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Improving amino acid composition of soybean under salt stress by salicylic acid and jasmonic acid

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Summary

A greenhouse experiment with factorial arrangement based on randomized complete block design with four replications was conducted in 2015 to investigate the effects of salicylic acid (SA) (1 mM) and jasmonic acid (JA) (0.5 mM) on protein accumulation and amino acid composition of soybean seeds under different levels of salinity (0, 4, 7, and 10 dS/m NaCl, respectively). Treatment of SA improved protein percentage and per seed at different stages of seed development under all salinity levels. The highest protein yield was also recorded for SA treated plants, due to higher seed yield and protein content. In contrast, treatment with JA reduced seed protein content and yield as a result of reduction in seed yield. Lysine, methionine, phenylalanine, threonine, aspartic acid, glutamic acid, proline and tyrosine contents increased, but leucine and valine contents decreased with enhancing salinity. Foliar spray of SA improved isoleucine, leucine, lysine, methionine, valine, alanine, aspartic acid, glutamic acid, glycine and serine contents, but application of JA increased sulfur containing amino acids such as methionine and aromatic amino acids such as phenylalanine and tyrosine in soybean seeds. Treatment with SA had the greatest effect on enhancing protein quantity and quality under different levels of salinity.

Introduction

An important aspect of agriculture is the cultivation of plants for food, fiber, biofuel, medicine and other products used to sustain and enhance human life. Agriculture was the key development in the rise of sedentary human civilization, whereby farming of domesticated species created food surpluses that nurtured the development of civilization (BAJPAI et al., 2014; FENG et al., 2014; MISHRA et al., 2015; NEMLI et al., 2015).

Soybean is an important agricultural crop and its seeds with 36-40% protein content are important sources for human and animal feed (KRISHNAN, 2005). Environmental stresses such as soil salinity can limit soybean production. The reduction in soybean seed and protein yields under salinity can be attributed to a shorter seed filling period (GHASSEMI-GOLEZANI et al., 2010). High salinity interferes with plant growth and development and can also lead to physiological drought conditions and ion toxicity, leading to a buildup of Na⁺ and Cl⁻ concentrations in the cytosol, which can be ultimately detrimental to the cell. Higher concentrations of sodium ions can also lead to a reduction in photosynthesis and production of reactive oxygen species (MEDHAT, 2002; KHALID et al., 2015).

Protein quality depends on the amino acid composition. Soybean protein contains all the essential amino acids including isoleucine, leucine, lysine, methionine, cysteine, phenylalanine and tyrosine, threonine, tryptophan, valine, and histidine. It has been widely documented that soybean seed composition varies with environmental factors, especially during the seed filling period (WILSON, 2004; CARRERA et al., 2009). Seed filling period was correlated with the seed and protein yield in indeterminate soybean lines. WOLF et al.,

(1982) reported that the majority of protein bound and amino acids increased as the salinity severed. KARR-LILIENTHAL et al. (2005) reported that essential, non-essential, and total amino acid contents in soybean seeds were lower in cooler zones in comparison with warmer zones. Greater deposition of sulfur amino acids (methionine and cysteine) was shown at upper temperatures (WOLF et al., 1982). The possible effects of plant growth regulators such as salicylic acid (SA) and jasmonic acid (JA) on protein and amino acid accumulation in oilseed crops are poorly understood.

Salicylic acid (SA) is an endogenous growth regulator of phenolic nature, which participates in the regulation of physiological processes in plants. SA plays an important role in the defense response to abiotic stresses in plant species (PASALA et al., 2016). Exogenous treatment of SA enhances plant growth and photosynthetic capacity in saline conditions (NOREEN et al., 2012). Treatment of SA also significantly increases dry weights of root and top part of soybean (GUTIERREZ-CORONADO et al., 1998), tomato (STEVENS et al., 2006) and maize (KHODARY, 2004) under saline conditions. KHODARY (2004) found that SA could induce salt tolerance in maize plants via accelerating their photosynthesis performance and carbohydrate metabolism. SA increases proteins inside the plant cells that improve plant ability to tolerant the salt stress (KUMAR et al., 1999). SA also has a positive impact on the activity of nitrate reductase (FARIDUDIN et al., 2003), synthesis of secondary metabolites and antioxidant enzymes activity (SINGH and USHA, 2003; ERASLAN et al., 2007).

