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Effects of Priming with Salicylic Acid on Safflower Seedlings Photosynthesis and Related Physiological Parameters

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Abstract

Generally, primed seeds produce larger and heavier plants than non-primed seeds. This may be simply due to rapid emergence and extension of leaf growth, or the influence of other physiological processes. The effect of seed pretreatment with salicylic acid (SA) on some physiological and photosynthetic characteristics of the safflower seedlings, cv. Goldasht, was examined under field condition. The treatments were different levels of SA (including zero or hydropriming, 400, 800, 1200, 1600, 2000 and 2400 µM and a treatment of the non-primed seeds as the control). Priming enhanced photosynthesis rate (P_N) chlorophyll content index (CCI), relative water content (RWC) and seedling dry weight. Also, primed seeds had higher stomatal conductance (gs) and transpiration rate (E) than the control and the hydroprimed treatments. The lowest intercellular CO_2 (Ci) and highest cell membrane stability was obtained in 2400 µM SA. But values of the control treatment were opposite. In addition, highest carboxylation efficiency (CE) and photosynthetic water use efficiency (WUE_b) were found in 2000 and 2400 µM of SA. It seems seed priming with SA, increased gs and hence P_N by improving RWC status. This was associated with enhanced WUE and CE at higher levels of SA. A positive relationship was found between WUE_b and P_N, CE and RWC but negative relationship with Ci. It seems that increase in plants dry weight by priming not only was the result of rapid growth rate, but also the enhancement of P_N, RWC and chlorophyll content.

Keywords: Carboxylation efficiency; Cell membrane stability; Photosynthetic rate; Relative water content; Water use efficiency

Introduction

Not only photosynthesis process is the basis of growth for individual plants, but, it also is the very important process that supplies energy in the ecosystems. Photosynthesis reactions and the balance between respiration and photosynthesis depend on the environmental and edaphic factors. As a result, for better understanding of plant's growth, it is necessary to have knowledge in this area (Schulze *et al*. 2005). There are some reports indicating that the salicylic acid (SA) has improved effects on photosynthesis and gas exchange. However, the effect created by the application of exogenous SA on plant physiological processes under non-stress conditions is controversial. Some reports suggest a positive effect of SA on growth and performance of plants. On the other hand, this hormone can act as a stress factor and has negative effects on the plant processes. Mode of action of this hormone greatly depends on several factors such as plant species, environmental conditions (temperature, light, etc.) and its concentration (Janda *et al*. 2014). Nazar *et al*. (2011) reported that the application of SA on two cultivars of mung bean increased photosynthesis under both normal and salt stress conditions. Also, application of SA increased photosynthesis rate (P_N), water use efficiency (WUE), stomatal conductance (gs) and transpiration rate (E) in *Brassica juncea* (Fariduddin *et al*. 2003). Khan *et al*. (2003) reported that SA, acetylsalicylic acid (ASA) and gentisic acid (GTA) increased P_N, gs and E rate in soybean and corn. Furthermore, they showed that treatment with these compounds raised leaf area and dry weight. In contrast, Lian *et al*. (2000) indicated that the higher concentrations of SA had an inhibitory effect on P_N.

Generally, SA has important impact on plants, including profound influence on membrane stability (Yusuf *et al*. 2012), water relations (Loutfy *et al*. 2012), stomata behavior (Aldesuquy *et al*. 1998) and growth promotion (Hayat *et al*. 2010). Hayat *et al*. (2005) reported that wheat seedlings treated with SA had more leaf number and higher fresh and dry weight. Increase of the fresh weight indicates the favorite status of plant water relation and this could be due to the water uptake improvement results from the root system (Shekari *et al*. 2010). Enhanced root length with application of SA in borage (Shekari *et al*. 2010) and safflower (Mohammadi *et al*. 2011) has been reported. It has been described that the pre-treatment of seeds improved some physiological traits of seedlings and the mature plants (MiarSadegi *et al*. 2011; Mohammadi *et al*. 2011).

