improvement of tuber photosynthate assimilation of the potato plant by the acetylsalicylic acid application. Also, the positive effect of acetylsalicylic acid treatment on the control of pathogens has been reported by several authors (López *et al.* 2001; 2003 Bokshi *et al.* 2003; Sánchez-Rojo *et al.* 2010). Furthermore, Kabiri and Naghizadeh (2015) showed that acetylsalicylic acid treatment increased the tolerance to water stress conditions by maintaining cellular membrane integrity and scavenging of reactive oxygen species through the increase in the activity of antioxidant enzymes, which resulted in the enhancement of relative water content and grain yield in barley. The usefulness of brassinosteroids has also been indicated in potato. Brassinolide increased potato root growth in-vitro and alleviated salinity stress (Hu *et al.* 2016). Based on Efimova *et al.* (2018), the priming of plants by brassinosteroids reduced oxidative stress and increased salt tolerance in potato. According to Miller *et al.* (2003), application of lower levels of brassinosteroid (1 µl, 10 µl) in the in-vitro condition significantly increased the plantlet growth in potato.

The objective of this research was to evaluate the effect of water deficit stress and foliar application of gibberellic acid, epibrassinolide and acetyl salicylic acid on photosynthesis, and yield and yield components of potato.

Materials and Methods

A two-year field study was conducted at Malayer, Hamedan, Iran (48′ and 82° E, 34′ and 29° N, 1725 m above sea level). The site is characterized by a typical temperate arid zone with mean annual precipitation of 300 mm. The climatic data for the two years and average of 10 years are presented in Table 1. The rainfall only occurred in small amounts (0.06 mm) in July 2015. All plots were disked twice prior to planting on 30 April in each year. Seed pieces of a medium-late potato cultivar ‘Banba’ were hand-cut to the average weight of about 30 g, and planted in the field plots on 24th and 29th of May 2015 and 2016, respectively, at about 10 cm depth with a six-row planter. Two weeks before planting, soil samples were taken to determine pH, electrical conductivity, organic carbon, total N, available P and available K (Tandon 1995). The soil type was silt loam, the bulk density of the soil was 1.3 Mg m^{-3} and soil pH was 7.3 (Table 2). According to Havlin *et al.* (2005), N, P and K were low, medium and high in both year, respectively. Each experimental plot consisted of 8 rows of 9 m long, spaced 0.7 m apart with a within-row spacing of 25 cm. The plots and blocks were 1 and 2 m apart, respectively to prevent water movement. Eight plant were considered in each m^2. For each plot, a balance sheet for NPK, based on soil analysis, was developed. Thirty percent of N and total P and K requirements were supplied (NPK in the form of urea, superphosphate triple and potassium, respectively) at planting. For the rest of the season urea was used as the nitrogen source.

Experimental factors were arranged as the split plot design with three replications. The main plots consisted of four irrigation regimes using the surface drip irrigation method. The available soil water content (ASW) for the rooting depth was determined as:

$$ASW = (AS-WS)/(FC-WS)$$

where AS, WS and FC are actual soil water content, soil water content at the wilting point and field capacity, respectively. For the two years, the crop water use was determined as $K_c \times ET_p$, where K_c is the crop coefficient and ET_p is the potential evapotranspiration. The irrigation levels were control (irrigation was initiated at 80% of the FC; well-watered), mild stress (irrigation was initiated at 65% of the FC), severe stress (irrigation was initiated at 50% of the FC) and extreme stress (irrigation was initiated at 35% of the FC). Sub-plots four spaying treatments as follows: no foliar application (control), gibberellic acid, epi-brassinolide and acetylsalicylic acid. Irrigation was initiated after emergence and lasted until final harvest. All foliar applications were conducted at tuber initiation. For leaf spraying, an amount equivalent to 200 mg/L, 1 mg/L and 100 ppm of solution (gibberellic acid, epi-brassinolide and acetylsalicylic acid, respectively) was applied, using a backpack sprayer with constant pressure. A neutron probe was used two times a week to monitor the soil moisture during the growth period by taking soil samples at the depth of 40 cm. The chlorophyll index (SPAD), stomatal conductance, net photosynthesis rate, intercellular CO_2 concentration and transpiration rate were measured on the third leaf from the top of four leaves, seven days after foliar application. A portable chlorophyll meter (Minolta SPAD-502, Japan) was used for measuring the chlorophyll index following the method of Turner and Jund (1991). The stomatal conductance, net photosynthesis rate, intercellular CO_2 concentration and transpiration rate were measured on the fully developed leaves with the open gas-exchange system of Li-6400 XT (Li-Cor, Lincoln, NE, USA). These traits were measured around 12 am, at which the photosynthetic active radiation above the canopy reached 300 μmol/m^2/s. Inside the chamber, the light intensity was 1000 μmol/m^2/s and the CO_2 concentration was 370 μmol/mol. Relative humidity and air temperature were kept at 40-45% and 25 °C, respectively.

Leaf area index (LAI) was measured by a leaf area meter (AAM-9, Hayashi Denko, Tokyo, Japan). Water saturation deficit (WSD) was determined on the 4th leaf from the top using the method of Turner (1981). For each plot, 10 leaves were cut in the morning and weighed immediately to obtain the fresh weight (FW). These leaves were floated in the dark for 24 h and the turgid weight (TW) was measured. Then the dry weight (DW) of the leaves was measured after oven-drying at 75°C for 48 h. WSD was calculated by the following formula (Turner 1981):

$$WSD = [(TW - FW)/(TW - DW)] \times 100\%.$$

Also, relative water content (RWC) was calculated as follows:

$$RWC\ (\%) = (FW-DW)/(TW-DW)\times 100.$$

Four plants from each plot were selected randomly considering marginal effects. The length of longest stem from the crown was measured to determine plant height after harvest. The number of stolons in each sampling was counted and finally averaged. Leaf and stem weights were determined separately. The stems or leaves were placed in oven at 75 °C and weighted after constant mass was reached. To measure the percent tuber dry matter, 200 g of tuber were randomly selected and weighed, then the tubers were sliced at 75 °C and re-weighted after constant mass was reached.

The middle four rows of each plot were harvested by hand on October 3 and September 27 in 2015 and 2016, respectively. In each plot, 10 random plants were chosen to measure number of tubers per plant and tuber weight per plant. Then, the potatoes were sliced, dried in an oven at 75 ºC for 72 h and weighed again to obtain tuber dry weight. Water use efficiency (WUE) was calculated by dividing the marketable yield by the volume of irrigation water.

