Differential Responses in Potassium Absorption and Use Efficiencies in the Halophytes *Catapodium rigidum* and *Hordeum maritimum* to Various Potassium Concentrations in the Medium

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Abstract: The changes in biomass production, root length, mineral nutrition, potassium absorption efficiency (KAE), and potassium use efficiency (KUE) of the halophytes *Catapodium rigidum* and *Hordeum maritimum* in response to potassium availability were assessed under natural conditions. Plants were cultivated in the greenhouse of the experimental station of the Biotechnology Centre of Borj Cédria (a Mediterranean coastal area) 30 km south-east of Tunis for four months from the autumn to winter of 2007–2008. *H. maritimum* biomass production was not significantly affected by the K⁺ concentration, but *C. rigidum* growth was increased significantly with increasing K⁺ concentration in the medium. Root/shoot dry weight ratio remained constant in *C. rigidum*, but decreased significantly at 1000 and 3000 µM K⁺ in *H. maritimum*. KAE increased but KUE decreased significantly with increasing K⁺ concentration in the medium in both species. However, KAE was higher in *H. maritimum* than in *C. rigidum* showing a contrasting response to K⁺ concentration between the two species. Overall, the maintenance of a cationic balance may be explained by cation antagonism. The lower K⁺ requirement of *H. maritimum* to express its optimal growth can be attributed to its higher efficiency to acquire and transfer K⁺ to shoots.

Key words: Biomass production, *Catapodium rigidum*, Cationic balance, *Hordeum maritimum*, Potassium absorption efficiency, Potassium use efficiency.

Potassium is the fourth most abundant mineral, constituting about 2.5% of the lithosphere (Sparks and Huang, 1985). Four different pools can be distinguished according to the availability: solution K⁺, exchangeable K⁺, fixed non-exchangeable K⁺, and K⁺ in primary minerals (Sparks, 1987). Potassium availability for plants is highly variable, due to complex soil dynamics, which is strongly influenced by root-soil interactions (Ashley et al., 2006). Consequently, potassium deficiency is a widespread problem in some soils. The importance of plants native to saline soil, *i.e.*, halophytes for livestock feeding purposes is currently increasing. In this way, the identification, characterization, and development of crops with high K⁺-use efficiency along with K⁺ fertilizer may be a viable strategy to improve yield and reduce production costs (Fageria et al., 1991). In saline areas, halophytes are often exposed to drought and the variable availability of nutrients depending on both time and space. Optimal plant growth is rarely achieved in these areas since most of them are deficient in one or more essential minerals, which may lead to nutrient stress. In saline soils, plants suffer for instance dual injury-sodium toxicity and potassium deficiency (Rubio et al., 1995; Schachtman, 2000; Wang et al., 2004) as a consequence of the competition between potassium and sodium ions to enter the plant cell because they are similar in ionic radius and ion hydration energy (Schachtman and Liu, 1999).

Potassium is an essential macronutrient for the growth of all plants (Schachtman and Liu, 1999). This cation plays vital roles in plant cells including osmoregulation, photosynthesis, enzyme activation, and formation of carbohydrates, nucleic acids, and proteins (Fageria et al., 1997). The effects of potassium deficiency on mineral nutrition have been extensively studied (Diem and Godbold, 1993; Pujos and Morard, 1997). A large variation has been reported in both K⁺ uptake and use efficiencies among crop species and genotypes, including tomato (Chen and Gabelman, 1995), common bean (Fageria et al., 2001), rice (Yang et al., 2004), wheat (Woodend and Glass, 1993; Damon and Rengel, 2007), and canola (Damon et al., 2007).

In saline areas such as Sebkhas, *Catapodium rigidum* and *Hordeum maritimum*, an annual Poaceae with fodder potential are frequently associated with perennial tufts of...
strict halophytes (Abdelly et al., 2006). To elucidate how these two species respond to potassium deficiency, we analyzed the impact of potassium availability on growth, mineral nutrition, and both $K^+$ absorption and use efficiencies for biomass production of these two halophytic species.