Safflower (*Carthamous tinctorios* L.) is a plant from Asteraceae family and is the only native oilseed crop which is originated from Iran. This plant has high adaptability to Iran's climate and is tolerant to undesirable environmental conditions such as drought and salinity stresses. Moreover, safflower has a high-quality edible oil (Alyari *et al*. 2000). Despite the importance of safflower in oil production, few studies have been conducted on photosynthetic traits and the possibility of improving its photosynthetic capacity. In our previous report (Mohammadi *et al*. 2011) it was noted that priming with SA has a significant effect on emergence percent and rate and improvement of the safflower seedling establishment in terms of plant/m^2, number of leaves, leaf area, root development and dry weight of plants. The question can be raised whether the increase in dry weight of the produced plants has been due to an increase in emerging rate and rapid establishment of seedlings and, therefore, duration of carbon assimilation period and/or SA directly affects the photosynthesis capacity in safflower seedlings?

The aim of this study was to evaluate the influence of safflower seed priming with SA, on photosynthesis and related parameters and determination of seed vigor differences induced by SA priming under field condition.

Materials and Methods

The effects of priming by SA on physiological traits and performance of safflower plants, cv. Goldasht, was carried out in a randomized complete block design with six replications in 2010 in the Agricultural Research Station of Zanjan University. Each plot consisted of 5 rows with a length of 5 m and 0.5 m intervals. The distance of drilling on rows was 10 cm. In mid-April seeds were planted manually.

The experimental treatments consisted of the seeds primed by the salicylic acid at 8 levels: untreated or control seeds, zero (hydropriming), 400, 800, 1200, 1600, 2000, and 2400 µM. For priming, after preparation of various SA solutions, safflower seeds were immersed for 24 hours at room temperature, under different concentrations of SA. The seeds were dried for 48 hours and after being disinfected with Carboxin Thiram fungicide, they were planted manually. Approximately, 25 days after emergence plants RWC was measured at 10-12 AM from the second leaf of 5 plants of each plot by the following equation (Noggle and Fritz 1983);

$$RWC= [(FW-DW) / (TW-DW)] \times 100$$

In which, FW=Fresh weight, DW= Dry weight, TW= Turgid weight

Photosynthetic rate and the related traits were measured by IRGA photosynthesis (Lic-ADC-UK) apparatus. To do this, the penultimate leaf was placed in the measurement chamber, so that the upper surface of the leaf was upward to get enough sunlight. Stomatal conductance (m molCO_2 m^{-2} s^{-1}), transpiration rate (mmol H_2O m^{-2} s^{-1}) and photosynthesis rate (µ molCO_2 m^{-2} s^{-1}) data were obtained by averaging three recordings. Photosynthetic water use efficiency (WUE_b) was obtained through dividing net photosynthesis or current photosynthesis by transpiration rate (Perez-Perez *et al*. 2007).

$$WUE_b = A/E$$

In which A is net photosynthesis and E is transpiration rate.

Carboxylation efficiency was calculated through dividing net photosynthesis (P_N) on inter-cellular carbon dioxide concentration (Ci) (Fariduddin *et al*. 2003) as follow:

$$CE = P_N/Ci$$

The chlorophyll content index was measured using the manual chlorophyll meter (CCM-200) (Opti Science-UK.Co). The cell membrane stability (CMS) was measured in fully expanded penultimate leaves. The middle parts of leaves were cut into pieces of one cm. Then, 0.5 g of leaf pieces were selected and washed three times with distilled water for removing dust or other surface electrolytes and subsequently were placed in small containers containing 20 ml of distilled water. Samples were placed at 10 °C for 24 h and electrical conductance of solution in containers was measured by a conductivity meter (E_1) (Electrical conductive meter, model: Inolab, WTW). The test tubes moved to thermostated water bath for one hour in 100 ˚C (E_2) (Shiferaw and Baker 1996:). The CMS was calculated by the following equation:

$$CMS= [1- (E1/E2)] \times 100$$

After 25 days of the seedling's emergence, six plants were selected from each plot and placed at 70 °C in an oven for 48 h to measure dry weight using a precise scale.

