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NUTRIENT UPTAKE AND MANAGEMENT UNDER SALINE CONDITIONS IN THE XEROHALOPHYTE: *TECTICORNIA INDICA* (WILLD.) SUBSP. *INDICA*

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In the present investigation, we studied uptake and management of the major cations in the xerohalophyte, *Tecticornia indica* (Willd.) subsp. *indica* as subjected to salinity. Plants were grown under greenhouse conditions at various salinity levels (0, 100, 200 and 400 mM NaCl) over 110 days. At harvest, they were separated into shoots and roots then analyzed for water contents, dry weights (DW), and Na^+, K^+, Ca^{2+}, and Mg^{2+} contents. Plants showed a growth optimum at 200 mM NaCl and much better tissue hydration under saline than non-saline conditions. At this salt concentration (200 mM NaCl), shoot Na^+ content reached its highest value (7.9 $mmol \cdot g^{-1}$ DW). In spite of such stressful conditions, salt-treated plants maintained adequate K^+, Ca^{2+}, and Mg^{2+} status even under severe saline conditions. This was mainly due to their aptitude to selectively acquire these essential cations and efficiently use them for biomass production.

Keywords: Biomass production – cation/sodium selectivity – Na-hyperaccumulation – nutrient use efficiency – xerohalophyte

INTRODUCTION

Halophytes are plants naturally subjected to high salinity levels that could be lethal for most cultivated plants [4]. Greenway and Munns [12] distinguished dicotyledeneous halophytes able to grow at 200 to 500 mM NaCl from monocotyledeneous ones that show a decrease in their growth rate even at 100 mM NaCl. The major differences between them are mainly due to their cell water contents and consequently their vacuolar volume. Dicotyledeneous halophytes can maintain higher sodium contents and Na^+/K^+ ratios since they can accumulate the major part of sodium in vacuoles and require relatively low potassium amounts for metabolism [9]. Nevertheless, differences in halophyte adaptive strategies exist even within the same family [35]. For instance, Chenopodiaceae differ from each other by their aptitude to absorb sodium and their shoot Na^+/K^+ ratio [30]. The Chenopodiaceae *Tecticornia indica* (Willd.) subsp. *indica* (also called *Artrocnemum indicum* (Willd.) Moq., *Salicornia indica* Willd., and *Halosarcia indica* (Willd.) Paul G. Wilson) is one of the fodder xero-

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halophytic species appreciated by dromedary livestock, and occasionally bovines [20]. In saline ecosystems, the tufts of this perennial species offer to several annual glycophytes a favorable microhabitat to grow and considerably contribute to the annual productivity [1]. Dealing with halophyte uses, Koyro et al. [19] said that in the light of the progressive shortage of fresh water resources and soil salinization, a major aim is to evaluate the potential of local (xero-) halophytic species to be widely and economically used in arid and semi-arid regions. In this context, *T. indica* subsp. *indica* is considered as a potential oilseed plant [36]. Moreover, we showed in a previous work that it exhibited a relatively high phytodesalination capacity in its natural biotope as well as in pot experiments [29]. It is, therefore, crucial to study the nutritional behavior of this species under long-term salt treatment.

MATERIALS AND METHODS

Plant growth conditions

T. indica subsp. *indica* cuttings were taken from plants grown in their natural biotope, Soliman sabkha (N-E Tunisia) and immediately transplanted onto sand for rooting. An initial harvest was performed for 12 of the obtained seedlings (4–5 cm of length) and 48 others were cultivated on sand under greenhouse conditions (25 ± 6 °C/10 ± 3 °C day/night temperature, 60 ± 5%/90 ± 5% day/night relative humidity, 14 h/10 h light/dark regime, and 1000–1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR). Each 12 plants were irrigated with Hewitt's [14] nutrient solution at 0, 100, 200, or 400 mM NaCl.

