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Ion uptake, osmoregulation and plant-water relations in faba beans (*Vicia faba* L.) under salt stress

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(With 2 Figures)

Summary

In pot experiments, the effects of irrigation with artificial seawater on faba beans were investigated. The sum of the salt concentration was 0, 20, 40 and 60 mM ($\text{NaCl}:\text{MgCl}_2:\text{MgSO}_4=2:1:1$ on molar basis). Salt stresses increased the concentrations of sodium, magnesium and chloride ions in the plants. Sodium reduced the uptake of potassium due to ion antagonism. Decreased iron concentrations induced chlorosis. Chloride antagonized the uptake of nitrate. Phosphate increased significantly in response to ion balance.

Significant increases in glucose, fructose, in some cases sucrose, proline and calcium contents in faba beans showed some tendency of this crop to adjust osmotically against salt stress. Salinity reduced leaf water potential (Ψ_t) as well as osmotic potential (Ψ_s). Leaf water potential (Ψ_t) decreased from -9×10^5 Pa under control conditions to -14×10^5 Pa under severe salt stress. Grain as well as straw yields of Faba beans were decreased significantly by artificial salinity. At the highest stress level (60 mM salt) grain yields were reduced by 85 %, while straw yields decreased by 43 % at 60 mM.

Key-words: salt stress, seawater salinity, osmotic adjustment, leaf water potential, osmotic potential.

Ionenaufnahme, osmotische Regulation und pflanzlicher Wasserhaushalt bei Ackerbohnen (*Vicia faba* L.) unter Salzstreß

Zusammenfassung

In Gefäßversuchen wurde der Einfluß von Bewässerung mit künstlichem Meerwasser ($\text{NaCl}:\text{MgCl}_2:\text{MgSO}_4=2:1:1$ auf molarer Basis) auf Ackerbohnen untersucht. Die Salzkonzentrationen betragen 0, 20, 40 und 60 mM. Salzstreß bewirkte einen Anstieg der Konzentrationen von Natrium-, Magnesium- und Chloridionen im Pflanzengewebe. Natrium-Kaliumantagonismus führte zu einer Abnahme der Kaliumaufnahme. Abnehmende Eisenkonzentrationen waren die Ursache für Chlorosen. Die Nitrataufnahme wurde durch steigende Chloridmengen vermindert. In Abhängigkeit von der Ionenbilanz ergab sich eine Erhöhung der Phosphatgehalte.

Die Ackerbohnenpflanzen zeigten tendenziell eine osmotische Anpassung durch steigende Glucose-, Fructose-, teilweise Saccharose-, Prolin- und Calciumgehalte als Antwort auf den Salzstreß. Versalzung des Bodens verminderte das Blattwasserpotential (Ψ_t) und das osmotische Potential (Ψ_s). Das Blattwasserpotential (Ψ_t) fiel von -9×10^5 Pa unter Kontrollbedingungen auf -14×10^5 Pa bei schwerem Salzstreß.

Sowohl Korn- als auch Stroherträge der Ackerbohne wurden unter Salzstreß deutlich vermindert. Bei der höchsten Streßstufe (60 mM Salz) verringerte sich der Kornertrag um 86 % und der Strohertrag um 43 %, jeweils bezogen auf die Kontrolle.

Schlüsselworte: Salzstreß, Salzwassereinfluß, osmotische Anpassung, Blattwasserpotential, osmotisches Potential.