Jasmonic Acid (JA) and its methyl ester (JAME) are the key molecules of the octadecanoid signaling pathway. JA is reported to be involved in diverse developmental processes, such as seed germination, root growth, fertility, fruit ripening and senescence (WASTERNAK and HAUSE, 2002). JA content may increase under stressful conditions such as salinity (PEDRANZANI et al., 2007). According to KANG et al., (2005) application of JA could enhance tolerances against biotic and abiotic stresses. Foliar application of jasmonic acid on soybean under salt stress reduced the damaging influence of salt and improved photosynthesis and yield (YOON et al., 2009).

The objective of this research is to investigate the influence of foliar application of salicylic acid and jasmonic acid on protein accumulation and amino acid composition of soybean seeds under salt stress.

Materials and methods

Experimental conditions

A greenhouse experiment with a factorial arrangement on the basis of randomized complete block design with four replications was conducted in 2015 to investigate changes in protein accumulation and quality of soybean seeds (cultivar M7, a high yielding cultivar widely used in commercial level) under different NaCl salinity levels (0, 4, 7 and 10 dS/m) in response to the foliar application of salicylic acid (SA) and jasmonic acid (JA). In this experiment, 48 pots, each filled with 1 kg perlite, were used. 30 seeds were sown in 3 cm depth of each pot, and all pots were then placed in a greenhouse with a day and night mean temperatures of 28 and 26 °C, respectively. According to the treatments, tap water and saline solutions were added to the pots to achieve 100% FC (field capacity). After seedling estab-

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ishment, plants were thinned to keep 10 plants in each pot. The pots were weighed regularly and the losses were made up with Hoagland solution (EC=1.3 dS/m). All the pots were washed every 30 days and salinity treatments were reapplied in order to avoid further increase in electrical conductivity (EC). Salicylic acid (1 mM) and jasmonic acid (0.5 mM) were sprayed on plants at vegetative and flowering stages in accordance with the treatments.

Leaf nitrogen and sulfur contents

The leaf samples were washed with deionized water at least two times to remove the dust. After oven drying at 80 °C for 48 h, leaf samples were powdered and then nitrogen and sulfur contents were measured by a CHNS elemental analyzer (Elementar-group, Hanau, Germany).

Protein accumulation

Two plants were harvested from each pot with 10 days intervals at five stages, beginning 18 days after flowering. Then seeds were detached from the pods and percentages of protein for each sample were determined, using a seed analyzer (Zeltex ZX-50, Maryland, USA). Seed and protein yields per plant at final harvest.

Protein hydrolysis

Peptides and proteins completely hydrolyzed to free amino acids prior to analysis. Seed samples were powdered and then 0.5 g of powder was hydrolyzed in hydrochloric acid (6 M) within glass tubes. The tubes were flushed with nitrogen and then heated at 110 °C for 24 h. The hydrolyzed samples were rotary evaporated to dry under vacuum at 40 °C, and then dissolved in a sodium citrate buffer (0.1 M citric acid monohydrate and 0.1 M trisodium citrate). In this way, tryptophan and cysteine were completely degraded during the hydrolysis with hydrochloric acid and glutamine and asparagine being delaminated to glutamic and aspartic acid, respectively (FOUNTOULAKIS and LAHM, 1998; WEISS et al., 1998).

Gas chromatography mass spectrometry (GC-MS) analysis

Varian saturn 2200 GC-MS system (Varian, Netherland) was used with silica capillary column (30 m × 0.32 mm, 0.25 μm film thickness). One micro liter of prepared samples was separated and analyzed using GC-MS with split mode (10:1). Helium was used as carrier gas (1.5 mL/min). The primary temperature of the column was 100 °C, followed by a ramp of 10 °C/min to 140 °C, a second ramp of 10 °C/min to 170 °C, a third ramp of 15 °C/min to 185 °C, and finally a ramp to 230 °C at 15 °C/min. At each stage of programming, the temperature was held for 2, 1, 1, 2 and 5 min, respectively. The injector temperature was 250 °C. Electron impact ionization (EI) interface temperature was 250 °C and ion source temperature was 200 °C.