Data analysis and Duncan's multiple range test at the 5% probability level for comparing means were performed using MSTAT-C.

Results and Discussion

Photosynthesis rate

The increase of SA concentration resulted in accelerating trend in photosynthetic rate. Between the priming levels, the highest P_N was related to the 2400 µM (24.68 µmolCO_2 m^{-2} s^{-1}) with 101% increment compared to the control treatment. The minimum P_N was obtained from the control seeds (12.26 µmol CO_2 m^{-2} s^{-1}) (Figure 1a). In general, seed priming with SA showed a high photosynthetic rate than the control treatment. With increasing concentration of SA from the control treatment to 2400 µM, P_N nearly doubled. Photosynthesis is a crucial process in metabolism of higher plants. In general, the photosynthesis rate is the major determinant of dry matter production and productivity capacity of the crop plants (Hopkins and Huner 2008). It is stated the high intensity of photosynthesis in seedling stage has an important role in the determination of the plant vigor and therefore in productivity potential (Natr and Lawlor 2005). An increase in the P_N can be due to the improvements in plant water content and water status that increase stomatal opening; or due to increase in the nutritional status, such as nitrogen uptake and the number of chlorophyll pigments as photoreceptor antennas; or it can be because of a direct effect on the photosynthetic device such as the improvement of the electron transport and increase in activity of the Rubisco and other enzymes involved in photosynthesis. In the present experiment, improvement of the tissue's water status (RWC), stomatal conductance and leaf chlorophyll content was observed (Figures 1b and 2a,c). Also, there are some reports about the increased rates of photosynthesis by application of SA in plants. According to Shakirova *et al*. (2003), SA increases photosynthesis by preventing the chloroplast degradation and improves the electron transport capacity by photosystem II. Fariduddin *et al*. (2003) also, reported that the P_N increased in mustard plants under the effect of SA. In addition, SA stimulated the rate of photosynthesis in soybean, barley and corn (Khodary 2004).

Photosynthetic rate had significant positive correlation with all evaluated traits except inter-cellular carbon dioxide concentration and electrolyte leakage (Table 1). Positive correlation between RWC, stomatal conductance and transpiration rate with photosynthesis shows that treatments, which can improve the plant water status, can have a positive effect on the rate of photosynthesis.

Table 1. Correlation coefficients of photosynthetic traits under different levels of salicylic acid in safflower seedlings

Trait	PN	g_S	E	C_i	WUE	CE	CCE	RWC	CMS
Photosynthesis rate (P_N)	1								
Stomatal conductance (g_S)	0.72**	1							
Transpiration rate (E)	0.60**	0.76**	1						
Intercellular CO_2 (Ci)	-0.74**	-0.19	-0.34*	1					
Water use efficiency (WUE)	0.60**	0.13	-0.27	-0.56**	1				
Carboxylation efficiency (CE)	0.97**	0.59**	0.54**	-0.83**	0.61**	1			
Chlorophyll index (CCE)	0.57**	0.29*	-0.09	-0.39**	0.75**	0.60**	1		
Relative water content (RWC)	0.38**	0.06	-0.04	-0.38**	0.46**	0.46**	0.55**	1	
Cell membrane stability (CMS)	-0.68**	-0.18	-0.46**	0.59**	-0.52**	-0.76**	0.57**	-0.56**	1
Total dry weight (TDW)	0.64**	0.34*	0.16	-0.42**	0.56**	0.68**	0.83**	0.46**	-0.83**