1. Introduction

Salinity in general inhibits plant growth by decreasing the potential of soil or nutrient solutions exposed to the roots (FLOWERS and YEO 1986, CUSIDO et al. 1987, CAESAR and RUSITZKA 1982, PESSARAKLI and TUCKER 1988, WOOD and GAFF 1989, ZERBI et al. 1990). Plants grown under salt stress often show symptoms of specific ion toxicities, deficiencies and nutritional imbalances (GREENWAY and MUNNS 1980, PLAUT and GRIEVE 1988, NEUE et al. 1990, MATSUMOTO and CHUNG 1990, HE and CRAMER 1992). As the ion antagonism in saline environments is usually followed by nutrient deficiencies, the ionic composition is very important with regard to salt tolerance. Mechanisms in plants for avoiding the uptake of excess ions and intracellular compartmentation are considered to be responsible for the tolerance of a crop to high salinity levels (CAESAR and RUSITZKA 1982, CHEESEMAN 1988, HE and CRAMER 1992). For survival of the plants during the periods of low water potential due to salt stress, roots should have the ability to exclude soil salts. Alternatively shoots should export or excrete salts to the periphery or cells should tolerate salts that reach them (WOOD and GAFF 1989). Plants should also have the ability to sequester the excess ions into vacuoles of the root cortex that regulates the transport of ions into xylem and photosynthetic tissues (EPSTEIN and RAINS 1987, CHEESEMAN 1988, MATSUMOTO and CHUNG 1990).

Osmotic adjustment is essential for a plant to survive in saline environments (HSIAO et al. 1976, FLOWERS et al. 1977). The most important ions, as far as osmotic adjustments in halophytes is concerned, are sodium, potassium and chloride (FLOWERS and YEO 1986, MCCREE 1986). Glycophytes often adjust by excluding salts and generating sufficient organic molecules as osmotica to maintain turgor (MCCREE 1986). Current belief is that the ions involved in osmotic adjustment are largely restricted to the vacuoles (FLOWERS et al. 1977, WYN JONES et al. 1977, MUNNS et al. 1983, STEWART and AHMAD 1983), the osmotic potential of the cytoplasm being adjusted with organic compatible solutes (STEWART and LEE 1974, STOREY and WYN JONES 1975).

Faba beans are known to be sensitive to salt stress. Because of the increasing demands, their cultivation even extends to areas with salt influenced soils or irrigation water. Therefore, the present investigations aimed at different physiological processes underlying yield formation — nutrient uptake, water relations and organic solute production — that are known to be affected by salt stress. In this experiment, plants were stressed by the addition of simulated seawater instead of a single salt because seawater is thought to be more representative for a generalized plant response to salinity (HE and CRAMER 1992).

2. Materials and Methods

Faba beans were grown in pots under the following greenhouse conditions: 12 hours photoperiod (06 h–18 h), 21 ± 1 °C temperature, photosynthetic active radiation $350 \mu\text{M}$ photon flux density $\text{m}^{-2} \text{s}^{-1}$ at plant top level, provided by mercury vapour lamps.

Plastic pots were filled with 6 kg air-dry sandy loam soil of Seibersdorf, which was screened through a 2 mm sieve and had the following general characteristics: sand 45.7 %, silt 31.1 % and clay 23.2 %, pH 7.63, organic matter 3.5 %, CaCO_3 12 %, Ca 4.68 %, Mg 1.44 %, K 0.49 %, P 839 ppm, N 0.28 %, Al 1.89 %, Na 113 ppm, maximum water holding capacity 43 % and moisture at field capacity 30 %. Eight faba bean seeds were germinated in each pot. Five days after germination, the number of plants per pot was reduced to four of uniform size. After thinning, pot surface was covered with aluminium foil in order to prevent evaporation. The pots were arranged in a completely randomized design in the greenhouse with four replications for each treatment.

The plants were allowed to grow for two weeks without salt treatments. During this period, pots were irrigated with deionized water. Faba bean plants were then exposed to constant levels of salt stress equivalent to seawater salinity. This was accomplished by irrigation with varying degrees of salt solutions (Treatments: 0, 20, 40 and 60 mM salts), while maintaining a constant soil moisture level of 70 % water-holding capacity during the whole growing period of faba beans. Seawater was simulated with a mixture of NaCl, MgCl_2 and MgSO_4 (2 : 1 : 1 on a molar basis). The sum of these salt concentrations were 0, 20, 40 and 60 mM.