Statistical analysis

Analyses of variance of the data for different parameters were carried out, using MSTATC software, and means were compared by Duncan multiple range test at $p \leq 0.05$. Figures were drawn by the Excel software.

Results

Leaf nitrogen and sulfur contents

Nitrogen content of soybean leaves significantly affected by Salinity and hormonal applications ($p \leq 0.01$). There was no significant changes in nitrogen content of leaves up to 4 dS/m NaCl salinity, but

thereafter it was significantly decreased with increasing salt stress. Nitrogen content of soybean leaves was augmented by foliar application of SA, but it was diminished by JA treatment (Fig. 1).

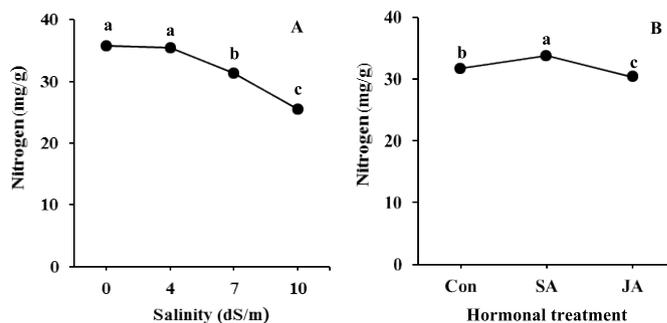


Fig. 1: Changes in nitrogen content of soybean leaves under different salinity (A) and hormonal treatments (B). Different letters indicate significant difference at $p \leq 0.05$.

Salinity and foliar application of hormones had significant effects on sulfur content of soybean leaves ($p \leq 0.01$). Sulfur content of leaves reduced as salinity enhanced. Treatment with JA and SA increased sulfur content of leaves compared with control plants. Plants with JA treatment showed the highest sulfur content in leaves (Fig. 2).

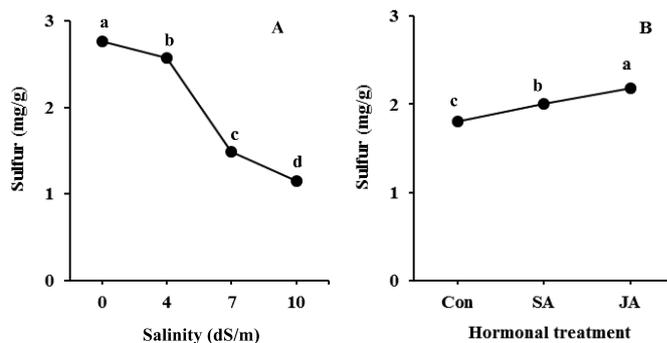


Fig. 2: Changes in sulfur content of soybean leaves under different salinity (A) and hormonal (B) treatments. Different letters indicate significant difference at $p \leq 0.05$.

Protein accumulation in seeds

Protein percentage of soybean seeds under all saline and non-saline conditions increased with increasing seed filling period. Stable value for protein percentage of all treatments was attained at about 52 days after flowering. Protein percentage of all soybean seeds at different stages of seed development and salinity levels was higher for SA treated plants, followed by control plants. The lowest protein percentage under these conditions was recorded for seeds from JA treated plants (Fig. 3).

Protein content per seed enhanced with increasing seed filling up to 48-58 days after flowering, depending on salinity levels and hormonal applications. The highest protein content per seed under salinity treatments was obtained 5-10 days earlier than that under non-saline condition. Foliar application of SA improved protein content of soybean seeds at different developmental stages under all salinity levels. This improvement was particularly high under moderate (7 dS/m) and high salinity (10 dS/m) levels, with no noticeable differences in seed protein content of JA treated and control plants (Fig. 4).