Post-harvest treatment

After 110 days of treatment, plants were harvested, separated into shoots and roots, weighed, oven-dried over one week at 70 °C, weighed again then ground. Nutrient extraction from the obtained powder was performed by a 0.5% HNO_3 solution. Ca^{2+} and Mg^{2+} contents were measured by a VARIAN 220 FS atomic absorption spectrophotometer (Varian, SpectrAA 220FS, Mulgrave, Australia) in the HNO_3 extractions. K^+ and Na^+ contents were determined by a Corning 480 flame photometer (Corning Medical and Scientific. Ltd., Halstead, Essex, England) *i*n the same extractions. K^+ and Na^+ solutions with adequate known concentrations (6 for each cation) were previously prepared by dissolving appropriate KCl and NaCl amounts in a 0.5% HNO_3 solution. K^+ and Na^+ concentrations ranged from 0 to 10 $mg \cdot l^{-1}$ and from 0 to 30 $mg \cdot l^{-1}$, respectively. These solutions were used to calibrate the Corning spectrophotometer. The lowest concentration (0 $mg \cdot l^{-1}$) was used for "0" and the highest one (10 or 30 $mg \cdot l^{-1}$ depending on the concerned cation) was used for "100". A standardizing linear curve was drawn for each of the two minerals and its slope was used to calculate mineral concentrations in the extracts. For readings over 100, adequate dilutions were performed.

Calculated parameters

Relative growth rate (RGW) was calculated according to Hunt's [15] equation: $RGR = (\ln DW_2 - \ln DW_1)/(t_2 - t_1)$, with DW = total plant dry weight (mg), t = time (d), and the subscripts 1 and 2 = initial and final harvests.

The selective accumulations of each cation over Na^+ were estimated through the calculation of cation/(cation + Na^+) ratios in plant organs and their comparison with those of the nutrient medium for each treatment [13].

Nutrient uptake efficiency was determined as the following ratio: $UpE = (Q_2 - Q_1)/\underline{RDW}$, with $(Q_2 - Q_1)$ = the quantity of the nutrient taken up between the initial and the final harvests (110 d), and $\underline{RDW}$ the mean root dry weight during the same period calculated as follows: $\underline{RDW} = (DW_2 - DW_1)/(\ln DW_2 - \ln DW_1)$ [31].

For each nutrient, use efficiency (UsE) was estimated as the following ratio: changes in biomass accumulation to changes in nutrient accumulation over the treatment period (110 d) [28].

The flux of each cation from the medium to plant roots was calculated according to Pitman [28]:

$F_{MR} = (Q_2 - Q_1)/\underline{RDW}^* (t_2 - t_1) = UpE/(t_2 - t_1)$, with $(t_1 - t_2)$ the treatment period (from the initial to the final harvest).

Statistical analysis

Two kinds of analysis were realized using SPSS 11.0 for Windows:

1. A variance analysis of data (One-way ANOVA): means being separated according to Duncan's test at $P \leq 0.05$.

2. A study of relationships between water and sodium contents in shoots and roots by Pearson's correlations.

RESULTS

Biomass production and tissue hydration

Shoot dry weights (DW) increased with the increasing salinity up to 200 mM NaCl, the optimal concentration at which it reached 166% of the control (Table 1). At the highest salinity level (400 mM NaCl), however, shoot growth showed no difference with that of non-treated plants. Similar variations were observed in RGR although results exhibited no significant difference between plants exposed to 100 and 200 mM NaCl. Roots, organs directly in contact with Na^+ and Cl^- ions in the medium, did not show an enhancement in their growth under saline conditions (Table 1). On the contrary, a significant decline in their DW was obtained at 400 mM NaCl. Actually, their RGR decreased from 24.2–25.1 $mg \cdot g^{-1}$ $DW \cdot d^{-1}$ under non-saline and moderate saline conditions to 20.1 $mg \cdot g^{-1}$ $DW \cdot d^{-1}$ under severe salinity. This difference

Table 1
Shoot and root water contents (H_2O) and growth parameters in *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days