Statistical analyses

After the analysis of variance, means were compared by the least significant difference (LSD) test. The statistical analyses were carried out by the SAS software (SAS Institute Inc. 2002).

Table 1. Mean air temperature (MAT) and mean rainfall (MR) of the experimental site from June to October in different years.

Year	Month				
	June	July	August	September	October
2015					
MAT (◦C)	23.4	27.2	26.0	22.8	19.1
MR (mm)	0	0.06	0	0.42	0
2016					
MAT (◦C)	22.1	26.4	25.7	22.0	19.0
MR (mm)	0	0	0	0	0

Table 2. Physical and chemical properties of the soil in the experimental site in 2015 and 2016.

Year	pH	EC	TNV (%)	OC (%)	N (%)	P (ppm)	K (ppm)	Si (%)	S (%)	Cl (%)
2015	7.3	0.4	5.5	0.2	0.02	4	247	61	12	24
2016	7.4	0.3	6	0.4	0.05	7	258	69	17	22

Results

Analysis of variance

Results of analysis of variance are shown in Table 3. Year significantly affected leaf and shoot dry weights, number of tubers, percentage of tuber dry matter, WUE, chlorophyll index and stomatal conductance of the potato plants. Drought stress had significant effect on all agro-morphological and physiological traits of potato, except number of tubers, tuber dry weight, chlorophyll index and stomatal conductance. However, hormone application affected all traits significantly.

Interaction of year × drought stress × hormone was significant for leaf dry weight, shoot dry weight, number of tubers, tuber dry weight, percentage of tuber dry matter, WUE, chlorophyll index and stomatal conductance. Excluding the traits with the three-way interaction of year × drought stress × hormone, none of the remaining traits had significant year × drought stress interaction; however, year × hormone interaction was significant for percentage of tuber dry matter and drought stress × hormone interaction was significant for plant height, LAI, WSD, RWC, net photosynthesis rate, transpiration rate and intercellular CO_2 concentration.

Main effects of drought stress and hormone

Number of stolons was significantly reduced by enhancing drought stress and the extreme drought stress showed the lowest value (Figure 1). Application of epibrassinolide and gibberellic acid affected the number of stolons significantly and the highest amount belonged to epibrassinolide (Figure 2). Percentage of tuber dry matter improved with increasing drought stress (Figure 3). Also, application of all hormones, increased percentage of tuber dry matter significantly, among which epibrassinolide was the most effective (Figure 4).

Drought stress × hormone interaction

Although there was significant interaction between drought stress levels and hormones, drought stress decreased plant height, LAI, RWC, net photosynthesis rate, transpiration rate, intercellular CO_2 concentration, and increased WSD values (Table 4). Epibrassinolide hormone at normal condition resulted in the highest amounts of plant height, RWC and intercellular CO_2 concentration. The lowest values for these traits were obtained in the extreme drought stress condition when no regulators were used. The highest and lowest values of LAI and transpiration rate belonged to the normal condition + gibberellic acid and extreme condition + no regulators. Treatment combinations of normal condition + epibrassinolide and extreme condition + no regulators had minimum and amounts maximum of WSD, respectively. At all levels of the drought stress, the hormones under study significantly affected majority of the traits under investigation as compared to the control (without regulators). However, the case of the net photosynthesis rate was different, and none of the hormones performed better than the control at all water deficit stress conditions (Table 4).

Drought stress × hormone × year interaction

The results for the significant three-way interactions are presented in Table 5. In both years, the lowest amounts of leaf dry weight, shoot dry weight, tuber dry weight and WUE were observed under extreme stress conditions without the use of regulators. In both years, the greatest amounts of leaf dry weight, shoot dry weight, tuber dry weight and WUE were obtained when epibrassinolide was applied at either mild stress or normal conditions. It seems that hormone application affected leaf dry weight, shoot dry weight, tuber dry weight, number of tubers and WUE at all humidity conditions. The SPAD values at mild and normal conditions were higher for the control (without regulators) in both years

Table 3. Analysis of variance for the effects of drought stress and hormone treatments on some agro-morphological and physiological traits of potato.

		Mean squares						
SOV	df	PH	NS	LDW	SDW	NT	TDW	TDM
Year (Y)	1	73.9^{ns}	6^{ns}	2055.4**	5074.6**	506.1**	275.7^{ns}	1.49**
Rep / Y	4	11.7*	2.92**	57.8^{ns}	223.5*	9.5**	526.0^{ns}	0.24^{ns}
Irrigation (I)	3	1458.8**	18.79**	2950.9**	11402.3**	781.8^{ns}	213489.1^{ns}	2.75**
I × Y	3	0.86^{ns}	0.19^{ns}	5.7^{ns}	51.6^{ns}	100.6**	24658.3**	0.14^{ns}
Rep × I /Y	12	4.2**	0.64**	52.7**	66.5**	0.97*	247.9**	0.10**
Hormone (H)	3	419.0**	8.81**	1086.7**	4569.3**	960.1**	30714.7*	0.99*
I × H	9	2.1**	0.31^{ns}	5.9^{ns}	19.1^{ns}	5.1^{ns}	346.4^{ns}	0.02^{ns}
H × Y	3	1.2^{ns}	0.11^{ns}	44.8**	66.4**	8.6**	2862.7**	0.10**
I × H × Y	9	0.9^{ns}	0.23^{ns}	12.0*	31.9**	5.3**	449.1**	0.02^{ns}
Error	48	0.61	0.16	4.58	9.2	0.5	52.46	0.02
CV (%)	-	0.93	1.74	3.91	2.44	1.32	0.99	0.81

PH: plant height; NS: number of stolons; LDW: leaf dry weight; SDW: shoot dry weight; NT: number of tubers; TDW: tuber dry weight; TDM: percentage of tuber dry matter; ns: not significant at 0.05 probability level; *significant at 0.05 probability level; **significant at 0.01 probability level.