Transpiration rate during the growing period of faba beans was determined by weighing the pots daily till the final harvest. As the pots were covered with aluminium foil, the loss of water each day was due to transpiration. Total leaf water potential (Ψ_t) was measured according to SCHOLANDER et al. (1965) with a pressure chamber. Osmotic potential (Ψ_s) of the leaves was determined with a dew point psychrometer (WESCOR, C-52 Leaf Chamber, Wescor USA, HR-33T-R) in the leaf sap after their hydration over-night in a cool chamber, freezing in liquid nitrogen and thawing for 20 min at room temperature.

Glucose, fructose and sucrose in faba bean leaves were determined before flowering (within two weeks after salt initiation) by enzymatic methods described by BOEHRINGER-MANNHEIM (1989). Proline was estimated in the leaves by the method outlined by BATES et al. (1973).

One plant per pot was harvested before flowering and the rest at the end of the experiment (after maturity of grains). The plants harvested before flowering were separated into leaves and stems. All the plant samples were oven-dried at 70° C and finely ground. Dry weight of the shoots was also recorded after final harvest.

Chloride, nitrate, sulphate and phosphate were determined in leaves and stems of faba beans before flowering and in shoots after final harvest by ion chromatography (DIONEX Model 2010i).

For the determination of these ions, the plant samples were extracted with 50 ml deionized-distilled hot water in a shaking water-bath (80 °C for 10 min). The extraction was repeated twice and the decanted supernatants were bulked and filtered (WOOD and GAFF 1989).

Sodium, potassium, calcium, magnesium, iron and total phosphorus (in shoot) were determined by Plasma Emission Spectrometry (Perkin Elmer Plasma II) after wet digestion of the samples in HNO_3 : HClO_4 (5 : 1) mixture.

Finally all the results were statistically analysed (SAS-Software).

3. Results

Shoot dry matter production of faba beans was significantly affected by salt stress (fig. 1). It decreased gradually with salt concentration. The dry matter yield at a salt concentration of 60 mM decreased to 43 % of the control treatment. Grain yield was more severely affected by seawater salinity than shoot yield (fig. 1). Salinity reduced grain yield up to 86 % of control. However, faba bean growth was little affected by salt stress in the 2nd week of the salt application (table 1).

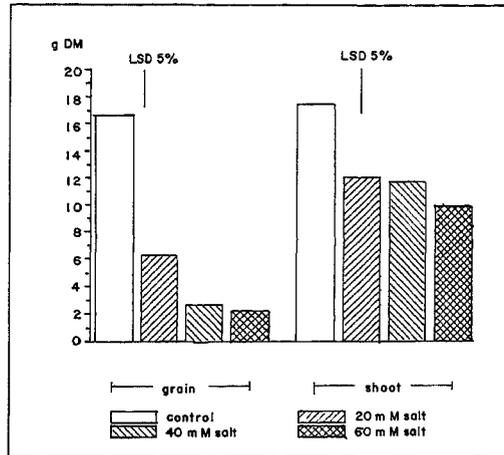


Fig. 1: Influence of salt stress on dry matter production of faba beans

Table 1

Effect of salt stress on dry matter production (leaves + stems) before flowering and K/Na, Na/Ca and Ca/Mg ratios in leaves, stems and shoots of faba beans

mM Salt	DM (g) (Leaves + Stems)	Leaves			Stems			Shoots		
		K/Na	Na/Ca	Ca/Mg	K/Na	Na/Ca	Ca/Mg	K/Na	Na/Ca	Ca/Mg
0	2.15 a	23.64 a	0.42 c	3.51 a	68.38 a	0.03 b	3.77 c	4.09 a	0.56 c	5.74 a
20	2.00 a	9.62 b	0.78 b	3.74 a	19.27 b	0.09 b	3.77 c	0.52 b	1.30 b	5.64 a
40	2.04 a	4.22 c	1.30 a	3.72 a	7.30 c	0.16 a	3.87 b	0.27 c	1.79 a	5.12 a
60	1.98 a	2.43 d	1.56 a	3.96 a	4.97 c	0.18 a	4.44 a	0.22 c	2.04 a	4.58 a