NaCl (mM)	0	100	200	400
Shoots (Sh)				
DW ($g \cdot plant^{-1}$)	1.21^{c}	1.67^{b}	2.01^{a}	1.21^{c}
RGR ($mg \cdot g^{-1}$ DW $\cdot d^{-1}$)	25.3^{a}	28.7^{b}	30.1^{b}	25.2^{a}
H_2O ($ml \cdot g^{-1}$ DW)	4.92^{a}	7.06^{b}	7.98^{c}	7.83^{c}
Roots (R)				
DW ($g \cdot plant^{-1}$)	0.35^{b}	0.34^{b}	0.38^{b}	0.21^{a}
RGR ($mg \cdot g^{-1}$ DW $\cdot d^{-1}$)	24.2^{b}	24.4^{b}	25.1^{b}	20.1^{a}
H_2O ($ml \cdot g^{-1}$ DW)	3.38^{a}	6.90^{b}	6.70^{b}	7.76^{b}
Whole plant				
DW ($g \cdot plant^{-1}$)	1.55^{a}	2.01^{b}	2.39^{b}	1.43^{a}
RGR ($mg \cdot g^{-1}$ DW $\cdot d^{-1}$)	25.2^{a}	27.8^{b}	29.1^{b}	24.3^{a}
Root/shoot ratio				
DW	0.31^{b}	0.21^{a}	0.19^{a}	0.19^{a}
RGR	0.96^{c}	0.85^{b}	0.83^{ab}	0.80^{a}

Values are means of 12 replicates. Those with different letters are significantly different according to Duncan's test at $P \leq 0.05$. DW: dry weight and RGR: relative growth rate.

between shoot and root responses to salinity led to a reduction in root/shoot ratio calculated on the basis of DW or RGR. In addition to the beneficial salt effect in terms of biomass production, it significantly ameliorated tissue hydration. In salt-treated plants, water contents varied from 144 to 162% of the control in shoots and from 198 to 230% in roots (Table 1).

Sodium accumulation and nutrient acquisition and distribution

Sodium accumulation

A gradual increase in Na^+ contents with the increasing salinity was observed in both shoots and roots, but the former reached their maximum at 200 mM NaCl, whereas the latter continued to increase up to 400 mM NaCl (Table 2). In addition, for each treatment, shoot sodium contents were about 3-fold those of roots, reaching at 200 and 400 mM NaCl 7.9 versus 2.7–3.1 $mmol \cdot g^{-1}$ DW. *T. indica* subsp. *indica* exhibited an increasing Na^+ flux from the medium to roots with the increasing salinity up to 200 mM NaCl. This was due to the gradual enhancement of Na^+ uptake efficiency (UpE) as salt concentration augmented, reaching 132.2 $mmol \cdot g^{-1}$ root DW at 200 mM

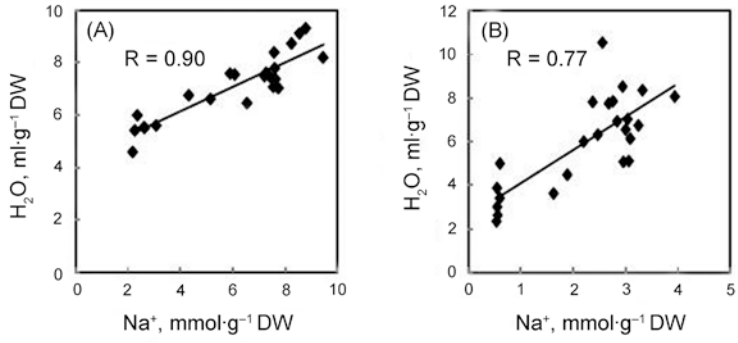

Fig. 1. Correlations between water and sodium contents in shoots (A) and roots (B) of *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days. Points are individual values. Pearson's correlations are significant at 0.01 level

Table 2
Sodium absorption and accumulation parameters in *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days