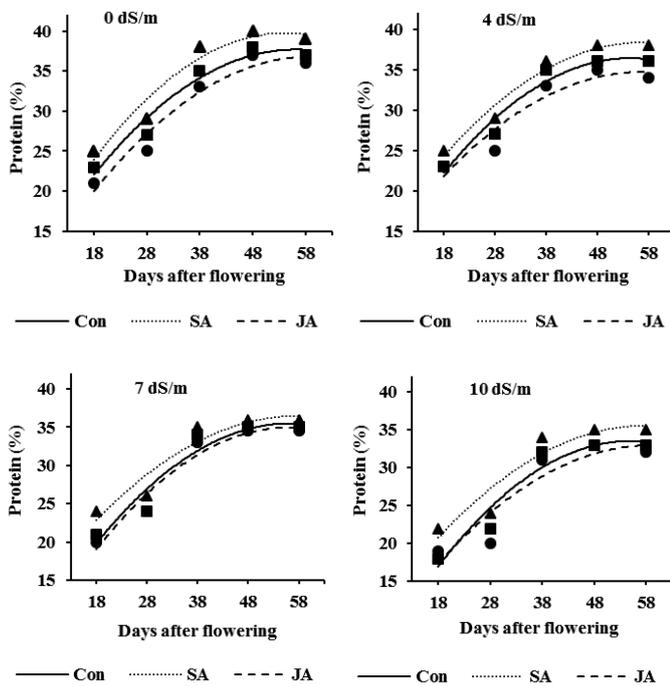


Fig. 3: Changes in protein percentage of soybean (M7 cultivar) seeds in response to salinity and hormonal applications

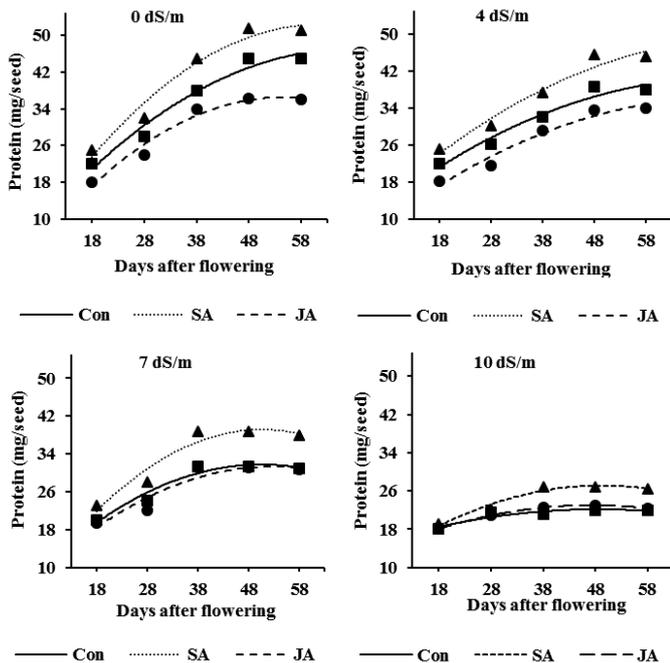


Fig. 4: Changes in protein content of soybean (M7 cultivar) seeds in response to salinity and hormonal applications

Seed and protein yields

Effects of salinity and hormonal application on seed yield was significant ($p \leq 0.01$). Seed yield per plant decreased with increasing salinity. Treatment with SA significantly improved seed yield (about 17%), but there was no significant difference between JA treated and control plants (Tab. 1).