Both cations and anions in faba beans were determined at two separate occasions within two weeks of salt initiation (before flowering) and after final harvest. Salinity increased the concentration of sodium in leaves and stems as well as in shoots (table 3). Highest concentrations of sodium were found at 60 mM salts at all stages of growth. A 10 fold increase in sodium concentration in shoots of faba beans was observed at 60 mM salts. Leaves had a much lower concentration of sodium than stems and the highest concentration of sodium was noticed at 60 mM in shoots (6.05 %, table 3). On the other hand, potassium contents decreased with salinity (table 3). Reduction in potassium concentrations was more pronounced in shoots and stems than in leaves. A reduction of 44 % K in shoots compared with the control was observed at salt concentrations of 60 mM. K/Na ratio was also decreased with salt concentrations (table 1). This ratio was significantly higher in faba beans before flowering stage than after maturity. A minimum of 0.22 was found in shoots at a salt concentration of 60 mM (table 1).

Magnesium contents in leaves were significantly enhanced by 40 mM and 60 mM salts as compared to the control (table 2), but its concentration in stems remained unaffected. Magnesium was higher in leaves than in stems. However, at maturity of faba beans, there was a significant increase in magnesium contents in shoots due to salt stress (table 2). Calcium concentration was also increased by salt application in leaves and shoots before flowering and after harvest (table 2). There was a gradual increase in calcium concentration in stems before flowering, but this increase was not significant except at 60 mM salts. Na/Ca ratio increased with salinity. This ratio was higher at maturity than before flowering stage (table 1) showing an enhanced uptake of Na by faba beans with age. Ca/Mg ratio did not change with salt concentration. The highest ratio was observed in shoots after final harvest (table 1).

Table 2

Effect of salt stress on Ca, Mg and P concentrations (%) in faba bean leaves, stems and shoots at two stages of growth

mM salts	Leaves		Stems		Shoots		
	% Ca	% Mg	% Ca	% Mg	% Ca	% Mg	% P
0	1.64 c	0.44 b	0.47 b	0.13 a	1.05 c	0.18 c	0.09 c
20	1.73 bc	0.46 b	0.50 ab	0.14 a	2.16 b	0.38 b	0.16 b
40	2.26 ab	0.58 a	0.58 ab	0.16 a	3.10 a	0.61 a	0.19 ab
60	2.64 a	0.59 a	0.63 a	0.16 a	2.97 a	0.65 a	0.23 a

Table 3

Effect of salt stress on sodium and potassium concentrations in faba beans (in % of dry weight)

mM Salts	% Na			% K		
	Leaves	Stems	Shoots	Leaves	Stems	Shoots
0	0.05 c	0.12 d	0.59 c	3.60 a	4.71 a	2.39 a
20	0.15 c	0.39 c	2.80 b	2.89 b	3.78 b	1.45 b
40	0.36 b	0.75 b	5.58 a	2.66 b	3.17 b	1.51 b
60	0.49 a	0.98 a	6.05 a	2.42 b	2.87 b	1.33 b

Salinity reduced iron concentrations in faba beans before flowering as well as at maturity (table 4). This reduction in iron contents in plants under salt stressed conditions resulted in chlorosis. Iron concentrations were higher in leaves than in stems and shoots (table 4).

Table 4

Effect of salt stress on iron and chloride concentrations in faba beans

mM Salts	Fe (ppm)			% Cl ⁻		
	Leaves	Stems	Shoots	Leaves	Stems	Shoots
0	105 a	62 b	100 a	0.92 c	0.50 b	1.18 c
20	88 b	45 b	64 b	2.25 b	2.57 a	6.63 b
40	93 ab	50 b	63 b	2.71 ab	3.04 a	11.81 a
60	89 b	43 b	59 b	3.35 a	2.90 a	13.51 a

