

K⁺/Na⁺ soil-plant interactions during low salt stress and their role in osmotic adjustment in faba beans

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Abstract

This work examines the responses of faba beans to the external K⁺/Na⁺ ratio, the role of inorganic ions Na⁺, K⁺, Ca²⁺, Mg²⁺, Cl⁻, PO₄³⁻ and SO₄²⁻, the role of organic solutes, amino acids, soluble proteins and soluble sugars. The plants were treated with 25 mM solutions of NaCl and KCl at 0, 0.425, 1.134, 2.55 and 6.8 K⁺/Na⁺ ratios. The different organs of treated plants showed different responses. Leaves were dependent on K⁺, Na⁺, Ca²⁺ and Cl⁻ to readjust their osmotic pressure and decrease their Mg²⁺ content. Stems were dependent on Na⁺, Ca²⁺ and Cl⁻ while roots were dependent on Mg²⁺ more than other organs. Leaves and stems increased their PO₄³⁻ contents with the increase in external K⁺. Soluble sugars played the most important role, as organic solutes, in osmotic readjustment. With the increase in external K⁺ the dependence of roots on soluble sugars decreased. The increase in external K⁺ increased the leaves' amino acid and soluble protein contents.

Key words: K⁺/Na⁺ ratio, salinity, osmoregulation, salt stressed plants, *Vicia faba*.

Resumen

Interacciones K⁺/Na⁺ suelo-plantas de haba sometidas a estrés salino y su papel en el ajuste osmótico

Este trabajo analiza la respuesta de plantas de haba a la relación K⁺/Na⁺, el papel de los iones inorgánicos Na⁺, K⁺, Ca²⁺, Mg²⁺, Cl⁻, PO₄³⁻ y SO₄²⁻, así como el papel de los solutos orgánicos, aminoácidos, proteínas y azúcares solubles. Se trataron plantas de haba con soluciones 25 mM de NaCl y KCl presentando una relación K⁺/Na⁺ de 0, 0.425, 1.134, 2.55 y 6.5. Los diferentes órganos de las plantas tratadas mostraron respuestas distintas: las hojas dependieron de K⁺, Na⁺, Ca²⁺ y Cl⁻ para reajustar su presión osmótica y disminuir su contenido en Mg²⁺; los tallos dependieron de Na⁺ y Ca²⁺; y las raíces dependieron de Mg²⁺ más que otros órganos. Las hojas y los tallos aumentaron su contenido en PO₄³⁻ al aumentar el K⁺ externo. Los azúcares solubles fueron el soluto orgánico más importante en el reajuste osmótico. Con el aumento de K⁺ externo disminuyó la dependencia de las raíces en azúcares solubles y aumentó el contenido de las hojas en aminoácidos y proteínas solubles.

Palabras clave: relación K⁺/Na⁺, salinidad, osmorregulación, plantas con estrés salino, *Vicia faba*.

Introduction

Salinity is one of the greatest problems, in arid and semiarid regions, to affect plant crop growth production (Sibole *et al.*, 1998). Sodium chloride is the most familiar accumulated salt in soils suffering from salinity. The tolerance of salt stressed plants is essentially dependent on their ability to accumulate the inorganic solutes from the external media in their tissues (Demmig and Winter, 1986). The accumulation of inorganic ions within plant tissues is the fastest way to maintain the soil-plant osmotic gradient. This process starts

immediately after the occurrence of stress to maintain the water status within plant cells (Wyn Jones and Pritchard, 1989). The large amounts of accumulated inorganic ions may cause ion toxicity (Kinraide, 1999). To avoid this toxicity, plants tend to accumulate compatible organic solutes by *de novo* synthesis of amino acids, sugars, polyols and quaternary amines acting as osmolytes (Wyn Jones and Pritchard, 1989; Bohnert and Shen, 1999). The uptake of ions needed for the synthesis of organic osmolytes and other metabolites is affected by external salt stress. This is due to competition and nutrient imbalances (Kinraide, 1999).

Potassium is one of the most important cations for plant growth. It is required as a vacuolar osmoticum and as an enzyme cofactor (Leigh and Wyn Jones,

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1984; Marschner, 1995) and also plays a role in salinity toxicity (Lauchli, 1990; Niu *et al.*, 1995). Na⁺-induced depletion of tissue K⁺ has been cited as a contributor to salinity toxicity (Ben-Hayyim *et al.*, 1987; Nakamura *et al.*, 1990). The supplementation of NaCl to the rooting media may cause reductions in the K⁺ content in plant tissues (Ben-Hayyim *et al.*, 1987; Nakamura *et al.*, 1990), or even possibly elevations of K⁺ concentrations in plant tissues (Cramer *et al.*, 1990; Ashraf and O'Leary, 1994). Supplementation of saline media with K⁺ > 20 mM has been observed to relieve Na⁺ toxicity (Satti and Lopez, 1994; Cordovilla *et al.*, 1995), but higher levels of K⁺ can be toxic (Lauter *et al.*, 1988). The responses of plant species may differ according to the salinising system (Grattan and Grieve, 1999). Numerous studies have shown that there are reductions in K⁺ uptake, due to competition, in Na-salt stressed plants (Mor and Marchanda, 1992; Graifenberg *et al.*, 1995). Other studies have shown that K⁺ may be preferentially acquired and transported against a strong Na⁺ concentration gradient. As a result, K⁺ levels in the cell sap of bean leaves increased with increasing NaCl-salinity (Kamel, 2002).