**Materials and Methods**

1. **Plant material and growth conditions**

   Seeds of *C. rigidum* and *H. maritimum* were collected from a Sebkha at Soliman (30 km south of Tunis) and were sown in pots filled with 3 kg inert sand. One-week-old seedlings (two per pot) were conserved and irrigated for one month with a 20-fold diluted modified Hewitt (1966) nutrient solution. Plants were then divided into four lots, which were irrigated with complete modified Hewitt nutrient solution containing in mM: 1.5 $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 3.5 $\text{Ca (NO}_3\text{)}_2 \cdot 4\text{H}_2\text{O}$, 5.4 $\text{NaNO}_3$, 2 $\text{NH}_4\text{H}_2\text{PO}_4$, and $K^+$ was supplied as $\text{KCl}$. The micronutrients (ppm) were: Mn (0.5), Cu (0.04), Zn (0.05), B (0.5), Mo (0.02) (Arnon and Hoagland, 1940) and Fe (3) as Na$_2$-Fe-EDTA. $K^+$ was applied at 10, 100, 1000, or 3000 $\mu\text{M} K^+$ for 4 months (5 September 2007 to 5 January 2008). Eight pots each containing 2 plants were used per treatment. The culture was carried out in a greenhouse under natural light conditions with an average day/night temperature of 25/18°C and a relative humidity of 65/90%. The experimental station is located in Borj Cédria, close to the Mediterranean Sea shore, 30 km south-east of Tunis (10°10'E, 36°48'N; 10 m of altitude), with a mean temperature and annual rainfall of 19.4°C and 456 mm, respectively.

2. **Analyses**

   At harvest, plants were divided into roots and shoots and fresh weight was immediately measured. Samples were then oven-dried for 48 h at 60°C for dry weight (DW) determination. Sodium and potassium were assayed by flame spectrometry (Corning photometer) and calcium and magnesium by atomic absorption spectrophotometry after nitric acid extraction ($\text{HNO}_3$, 0.5%) of the finely grounded dry matter. Reduced N was assayed with the Kjeldahl method.

   Potassium absorption efficiency (KAE) was estimated as the ratio of total $K^+$ quantity accumulated in the plant during the experiment to the root dry weight (Rabhi et al., 2007). Potassium-use efficiency (KUE) was calculated from the ratio of the changes in biomass to the amount of potassium accumulated in shoots over the growth period (Rengel and Damon, 2008).

   All data were subjected to a one-way analysis of variance (ANOVA), and means were compared using Duncan test at 5% level of significance, using the SPSS.10.0 Windows (1996) software.

**Results**

1. **Potassium deficiency-related symptoms and plant growth**

   Independent of $K^+$ concentration in the medium, *C. rigidum* was more productive than *H. maritimum* (Table 1). In addition, *C. rigidum* shoot dry weight increased with increasing concentration of potassium in the culture medium whereas root dry weight was maximal at 3000 $\mu\text{M} K^+$. Shoot dry weight of *H. maritimum* was significantly increased only at the highest $K^+$ concentration whereas root dry weight was not affected by the treatments applied. Consequently, whole plant growth of *C. rigidum* increased

### Table 1. Effect of potassium concentration in the culture medium on shoot, root, and whole plant dry weight (DW, g plant$^{-1}$), root/shoot dry weight ratio, and root length (cm) of *Cattapodium rigidum* and *Hordeum maritimum* plants. Means of eight replicates ±SE. Means followed by the same letters are not significantly different at 5% according to the Duncan’s multiple-range test.