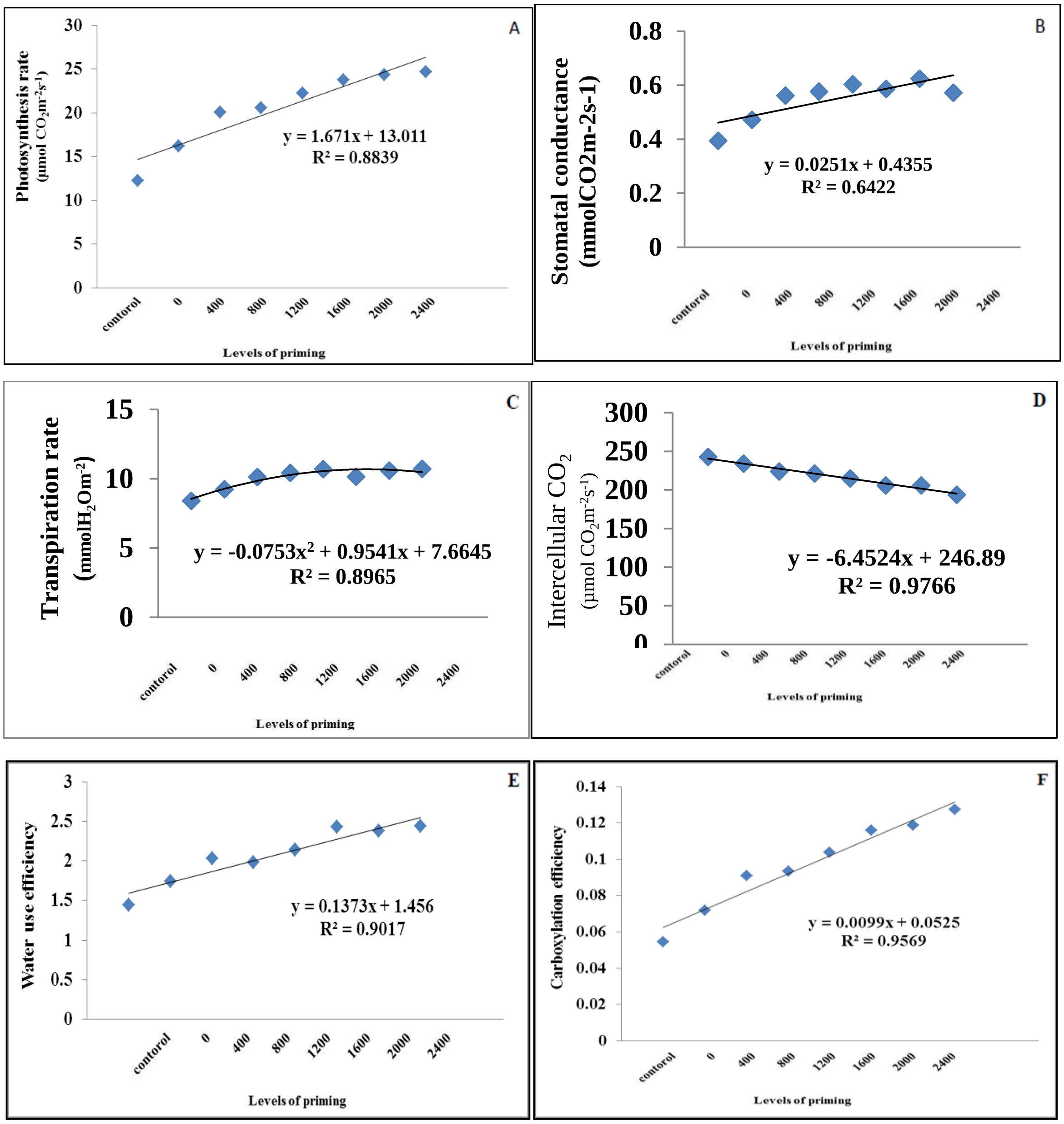

Figure 1. Effects of seed priming with different levels of salicylic acid on photosynthetic traits of safflower seedlings, cv. Goldasht

Transpiration and stomatal conductance

The g_s and E in the plants increased in comparison with the control, due to an increase in SA concentration (Figure 1b,c). The lowest g_s value was observed in the control plants (0.3942) and the maximum g_s in 1200 (0.6033 mol CO_2 m^{-2} s^{-1}) and 2000 (0.6242 mol CO_2 m^{-2} s^{-1}) µM treated plants (Figure 1b). The maximum amount of E was seen in the primed seeds with 800 µM (10.71 mmol H_2O m-^{2} s^{-1}) SA, however, it did not show significant difference with 400 to 2400 µM of SA treatments (p> 5%). The lowest transpiration rate was detected in the control plants (8.405 mmol H_2O m-^{2} s^{-1}) (Figure 1c).