Salt stress increased chloride concentrations in faba beans (table 4). The increase in chloride contents was less pronounced in leaves (up to 4 folds) than that in stems (up to 6 folds) and shoots (up to 11 folds). Probably the transport of

chloride from the stems to the leaves was restricted. Highest concentrations of chloride in the shoots of faba beans were due to the accumulation of this ion as the plants aged. However, the nitrate contents declined significantly with increased salt concentrations. Nitrate concentrations were lowest in shoots under control conditions after final harvest (table 5) probably due to the accumulation of nitrogen in the grains. Phosphate concentration was also influenced by salt stress. Its concentration was found to be significantly higher in stems and shoots of faba beans compared with the control, while its increase in leaves was not significant (table 5). Like phosphate ions total phosphorus was also significantly increased by salinity showing the highest concentration at 60 mM salts (table 2). Sulphate ion was enhanced by salt stress in stems and shoots of faba beans, but its concentration in leaves declined with salinity (table 5). Sulphate ions in salt solutions might have induced their increased uptake in salt-treated plants.

Table 5

Effect of salt stress on NO_3^- , PO_4^{3-} and SO_4^{2-} ion concentrations in faba beans leaves, stems and shoots

mM Salts	Leaves			Stems			Shoots		
	NO_3^-	PO_4^{3-}	SO_4^{2-}	NO_3^-	PO_4^{3-}	SO_4^{2-}	NO_3^-	PO_4^{3-}	SO_4^{2-} %
0	0.18 a	0.57 a	0.18 a	0.33 a	0.35 b	0.06 b	0.01 c	0.13 c	0.42 b
20	0.14 b	0.63 a	0.13 ab	0.21 b	0.58 ab	0.11 ab	0.03 b	0.33 b	0.60 b
40	0.15 b	0.68 a	0.08 b	0.17 b	0.70 a	0.14 a	0.05 a	0.40 ab	0.91 a
60	0.14 b	0.69 a	0.08 b	0.21 b	0.76 a	0.15 a	0.06 a	0.53 a	1.00 a

Salinity at 20 and 40 mM salts increased glucose and fructose contents in leaves of faba beans (table 6), while only slight increases (not significant) in glucose and fructose contents was found at 60 mM salts (table 6). Apparently at this salt concentration, the conversion of glucose and fructose to sucrose was favoured. Proline contents in faba beans were enhanced by salinity, especially at the 40 and 60 mM salt treatments (table 6). The highest amount of proline (2.2 %) was observed at 60 mM salts.

Table 6

Effect of salt stress on glucose, fructose, sucrose and proline contents in faba beans (dry weight basis)

mM Salts	% Glucose	% Fructose	% Sucrose	% Proline
0	0.25 b	0.21 b	10.51 b	0.46 c
20	0.50 a	0.46 a	10.75 b	1.00 bc
40	0.48 a	0.44 a	11.77 ab	1.53 ab
60	0.29 b	0.27 b	14.76 a	2.17 a

Leaf water potential (Ψ_t) decreased significantly in faba beans as compared with the control treatment due to salinity (table 7). Leaf water potential did not drop below -14×10^5 Pa and the lower values were always being recorded under 60 mM salt treatment, while Ψ_t in control plants ranged from -9×10^5 Pa at full turgor to -11×10^5 Pa under water stress. A similar drop in water potential to -12.3×10^5 Pa was observed at the 20 mM salt treatments. However, simultaneous salt and water stresses could not decrease water potential at 40 and 60 mM salt treatments more than salt stress alone. Osmotic potential (Ψ_s), measured twice during the growing period, decreased sharply with salt concentrations. Low values were obtained at maturity as compared to vegetative stage (table 7).