Analysis of variance of the data for final harvest showed significant effects of salinity and hormonal treatments on protein percentage and yield of soybean seeds ($p \leq 0.01$). Interaction of salinity and hor-

Tab. 1: Means of soybean seed yield and protein percentages under different salinity and hormonal treatments

Treatments	Seed yield (mg/plant)	Protein (%)
Salinity		
0 dS/m	3710 a	38.46 a
4 dS/m	3260 b	38.24 ab
7 dS/m	2840 c	37.96 b
10 dS/m	2070 d	36.25 c
Hormonal treatment		
Control	2870 b	37.73 b
SA	3360 a	38.92 a
JA	2680 b	36.54 c

Different letters in each column indicate significant difference at $p \leq 0.05$.

monal application for protein yield was also significant ($p \leq 0.05$). Protein percentage decreased with enhancing salinity. Seeds from SA and JA treated plants had the highest and the lowest protein percentages, respectively (Tab. 1). Protein yield per plant decreased as a result of increasing salinity. The highest protein yield was recorded for SA treated plants under saline and non-saline conditions. Treatment with JA under non-saline and low saline (4 dS/m) conditions significantly reduced protein yield per plant, but there was no significant difference between JA treated and control plants under 7 dS/m and 10 dS/m salinities (Fig. 5).

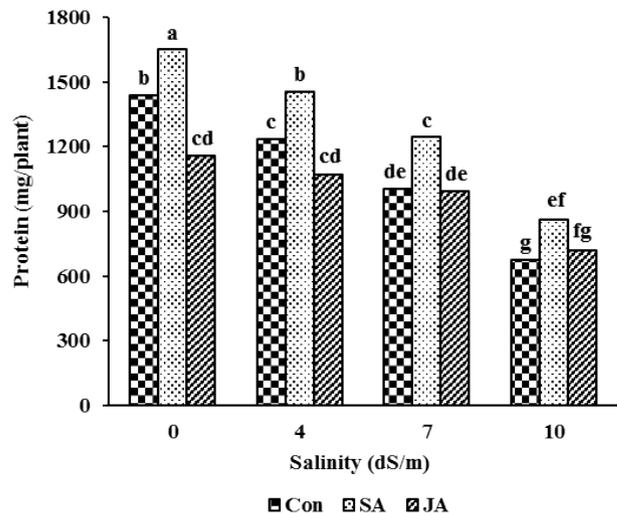


Fig. 5: Protein yields of soybean seeds per plant under different salinity and hormonal treatments

Different letters indicate significant difference at $p \leq 0.05$.

Essential amino acids

With the exception of isoleucine (Ile), all of the essential amino acids significantly affected by salinity. Lysine (Lys), methionine (Met), phenylalanine (Phe) and threonine (Thr) increased, but leucine (Leu) and valine (Val) decreased with enhancing salinity. Foliar treatment of SA improved isoleucine, leucine, lysine, methionine and valine contents in soybean seeds. However, SA had no significant effect phenylalanine and threonine contents. Methionine, phenylalanine and threonine contents enhanced, but isoleucine content

reduced in response to JA treatment. Seeds from JA treated plants did not show significant difference in leucine, lysine and valine contents, compared with those from control plants (Tab. 2).

Non-essential amino acids

Increasing salinity led to the increment of aspartic acid (Asp), glutamic acid (Glu), proline (Pro) and tyrosine (Tyr) contents, but had no significant effects on alanine (Ala), glycine (Gly) and serine (Ser) contents. All of the non-essential amino acids except proline affected by hormonal treatments. The contents of alanine, aspartic acid, glutamic acid, glycine and serine were augmented by SA application. In contrast, treatment with JA increased tyrosine content, decreased aspartic acid and glycine contents, but had no significant effect on alanine, glutamic acid and serine contents (Tab. 3).

Discussion

Nitrogen is the element that plants require in large quantity. It plays a dominant role in plant metabolism as a constituent of many cell components like proteins and enzymes (HAWKESFORD et al., 2012). Reduction in leaf nitrogen content under salinity (Fig. 1A) could be the result of inhibiting the activity nitrate reductase by high sodium contents (BAKI et al., 2000). Treatment with SA promoted the activity of nitrate reductase in plants (AYDIN and NALBANTOĞLU, 2011) and