Enhancement of g_s and *E* has a close relationship with the plant water status, probably because of deeper rooting (Mohammadi *et al*. 2011; Abdolahi and Shekari 2013) and also better water uptake due to accumulation of osmotic substances such as soluble sugars and proline (Pak Mehr *et al*. 2012). The water content of the plants which were under the treatment of SA were higher than the control plants or even the hydroprimes. As a result, those plants had higher stomatal conductance and transpiration rate. Khan *et al*. (2003) illustrated increases in transpiration rate and stomatal conductance in response to SA, ASA and GTA in corn and soybean leaves. Singh and Usha (2003) reported that foliar spray with SA at a concentration of 1-3 mM increased g_s, chlorophyll content and Rubisco activity compared to the control treatment. The higher transpiration rate in SA treatments may be due to the favorite water status of the plants that are reflected in attributes such as plant dry weight (Singh *et al*. 1997). Richards *et al*. (2002) stated that the stable production requires high transpiration, stomatal conductance and mesophyll conductance.

Transpiration rate had positive correlation with stomatal conductance (Table 1). This shows that with the increase in stomata opening and g_s, the transpiration rate rises. Neither the stomatal conductance nor transpiration rate showed a significant relationship with WUE. In contrast, they had a significant positive correlation with carboxylation efficiency probably due to the indirect effect of this trait on the increase of the photosynthesis rate.

Intercellular CO_2 concentration

The maximum rate of Ci was related to the control plants (242.7 μmol CO_2 m^{-2} s^{-1}) and the lowest concentration of Ci with a 20% decrease was observed in plants treated with 2400 μM SA (Table 2). In general, with an increase in the concentration of SA, the amount of Ci decreased (Table 2). Increased concentration of Ci can be related to the reduced mesophyll conductance and photosynthetic capacity of chloroplasts that in this state the received CO_2 by the leaf is not used properly in the photosynthesis process (Koc *et al*. 2003). In the present experiment, application of SA led to maintenance of photosynthesis at a higher quantity and as a result the amount of Ci was reduced. Treatments with higher photosynthesis and stomatal conductance had a greater efficiency in using the interred CO_2 to mesophyll, so the concentration of their Ci was diminished. Singh and Usha (2003) claimed that the lower amount of inter-cellular carbon dioxide concentration in the prepared wheat plants could be due to the efficient use of the carbon dioxide because of the high rate of photosynthesis.

The relationship between the Ci and P_N, E, photosynthetic WUE, CE, chlorophyll index, RWC and dry weight was negative (Table 1). Therefore, treatments with greater ability to use carbon dioxide and higher photosynthetic rate (carboxylation efficiency) showed less Ci. Also, the relation between CMS and Ci indicated that in treatments where cell membrane integrity is weaker than other treatments photosynthesis or other cell physiological process are done in the lower rate.

Water use efficiency and carboxylation efficiency

The highest photosynthetic WUE (2.443) and maximum CE (0.1275) were observed in 2400 μM concentrations of SA (Figure 1e,f). Seed priming either by water or by SA enhanced both traits and by increasing SA concentrations an upward trend was found with these traits. Photosynthetic WUE is a criterion which shows photosynthesis rate per unit of *gs* or *E* (Larcher 1995). Generally, plants by increment in carbon assimilation and/or by reduction in transpiration enhance their photosynthetic WUE (Marco *et al*. 2000). In our experiment, priming significantly increased *gs* and *E* ratio. Therefore, it is reasonable that increment in photosynthetic WUE is mostly related to enhancement in P_N. Boyer (1996) stated that one of the reasons for the increase in crops yield can be found in the improvement of WUE and Broeckx *et al*. (2014) reported a relation between higher productivity and high water use. Also, Sairam *et al*. (2002) indicated that the reduction in photosynthetic WUE may be due to enhancement in canopy temperature and transpiration and/or reduction of root capacity in water uptake from soil layers.