|                | Treatments ($\mu\text{M} K^+$) | 10      | 100     | 1000    | 3000    |
|----------------|-------------------------------|---------|---------|---------|---------|
|                |                               |         |         |         |         |
| *C. rigidum*   |                               |         |         |         |         |
| Shoot DW       | 2.09 ± 0.18                   | 2.57 ± 0.28 | 2.98 ± 0.40 | 4.01 ± 0.34 |
| Root DW        | 0.55 ± 0.12                   | 0.59 ± 0.10 | 0.80 ± 0.24 | 1.05 ± 0.09 |
| Whole plant DW | 2.62 ± 0.20                   | 3.17 ± 0.28 | 3.79 ± 0.61 | 5.06 ± 0.36 |
| Root/Shoot     | 0.30 ± 0.04                   | 0.24 ± 0.06 | 0.26 ± 0.06 | 0.26 ± 0.03 |
| Root length    | 25.20 ± 1.7                   | 27.51 ± 1.6 | 24.30 ± 1.9 | 21.30 ± 2.5 |
| *H. maritimum* |                               |         |         |         |         |
| Shoot DW       | 0.73 ± 0.09                   | 0.85 ± 0.15 | 0.97 ± 0.22 | 1.06 ± 0.24 |
| Root DW        | 0.20 ± 0.04                   | 0.23 ± 0.09 | 0.16 ± 0.03 | 0.16 ± 0.03 |
| Whole plant DW | 0.93 ± 0.11                   | 1.08 ± 0.20 | 1.13 ± 0.25 | 1.23 ± 0.27 |
| Root/Shoot     | 0.28 ± 0.05                   | 0.27 ± 0.01 | 0.18 ± 0.04 | 0.16 ± 0.03 |
| Root length    | 28.70 ± 2.8                   | 29.71 ± 2.7 | 18.30 ± 2.2 | 16.30 ± 1.9 |
with increasing K⁺ concentration in the nutrient solution, while no significant effect was detected in *H. maritimum.*  

None of these treatments had any significant effect on the root/shoot dry weight ratio (R/S) in *C. rigidum.* By contrast, in *H. maritimum* R/S ratio was larger at a lower K⁺ concentration (Table 1). In both species, root length was higher at 10, 100, and 1000 µM K⁺ at 3000 µM K⁺ (Table 1).

Symptoms of K⁺ deficiency as necrotic spots were only detected in aged leaves of *C. rigidum* plants grown under 10 and 100 µM K⁺. These symptoms were generally observed around two months after plant treatment.

### 2. Mineral contents

In both species, K⁺ concentration in all plant organs increased with increasing K⁺ supply (Tables 2, 3). In addition, this cation was more accumulated in shoots than in roots. K⁺ concentration in both shoots and roots was markedly higher in *H. maritimum* than in *C. rigidum.*

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**Table 2.** Effect of potassium concentration in the culture medium on potassium, sodium, calcium, magnesium, sum of four cations, and reduced N concentrations (mmol g⁻¹ DW) of shoots and roots of *C. rigidum* plants. Means of eight replicates ± SE. Means followed by the same letters are not significantly different at 5% according to the Duncan’s multiple-range test.

| Treatments (µM K⁺) | 10    | 100   | 1000  | 3000  |
|-------------------|-------|-------|-------|-------|
| **Shoots**        |       |       |       |       |
| K⁺                | 0.15±0.02 a | 0.16±0.02 a | 0.40±0.03 b | 0.74±0.17 c |
| Na⁺               | 2.06±0.34 c | 1.69±0.22 b | 1.17±0.23 a | 1.19±0.18 a |
| Mg²⁺              | 0.24±0.04 b | 0.20±0.02 b | 0.16±0.03 a | 0.14±0.03 a |
| Ca²⁺              | 0.33±0.05 a | 0.33±0.03 a | 0.34±0.05 a | 0.34±0.09 a |
| Sum of four cations| 2.78±0.43 ab | 2.38±0.26 a | 2.06±0.31 a | 2.26±0.61 a |
| N                 | 3.21±0.27 a | 2.75±0.57 a | 2.31±0.21 a | 2.38±0.23 a |

| **Roots**         |       |       |       |       |
| K⁺                | 0.03±0.01 a | 0.04±0.01 a | 0.08±0.01 b | 0.26±0.06 c |
| Na⁺               | 0.65±0.10 b | 0.64±0.06 b | 0.59±0.09 ab | 0.41±0.07 a |
| Mg²⁺              | 0.11±0.01 b | 0.09±0.01 b | 0.06±0.01 a | 0.06±0.01 a |
| Ca²⁺              | 0.16±0.03 a | 0.17±0.04 a | 0.27±0.07 b | 0.28±0.04 b |
| Sum of four cations| 0.95±0.13 a | 0.93±0.07 a | 1.01±0.12 a | 1.00±0.12 a |
| N                 | 1.32±0.30 a | 1.31±0.38 a | 1.28±0.16 a | 1.27±0.06 a |