Table 3 continued

SOV	df	WUE	LAI	WSD	RWC	SPAD	Pn	Gs	Tr	Ci
Year (Y)	1	0.04**	0.025^{ns}	0.43^{ns}	4.5^{ns}	374.8**	3.73^{ns}	144.1**	0.02^{ns}	1037.0^{ns}
Rep / Y	4	0.002^{ns}	0.07**	25.3**	39.5**	2.3^{ns}	37.5**	0.07**	0.07**	252.7**
Irrigation (I)	3	1.09*	6.49**	409.6**	445**	51.2^{ns}	154.5**	1.41^{ns}	4.6**	3493.1**
I × Y	3	0.11**	0.00003^{ns}	0.03^{ns}	0.22^{ns}	15.4**	0.06^{ns}	0.92**	0.0001^{ns}	0.37^{ns}
Rep × I /Y	12	0.001**	0.00009^{ns}	0.95*	1.58**	1.5**	1.42**	0.003*	0.0001^{ns}	10.7**
Hormone (H)	3	0.15*	1.62**	64.6**	79.08**	6.8^{ns}	42.14**	0.19**	0.82**	447.2**
I × H	9	0.001^{ns}	0.013**	2.3**	1.35*	0.6^{ns}	7.59**	0.004^{ns}	0.008**	10.3**
H × Y	3	0.013**	0.00002^{ns}	0.004^{ns}	0.03^{ns}	1.7**	0.015^{ns}	0.22**	0.0001^{ns}	0.11^{ns}
I × H × Y	9	0.002**	0.00008^{ns}	0.0001^{ns}	0.0004^{ns}	1.0**	0.002^{ns}	0.005**	0.0001^{ns}	0.03^{ns}
Error	48	0.0002	0.0002	0.58	0.64	0.17	0.52	0.001	0.0001	3.94
CV (%)	-	1	0.48	4.63	0.99	0.68	7.36	2.21	0.49	0.77

WUE: water use efficiency; LAI: leaf area index; WSD: water saturation deficit; RWC: relative water content; SPAD: chlorophyll index, P_n: net photosynthesis rate, G_s: stomatal conductance; T_r: transpiration rate; C_i: intercellular CO_2 concentration; ns: not significant at 0.05 probability level;
*significant at 0.05 probability level; **significant at 0.01 probability level.

Table 4. Means of agro-morphological and physiological traits of potato for the treatment combinations of drought stress and hormone levels.

Drought stress	Hormone	PH (cm)	LAI (%)	WSD (%)	RWC (%)	P_n (µmol/m^2/s)	T_r (mg/dm^2/h)	C_i (ppm)
Normal	Without regulators	85.75^{f}	3.44^{f}	14.37^{g}	82.75^{cd}	14.83^{a}	2.93^{e}	263.33^{c}
	Gibberellic acid	93.37^{c}	4.03^{a}	12.40^{ij}	84.87^{b}	11.08^{b}	3.44^{a}	268.12^{b}
	Epibrassinolide	95.61^{a}	3.93^{b}	10.80^{k}	86.92^{a}	10.16^{c}	3.34^{b}	272.26^{a}
	Acetylsalicylic acid	90.23^{d}	3.84^{c}	12.70^{hi}	85.12^{b}	14.38^{a}	3.26^{c}	268.59^{b}
Mild	Without regulators	83.07^{h}	3.13^{i}	15.43^{f}	81.96^{de}	11.68^{b}	2.84^{f}	258.42^{d}
	Gibberellic acid	90.82^{d}	3.84^{c}	14.37^{g}	83.25^{cd}	9.91^{c}	3.24^{c}	264.60^{c}
	Epibrassinolide	94.56^{b}	3.75^{d}	11.64^{jk}	86.32^{a}	11.38^{b}	3.25^{c}	268.04^{b}
	Acetylsalicylic acid	88.39^{e}	3.64^{e}	13.54^{gh}	84.29^{b}	11.86^{b}	3.04^{d}	263.68^{c}
Severe	Without regulators	75.44^{l}	2.74^{k}	19.79^{c}	77.22^{g}	10.07^{c}	2.44^{i}	246.82^{g}
	Gibberellic acid	81.80^{i}	3.35^{g}	17.21^{e}	80.14^{f}	8.87^{d}	2.83^{f}	250.48^{f}
	Epibrassinolide	84.07^{g}	3.25^{h}	16.65^{e}	81.15^{e}	6.27^{g}	2.74^{g}	259.29^{d}
	Acetylsalicylic acid	80.26^{j}	3.14^{i}	18.15^{d}	79.69^{f}	7.98^{e}	2.64^{h}	253.77^{e}
Extreme	Without regulators	69.31^{n}	2.35^{m}	24.79^{a}	72.54^{i}	8.87^{d}	2.04^{l}	236.40^{i}
	Gibberellic acid	75.68^{l}	2.82^{j}	21.08^{b}	76.06^{h}	7.13^{f}	2.43^{i}	241.06^{h}
	Epibrassinolide	78.95^{k}	2.74^{k}	19.29^{c}	77.75^{g}	5.39^{h}	2.35^{j}	247.63^{g}
	Acetylsalicylic acid	74.16^{m}	2.65^{l}	21.26^{b}	75.95^{h}	7.09^{fg}	2.27^{k}	239.48^{h}

PH: plant height; LAI: leaf area index; WSD: water saturation deficit; RWC: relative water content; P_n: net photosynthesis rate; T_r: transpiration rate; C_i: intercellular CO_2 concentration; Means with similar letters in each column are not significantly different at 0.05 probability level based on least significant difference test.

as compared to the hormone application; however, some differences were not significant. In both years, the application of gibberellic acid significantly increased the number of tubers at all drought stress levels as compared to other hormone treatments. The results for the stomatal conductance were not consistent over years. In the first year, the highest values were observed for gibberellic acid and epibrassinolide at all stress conditions; however, these values were not significantly different from some values obtained for other hormonal treatments. In the second year, no significant differences were obtained among hormones at normal, mild stress and extreme stress conditions. But, at the severe stress, gibberellic acid showed the highest stomatal conductance, although its difference with acetylsalicylic acid was not significant.