NaCl (mM)	0	100	200	400
Shoot content (mmol · g^{-1} DW)	2.51[a]	5.92[b]	7.90[c]	7.92[c]
Root content (mmol · g^{-1} DW)	0.56[a]	2.48[b]	2.73[bc]	3.10[c]
Shoot quantity (mmol · $shoot^{-1}$)	2.92[a]	9.67[b]	15.52[c]	9.48[b]
Root quantity (mmol · $root^{-1}$)	0.20[a]	0.86[bc]	0.93[c]	0.70[b]
F_{MR} (mmol · d^{-1} · g^{-1} root DW)	0.22[a]	0.79[b]	1.20[d]	1.02[c]
UpE (mmol · g^{-1} root DW)	24.22[a]	86.83[b]	132.2[d]	112.6[c]

Values are means of 6 replicates. Those followed by different letters are significantly different according to Duncan's test at $P \leq 0.05$. F_{MR}: medium-root flux, UpE: uptake efficiency.

NaCl (Table 2). Under severe salinity conditions (400 mM NaCl), a slight decrease in these two parameters was observed. Therefore, the highest shoot sodium quantity (15.52 mmol) was found in plants treated with 200 mM NaCl. Root Na^+ quantities were much lower than those of shoots and showed the highest value at the same salt concentration (Fig. 1). Nevertheless, a high positive correlation between water and sodium content was observed in both shoots and roots (Fig. 1).

Potassium acquisition, distribution, and use

Under non-saline conditions, shoot and root K^+ contents were 6.7 and 2.2 mmol · g^{-1} DW, respectively (Table 3). Under saline conditions, an obvious decrease in shoot contents with the increasing salinity was noticed, whereas no significant variation was observed in those of roots. As a consequence, accumulated quantities were

Table 3
Potassium status parameters in *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days

NaCl (mM)	0	100	200	400
Shoot content (mmol · g^{-1} DW)	6.65^{c}	3.60^{b}	2.94^{b}	2.00^{c}
Root content (mmol · g^{-1} DW)	2.18^{a}	2.16^{a}	2.02^{a}	2.03^{a}
ΔQ (mmol · $plant^{-1}$)	8.24^{c}	6.34^{b}	6.28^{b}	2.59^{a}
F_{MR} (mmol · d^{-1} · g^{-1} root DW)	0.66^{c}	0.50^{b}	0.46^{b}	0.27^{a}
UpE (mmol · g^{-1} root DW)	72.25^{c}	54.60^{b}	51.07^{b}	29.50^{a}
UsE (g · $mmol^{-1}$)	0.17^{a}	0.32^{b}	0.40^{c}	0.55^{d}

Values are means of 6 replicates. Those followed by different letters are significantly different according to Duncan's test at $P \leq 0.05$. ΔQ: absorbed quantity within the whole plant over the treatment period, F_{MR}: medium-root flux, UpE: uptake efficiency, UsE: use efficiency.

reduced by 23% at moderate salinity level (100–200 mM NaCl) and 66% at severe level (400 mM NaCl). Actually, its influx into roots (F_{MR}) gradually decreased with salinity from 0.66 mmol · d^{-1} · g^{-1} root DW in the control to 0.27 mmol · d^{-1} · g^{-1} root DW at 400 mM NaCl. This was due to a similar gradual diminution in root potassium UpE. Facing such stressing conditions, salt-treated plants considerably enhanced their K^+ use efficiency (UsE) with the increasing salinity, reaching at the highest salt level more than 3 times that of the control (Fig. 2A).