It is clear that plants tend to avoid ionic toxicity resulting from the accumulation of inorganic ions in high quantities within their tissues. Also, they tend to maintain the lowest level of essential ions necessary for biological processes. The aim of this study was, therefore, to determine the sodium-potassium interactions within different organs of *Vicia faba* plants according to the availability of Na⁺ and K⁺ in the external medium, and to determine the role of K⁺ in osmotic adjustment.

Material and Methods

Faba beans (*Vicia faba* L. cv. Giza 40) seeds were cultivated in 15 pots, eight seeds in each pot. Each pot (15 cm width × 12 cm height) contained 2 kg of sand-clay soil (2:1 respectively). The seedlings were irrigated to field capacity with tap water for three weeks then the pots containing plants were divided into five groups, each group with three pots (replicates). The first group (control) was irrigated with tap water containing 25 mM NaCl. The second to the fifth group were irrigated with 20 mM NaCl + 5 mM KCl, 15 mM NaCl + 10 mM KCl, 10 mM NaCl + 15 mM KCl, 5 mM NaCl + 20 mM KCl respectively for three weeks. The plants were grown in greenhouse in the tempera-

ture range 33°C and 5°C day/night, humidity range 25-85% and average day length about 13 h.

At harvest, the plants were separated into roots, stems and shoots. Roots were washed in the solution used for their irrigation and dried with filter paper. All plant parts were dried at 70°C for 48 h. The dried parts were ground and the solutes were extracted in water according to El-Sharkawi and Michel (1975).

Sodium and potassium were measured by flame photometry (flame photometer, corning M410, UK) according to Williams and Twine (1960). A volumetric estimation of Cl⁻, Ca²⁺ and Mg²⁺ was performed according to Jackson (1958) and Johnson and Ulrich (1959). Sulphate, phosphate, soluble sugars, amino acids and soluble proteins were measured colorimetrically (spectrophotometer Jenway M6405 UK) according to Black *et al.* (1965), Woods and Mellon (1941), Dubois *et al.* (1956), Lee and Takahashi (1966) and Lowry *et al.* (1951), respectively.

Potassium/sodium selectivity in root, stem and leaf were calculated as:

$$S_{K:Na}(\text{root}) = (K_r * Na_{\text{ext}}) / (Na_r * K_{\text{ext}}) \quad (1)$$

$$S_{K:Na}(\text{Stem}) = (K_s * Na_r) / (Na_s * K_r) \quad (2)$$

$$S_{K:Na}(\text{leaf}) = (K_l * Na_s) / (Na_l * K_s) \quad (3)$$

Where the subscripts ext., r, s and l indicate, respectively, ion concentration in the external solution, in root, stem and leaves.

Results were analyzed statistically using ANOVA1, analysis of variance (one way equal cell size). The F value is the ratio of the model mean square to the error mean square.

Results

Growth and water content parameters

Shoot length as growth indicator was affected by the external K⁺/Na⁺ ratio. This decreased at the 0.425 K⁺/Na⁺ value more than the control (K⁺/Na⁺ value = 0). Shoot length increased gradually and exceeded that of the control in the next highest ratios, except for at the 6.8 K⁺/Na⁺ value where shoot length decreased but was still higher than control (Fig. 1).

Accumulated organic solutes

The organic solutes, soluble protein, amino acids and sugars were affected by the external K⁺/Na⁺ value.

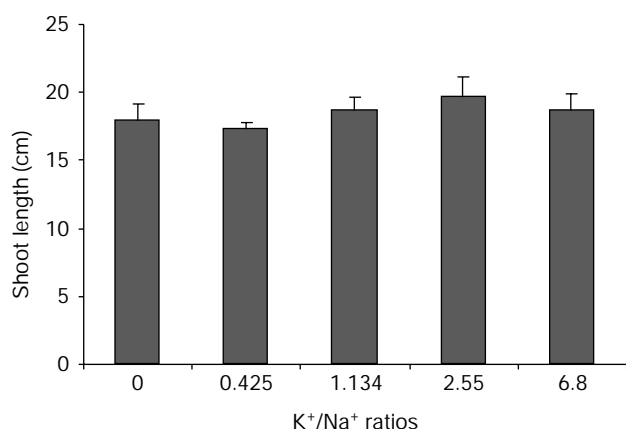


Figure 1. The shoot length (cm) at different external K⁺/Na⁺ ratios.