Transpiration efficiency is the main component of WUE especially in areas where the stored water of the soil is a major component of plant consumed water (Richards *et al*. 2002). One of the reasons for the increase in the photosynthetic WUE in this experiment is probably an improvement in some root traits (Mohammadi *et al*. 2011). Higher photosynthetic WUE at higher concentrations of SA treatment compared to the control treatment can be related to the reduction in resistance to flow of water vapor from leaf because stomatal closure has more restricting effect on carbon dioxide flow than transpiration (Weber *et al*. 2006). There was an increase in CE with intensifying in the amount of SA from zero to 2400 μM concentration. In the present experiment, plants whose seeds were primed with SA had higher g_s and P_N compared to the hydroprimed and none primed seeds. On the other hand, the amount of Ci was reduced in the plants treated with SA. In other words, the received carbon dioxide was used with more efficiency and increased the CE. CE improvements by application of SA in *Brassica juncea* have been reported before (Fariduddin *et al*. 2003).

The correlation between photosynthetic WUE and P_N, CE, chlorophyll index, RWC and dry weight was positive and in contrast, it was negative and significant with Ci and electrolyte leakage (Table 1). Similar to photosynthetic WUE, CE had positive correlation with P_N, g_s, E, chlorophyll index, RWC and dry weight; but had a negative relationship with Ci and electrolyte leakages. Thus, treatments that were more efficient to use the inter-cellular carbon dioxide (carboxylation efficiency), also showed higher water use efficiency.

Chlorophyll index

With increasing SA concentration, the P_N and the chlorophyll content index increased (Figure 2c). The high chlorophyll index with near to 70% increment compared with the control was found in the 2400 μM treatment (130.4) and the lowest value was observed in the control treatment (76.86). Chlorophyll pigment is the first responsible pigment for the absorption of the light energy in photosynthesis (Hopkins and Huner 2008). Leaf chlorophyll content is one of the key factors in determining photosynthetic rate and dry matter production (Jiang and Huang 2001). Since the chlorophyll content index indicates the chlorophyll concentration of a leaf (Ruiz-Espinoza *et al*. 2010) and also there is a relationship between chlorophyll content and photosynthesis rate (Table 3), the more chlorophyll content may lead to greater photosynthesis. It has been reported that SA enhances photosynthesis with influence on the production of chlorophyll pigments (Hayat *et al*. 2010). In addition, this hormone increases dry weight by enhancing the Rubisco activity and also by increasing the water uptake of plant (Hayat and Ahmad 2007).

Chlorophyll index was positively correlated with all traits except for Ci and CMS (Table 1). Positive relationship between the chlorophyll index and gas exchange and dry matter production indicate that maintenance of chlorophyll in proper amounts can increase the plant dry matter.

Relative water content

The highest and the lowest RWC were observed in 2400 μM concentrations of SA (84.7%) and control treatment (75.7%), respectively (Figure 2a). In general, an upward trend was seen in RWC with increasing of SA concentration applied for seed priming. The difference in RWC indicates the effect of treatments on root growth development for water uptake from the soil; or the ability of plants for osmotic adjustment and accumulation of compatible solutes to maintain the tissue turgor; and/or the ability to prevent water waste through reduction of stomatal opening. According to the Figure 1b, stomata opening and g_s increased in our experiment by application of SA. Therefore, stomatal control and transpiration reduction could not be a reason for the increase of RWC in plants treated with the SA. It seems two first hypotheses may explain better water status in the SA treated plants. It has been suggested that the higher RWC can maintain and retain g_s and, therefore, higher E and photosynthesis in the plants (Medrano *et al*. 2002). Plants dry weight increase represents the ideal status of plant water relations and could be due to the increased amount of water uptake by the root system (Shekari *et al*. 2010).