Calcium acquisition, distribution, and use

In control plants, Ca^{2+} ions were equally distributed within tissues showing contents of 0.44 and 0.40 mmol · g^{-1} DW in roots and shoots, respectively (Table 4). Salt presence in the medium reduced shoot calcium contents by 26–30% as compared to the

Table 4
Calcium status parameters in *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days

NaCl (mM)	0	100	200	400
Shoot content (mmol · g^{-1} DW)	0.44^{b}	0.33^{a}	0.31^{a}	0.30^{a}
Root content (mmol · g^{-1} DW)	0.40^{a}	0.41^{a}	0.40^{a}	0.39^{a}
ΔQ (mmol · $plant^{-1}$)	0.58^{b}	0.61^{b}	0.66^{b}	0.38^{a}
F_{MR} (mmol · d^{-1} · g^{-1} root DW)	0.046^{b}	0.47^{b}	0.049^{b}	0.039^{a}
UpE (mmol · g^{-1} root DW)	5.04^{b}	5.21^{b}	5.43^{b}	4.31^{a}
UsE (g · $mmol^{-1}$)	2.48^{a}	3.31^{b}	3.68^{b}	3.70^{b}

Values are means of 6 replicates. Those followed by different letters are significantly different according to Duncan's test at $P \leq 0.05$. ΔQ: absorbed quantity within the whole plant over the treatment period, F_{MR}: medium-root flux, UpE: uptake efficiency, UsE: use efficiency.

control, those of roots being non-affected even at 400 mM NaCl. In terms of absorbed quantities, only the highest salt level induced a significant decrease, while the highest value was found at 200 mM NaCl although differences with those of 0 and 100 mM NaCl were not statistically significant. F_{MR} and UpE exhibited a slight and non-significant increase up to 200 mM NaCl then obviously declined, indicating a noticeable detrimental effect of severe salinity on calcium absorption. Plant use efficiency of this nutrient experienced a significant improvement, mainly at 200 and 400 mM NaCl (Fig. 2B).

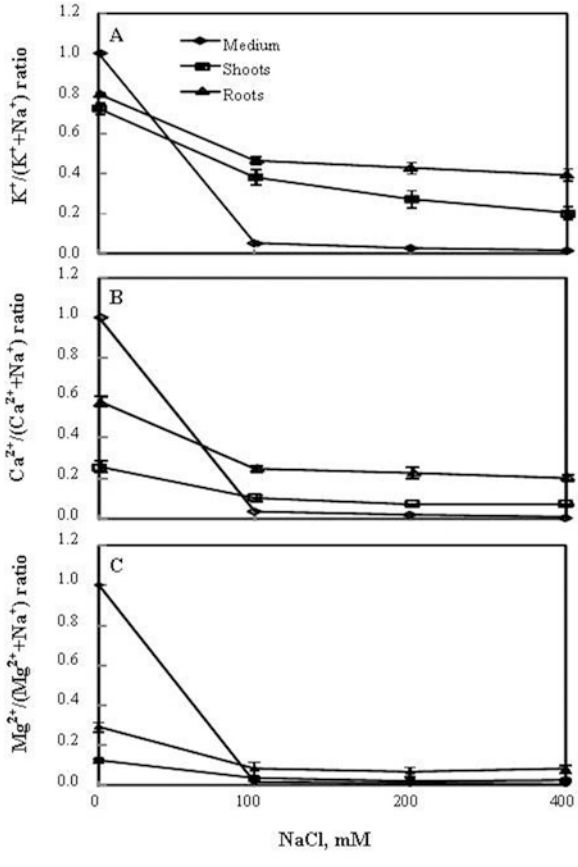

Fig. 2. (A) $K^+/(K^+ + Na^+)$ ratios in the medium and in shoots and roots of *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days. Points are means of 6 replicates ± standard error. – (B) $Ca^{2+}/(Ca^{2+} + Na^+)$ ratios in the medium and in shoots and roots of *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days. Points are means of 6 replicates ± standard error. – (C) $Mg^{2+}/(Mg^{2+} + Na^+)$ ratios in the medium and in shoots and roots of *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days. Points are means of 6 replicates ± standard error

Magnesium acquisition, distribution, and use

Shoots of control plants exhibited a magnesium content of 0.18 mmol·g^{-1} DW (Table 5). This value decreased in salt-treated plants as salt concentration increased in the medium, being reduced at 400 mM NaCl by 50%. In roots, the reduction (27%) was less pronounced. The quantities of this nutrient absorbed during the treatment period were gradually decreased with salinity. This was concomitant with a progressive diminution of both F_{MR} and UpE up to 200 mM NaCl. At the highest salt level, however, these two parameters slightly increased again without reaching the values of the control. To overcome this magnesium shortage, salt-treated plants showed a noticeable increase of its UsE. The highest value was obtained at 200 mM NaCl (15.76 g DW·mmol^{-1}) (Fig. 2C).