**Table 3.** Effect of potassium concentration in the culture medium on potassium, sodium, calcium, magnesium, sum of four cations, and reduced N concentrations (mmol g⁻¹ DW) of shoots and roots of *H. maritimum* plants. Means of eight replicates ± SE. Means followed by the same letters are not significantly different at 5% according to the Duncan’s multiple-range test.

| Treatments (µM K⁺) | 10    | 100   | 1000  | 3000  |
|-------------------|-------|-------|-------|-------|
| **Shoots**        |       |       |       |       |
| K⁺                | 0.31±0.01 a | 0.38±0.04 a | 0.96±0.11 b | 1.16±0.05 c |
| Na⁺               | 0.97±0.07 a | 0.98±0.03 a | 0.91±0.01 a | 0.92±0.02 a |
| Mg²⁺              | 0.24±0.01 b | 0.23±0.01 b | 0.17±0.01 a | 0.17±0.01 a |
| Ca²⁺              | 0.37±0.02 b | 0.41±0.04 b | 0.29±0.01 a | 0.29±0.02 a |
| Sum of four cations| 1.88±0.07 a | 2.01±0.08 a | 2.33±0.12 ab | 2.5±0.05 ab |
| N                 | 2.40±0.34 a | 2.63±0.14 a | 2.56±0.21 a | 2.60±0.62 a |

| **Roots**         |       |       |       |       |
| K⁺                | 0.11±0.01 a | 0.12±0.02 a | 0.31±0.11 b | 0.56±0.15 c |
| Na⁺               | 1.01±0.11 d | 0.91±0.07 c | 0.73±0.05 b | 0.61±0.10 a |
| Mg²⁺              | 0.12±0.02 ab | 0.11±0.01 ab | 0.10±0.01 a | 0.09±0.02 a |
| Ca²⁺              | 0.40±0.04 a | 0.42±0.04 a | 0.46±0.04 a | 0.47±0.04 a |
| Sum of four cations| 1.64±0.15 a | 1.55±0.07 a | 1.60±0.13 a | 1.73±0.30 a |
| N                 | 1.85±0.17 a | 2.22±0.30 a | 1.83±0.31 a | 2.07±0.18 a |
Table 4. Effect of potassium concentration (µM) in the culture medium on potassium absorption efficiency (KAE, mmol K g⁻¹ root DW) and potassium use efficiency (KUE, shoot g DW mmol⁻¹ K⁺) in C. rigidum and H. maritimum. Means of eight replicates ± SE. Means followed by the same letters are not significantly different at 5% according to the Duncan’s multiple-range test.

|        | C. rigidum | H. maritimum |
|--------|------------|--------------|
| KAE    |            |              |
| 10     | 3.29 ± 0.53 a | 6.31 ± 1.37 a |
| 100    | 4.58 ± 0.94 b | 10.84 ± 1.00 b |
| 1000   | 11.09 ± 1.27 c | 18.91 ± 3.78 c |
| 3000   | 19.69 ± 2.86 d | 32.58 ± 3.59 d |
| KUE    |            |              |
| 10     | 6.81 ± 0.68 c | 3.28 ± 0.16 d |
| 100    | 6.52 ± 0.61 c | 2.71 ± 0.24 c |
| 1000   | 2.51 ± 0.16 b | 1.08 ± 0.16 b |
| 3000   | 1.57 ± 0.58 a | 0.87 ± 0.03 a |

Excepting H. maritimum shoots, in which the change in Na⁺ concentration was negligible, the Na⁺ concentration decreased with increasing K⁺ concentration in the culture medium (Tables 2, 3). Excepting H. maritimum roots, Mg²⁺ concentrations were higher at a lower K⁺ concentration in the culture medium (Tables 2, 3). Ca²⁺ concentration in H. maritimum shoots decreased significantly at 1000-3000 µM K⁺, while it increased in C. rigidum roots. No significant effect was observed in roots of H. maritimum or shoots of C. rigidum (Tables 2, 3).