increased nitrogen content of soybean leaves. However, foliar application of JA enhances ethylene synthesis and inhibits root growth (XIE et al., 1998), which limits nitrogen uptake and translocation to soybean leaves (Fig. 1B). Decreasing sulfur content of leaves due to salinity (Fig. 2A) is related with the inhibition of sulfur uptake. High salinity and drought overlaps with each other, as high salt limits water uptake by the plants. This makes it ever more difficult for the plants to acquire water as well as nutrients such as sulfur. Improving sulfur uptake by SA treatment may be resulted from inhibition of ethylene synthesis and enhancing root growth by this hormone. In contrast, increasing sulfur content of leaves with JA application (Fig. 2B) is related with enhancing genes expression, glutathione synthesis, and glucosinolate activities in plant organs, especially in roots (XIANG and OLIVER, 1998; JOST et al., 2005).

Protein is the most important constituent of soybean seeds. It is synthesized and accumulated in the seeds during filling period (GHASSEMI-GOLEZANI et al., 2010). Decreasing protein percentage and protein content with increasing salinity (Fig. 3 and 4) could be associated with the disturbance in nitrogen metabolism and inhibition of nitrate absorption. Reduction in nitrogen under saline conditions is likely due to the reduction of absorbed water and a decrease in root permeability (STROGOV et al., 1970). HOBBS and MUENDEL (1983) reported similar results for soybean seeds under moisture stress. Foliar applications of SA increased nitrogen content (Fig. 1B) and consequently protein percentage and protein per seed under all

Tab. 2: Essential amino acids content of soybean seeds under different salinity and hormonal applications

Treatments	Ile (mg/g)	Leu (mg/g)	Lys (mg/g)	Met (mg/g)	Phe (mg/g)	Thr (mg/g)	Val (mg/g)
Salinity							
0 dS/m	18.95 a	30.25 a	24.65 d	9.69 d	17.44 c	15.32 d	17.40 a
4 dS/m	18.86 a	30.15 a	25.45 c	10.25 c	17.67 c	15.71 c	16.30 bc
7 dS/m	18.92 a	29.24 b	26.56 b	10.63 b	18.12 b	16.52 b	16.36 b
10 dS/m	19.02 a	29.30 b	27.49 a	10.95 a	18.86 a	16.96 a	15.10 d
Hormonal treatment							
Control	18.85 b	29.66 b	25.93 b	9.83 c	17.72 b	15.89 b	16.33 b
SA	19.36 a	30.22 a	26.60 a	10.35 b	17.95 b	15.97 b	16.93 a
JA	18.61 c	29.33 b	25.58 b	10.93 a	18.40 a	16.53 a	16.35 b

Different letters in each column indicate significant difference at $p \leq 0.05$.

Tab. 3: Non-essential amino acids content of soybean seeds under different salinity and hormonal applications

Treatments	Ala (mg/g)	Asp (mg/g)	Glu (mg/g)	Gly (mg/g)	Pro (mg/g)	Ser (mg/g)	Tyr (mg/g)
Salinity							
0 dS/m	17.13 a	43 d	67.50 c	20.56 a	20.06 d	26.27 a	18.82 d
4 dS/m	17.12 a	44.36 c	67.66 c	20.50 a	21.13 c	26.28 a	19.51 c
7 dS/m	17.21 a	46.58 b	70.50 b	20.42 a	21.83 b	26.32 a	20.19 b
10 dS/m	17.20 a	47.11 a	72.42 a	20.57 a	22.78 a	26.31 a	21.52 a
Hormonal treatment							
Control	17.03 b	45.10 b	68.88 b	20.41 b	21.46 a	26.20 b	19.64 b
SA	17.43 a	46.46 a	70.58 a	21.51 a	21.42 a	26.63 a	19.89 b
JA	17.03 b	44.22 c	68.87 b	19.70 c	21.47 a	26.05 b	20.50 a

Different letters in each column indicate significant difference at $p \leq 0.05$.

salinity levels (Fig. 3 and 4). Decreasing protein percentage and protein per seed by JA application under non-saline and mild salinity (4 dS/m) directly related with reduction in nitrogen content of seeds from JA treated plants (Fig. 1B). Little differences in seed protein content of JA treated and untreated plants under moderate and severe salinity were probably due to similar decrease in nitrogen uptake of these plants under subjected salt stresses (Fig. 3 and 4).