The accumulated amounts of these solutes varied according to the external K⁺/Na⁺ values in the different organs of the treated *Vicia faba* plants.

Soluble sugars were the most accumulated organic solute in the different organs. Roots showed more dependence on soluble sugars to increase their osmotic pressure than stems and leaves. The roots' soluble sugar contents were the highest in all the treatments (Fig. 2). The highest osmotic pressure was produced by soluble sugars and reached 35.67 kPa in the roots at the 0.425 K⁺/Na⁺ ratio. Generally, the soluble sugars osmotic pressure was higher in roots than in stems and leaves. Leaves were more dependent on soluble sugars for increasing their osmotic pressure. The roots' soluble sugar content was clearly affected with the increasing external K⁺/Na⁺ ratio. Leaves showed a reduced soluble sugar content with the increase in the external K⁺/Na⁺ ratio. There wasn't a clear association between the external K⁺/Na⁺ ratio and the amounts of soluble sugars accumulated in the stems.

Amino acids were accumulated in small amounts compared with the soluble sugars and were affected slightly with the increase in the external K⁺/Na⁺ ratio (Fig. 2). The peak occurred at the 1.134 K⁺/Na⁺ ratio in both roots and leaves. The amino acid content decreased more than control at the 2.55 and 6.8 K⁺/Na⁺ ratios in roots and stems but was higher in leaves. Amino acid osmotic pressure ranged between 2.3 and 3.4 kPa in the different organs of treated plants.

Soluble proteins were accumulated in stems and leaves more than amino acids (Fig. 2). The leaf soluble protein content increased slightly and gradually with the increasing K⁺/Na⁺ ratio. Roots and stems showed an inverse behavior, the root content of soluble protein decreased with the increase in K⁺/Na⁺ ra-

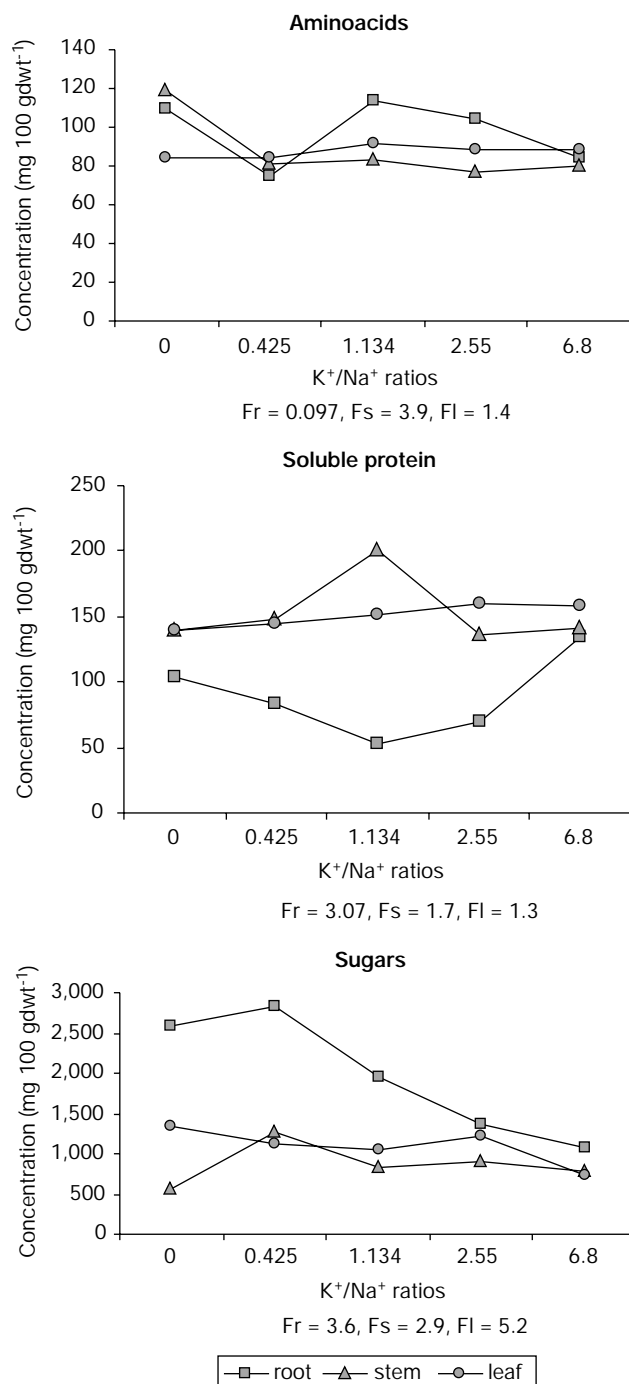


Figure 2. Amino acids, soluble proteins and soluble sugars content (mg 100 g dwt⁻¹) in roots, stems and leaves of *Vicia faba* at different external K⁺/Na⁺ ratios. Fr, Fs and Fl are the computed statistical F values for roots, stems and leaves respectively.

tio to reach the lowest level (53.55 mg 100 g dwt⁻¹) at the 1.134 K⁺/Na⁺ ratio and increased again. The stems inversely to the roots increased their content of soluble protein to reach the peak (200.15 mg 100 g dwt⁻¹)

at the 1.134 K^+/Na^+ ratio and decreased with increasing external K^+/Na^+ .