Interestingly, the sum of four cations (C⁺ = K⁺ + Na⁺ + Ca²⁺ + Mg²⁺ mmol g⁻¹ DW) obtained by adding the concentrations of each cation per organ was unaffected in shoots and roots of both species despite the wide range of potassium concentrations (Tables 2, 3). No significant impact on reduced N concentration was observed in either species (Tables 2, 3).

3. Potassium absorption efficiency (KAE) and potassium use efficiency (KUE)

KAE increased with increasing K⁺ concentration in the culture medium, but the KAE in H. maritimum was almost two-fold higher that in C. rigidum (Table 4). The changes in biomass production per mmol of K⁺ accumulated in shoots over the growth period, expressed as KUE, showed an opposite tendency (Table 4).

Discussion

Lowering of the K⁺ concentration in the medium restricted substantially the biomass production of C. rigidum shoots and roots (and consequently of the whole plant) and only of H. maritimum shoots, indicating higher tolerance to potassium deficiency of H. maritimum (Table 1).

In our conditions, H. maritimum required only 10 µM K⁺ for maximal growth, in terms of biomass production (Table 1). This suggests that even in the presence of very low K⁺ concentrations in the culture medium, the amount of K⁺ in plant tissues was sufficient to sustain the plant vegetative growth. These findings also demonstrate the capacity of K⁺ uptake mechanisms to take up this cation over a wide range of K⁺ concentrations. In C. rigidum, limits imposed by potassium nutrition to the growth could be due to the incapacity of absorption systems to acquire sufficient amounts of K⁺ for maintaining growth at optimum rates.

The reduction of shoot growth observed in both C. rigidum and H. maritimum exposed to K⁺ shortage could be partly due to smaller leaf expansion (visual observation) and to impaired photosynthetic activity since K⁺ is involved in the photosynthesis processes. K⁺ deficiency has been shown to reduce stomata aperture, thereby impairing CO₂ fixation, and to disturb conversion of light energy into chemical energy, and phloem export of photosynthates from source leaves to sink organs (Cakmak, 2005). Less export of photoassimilates from leaves under K⁺ lacking conditions, thereby inhibiting root growth has been also reported (Cakmak et al., 1994; Gerardeaux et al., 2010). This may have happened in the roots of C. rigidum at 10 and 100 µM K⁺. Visible symptoms of K⁺ deficiency such as necrotic spots were detected only in old leaves of C. rigidum plants grown under 10 and 100 µM K⁺ after two months of treatment. This may represent a survival strategy adopted by plants exposed to K⁺-shortage stress, consisting of the mobilization of K⁺ from mature and senescing organs, to make it available for the youngest ones (Hewitt, 1963). As a consequence, symptoms of K⁺ deficiency usually appear first in the older leaves (Fageria et al., 2001). Cakmak (2005) recently suggested that those signs could be associated with the oxidative degradation of chlorophyll by reactive oxygen species (ROS), whose production is enhanced by K⁺ deficiency.

K⁺ supply can affect the partitioning of dry matter to shoots and roots resulting from differences in assimilate distribution between these two organs. The root/shoot DW ratio under potassium deficiency depends on the species and conditions of culture (Andrews et al., 1999). This was also true in the present study, which revealed that this parameter increased with low K⁺ concentration in H. maritimum, in contrast to C. rigidum (Table 1). Similar results were observed in wheat (Andrews et al., 1999) and mulberry plants (Tewari et al., 2007). However, Cakmak et al. (1994) and Marschner et al. (1996) reported a decrease in root/shoot DW ratio in K⁺-deficient plants, while no statistically significant effect was found in maize plants (Tewari et al., 2004).