Cell membrane stability

The highest CMS was related to the primed seeds with 2400 μM concentration (58.6%) and the lowest was related to the control treatment (22%) which had a significant difference with other levels (Figure 2b). Cell membrane stability is considered as a tool for resistance against environmental stresses such as drought (Saneoka *et al*. 2004). Variations created in the cell membrane structure by the lipid changes and other changes increase cell membrane permeability to ions and macromolecules. In this experiment, all levels of SA reduced the ion leakage compared to the control treatment. It has been reported that SA has reduced ion leakage and accumulation of toxic ions in plants and also increased cytokinins levels (Krantev *et al*. 2008). Nemeth *et al*. (2002) explained that SA protects membrane through affecting polyamines such as putrescine, spermine and spermidine, as well as creating stable complexes. In the present study, primed seeds with 2400 μM SA showed the lowest leakage. Popova *et al*. (2009) reported that treatment of barley plants with SA reduced lipid peroxidation rate and electrolyte leakage.

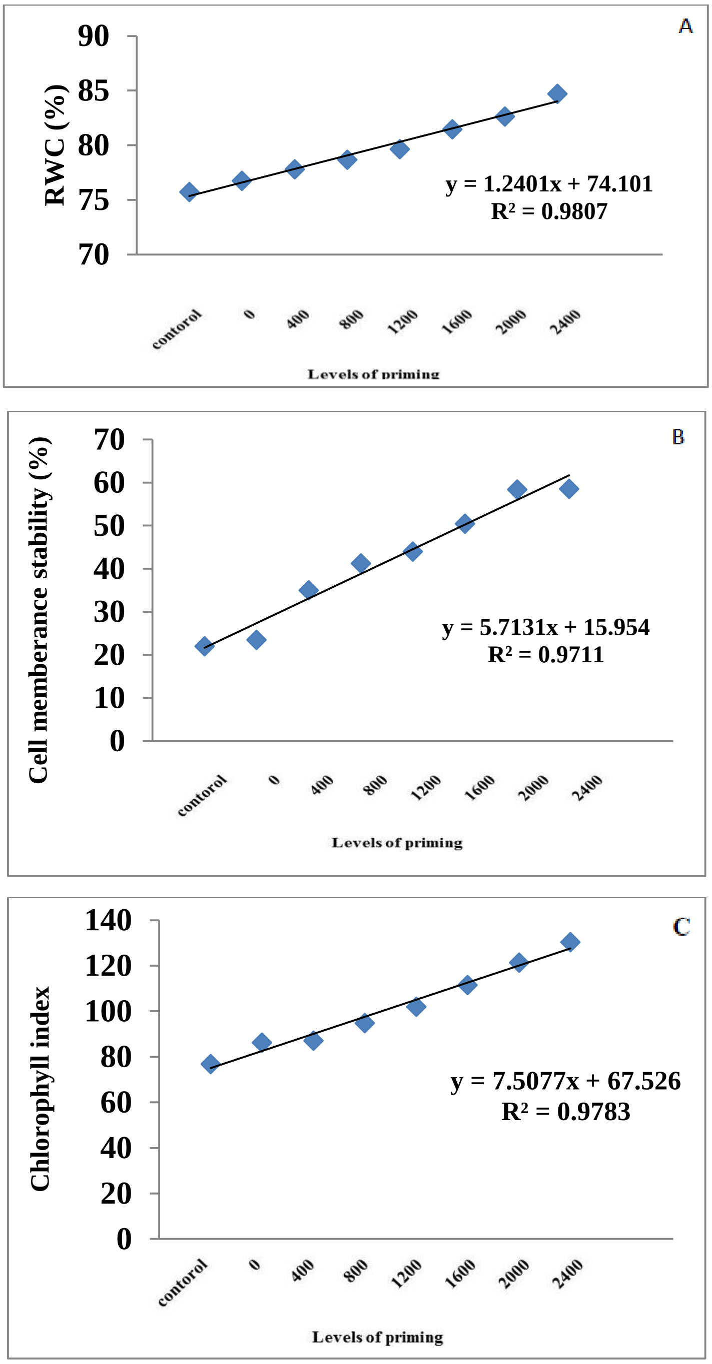

Figure 2. Effects of seed priming with different levels of salicylic acid on relative water content, cell membrane stability and chlorophyll content index of safflower, cv. Goldasht