Table 7

Effect of salt stress on leaf water potential (Ψ_l) and osmotic potential (Ψ_s) at various stages of growth of faba beans

mM Salts	$\Psi_l (-1 \times 10^5)$					$\Psi_s (-1 \times 10^5)$	
	34	39	48	54	82	34	82 DAE
0	9.4 a	9.4 a	11.5 a	9.0 a	9.7 a	8.2 a	8.7 a
20	11.1 b	10.9 b	12.4 ab	11.4 b	11.6 b	9.2 b	11.5 b
40	11.8 b	11.9 c	12.8 bc	12.6 c	12.5 c	11.1 bc	12.1 b
60	13.5 c	13.4 d	13.6 c	13.3 d	14.0 d	12.3 c	13.0 c

DAE — Days after emergence of faba beans

48 DAE — simultaneous salt and water stress

Salt stress affected transpiration in faba beans. The highest transpiration was observed in the control treatment, with maximum values of about 300 ml plant⁻¹ day⁻¹ at flowering stage. Fluctuations in transpiration were also highest under control treatment and mainly occurred in response to microclimatic changes. Salinity reduced transpiration considerably under the ambient atmospheric conditions (fig. 2). There were only small differences among the salt treatments, transpiration being slightly higher at 20 mM salt treatments. Under these conditions, transpiration rate never exceeded 120 ml plant⁻¹ day⁻¹ and was relatively constant throughout the growing period of faba beans. During the first 35 days after germination (e. g. 21 days after salt initiation), there was no appreciable difference in transpiration between the control and the salt stressed plants (fig. 2).

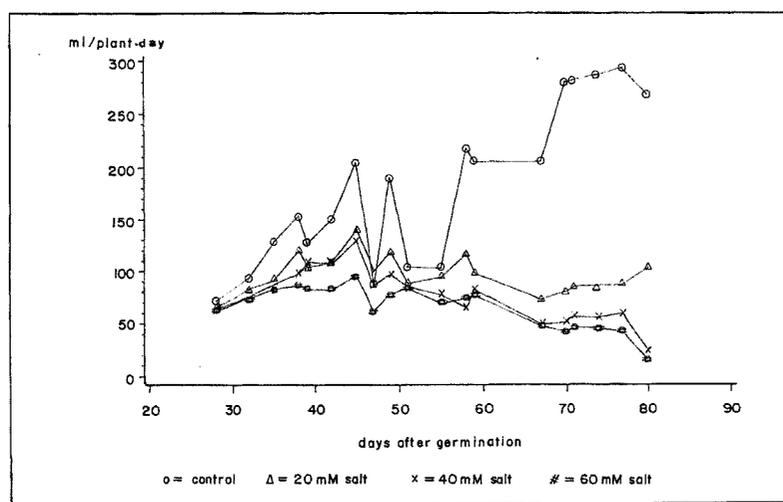


Fig. 2: Total water transpiration of faba beans in relation to salt stress

4. Discussion

Reduction in dry matter production (upto 43 %) and grain yield (upto 86 %) of faba beans as compared with control may be caused by ion toxicities, reduced water absorption and impaired biochemical and physiological processes associated with increasing salt stresses. Similar responses to salinities in glyco-phytes are reported by GREENWAY and MUNNS 1980, MARSCHNER 1986, MUNNS and TERMAAT 1986, GRATTAN and MAAS 1988, SALIM 1989 and HE and CRAMER 1992.

HAMID and TALIBUDEEN (1976) found that the sensitivity of faba beans increased with age and the yield was reduced to half. EL-KAROURI (1979) showed that the growth and yield of faba beans in a field trial in Sudan were reduced to 50 % due to salinity (9 mmhos/cm). In this respect, the European cultivars are reported to be more sensitive than other cultivars (CAESAR and RUSITZKA 1982). In our experiment, the grain yield was more severely affected than shoot yield, apparently these yield reductions are associated with physiological disorders in the plants due to salinities.