The morphological and physiological root characteristics are important for absorbing nutrients from the soil (Sattelmacher et al., 1994). Yang et al. (2003)
showed that the K-efficient rice genotypes had a longer root system than the inefficient ones under low K-conditions. In our experiment, the higher root length in both species at 10, 100, and 1000 μM K- in comparison to that at 3000 μM K- (Table 1) may be a mechanism by which plants increase soil exploration in order to enhance potassium uptake. This morphological adaptive trait was more pronounced in H. maritimum than in C. rigidum since K- concentrations in both shoots and roots were higher in H. maritimum. While changes in root DW and root length of H. maritimum showed a similar pattern, the opposite tendency was observed in C. rigidum, probably due to the reduced number and growth of lateral roots in C. rigidum, as previously reported in maize and Arabidopsis thaliana grown under low K- concentrations (Shin and Schachtman, 2004). Species and genotypes tolerant to nutrient deficiency have also developed specific physiological mechanisms allowing them to acquire sufficient quantities of a specific nutrient (uptake efficiency) and/or to utilize it more effectively (utilization efficiency) (Sattelmacher et al., 1994). The relative tolerance of H. maritimum compared with C. rigidum to K- deficiency was associated with a higher root ability to absorb K+ judging from the higher KAE values in H. maritimum than in C. rigidum (Table 4).

Plants cope with K- deficiency by increasing K+ use efficiency, i.e., the quantity of biomass produced per unit of absorbed K+ (Rengel and Damon, 2008). This parameter is commonly measured in relation to vegetative growth, particularly in forage crops (Woodend and Glass, 1993). In both H. maritimum and C. rigidum, KUE for shoot biomass production increased as K- concentration in the culture medium decreased (Table 4). Contrary to KAE, C. rigidum showed higher KUE values than H. maritimum. This behaviour indicates the higher ability of C. rigidum to counteract K- deficiency in the culture medium by improving K+ translocation towards shoots and its redistribution from older leaves towards the young growing organs. Potassium is highly mobile in the phloem sap, in which it represents about 80% of the total cationic species (Mengel and Kirkby, 1982). Furthermore, this difference in KUE could be attributed to a difference in plant capacity to substitute K+ with other ions (Rengel and Damon, 2008).

Despite the wide range of K- concentrations in the culture medium, changes in shoot or root K+ concentrations were not drastic. For instance, a 300-fold increase in K+ concentration in the external medium (from 10 to 3000 μM) resulted in only a 5- and 8-fold increase in C. rigidum shoot and root K+ concentrations, respectively. In H. maritimum, a 4- and 5-fold increase was observed in shoot and root K+ concentrations, respectively. The comparison between the two species showed that K+ concentrations in both shoots and roots were higher in H. maritimum than in C. rigidum, suggesting that K+ acquisition and transfer to the shoots are differently regulated in both species.

The presence of Na+ and Mg2+ is important in alleviating the effects of K- deficiency. Increased concentrations of Na+, Mg2+, and Ca2+ in response to potassium deficiency and decreased concentrations of these cations under high concentrations of K- have been reported (Diem and Godbold, 1993; Pujos and Morard, 1997). K- and Mg2+ have in part similar roles such as osmoregulation, enzyme activation, and cellular pH control (Marschner, 1986). Na+ could replace K+ in non-specific physiological and biochemical functions (Flowers and Läuchli, 1983). In C. rigidum, there was K+-Na+ and K+-Mg2+ antagonism in both shoots and roots, whereas in H. maritimum, there was K+-Mg2+ and K+-Ca2+ antagonism in shoots but only K+-Na+ antagonism in roots. The occurrence of such antagonisms may have contributed to maintain constant the cation balance for a given organ irrespective of K- external changes (Tables 2, 3). The non-significant effect of K+ supply on reduced N concentrations reveals that N acquisition and assimilation were not affected. Gerardeaux et al. (2010) reported similar results in cotton plants.