Estimated cations (Na^+ , K^+ , Ca^{2+} and Mg^{2+})

The uptake of sodium ions was enhanced in *Vicia faba* roots at the K^+/Na^+ ratio 0.425 and reached the peak at 1284.67 mg 100 g dwt⁻¹ (Fig. 3). With the increased K^+/Na^+ ratio, the root content of sodium decreased gradually. This was less than the control in all treatments, except at the K^+/Na^+ ratio 0.425. Stems and leaves increased their Na^+ content gradually with the increasing K^+/Na^+ ratio, but the Na^+ concentration declined slightly in stems at the 6.8 K^+/Na^+ ratio. The highest accumulated amount of Na^+ occurred in stems at the 2.55 K^+/Na^+ ratio. The leaf content of Na^+ declined

gradually at the 2.55 K^+/Na^+ ratio. The highest content occurred at the 1.134 K^+/Na^+ ratio.

Leaves were dependent on K^+ more than root and stems (Fig. 3). Roots showed the same behavior as for Na^+ in that potassium uptake was enhanced at the 0.425 K^+/Na^+ ratio and declined gradually at higher values. Stems showed instability throughout the different treatments but generally the potassium contents were higher at the higher K^+/Na^+ ratios compared with the control and the 0.425 K^+/Na^+ ratio. In the control and lowest K^+/Na^+ ratios, the roots showed a tendency to accumulate potassium more than stems. The inverse behavior occurred at higher values. The highest amount of potassium accumulating in the plant occurred in the leaves. The leaf content of potassium increased gradually to reach a peak at the 1.134 K^+/Na^+ ratio and declined again.