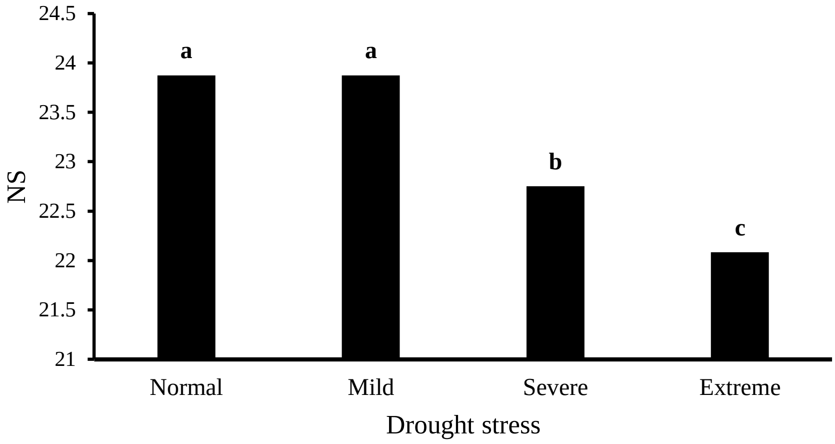

Figure 1. Number of potato stolons (NS) at different drought stress levels; means with similar letters are not significantly different at 0.05 probability level based on least significant difference test.

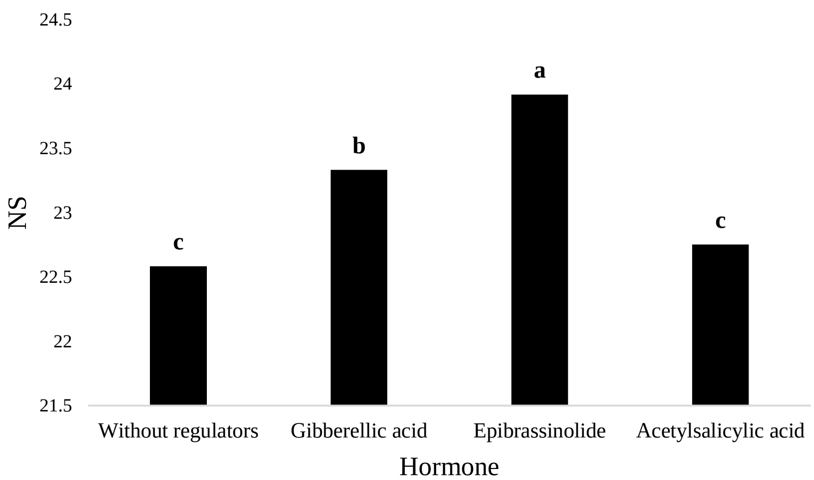

Figure 2. Number of potato stolons (NS) at different hormone conditions; means with similar letters are not significantly different at 0.05 probability level based on least significant difference test.

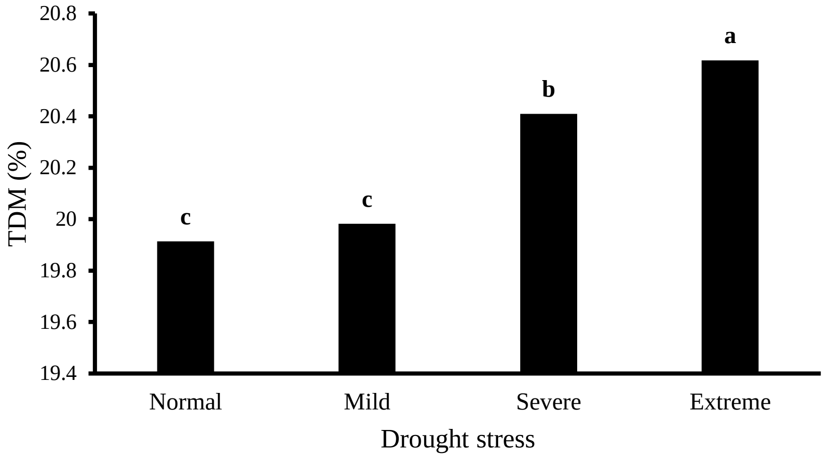

Figure 3. Tuber dry matter (TDM) of potato at different drought stress levels; means with similar letters are not significantly different at 0.05 probability level based on least significant difference test.

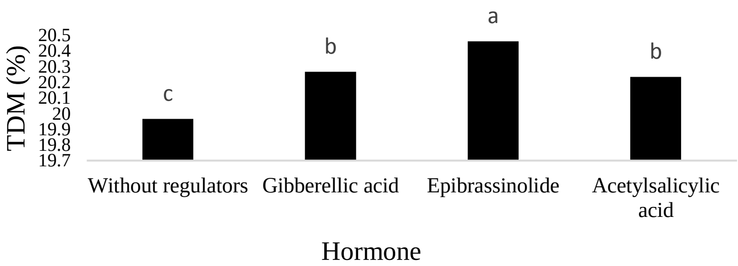

Figure 4. Tuber dry matter (TDM) of potato at different hormone conditions; means with similar letters are not significantly different at 0.05 probability level based on least significant difference test.

Discussion

Potato is considered as a drought sensitive plant (Soltys-Kalina 2016) and if the water requirements of this plant are not met, its yield reduction can reach 79% (Luitel *et al.* 2015). Barriopedro *et al*. (2011) indicated that the reduction of potato production due to drought stress was about 30% in Russia. In our study, drought stress limited the growth of potato, and had significant negative effect on most of the agro-morphological and physiological traits under investigation on the average of two years. Intensification of the drought stress on potato plants decreased LAI, RWC, net photosynthesis rate, transpiration rate, intercellular CO_2 concentration, stomatal conductance, and increased WSD, which may have been the cause of decrease in the agro-morphological characteristics under study. According to Lahlou *et al.* (2003), the decrease in water availability resulted in the decline of LAI and leaf area duration, which eventually led to the reduction in tuber number and tuber yield of potato. Rykaczewska (2017) observed the reduction of plant height, LAI, tuber weight and tuber number of the potato crop due to drought stress. Also, based on Crusciol *et al.* (2009), water deficit stress reduced tuber dry weight and number of tubers per plant in potato. Ierna and Mauromicale (2006) reported that drought stress reduced the photosynthesis rate, leaf area, tuber number per stem and tuber weight and yield of the potato plants. Drought led to a sharp decline in potato yield and/or quality (Stark *et al.* 2013; Soltys-Kalina *et al.* 2016). According to Cairns *et al.* (2012), drought stress negatively affected several physiological and agronomic traits of maize, including grain yield. Soleimanzadeh *et al.* (2010) stated that drought stress significantly reduced plant height in sunflower.