In conclusion, the present study revealed the higher tolerance of H. maritimum to potassium deficiency than C. rigidum. This behaviour can be partially attributed to differences in KAE than KUE, suggesting a differential regulation of K+ uptake and transport systems in the two species. This proves the fundamental role of these systems for crop growth under low K- conditions.

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References

Abdelly, C., Barhoumi, Z., Ghnaya, T., Debez, A., Ben Hamed, K., Ksouri, R., Talbi, O., Zribi, F., Ouerghzi, Z., Smaoui, A., Huchzermeyer, B. and Grignon, C. 2006. Potential utilisation of halophytes for the rehabilitation and valorisation of salt-affected areas in Tunisia. In M Öztürk, Y Waisel, MA Khan, G Gök (eds.,) Biosaline Agriculture and Salinity Tolerance in Plants. Birkhäuser Verlag Inc., Switzerland, 163-172.

Andrews, M., Sprent, J.I., Raven, J.A. and Eady, P.E. 1999. Relationships between shoot to root ratio, growth and leaf soluble protein concentration of Pisum sativum, Phaseolus vulgaris and Triticum aestivum under different nutrient deficiencies. Plant Cell Environ., 22: 949-958.

Arnon, D.I. and Hoagland, D.R. 1940. Crop production in artificial solutions and in soil with special reference to factors affecting yields and absorption of inorganic nutrients. Soil Sci. 50: 463-484.

Ashley, M.K., Grant, M. and Grabov, A. 2006. Plant responses to potassium deficiencies: a role for potassium transport proteins. J. Exp. Bot. 57(2): 425-436.

Cakmak, I., Hengeler, C. and Marschner, H. 1994. Partitioning of
shoot and root dry matter and carbohydrates in bean plants suffering from phosphorus, potassium and magnesium deficiency. *J. Exp. Bot.* 45: 1245-1250.

Cakmak, I. 2005. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *J. Plant Nutr. Soil Sci.* 168: 521-530.

Chen, J. and Gabelman, W.H. 1995. Isolation of tomato strains varying in potassium acquisition using a sand-zeolite culture system. *Plant Soil* 176: 65-70.

Damon, P.M., Osborne, L.D. and Rengel, Z. 2007. Canola genotypes differ in potassium efficiency during vegetative growth. *Eu phylta* 156: 387-397.

Damon, P.M. and Rengel, Z. 2007. Wheat genotypes differ in potassium efficiency under glasshouse and field conditions. *Aust. J. Agric. Res.* 58: 816-825.

Diem, B. and Godbold, D.L. 1993. Potassium, calcium and magnesium antagonism in clones of *Populus trichocarpa*. *Plant Soil* 155/156: 411-414.

Fageria, N.K., Baligar, V.C. and Jones, C.A. 1997. In N.K. Fageria, C.A. Jones eds., *Growth and Mineral Nutrition of Field Crops*, 2nd edition; Marcel Dekker, New York.

Fageria, N.K., Barbosa Filho, M.P. and da Costa, J.G.C. 2001. Potassium-use efficiency in common bean genotypes. *J. Plant Nutr.* 24: 1937-1945.

Flowers, T.J. and Läuchli, A. 1983. Sodium versus potassium: substitution and compartmentation. In A. Läuchli, A. Pirson eds., *Inorganic plant nutrition. Encyclopedia of plant physiology*, vol. 15B. Springer Inc., Berlin. 651-681.

Gerardeaux, E., Jordan-Meille, L., Constantin, J., Pellerin, S. and Dingkuhn, M. 2010. Changes in plant morphology and dry matter partitioning caused by potassium deficiency in *Gossypium hirsutum* (L.). *Environ. Exp. Bot.* 67: 451-459.

Hewitt, E.J. 1963. Essential nutrient elements for plants: requirement and interaction in plants. In F.C. Stewart eds., *Plant Physiol*, vol. III. Academic Press Inc., New York, USA. 137-360.

Hewitt, E.J. 1966. Sand and water culture methods used in the study of plant nutrition. *Commonw. Bur. Hort. Tech. Commn.* 22: 431-446.