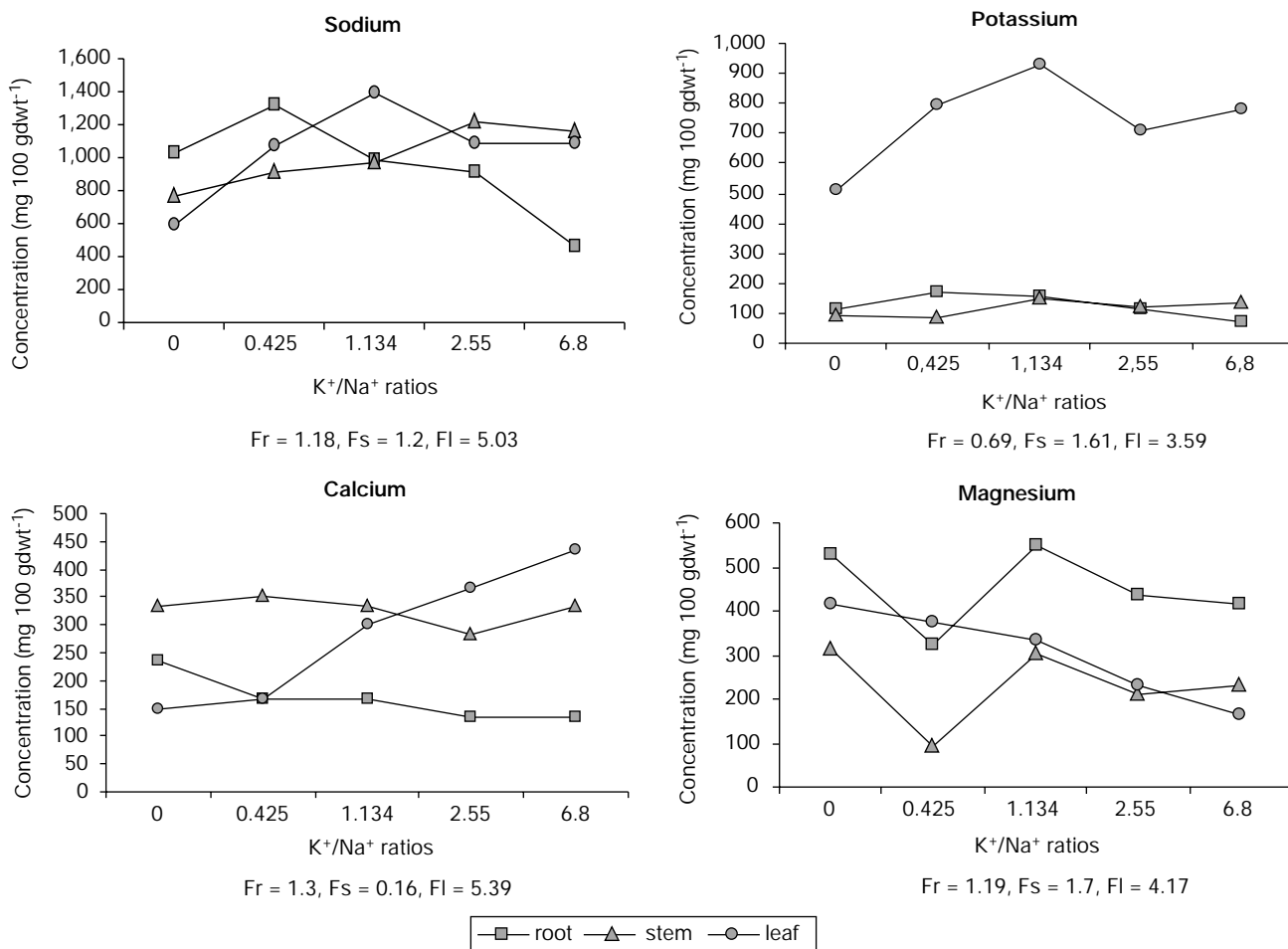


Figure 3. Sodium, potassium, calcium and magnesium content (mg 100 g dwt⁻¹) in roots, stem and leaves of *Vicia faba* at different external K^+/Na^+ ratios. Fr, Fs and Fl are the computed statistical F values for roots, stems and leaves respectively.

The stems showed a tendency to maintain their calcium content at a high concentration (Fig. 3). The concentration of calcium in stems ranged between 284 and 351 mg 100 g dwt⁻¹. The osmotic pressure caused by calcium in stems ranged between 16-20 kPa. There was a decrease in Ca²⁺ concentration in roots with the increase in external K⁺/Na⁺ ratio. On the other hand, there was an increase in leaf content of Ca²⁺ with the increase in external K⁺/Na⁺ ratio. In roots, the osmotic pressure caused by calcium decreased from 13.24 kPa in control to 7.56 kPa at the highest K⁺/Na⁺ ratios. The lowest calcium content in leaves occurred in the control and was about 150.3 mg 100 g dwt⁻¹. This caused an osmotic pressure equal to 8.51 kPa. The gradual increase in leaf calcium content with the increase in external K⁺/Na⁺ ratio reached the highest level 434.2 mg 100 g dwt⁻¹ at the K⁺/Na⁺ ratio 6.8. This concentration caused an osmotic pressure of about 24.58 kPa.

The magnesium content in roots decreased at the 0.425 K⁺/Na⁺ ratio and increased again exceeding the control at the 1.134 K⁺/Na⁺ ratio (Fig. 3). After this, the concentration decreased gradually again. The stems showed approximately the same behavior, but the root Mg²⁺ content was higher than in the stems for all the K⁺/Na⁺ ratios. The root content of Mg²⁺ ranged between 547.2 mg 100 g dwt⁻¹ at K⁺/Na⁺ ratio 2.55 and 415.47 mg 100 g dwt⁻¹ at K⁺/Na⁺ ratio 6.8. In the stems the concentration ranged between 91.2 mg 100 g dwt⁻¹ at the K⁺/Na⁺ ratio 0.425 and 314.13 mg 100 g dwt⁻¹ for the control. The leaf content of magnesium decreased gradually with the increasing external K⁺/Na⁺ ratio. The highest amount was accumulated in the control 415.47 mg 100 g dwt⁻¹ and decreased to reach the lowest concentration 162.13 mg 100 g dwt⁻¹ at the K⁺/Na⁺ ratio 6.8.

Anions studied (chlorides, sulphates and phosphates)

Cl⁻ was the most accumulated anion of the anions studied i.e. chlorides, phosphates and sulphates (Fig. 4). The response of different organs varied according to the external K⁺/Na⁺ ratio. With respect to chlorides, roots showed a gradual decrease in their chloride content with the increase in the external K⁺/Na⁺ ratio. Stems showed an inverse behavior in which their chloride content increased with the increase in the K⁺/Na⁺ ratio. The leaves showed a gradual increase in their chloride content to reach the highest amount at the 2.55 K⁺/Na⁺ value and decreased gra-