Table 5. Means of agro-morphological and physiological traits of potato for the treatment combinations of drought stress and hormone levels at two years.

Year	Drought stress	Hormone	LDW (gr/m^2)	SDW (gr/m^2)	NT	TDW (gr/m^2)	WUE	SPAD	G_s ($mol\ H_2O/m^2/s$)
2015	Normal	Without regulators	58.83^{d-f}	135.65^{ef}	51.72^{de}	786.20^{d}	1.75^{e}	61.82^{ab}	2.91^{cd}
		Gibberellic acid	71.68^{a-c}	157.33^{ab}	67.33^{a}	819.35^{bc}	1.83^{bc}	60.35^{d-f}	3.42^{a}
		Epibrassinolide	75.13^{ab}	165.73^{a}	56.78^{b}	875.15^{a}	1.95^{a}	60.42^{d-f}	3.32^{ab}
		Acetylsalicylic acid	70.28^{a-c}	155.65^{a-c}	53.94^{c}	801.72^{cd}	1.79^{cd}	60.61^{c-e}	3.24^{b}
	Mild	Without regulators	58.32^{d-f}	125.77^{fg}	50.89^{e}	788.10^{d}	1.76^{de}	62.12^{a}	2.82^{de}
		Gibberellic acid	68.10^{bc}	147.85^{b-d}	66.78^{a}	837.95^{b}	1.87^{b}	61.19^{a-d}	3.23^{b}
		Epibrassinolide	77.27^{a}	166.67^{a}	56.33^{b}	875.07^{a}	1.95^{a}	60.86^{b-d}	3.24^{b}
		Acetylsalicylic acid	65.28^{c-e}	144.45^{c-e}	53.39^{cd}	818.75^{bc}	1.83^{bc}	61.65^{a-c}	3.01^{c}
	Severe	Without regulators	47.02^{gh}	105.12^{hi}	42.78^{h}	632.60^{g}	1.41^{h}	59.46^{ef}	2.43^{g}
		Gibberellic acid	57.05^{ef}	120.98^{g}	57.72^{b}	711.10^{f}	1.59^{g}	59.32^{f}	2.81^{de}
		Epibrassinolide	66.38^{cd}	143.62^{de}	48.44^{f}	759.45^{e}	1.69^{f}	59.42^{f}	2.72^{ef}
		Acetylsalicylic acid	52.57^{fg}	116.53^{gh}	45.28^{g}	697.02^{f}	1.55^{g}	59.58^{ef}	2.63^{f}
	Extreme	Without regulators	34.05^{i}	85.10^{j}	35.56^{i}	489.85^{i}	1.09^{j}	56.44^{gh}	2.01^{i}
		Gibberellic acid	46.40^{gh}	106.85^{hi}	50.61^{e}	561.05^{h}	1.25^{i}	55.68^{h}	2.41^{g}
		Epibrassinolide	57.47^{ef}	124.69^{fg}	42.05^{h}	639.77^{g}	1.43^{h}	57.02^{g}	2.33^{gh}
		Acetylsalicylic acid	42.53^{h}	99.47^{i}	36.83^{i}	556.95^{h}	1.24^{i}	56.66^{gh}	2.24^{h}
2016	Normal	Without regulators	52.87^{c-e}	119.4^{c}	53.50^{f-h}	742.70^{cd}	1.71^{cd}	64.54^{ab}	0.42^{ab}
		Gibberellic acid	59.33^{b}	136.50^{b}	69.36^{a}	760.94^{b}	1.75^{b}	62.99^{c-e}	0.37^{a-e}
		Epibrassinolide	64.75^{a}	150.92^{a}	57.06^{d}	802.13^{a}	1.85^{a}	63.48^{b-e}	0.36^{a-e}
		Acetylsalicylic acid	57.32^{bc}	132.02^{b}	54.50^{ef}	757.62^{bc}	1.75^{bc}	63.06^{c-e}	0.43^{a}
	Mild	Without regulators	50.35^{d-f}	114.90^{cd}	52.61^{h}	742.44^{c-}	1.71^{cd}	65.56^{a}	0.43^{a}
		Gibberellic acid	61.20^{ab}	137.85^{b}	67.67^{b}	766.71^{b}	1.76^{b}	63.36^{b-e}	0.35^{a-f}
		Epibrassinolide	64.63^{a}	146.08^{a}	56.85^{d}	812.72^{a}	1.87^{a}	63.74^{b-d}	0.38^{a-d}
		Acetylsalicylic acid	58.62^{b}	133.67^{b}	54.33^{e-g}	763.04^{b}	1.76^{b}	63.50^{b-e}	0.36^{a-f}
	Severe	Without regulators	39.43^{gh}	94.43^{f}	51.00^{i}	692.27^{f}	1.59^{f}	64.64^{ab}	0.28^{ef}
		Gibberellic acid	47.58^{f}	107.58^{e}	64.30^{c}	733.22^{de}	1.69^{de}	64.14^{b-d}	0.39^{a-c}
		Epibrassinolide	53.63^{cd}	120.58^{c}	55.18^{e}	761.83^{b}	1.75^{b}	63.04^{c-f}	0.33^{b-f}
		Acetylsalicylic acid	48.90^{ef}	108.60^{de}	53.02^{gh}	726.33^{e}	1.67^{e}	64.24^{a-c}	0.30^{c-f}
	Extreme	Without regulators	29.73^{j}	74.85^{g}	46.65^{k}	609.99^{i}	1.40^{i}	63.53^{b-e}	0.30^{d-f}
		Gibberellic acid	36.58^{hi}	93.45^{f}	55.29^{e}	635.79^{h}	1.46^{gh}	62.32^{e}	0.26^{f}
		Epibrassinolide	41.78^{g}	106.00^{e}	48.78^{j}	653.21^{g}	1.50^{g}	60.83^{f}	0.30^{d-f}
		Acetylsalicylic acid	33.58^{ij}	91.90^{f}	49.81^{ij}	634.90^{h}	1.46^{h}	62.84^{de}	0.32^{c-f}

LDW: leaf dry weight; SDW: shoot dry weight; NT: number of tubers; TDW: tuber dry weight; WUE: water use efficiency; SPAD; G_s: stomatal conductance; Means with similar letters in each column are not significantly different at 0.05 probability level based on least significant difference test.