Table 5
Magnesium status parameters in *T. indica* subsp. *indica* plants grown under greenhouse conditions at 0, 100, 200, and 400 mM NaCl over 110 days

NaCl (mM)	0	100	200	400
Shoot content (mmol·g^{-1} DW)	0.18^{c}	0.13^{b}	0.12^{b}	0.09^{a}
Root content (mmol·g^{-1} DW)	0.12^{b}	0.10^{a}	0.09^{a}	0.08^{a}
ΔQ (mmol·plant^{-1})	0.23^{c}	0.17^{b}	0.15^{b}	0.12^{a}
F_{MR} (mmol·d^{-1}·g^{-1} root DW)	0.018^{c}	0.013^{b}	0.012^{a}	0.012^{ab}
UpE (mmol·g^{-1} root DW)	1.98^{c}	1.44^{b}	1.27^{a}	1.35^{ab}
UsE (g DW·mmol^{-1})	6.28^{a}	11.98^{b}	15.76^{c}	11.80^{b}

Values are means of 6 replicates. Those followed by different letters are significantly different according to Duncan's test at $P \leq 0.05$. ΔQ: absorbed quantity within the whole plant over the treatment period, F_{MR}: medium-root flux, UpE: uptake efficiency, UsE: use efficiency.

DISCUSSION

Moderate salinity (100–200 mM NaCl) induced a marked stimulation in biomass production of *T. indica* subsp. *indica*, indicating its strict halophytic behavior (Table 1). At 400 mM NaCl, no difference comparing with the control was observed. This makes such a salt concentration the salinity threshold in this species under our experimental conditions. Nagarajan et al. [27] found that growth of *T. indica* subsp. *indica* increased up to 300 mM NaCl. Over this concentration, biomass production of *T. indica* subsp. *indica* noticeably decreased. In *Arthrocnemum macrostachyum*, shoot biomass showed the highest values at 200 to 400 mM NaCl, but it was inhibited at salinities of 600 mM NaCl or higher [17]. The beneficial salt effect on *T. indica* subsp. *indica* growth was more noticeable in shoots than in roots. Similar results were also found by Messedi et al. [25] in *Sesuvium portulacastrum* as subjected to up to 400 mM NaCl. However, although *T. indica* subsp. *indica* maintained a high ability to produce biomass even under severe salinity conditions, it exhibited a low RGR,

which is probably related with its high salinity tolerance [18]. Flowers and Colmer [7] stated also that the RGR values of *T. indica* subsp. *indica* were low.

Under saline conditions, *T. indica* subsp. *indica* exhibited also a better tissue hydration in both shoots and roots (Table 1). This suggests the use of Na^+ ions in osmotic adjustment, mainly in shoots [26]. This hypothesis was confirmed by the existence of high correlations between water and sodium contents in these organs (Fig. 1). Similar results were also found by Sleimi and Abdelly [34] and Messedi et al. [24]. In addition, Nagarajan et al. [27] observed an increase in shoot proline content with the increasing salinity in *T. indica* subsp. *indica*. The property to use Na^+ in osmotic adjustment within shoots conferred to this halophyte a better water status, suggesting the requirements of this element for an adequate physiological function of photosynthetic organs. Another less obvious process of sodium sequestration in vacuoles was also proved by a relatively high correlation between water and sodium contents in roots (Fig. 1). The aptitude of *T. indica* subsp. *indica* to substitute potassium with sodium in osmotic adjustment offered it a better management of the absorbed K^+ quantities by their use only in biomass production [33]. A possibility of remobilization of this essential nutrient from old leaves was also signaled by Ben Hamed et al. [2], since it is with high mobility within phloem sap in which it represents about 80% of the whole cations [23].