There was a correlation between CMS with the dry weights and other traits. In addition, the CMS was negatively associated only with the Ci (Table 1). It seems that any treatment which improves CMS may affects plant productivity and dry weight production.

Total dry weight

The highest dry weight, which had significant difference with other treatments, was found in 2400 µM SA (Figure 3). In general, the lowest observed values in this experiment belonged to the control treatment and then to the hydroprime treatment. So that, the dry weight in the control treatment reached from 0.21 g to 0.52 g at 2400 µM. In other words, plant dry weight increased up to 148 percent. The heaviest and highest fleshy leaves were observed in plants with the 2400 µM treatment (Mohammadi *et al*. 2011). Increase in fresh and dry weight indicate the proper status of plant water relations that can be due to the increased water uptake by the root system (Shekari *et al*. 2010; Mohammadi *et al*. 2011; Abdolahi and Shekari 2013). Hayat *et al*. (2005) reported that wheat plants treated with SA had more leaf number and higher fresh and dry weight. Mohammadi *et al*. (2011) showed that treatment with SA had a positive effect on the emergence rate and increased root and shoot growth and dry weight of the safflower plant. Since in the present study, the dry weight was significantly affected by the priming with SA, variations in dry weight may be resulted from improvement of plant water relations which increases the stomatal openness, gas exchanges and photosynthetic rate. In addition, treated seeds had rapid emergence under field conditions and therefore had more leaf number to light absorption and more photosynthesis duration (Mohammadi *et al*. 2011). In our experiment, 2400 µM concentrations of SA led to the highest increase in dry weight (Figure 3). Shakirova (2007) reported that treatment with SA enhanced auxins and cytokinins level in plant tissues and consequently increased plant growth.

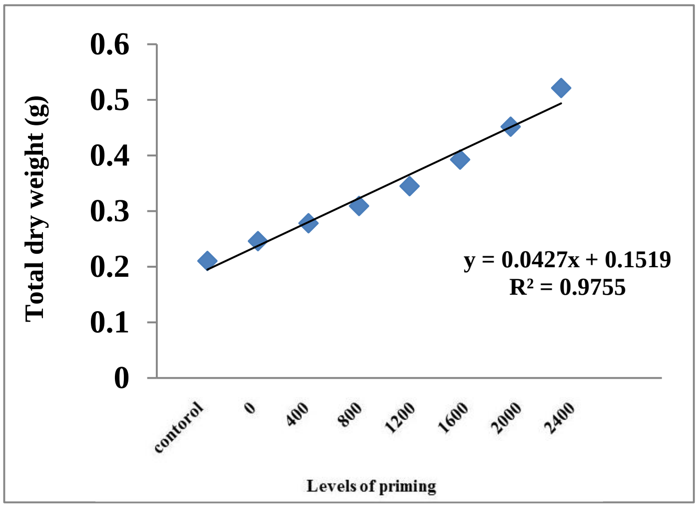

Figure 3. Effects of seed priming with different levels of salicylic acid on seedling dry weight of safflower, cv. Goldasht

Conclusion

Seed priming with SA caused a rise in the safflower plant's physiological traits. Among treatments, higher concentrations of SA had a more pronounced effect on the measured traits than the control and hydro-primed seeds. Furthermore, there was a significant positive correlation between the traits of photosynthetic rate, carboxylation efficiency, chlorophyll index and total dry weight of safflower. It seems that seed priming with SA by improving photosynthesis rate and leaf area duration increased plant dry weight production.

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