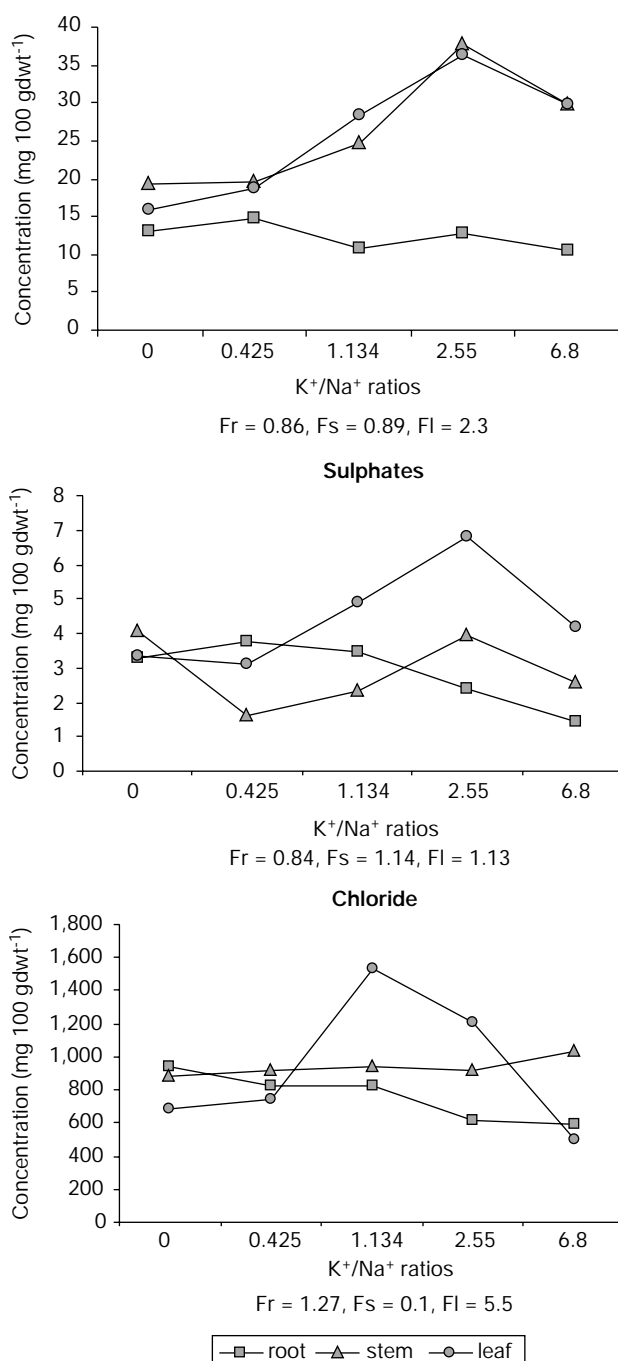


Figure 4. Phosphorus, sulphates and chlorides content (mg 100 g dwt⁻¹) in roots, stems and leaves of *Vicia faba* at different external K⁺/Na⁺ ratios. Fr, Fs and Fl are the computed statistical F values for roots, stems and leaves respectively.

dually again. At the 6.8 K⁺/Na⁺ value, the leaves had the lowest chloride content of all the organs over all the treatments. Osmotic pressure generated by chloride in roots dropped from 60.5 kPa in control to 37.8 kPa at the 6.8 K⁺/Na⁺ value. This was 56.7 kPa in the

stems of control and increased gradually up to 66.2 at the 6.8 K⁺/Na⁺ value. The highest role of chlorides in osmotic pressure was in the leaves at 1.134 K⁺/Na⁺ where it reached 98.34 kPa.

Root phosphorus content declined more than control except at the 0.425 K⁺/Na⁺ value. Generally, the root P content was lower than that in stems and leaves. Both stems and leaves showed the same pattern with a gradual rise in P content compared to control. P content in stems and leaves decreased at 6.8 K⁺/Na⁺ compared to previous treatments but was still higher than the control. Phosphorus played a less important role in osmotic adjustment than chlorides. The osmotic pressure caused by P was less than one kPa in all organs at all treatments.

Sulphates were the lowest accumulated anion. Roots showed the inverse response of stems and leaves. At the 0.425 K⁺/Na⁺ ratio, the sulphate content increased above that of the control value then decreased gradually again. It became less than control at the higher K⁺/Na⁺ ratios in stems, but was still higher in leaves. The highest osmotic pressure caused by sulphates was 0.16 kPa in the leaves at the 2.55 K⁺/Na⁺ value.

The computed ratios (Mg/Ca, Na/K, SAR, Cl/Na+K and S_{K:Na})

As shown in Table 1, the Mg²⁺/Ca⁺ ratio decreased gradually in both leaves and stems with the increase

in external K⁺/Na⁺ ratio and was lower than the control value. In roots, the Mg²⁺/Ca⁺ ratio decreased only at the 0.425 K⁺/Na⁺ value after which the ratio exceeded the control.

The K⁺/Na⁺ ratio decreased gradually in roots until the lowest value 10.7 at the 1.134 K⁺/Na⁺ ratio, then increased again but was still lower than control (Table 1). The stems showed the same behavior. Leaves showed an increase at the 0.425 K⁺/Na⁺ ratio up to 21.57 and decreased gradually but was still higher than control.

With the exception of the last treatment i.e. the 6.8 K⁺/Na⁺ ratio, all the different treatments showed a higher Na/Ca ratio than control, but there was no clear association probably due to the continuous inclusion and exclusion of ions in/out roots. The Na/Ca ratio in stems increased gradually with the increase in external K⁺/Na⁺ ratio. The K⁺/Na⁺ ratio in all the different treatments was higher than control. Leaves showed an increase in the Na⁺/Ca²⁺ ratio up to 5.49 in the treatment with the external K⁺/Na⁺ ratio of 0.425, which then decreased gradually and became less than control at the 2.55 and 6.8 K⁺/Na⁺ ratios.