Plants must decline the stomatal conductance to counteract with negative effects of stress, and as a result, it caused partial closure of the stoma that reduced net photosynthesis rate, transpiration rate, intercellular CO_2 concentration and also SPAD (in the first year), which consequently, decreased tuber dry weight, plant height, leaf dry weight, shoot dry weight, number of tubers and number of stolons. However, percentage of tuber dry matter increased with increasing drought stress because amount of moisture in potato tuber reduced with drought stress, which decreased tuber fresh weight relative to tuber dry weight. Stomata are the main locations that are affected by the moisture shortage. Ahmadi *et al.* (2010) observed that drought stress decrease stomatal conductance in potato when amount of leaf water potential was lower than -0.6 MPa. Li *et al.* (2016) revealed that water deficit stress decreased potato yield by influencing on the net photosynthesis rate, total leaf area and leaf life span. Ohashi *et al.* (2006) reported the reduction of photosynthesis rate, stomatal conductance, intercellular CO_2 concentration and transpiration rate in soybean due to drought stress. Based on Sadeghipour and Aghaei (2012), total chlorophyll content, net photosynthesis rate, stomatal conductance, and CO_2 absorption in the common been decreased when the plant was exposed to moisture deficiency, which eventually reduced plant growth.

RWC and tuber dry weight decreased due to water deficit stress. Lawlor (2002) explained that RWC is related to metabolic activities in plant tissues and decreasing RWC of leaves increases metabolic limitation, decreases stomatal conductance (gs) and slows down CO2 assimilation under drought stress conditions. Tátrai *et al.* (2016) has shown that water deficiency reduces RWC in *Thymus citriodorus*. Sinclair and Ludlow (1985) stated that RWC can be used as a screening tool to select drought resistant genotypes.

According to Jefferies and MacKerron (1994) drought tolerance has been associated with enhanced water use efficiency. However, in our study, WUE did not increase significantly under mild stress and decreased at severe and extreme water deficit stress conditions. The reduction of WUE under severe and extreme stresses can be attributed to closure of the stomata, which consequently lowered the photosynthesis and tuber yield. Plants with high WUE can be regarded as suitable genotypes to improve yield when the soil moisture is low. Condon *et al.* (2008) suggested the breeding of crop varieties with higher WUE to cope with the pressing need to improve WUE due to the enhancement of world's water shortage.

The amount of rainfall from June to October was very low in 2015 (0.06 mm) and no rainfall occurred in 2016. As mentioned before, drought stress had negative effect on the growth and production of the potato plant. Therefore, using different management systems, such as application of plant hormones, can alleviate the harmful effects of drought stress. In this study, hormone application had positive and significant effect on most of the agro-morphological and physiological traits of potato as compared to the control treatment. Epibrassinolide was more effective than gibberellic acid and acetylsalicylic acid in improving majority of the potato traits under normal and drought conditions, except for LAI, WSD, net photosynthesis rate, transpiration rate, number of tubers, chlorophyll index and stomatal conductance. Gibberellic acid had better performance than other two hormones in relation to LAI, WSD, transpiration rate (except at mild stress) and number of tubers. For all of the traits under investigation, acetylsalicylic acid did not show better results than epibrassinolide and gibberellic acid at both normal and water stress conditions. Bajguz (2011) stated that epibrassinollide has been widely applied to improve the harmful effects of abiotic and biotic stresses in plants. Upadhyaya *et al.* (2015) reported that application of epibrassinolide improved growth characteristics of the salt treated potato plants, such as shoot length, tuber number tuber suize size, and fresh and dry mass. Li *et al.* (2012) showed that epibrassinollide could improve plant growth of *Chorispora bungeana* under drought stress. According to Talaat and Abdallah (2010), the epibrassinolide treatment improved the growth characters and yield of two faba bean cultivars over the control treatment. Jan *et al.* (2018) concluded that epibrassinolide modulates total chlorophyll, carotenoid, photosynthetic efficiency, photochemical quenching, leaf RWC and gas exchange parameters in *Pisum sativum* L. under cadmium stress. Javanmardi and Rasuli (2017) found that gibberellic acid significantly affected potato yield and tuber quality. In another study, application of gibberellic acid increased number of tubers, tuber weight and tuber yield of potato (Barani *et al.* 2013). Based on Pazoki *et al.* (2012), the dual application of gibberellic acid and ascorbate significantly increased RWC and reduced cell membrane leakage as the main indicator of cell membrane stability in *Thymus vulgaris* L. under both drought stress and non-stress conditions.

Conclusions

The results of this study showed that drought stress had significant effect on most of the physiological and agro-morphological characteristics of the potato plants. Water deficiency reduced RWC that caused the decline in stomatal conductance and consequently decreased net photosynthesis rate, intercellular CO_2 concentration and SPAD which ultimately led to decrease in the agro-morphological traits of potato such as LAI, tuber dry weight, number of tubers, number of stolons, plant height, leaf dry weight and shoot dry weight. Therefore, one of the great challenges in recent years is to improve potato production under drought stress. The use of plant hormones, including epibrassinolide and gibberellic acid, positively affected the potato characteristics under investigation and mitigated the negative effects of drought stress. Epibrassinolide was more effective on WUE, RWC, intercellular CO_2 concentration, tuber dry matter, number of stolons, leaf dry weight, shoot dry weight, tuber dry weight and plant height, while gibberellic acid had better performance on LAI, WSD, transpiration rate and number of tubers.

References

Ahmadi SH, Andersen MN, Plauborg F, Poulsen RT, Jensen CR, Sepaskhah AR and Hansen S, 2010. Effects of irrigation strategies and soils on field-grown potatoes: gas exchange and xylem [ABA]. Agricultural Water Management 97(10): 1486-1494.

Alexopoulos A, Aivalakis G, Akoumianakis KA and Passam HC, 2007. The effect of foliar applications of gibberellic acid and daminozide on plant growth, tuberisation and carbohydrate accumulation within tubers grown from true potato seed (TPS). Journal of Horticultural Science and Biotechnology 82(4): 535-540.

Aliche EB, Oortwijn M, Theeuwen TPJM, Bachem CWB, Visser, RGF and van der Linden CG, 2018. Drought response in field grown potatoes and the interactions between canopy growth and yield. Agricultural Water Management 206(C): 20-30.