Reduction in seed yield under salinity was the main reason of decreasing protein yield per plant (Tab. 1, Fig. 5). The negative effect of salinity on plants may provoke osmotic potential by salt, so root cells do not obtain required water from the medium (ÇELİK and ATAĞ, 2012). Consequently, the uptake of some mineral nutrients such as nitrogen dissolved in water is also restricted. Higher concentrations of sodium ions are toxic to cell and inhibit the activity of essential enzymes, membrane disorganization, and osmotic imbalance, which finally can reduce protein syntheses in seeds (MEDHAT, 2002). Increasing seed and protein yields with SA treatment in soybean seeds (Tab. 1, Fig. 5) may be related with increasing activities of many anti-oxidant enzymes (SHI et al., 2006), decreasing synthesis of ethylene (LESLIE and ROMANI, 1986), improving nitrogen and sulfur uptakes (Fig. 1B and 2B) and enhancing maximum efficiency of PSII (GHASSEMI-GOLEZANI and LOTFI, 2015). In contrast, treatment with JA stimulated ethylene synthesis (XIE et al., 1998) and limited nitrogen uptake (Fig. 1B), thereby reducing seed and protein yields under non-saline and low salinity conditions (Tab. 1, Fig. 5). This may also be related to allocation of nitrogen and protein to vegetative sinks (STASWICK, 1994). These limitations also occurred for JA untreated plants at moderate and high salinity, leading to almost similar protein yield with JA treated plants under these salinity levels (Fig. 5).

Increasing some of essential (lysine, methionine, phenylalanine and threonine) and non-essential amino acids (aspartic acid, glutamic acid, proline and tyrosine) under salinity (Tab. 2 and 3) suggests that these amino acids may be acting as the sinks for excess nitrogen when decreased growth occurring during the imposed stress. Aspartic and glutamic acids were the major amino acids accumulated in seed tissues of soybean under salt stress (Tab. 3). Increasing aspartic and glutamic acids in the seeds may reflect the mobility of these important amino acids in the phloem (GIROUSSE et al., 1996). However, salinity has a negative impact on synthesis of leucine and valine (Tab. 2).

Improving nitrogen content in plant leaves by SA treatment (Fig. 1B) resulted in increased isoleucine, leucine, lysine, methionine, valine, alanine, aspartic acid, glutamic acid, glycine and serine content in seeds (Tab. 2 and 3). Foliar application of JA enhanced the phenylalanine and tyrosine (aromatic amino acids) contents of seeds (Tab. 2 and 3) via stimulating shikimate pathway (HERRMANN and WEAVER, 1999; TZIN and GALILI, 2010). However, increasing methionine (sulfur containing amino acid) synthesis in the seeds by JA treatment (Tab. 2) directly related with the increment of sulfur content in plants (Fig. 2B). On the other hand, allocation of more protein and nitrogen to vegetative sinks at different stages of maturity of JA treated plants (STASWICK, 1994) reduced some amino acids such as Isoleucine, aspartic acid and glycine in soybean seeds (Tab. 2 and 3).

Conclusions

Foliar application of SA enhanced protein yield of soybean seeds through increasing seed yield and protein percentage and per seed under saline and non-saline conditions. However, treatment with JA reduced seed protein yield, due to the reduction in seed yield and protein content. Increasing salinity led to an increase in lysine, methionine, phenylalanine, threonine, aspartic acid, glutamic acid, proline and tyrosine contents, and a decrease in leucine and valine contents. Seeds of SA treated plants had higher isoleucine, leucine, lysine, methionine, valine, alanine, aspartic acid, glutamic acid, gly-

cine and serine contents, but seeds of JA treated plants produced more sulfur containing amino acids such as methionine and aromatic amino acids such as phenylalanine and tyrosine. Application of SA was determined as a best way for enhancing protein quantity and quality of soybean seeds under saline and non-saline conditions.

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