In addition to this adaptive response to salinity, salt-treated plants showed high accumulation K/Na selectivity. Actually, $K^+/(K^+ + Na^+)$ ratios measured in their shoots and roots were, respectively, 8–16 and 10–31 those of the medium (Fig. 2A). Our results are in agreement with those obtained in *Hordeum maritimum* L. by Hafsi et al. [13]. These authors attributed such a response to a salt induction of specific K^+ absorption systems. Actually, Maathuis and Sanders [22] demonstrated that the activity of root potassium transporters can be repressed or induced according to plant K^+ status. But, despite the high K/Na absorption selectivity, potassium absorbed quantities as well as K^+ flux from the medium to roots were significantly reduced by salinity. This resulted in an obvious decline in K^+ contents within tissues mainly in shoots. Salt impact on the uptake of this macronutrient has often been attributed to a Na^+ antagonist effect. In this context, it was demonstrated that potassium transporters are also responsible for sodium influx into root cells [5, 16]. These transporters belong at least to two different mechanisms: a high affinity absorption system induced at the micromolar range and a low affinity system induced at the micromolar range [6].

Calcium status was less affected than potassium status. Ca^{2+} UpE was not affected by moderate salinity and showed significant decrease (85% of the control) only at 400 mM NaCl (Table 4). Nevertheless, salt-treated plants maintained an adequate supply of their tissues with this macronutrient. Actually, tissue $Ca^{2+}/(Ca^{2+} + Na^+)$ ratios, particularly in roots, remained obviously higher than those of the medium in each treatment. This clearly indicates a selective uptake of Ca^{2+} towards Na^+ ions (Fig. 2B), since calcium uptake has been often shown to decrease because of ion interaction (mainly sodium antagonism) and precipitation processes [10]. It is thought that Na^+ inhibits Ca^{2+} radial transport from the medium to root xylem through a saturation of cation exchange sites [21]. But such an effect seems to appear in *T. indica*

subsp. *indica* only at the highest salt level. In addition, all salt-treated plants considerably enhanced their efficiency to use this nutrient (Table 4), although it was shown to be more required under saline conditions [8].

Magnesium nutrition was more affected than that of calcium. Actually, all treated plants exhibited lower shoot and root Mg^{2+} contents than the control, since the efficiency of their roots to take it up was significantly affected, reaching the lowest value at 200 mM NaCl (Table 5). Nevertheless, the halophyte exhibited a high accumulation selectivity of Mg^{2+} over Na^{+} ions in roots as well as in shoots (Fig. 2C). Moreover, it improved its Mg^{2+} use efficiency, particularly at 200 mM NaCl (Table 5). In the literature, little importance is often given to magnesium nutrition [11]. Ruiz et al. [32] postulated that salinity reduced leaf Mg^{2+} content in *Citrus*. On the contrary, Bernstein et al. [3] found in several species that increasing NaCl concentrations in the medium had no effect on these contents. Actually, the competition between Mg^{2+} and Na^{+} is less pronounced than that between Mg^{2+} and Ca^{2+} [11].

CONCLUSION

T. indica subsp. *indica* experienced an obligate halophytic behavior and showed a growth optimum at 200 mM NaCl. Its tissue hydration was obviously enhanced due to salinity thanks to its ability to use sodium ions as inorganic osmolytes and consequently to keep potassium ions for biomass production. In addition to the "includer" strategy adopted for Na^{+} two main traits characterized the nutritional behavior of this species under saline conditions. On one hand, it showed high cation/Na selectivity allowing it to acquire potassium, calcium, and magnesium despite the high sodium concentrations in the medium, in particular at 400 mM NaCl. On the other hand, it enhanced nutrient use efficiency, especially that of K^{+}.

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