Bajguz A, 2011. Suppression of *Chlorella vulgaris* growth by cadmium, lead, and copper stress and its restoration by endogenous brassinolide. Archives of Environmental Contamination and Toxicology 60(3): 406-416.

Barani, M, Akbari N and Ahmadi H, 2013. The effect of gibberellic acid (GA3) on seed size and sprouting of potato tubers (*Solanum tuberosum* L.). African Journal of Agricultural Research 8(29): 3898-3903.

Barriopedro D, Fischer EM, Luterbacher J, Trigo RM and Garcia-Herrera R, 2011. The hot summer of 2010: redrawing the temperature record map of Europe. Science 332(6026): 220-224.

Bokshi AI, Morris SC and Deverall BJ, 2003. Effects of benzothiadiazole and acetylsalicylic acid on β-1,3-glucanase activity and disease resistance in potato. Plant Pathology 52(1):22-27.

Cairns JE, Sanchez C, Vargas Hernández M, Ordoñez R and Araus JL, 2012. Dissecting maize productivity: ideotypes associated with grain yield under drought stress and well-watered conditions. Journal of Integrative Plant Biology 54(12): 1007-1020.

Condon AG, Richards RA, Rebetzke GJ and Farquhar GD, 2004. Breeding for high water-use efficiency. Journal of Experimental Botany 55(407): 2447-2460.

Crusciol CAC, Pulz AL, Lemos LB, Soratto RP and Lima GPP, 2009. Effects of silicon and drought stress on tuber yield and leaf biochemical characteristics in potato. Crop Science 49(3): 949-954.

Dahal K, Li XQ, Tai H, Creelman A and Bizimungu B, 2019. Improving potato stress tolerance and tuber yield under a climate change scenario - a current overview. Frontiers in Plant Science 10: 563. https://doi.org/10.3389/fpls.2019.00563

Efimova MV, Khripach VA, Boyko EV, Malofii MK, Kolomeichuk LV, Murgan OK, Vidershpun AN, Mukhamatdinova EA and Kuznetsov VV, 2018. The priming of potato plants induced by brassinosteroids reduces oxidative stress and increases salt tolerance. Doklady Biological Sciences 478: 33-36.

Hu Y, Xia S, Su Y, Wang H, Luo W, Su S and Xiao L, 2016. Brassinolide increases potato root growth *in-vitro* in a dose-dependent way and alleviates salinity stress. Biomed Research International 2016:8231873. doi:10.1155/2016/8231873.

Ierna A and Mauromicale G, 2006. Physiological and growth response to moderate water deficit of off-season potatoes in a Mediterranean environment. Agricultural Water Management 82(1-2):193-209.

Jan S, Alyemeni MN, Wijaya L, Alam P, Siddique KH and Ahmad P, 2018. Interactive effect of 24-epibrassinolide and silicon alleviates cadmium stress via the modulation of antioxidant defense and glyoxalase systems and macronutrient content in *Pisum sativum* L. seedlings. BMC Plant Biology 18(1): 146.

Javanmardi J and Rasuli F, 2017. Potato yield and tuber quality as affected by gibberellic acid and zinc sulfate. Iran Agricultural Research 36(2): 7-12.

Jefferies RA and MacKerron DKL, 1994. Genotypic differences in water use efficiency in potato. Aspects of applied biology 38: 63-70.

Kauirik R and Naghizadeh M, 2015. Exogenous acetylsalicylic acid stimulates physiological changes to improve growth, yield and yield components of barley under water stress condition. Journal of Plant Physiology and Breeding 5(1): 35-45.

Lahlou O, Ouattar S and Ledent JF, 2003. The effect of drought and cultivar on growth parameters, yield, and yield components of potato. Agronomie 23(3): 257-268.

Lawlor DW, 2002. Limitation to photosynthesis in water-stressed leaves: stomata vs. metabolism and the role of ATP. Annals of Botany 89: 871-885.

Li YH, Liu YJ, Xu XL, Jin M, An LZ and Zhang H, 2012. Effect of 24-epibrassinolide on drought stress-induced changes in *Chorispora bungeana*. Biologia Plantarum 56(1): 192-196.

Li W, Xiong B, Wang S, Deng X, Yin L and Li H, 2016. Regulation effects of water and nitrogen on the source-sink relationship in potato during the tuber bulking stage. PLoS One 11(1): https://doi.org/10.1371/journal.pone.0146877.

López MM, López-López MJ, Martí R, Zamora J, López-Sanchez J and Beltra R, 2001. Effect of acetylsalicylic acid on soft rot produced by *Erwinia carotovora* subsp. *carotovora* in potato tubers under greenhouse conditions. Potato Research 44: 197-206.

Luitel BP, Khatri BB, Choudhary D, Paudel BP, Jung-Sook S, Hur OS, Baek HJ, Cheol KH and Yul RK, 2015. Growth and yield characters of potato genotypes grown in drought and irrigated conditions of Nepal. International Journal of Applied Sciences and Biotechnology 3: 513-519.

Monneveux P, Ramírez DA and Pino MT, 2013. Drought tolerance in potato (*S. tuberosum* L.): can we learn from drought tolerance research in cereals? Plant Science 205-206: 76-86.

Ohashi Y, Nakayama N, Saneoka H and Fujita K, 2006. Effects of drought stress on photosynthetic gas exchange, chlorophyll fluorescence and stem diameter of soybean plants. Biologia Plantarum 50(1):138-141.

Pazoki AR, Rezaei H, Habibi D and Paknejad F, 2012. Effect of drought stress, ascorbate and gibberllin foliar application on some morphological traits, RWC and cell membrane stability of thyme (*Thymus vulgaris* L.). Iranian Journal of Agronomy and Plant Breeding 8(1)1-13 (In Persian with English abstract).

Rykaczewska K, 2017. Impact of heat and drought stresses on size and quality of the potato yield. Plant, Soil and Environment 63(1): 40-46.

Sadeghipour O and Aghaei P, 2012. Response of common bean (*Phaseolus vulgaris* L.) to exogenous application of salicylic acid (SA) under water stress conditions. Advances in Environmental Biology 6(3): 1160-1168.

Sánchez-Rojo S, López-Delgado HA, Mora-Herrera ME, Almeyda-León HI, Zavaleta-Mancera HA and Espinosa-Victoria D, 2010. Salicylic acid protects potato plants from phytoplasma-associated stress and improves tuber photosynthate assimilation. American Journal of Potato Research. https://doi 10.1007/s12230-010-9175-y.