The sodium absorption ratio (SAR) increased in roots at the 0.425 external K⁺/Na⁺ ratio to the value of 10.19 and decreased again to 3.55 at the external 6.8 K⁺/Na⁺ ratio (Table 1). The latter value was lower than that of the control. Stems showed an increase in their SAR. This was higher than control in the different treatments. The SAR in leaves increased with the

Table 1. Potassium-sodium selectivity, Mg/Ca, Na/K, Na/Ca, sodium absorption ratio (SAR) and Cl/Na+K ratios in faba beans at different external K/Na ratios

Organ	External K/Na	S K:Na	Mg/Ca	Na/K	Na/Ca	SAR	Cl/Na+K
Root	0	0.001623	3.716425	15.40620	3.770583	6.315212	0.569360
	0.425	0.586360	3.201843	12.71455	6.705524	10.185980	0.387196
	1.134	1.044059	5.403110	10.71103	5.039130	6.285406	0.508305
	2.55	0.832251	5.378096	13.43700	5.899435	6.480282	0.414219
	6.8	0.634631	5.127952	11.74746	3.138756	3.552499	0.734156
Stem	0	8.959151	1.550893	14.02001	1.980270	5.422812	0.707181
	0.425	13.327050	0.428818	18.42757	2.233816	8.241919	0.626946
	1.134	15.011890	1.500864	10.96686	2.479617	6.984927	0.591457
	2.55	7.029707	1.236006	16.37566	3.652371	9.754718	0.470632
	6.8	2.630723	1.150662	14.16815	2.944724	8.776114	0.555213
Leaf	0	6.992725	4.558180	11.11096	3.487507	4.415769	0.672402
	0.425	3.845312	3.702131	21.56608	5.489970	7.647454	0.435282
	1.134	9.975908	1.834389	15.61105	3.921860	9.600037	0.692404
	2.55	11.163580	1.046057	14.64477	2.523975	8.071115	0.691314
	6.8	12.792760	0.615739	13.28951	2.124696	8.365958	0.286257

increase in external K⁺/Na⁺ ratio and declined slightly at the higher ratios.

The Cl/Na+K ratio was less than 1 in all the different organs over all the different treatments (Table 1). The lowest value of Cl/Na+K in roots was 0.387 at the external K⁺/Na⁺ ratio 0.425. The highest ratio was about 0.734 at the 6.8 K⁺/Na⁺ ratio. There was no clear association between the Cl/Na+K ratio and the external K⁺/Na⁺ ratio. Stems showed a gradual decrease in the Cl/Na+K ratio with the increase in the external K⁺/Na⁺ ratio. In leaves the Cl/Na+K ratio declined and then increased again at the K⁺/Na⁺ ratio 6.8 to exceed the control value.

Potassium sodium selectivity was very low in roots in the control and increased gradually to reach 1.044 at the K⁺/Na⁺ ratio 1.134, then decreased again (Table 1). Stems showed the same behavior but $S_{K:Na}$ was higher in stems compared with roots. Leaves showed a different behavior where the $S_{K:Na}$ declined at the 0.425 K⁺/Na⁺ ratio and increased gradually to reach its peak at the 6.8 K⁺/Na⁺ ratio (about 12.79). The highest $S_{K:Na}$ value occurred in stems at 1.134 and was around 15.01.

Discussion

The results presented in the current work for different estimated physiological parameters clearly show different responses to the external K⁺/Na⁺ ratio in the five groups of faba bean studied. The ability of plants to maintain a high cytosolic K⁺/Na⁺ ratio is considered as one of the key determinants of plant tolerance (Maathius and Amtmann, 1999).

With regard to the physiological parameter of shoot growth, the increase in K⁺ in the external medium increased the growth rate at higher external K⁺/Na⁺ ratios (Fig. 1). Improvement in the growth of Na⁺-stressed faba bean occurred with the increase in K⁺/Na⁺ ratio (Benlloch *et al.*, 1994). Accumulation of ions in the vacuole is clearly one of the most important strategies employed by plant cells against salt stress (Niu *et al.*, 1995; Hasegawa *et al.*, 2000). So, treated plants showed dependence on Cl⁻, Na⁺, K⁺ and Ca²⁺ in their osmotic readjustment. With the specific functions of every plant organ, it must readjust its osmotic pressure without disturbing its functions. The leaves showed a higher dependence on potassium than other organs. This reflects its importance as a vacuolar osmoticum and also how it is needed as a co-factor for the enzymes (Leigh and Wyn Jones, 1984; Marschner, 1995). The gradual increase in

K⁺: Na⁺ selectivity in leaves indicates the preference of leaves to accumulate K⁺ as compatible osmoticum, essential for stomata opening and closing (Allen *et al.*, 1998). The absence of a K⁺ gradient through the soil and plant parts (Fig. 3), where the roots and stems had very low concentrations of potassium compared with those accumulated in leaves, reflects the high dependence of leaves on K⁺ uptake through K⁺ channels (Amtmann and Sanders, 1998). The parallel behavior of sodium and potassium accumulation (Fig. 3) is due to the competition between Na⁺ and K⁺. Thermodynamics and the interaction between Na⁺ and K⁺ uptake may cause Na⁺ to enter the cell cytoplasm through potassium channels (Schachtman and Liu, 1999).