Salinity affected ion concentrations of leaves, stems and shoots not only in faba beans, but also in a number of other species, such as sugar beet, triticale, cotton, kidney bean, grass and Brassica sp. (AYOUB 1974, PLAUT and HEUER 1985, RATHERT 1983, FLOWERS and YEO 1986, FRANCOIS et al. 1988, SALIM 1989, DUBEY and RANI 1989, HE and CRAMER 1992). Compared with control treatment, salinity increased sodium concentration significantly in leaves, stems and shoots. This increase was accompanied by a concomitant decline in potassium concentration, showing an apparent antagonism between potassium and sodium (HE and CRAMER 1992). This antagonism could be due to the direct competition between K and Na at the site of ion uptake at plasmalemma (EPSTEIN and RAINS 1987). Sodium could as well enhance the efflux of potassium into the growth medium (CRAMER et al. 1985, HAJJI and GRIGNON 1985), possibly due to membrane integrity (HE and CRAMER 1992). A positive relation existed between magnesium and salt concentrations. The increase in magnesium concentrations in leaves and shoots of faba beans was due to its presence in the simulated artificial seawater salinity. Calcium concentration increased with salt concentrations, although high concentration of sodium in the external solution has been known to depress its contents in the plant materials due to its antagonism with sodium (GREENWAY and MUNNS 1980, RATHERT 1983, HE and CRAMER 1992), sometimes to a degree that causes calcium deficiencies (MAAS and GRIEVE 1987, HE and CRAMER 1992) and accelerates the passive accumulation of sodium ions. The increase in calcium concentrations with increasing salinities shows some tendency of faba beans for an osmotic adjustment.

Like sodium, the concentration of chloride increased with salt concentration in response to ion balance. Chloride had an antagonistic effect on nitrate uptake during the vegetative growth of faba beans resulting in a suppression of nitrate with increasing salinity. ABDUL-KADIR and PAULSEN (1982) reported a reduced growth and decreased nitrogen contents in wheat by salt stress. Phosphate and sulphate concentrations were enhanced by salt concentration. The increase in sulphate contents in faba beans is at least partly caused by its presence in the simulated salt solutions, while phosphate was taken up in response to ion balance and probably for osmotic adjustment (ULLAH et al. 1989).

Salt treated faba beans synthesized more glucose, fructose, proline and in some cases sucrose than control plants. These organic molecules act as osmotica and play an important role in osmotic adjustment. (GREENWAY and MUNNS 1980, FLOWERS et al. 1977, McCREE 1986). Such increases in organic solutes (proteins, aminoacids, prolines, etc.) in salt stressed plants have been frequently reported (DUBEY and RANI 1989, VYAS and RAO 1987, GREENWAY and MUNNS 1980, MEHTA and VORA 1987). Potassium deficiency in plants induced by salinity has the potential to increase aminoacids, specially aspartic acid, glutamic acid and proline contents (CUSIDO et al. 1987).

Transpiration rate in faba beans was severely affected by salinity. Its reduction under salt stressed conditions was probably because of a partial closure of stomata, which subsequently might have decreased net photosynthesis (HAYWARD

and SPURR 1943). A decreased absorption of water by salt stressed plants was observed by PESSARAKLI and TUCKER (1985, 1988) and PESSARAKLI et al. (1989). Reduced transpiration under saline conditions enhanced water contents in soils and in plants (LOOS and WIDMOSER 1986, PLAUT and HEUER 1985, WOOD and GAFF 1989). Fluctuations in transpiration rate during the growing period of faba beans under control treatments were caused by the changes in ambient humidity and temperature. Such changes were also observed by PLAUT and GRIEVE (1988), who attributed these changes in transpiration to the fluctuations in radiation, humidity and temperature of the air.

The decrease in leaf water potential (Ψ_l) as well as osmotic potential (Ψ_s) with increasing salt concentrations in the soil was due to the accumulation of inorganic and organic solutes by faba beans resulting in some osmotic adjustment. These reductions in leaf water potential (Ψ_l) were also reported by other authors (SHALHEVET and HSIAO 1986, WEST et al. 1986, PLAUT and HEUER 1985, ASPINAL 1986, LOOS and WIDMOSER 1986, ULLAH et al. 1989, ZERBI et al. 1990). ULLAH et al. (1989) observed a reduction in osmotic potential in faba bean leaves at full turgor as a reaction to salt stress to about -5×10^5 Pa.

The salt stress reduced both grain and straw yields in faba beans primarily due to the shift in ion balance, which also affected water relations and other physiological functions in plants.

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