SAS Institute Inc., 2002. SAS System for Windows Computer Program. Version 9.00. SAS Institute Inc., Cary, NC, USA.

Sinclair TR and Ludlow MM, 1985. Who taught plants thermodynamics? The unfulfilled potential of plant water potential. Australian Journal of Plant Physiology 33: 213-217.

Soleimanzadeh H, Habibi D, Ardakani MR, Paknejad F and Rejali F, 2010. Response of sunflower (Helianthus annuus L.) to drought stress under different potassium levels. World Applied Sciences Journal 8(4): 443-448.

Soltys-Kalina D, Plich J, Strzelczyk-Żyta D, Śliwka J and Marczewski W, 2016. The effect of drought stress on the leaf relative water content and tuber yield of a half-sib family of 'Katahdin'-derived potato cultivars. Breeding Science 66(2): 328-331.

Stark JC, Love SL, King BA, Marshall JM, Bohl WH and Salaiz T, 2013. Potato cultivar response to seasonal drought patterns. American Journal of Potato Research 90: 207-216.

Stuart NW and Cathey HM, 1961. Applied aspect of the gibberellins. Annual Review of Plant Physiology 12: 369-394.

Talaat NB and Abdallah AM, 2010. Effect of 28-homobrassinolide and 24-epibrassinolide on the growth, productivity and nutritional value of two faba bean (*Vicia faba* L.) cultivars. Archives of Agronomy and Soil Science 56(6): 649-669.

Tandon HLS (Ed.), 1995. Methods of Analysis of Soils, Plants, Waters, Fertilizers and Organic Manures. Fertilizer Development and Consultation Organization, New Delhi, India.

Tátrai ZA, Sanoubar R, Pluhár Z, Mancarella S, Orsini F and Gianquinto G, 2016. Morphological and physiological plant responses to drought stress in *Thymus citriodorus*. International Journal of Agronomy. 2016: http://dx.doi.org/10.1155/2016/4165750.

Turner NC, 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil 58(1): 339-366.

Turner FT and Jund MF, 1991. Chlorophyll meter to predict nitrogen topdress requirement for semidwarf rice. Agronomy Journal 83: 926-928.

Upadhyaya CP, Bagri DS and Upadhyay DC, 2015. Ascorbic acid and/or 24-epibrassinolide trigger physiological and biochemical responses for the salt stress mitigation in potato (*Solanum tuberosum* L.). International Journal of Applied Sciences and Biotechnology 3(4): 655-667.

Xie K, Wang XX, Zhang R, Gong X, Zhang S, Mares V, Gavilán C, Posadas A and Quiroz R, 2012. Partial root-zone drying irrigation and water utilization efficiency by the potato crop in semi-arid regions in China. Scientia Horticulturae134: 20-25.

Yactayo W, Ramírez DA, Gutiérrez R, Mares V, Posadas A and Quiroz R, 2013. Effect of partial root-zone drying irrigation timing on potato tuber yield and water use efficiency. Agricultural Water Management 123: 65-70.

پاسخ فیزیولوژیکی و زراعی- مورفولوژیکی سیب‌زمینی به تنش کم‌آبی و کاربرد تنظیم‌کننده‌های رشد

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چکیده

سیب‌زمینی به‌عنوان یک گیاه حساس به تنش کم‌آبی در نظر گرفته می‌شود. به منظور بررسی تأثیر تنش کم‌آبی و تنظیم‌کننده‌های رشد بر صفات فیزیولوژیکی و زراعی-مورفولوژیکی سیب‌زمینی، آزمایشی به‌صورت کرت‌های خرد شده بر پایه طرح بلوک‌های کامل تصادفی با سه تکرار در سال‌های ۱۳۹۴ و ۱۳۹۵ اجرا شد. سطوح تنش کم‌آبی، شامل شاهد (آبیاری مطلوب)، تنش خفیف، تنش متوسط و تنش شدید، در کرت‌های اصلی منظور شدند. کرت‌های فرعی شامل محلول‌پاشی تنظیم‌کننده‌های رشد در چهار سطح، یعنی شاهد، اپی‌براسینولید، اسید ژیبرلیک و اسید استیل‌سالیسیلیک، بودند. نتایج نشان داد که تنش کم‌آبی و تنظیم‌کننده‌های رشد تأثیر معنی‌داری بر اغلب صفات زراعی-مورفولوژیکی و فیزیولوژیکی سیب‌زمینی داشتند. وزن خشک برگ، وزن خشک ساقه، وزن خشک غده، ارتفاع گیاه، تعداد استولن، تعداد غده، شاخص سطح برگ، محتوای نسبی آب برگ، غلظت دی‌اکسیدکربن بین سلولی و هدایت روزنه‌ای در اثر تنش کم‌آبی کاهش یافت، در حالی‌که مقدار کمبود اشباع آب برگ افزایش یافت. به نظر می‌رسد که اثر منفی تنش کم‌آبی روی صفات فیزیولوژیکی، مانند محتوای نسبی آب برگ، بر ویژگی‌های زراعی-مورفولوژیکی سیب‌زمینی تأثیر نامطلوب گذاشته‌است. به جز شاخص کلروفیل، تنظیم‌کننده‌های رشد به‌طور معنی‌داری صفات زراعی-مورفولوژیکی و فیزیولوژیکی سیب‌زمینی را تحت تأثیر قرار دادند. اپی‌براسینولید محتوای نسبی آب برگ، کارایی مصرف آب، غلظت دی‌اکسیدکربن بین سلولی، درصد ماده خشک غده، ارتفاع گیاه، تعداد استولن، وزن خشک برگ، وزن خشک ساقه و وزن خشک غده را نسبت به سایر تنظیم‌کننده‌های رشد افزایش داد، در حالی که اثر اسید ژیبرلیک روی شاخص سطح برگ، مقدار کمبود اشباع آب برگ، میزان تعرق و تعداد غده بهتر از اپی‌براسینولید بود. در واقع، تنظیم‌کننده‌های رشد اثرات منفی تنش کم‌آبی را کاهش دادند.

واژه‌های کلیدی: شاخص سطح برگ؛ فتوسنتز؛ محتوای نسبی آب برگ؛ هدایت روزنه‌ای؛ هورمون‌های رشدی؛ وزن غده