In spite of the increase in the external K⁺/Na⁺ ratio, the stems were dependent on Na⁺ for osmotic readjustment more than K⁺. The accumulation of Na⁺ in stems is a remarkable feature possibly related to selective transport (Jeschke, 1984). The increase in the K⁺/Na⁺ ratio reduced the influx of Na⁺ (Mendoza *et al.*, 1994) by roots (Fig. 3). The conversion of HKT1 to LCT1 (Mendoza *et al.*, 1994) and the regulation of high-affinity K⁺ uptake (Tie-Bang *et al.*, 1998) under the effect of increasing external K⁺ and the high selectivity of leaves to accumulate K⁺ may cause a slight decrease in the K⁺ accumulated in the roots.

With the dependence of stems on Cl⁻ to readjust their osmotic pressure and the reduction of the influx of Cl⁻ in roots, the root dependence on chloride ions in osmotic adjustment decreased (Fig. 4). Chloride ions declined in leaves at higher K⁺/Na⁺ ratios. This may be due to the dependence on sucrose and malate²⁻ as K⁺ counterion in osmotic adjustment (Talbot and Zeiger, 1998). The Cl/K+Na ratio was, therefore, less than one (Table 1). The availability of potassium insured protein synthesis. Both amino acids and soluble proteins increased with the increase in K⁺/Na⁺ ratio (Fig. 2). Consequently, there was a tendency to accumulate phosphates required for biological synthesis and sulphates for the synthesis of sulphur containing amino acids and proteins (Fig. 3).

The tendency of leaves to accumulate Ca²⁺, as counterion, and release Mg²⁺ reflects the calcium ameliorative role intracellularly (Rengel, 1992). The presence of sufficient Ca²⁺ may decrease or remove the inhibitory effect of high whole-tissue concentration of Na⁺ or K⁺ (Kinraide 1999) and activate the intracellular signaling pathways that control the regulation of Na⁺ or K⁺ transport (Zhu, 2000). Several data showed a decrease in the leaf content of Mg²⁺ with the increa-

se in Ca^{2+} (Ruiz *et al.*, 1997; Bernstein *et al.*, 1974; Bernstein and Hayward, 1958). The contrast in the behavior toward the accumulation of Ca^{2+} and Mg^{2+} may reflect the exchange of magnesium by calcium through non-selective cation channels. This decreased the Mg/Ca ratio from 4.56 in control to 0.6 at the 6.8 K/Na ratio (Table 1). The Mg/Ca ratio decreased slightly in stems, except at the 0.425 K^+/Na^+ ratio, showing the dependence of stems in both divalent cations. The highest value of Mg/Ca was in the roots (Table 1). This may be due to the dependence of roots on Mg^{2+} or the tendency of plants to release the Mg^{2+} outward.

The accumulation of soluble sugars in the different parts of treated plants showed their importance in osmotic adjustment. Carbohydrates are obvious candidates for cytosolic solutes (Raschke, 1975; Outlaw, 1983). The accumulation of inorganic ions in the vacuole requires the accumulation of solutes in the cytosol to balance osmotic potentials between these two compartments (Talbot and Zeiger 1998). The high-accumulated inorganic ions, especially Na^+ , in the vacuole would be toxic to the cytosolic metabolism. There was, therefore, an association between the amount of soluble sugars accumulated and the Na^+ concentration in roots. The availability of K^+ in the external medium reduced the accumulated Na^+ in root vacuoles (Mendoza *et al.*, 1994). Root vacuoles volume represents a low percentage of the total plant volume (Flowers *et al.*, 1986), so, soluble sugars were the main accumulated solutes in the cytoplasm. The availability of K^+ in the external medium as a compatible ion may decrease the dependence on soluble sugars at higher K^+/Na^+ ratios (Fig. 2). Stems and leaves were more dependent on soluble sugars. The increase in K^+ in the external medium supported protein synthesis where the amino acids and proteins increased gradually in the leaves with the increased K^+/Na^+ ratio. The decrease of soluble proteins in roots was associated with an increase in the stems' soluble protein content. This may be due to the translocation of proteins from roots to stems or proteolysis. There was an increased amino acid content in the roots, probably due to proteolysis, to insure the availability of the amino acids required for K^+ transport.

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