Marschner, H. 1986. In H. Marschner ed., *Mineral nutrition of higher plants*. Academic Press, London.

Marschner, H., Kirkby, E.A. and Cakmak, I. 1996. Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients. *J. Exp. Bot.* 47: 1255-1263.

Mengel, K. and Kirkby, E.A. 1982. Principles of Plant Nutrition, 3rd edition; International Potsash Institute, Bern, Switzerland.

Pujos, A. and Morard, P. 1997. Effects of potassium deficiency on tomato growth and mineral nutrition at the early production stage. *Plant Soil* 189: 189-196.

Rabhi, M., Barhoumi, Z., Ksouri, R., Abdelly, C. and Gharsalli, M. 2007. Interactive effects of salinity and iron deficiency in *Medicago ciliaris*. *C. R. Biol.* 330: 779-788.

Rengel, Z. and Damon, P.M. 2008. Crops and genotypes differ in efficiency of potassium uptake and use. *Physiol. Plant.* 133: 624-636.

Rubio, F., Gassmann, W. and Schroeder, J.J. 1995. Sodium-driven potassium uptake by the plant potassium transporter HKT1 and mutations conferring salt tolerance. *Science* 270: 1660-1663.

Sattelmacher, B., Horst, W.J. and Becher, H.C. 1994. Factors that contribute to genetic variation for nutrient efficiency of crop plants. *Z Pflanzenphysiol Bodenkd* 157: 215-224.

Schachtman, D. and Liu, W. 1999. Molecular pieces to the puzzle of the interaction between potassium and sodium uptake in plants. *Trends Plant Sci.* 4: 281-287.

Schachtman, D.P. 2000. Molecular insights into the structure and function of plant K+ transport mechanisms. *Biochem. Biophys. Acta* 1463: 127-139.

Shin, R. and Schachtman, D.P. 2004. Hydrogen peroxide mediates plant root cell response to nutrient deprivation. *Proc. Natl. Acad. Sci.* USA 101: 8827-8832.

Sparks, D.L. and Huang, P.M. 1985. Physical chemistry of soil potassium. In R.D. Munson ed., *Potassium in agriculture*. American Society of Agronomy, Madison, Wisconsin, USA, 201-276.

Sparks, D.L. 1987. Potassium dynamics in soil. In B.A. Stewart ed., *Advances in Soil Science*, Springer-Verlag, New York, 1-63.

Tewari, R.K., Kumar, P., Tewari, N., Srivastava, S. and Sharma, P.N. 2004. Macronutrient deficiencies and differential antioxidant responses-influence on the activity and expression of superoxide dismutase in maize. *Plant Sci.* 166: 687-694.

Tewari, R.K., Kumar, P. and Sharma, P.N. 2007. Oxidative stress and antioxidant responses in young leaves of mulberry plants under nitrogen, phosphorus or potassium deficiency. *J. Integr. Plant Biol.* 49: 313-322.

Wang, S.M., Wan, C.G., Wang, Y.R., Chen, H., Zhou, Z.Y., Fu, H. and Sosebee, R.E. 2004. The characteristics of Na+, K+ and free proline distribution in several drought-resistant plants of the Alxa Desert, China. *J. Arid Environ.* 56: 525-539.

Woodend, J.J. and Glass, A.M.D. 1993. Genotype-environment interaction and correlation between vegetative and grain production measures of potassium use-efficiency in wheat (*T. aestivum* L.) grown under potassium stress. *Plant Soil* 151: 39-44.

Yang, X.E., Lu, J.X., Wang, W.M., Li, H., Luo, A.C., Ye, Z.Q. and Yang, Y. 2003. Genotypic difference and some associated plant traits in potassium internal use efficiency of lowland rice (*Oryza sativa* L.). *Nat. Cycl. Agroecosys.* 67: 273-282.

Yang, X.E., Lu, J.X., Wang, W.M., Ye, Z.Q. and Luo, A.C. 2004. Potassium internal use efficiency relative to growth vigor, potassium distribution, and carbohydrate allocation in rice genotypes. *J. Plant Nutr.* 27: 837-852.