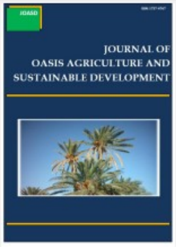

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Performance of the edible halophyte Cakile maritima under critical magnesium and potassium thresholds

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Abstract

In their natural biotope, plants are challenged with low nutrient availability which is one of the most important limiting factors for plant production. Nutrient limitation causes disruption in several metabolic pathways resulting in a decrease in plant growth and establishment. Such responses were mostly studied in glycophytes while in halophytes the data remained scare. In the present investigation, using *Cakile maritima* as a plant model for halophytes, we attempt to elucidate the behavior of this species under critical magnesium and potassium thresholds. Our data showed that low K or Mg supply (0.01 mM) reduced leaf number and biomass production in leaves, stems and roots while both parameters were improved at 0.05 mM Mg and K concentration before reaching an optimum at 0.25 mM Mg and 1 mM K, respectively. Several indices of K and Mg stress tolerance were reduced upon deficiency in both elements and were significantly improved by moderate K and Mg supply. Photosynthetic pigment content was reduced upon both deficiencies with the highest reductions recorded in plants suffering from severe Mg and K starvation. Increasing Mg and K supply resulted in better chlorophyll synthesis as reflected by the increase in chlorophyll stability index parameter (CSI). Furthermore, both deficiencies triggered oxidative damages as malondialdehyde content (MDA) and electrolyte leakage (EL) increased while membrane stability index (MSI) decreased under both deficiencies. Such results suggested that the cell redox homeostasis was altered when Mg and K were omitted from the nutrient solution. Interestingly, moderate and high Mg and K concentrations promoted *C. maritima* growth and reduced the oxidative damage caused by the lack of both elements in the external medium. Overall, *C. maritima* exhibited a typical halophytic behaviour, requiring less macroelements to express its growth performance when cultivated under critical magnesium and potassium thresholds.

1. INTRODUCTION

Nutrient availability is a determinant factor for plant growth and development (Kumar et al., 2021). Plants require many elements for their optimal growth and development and each nutrient plays an essential role in carrying out both physiological and metabolic functions. Thus, its deficiency results in many disorders. Nutrients are classified into macro-elements and micro-elements. Nitrogen (N), phosphorus (P), potassium (K), calcium, sulfur (S), and magnesium (Mg) are known as macro-nutrients because they are required by plants in larger amounts. Iron (Fe), zinc (Zn), copper, boron, manganese molybdenum, and chloride are recognized as micro-nutrients since plants need those elements in smaller quantity.

Within their roles in plants, some similarities and differences between Mg and K were described. The common function associated with Mg and K is their critically contribution to the process of photosynthesis and subsequent long-distance transport of photoassimilates elaborated under such process (Tränkner et al., 2018). Under insufficient K or Mg supply, the disturbance of the photosynthetic machinery results in an over-production of reactive oxygen species which cause damages to membrane integrity and ion transport across those biological barriers. Regarding their flexibility inside the plant cell, the majority of the metabolically active Mg is incorporated into cellular compartments (Waters, 2011), with highest concentrations found generally in chloroplasts (Karley and White, 2009) whereas, K is not bound to organic macromolecules and therefore is more exchanged (Marschner, 2012).

Potassium is the fourth most abundant macro-element in the lithosphere and the second important element after nitrogen (Kumar et al., 2020). In the soil solution, K is found in four forms (*i*) the ionic form (0.1-0.2%), (*ii*) the exchangeable form (1-2%), (*iii*) the non-exchangeable form (1-10%) and (*iv*) the unavailable form (90-98%) (Kumar et al., 2020). K as a mineral nutrient is required in large quantities by plants to ensure optimal growth (White and Karley, 2010; Tränkner et al., 2018). Thus, inside the plant cell, it must be maintained within a range of 100–200 mM in the cytosol to ensure several physiological and metabolic functions (Wang and Wu, 2013). Several roles are attributed to K as it is a cell growth-promoting macro-element through different mechanisms (Oosterhuis et al., 2014), controls photosynthesis (Andrés et al., 2014; Tränker et al., 2018), supports the integrity of chloroplasts and promotes nutrient uptake (Sustr et al., 2019). Besides, K controls stomata movements (Kumar et al., 2020) and contributes to abiotic stress tolerance in plants (Pandey and Mahiwa, 2020). Thus actually K is recognized as a part of the signaling pathways because it interacts with several signaling molecules including calcium and reactive oxygen species to mitigate adverse impacts of many abiotic stresses (Liu and Liao, 2022). In spite of the important roles ascribed to potassium, its availability to plants is low because it is influenced by the physio-chemical properties of the soil (Chen et al., 2016).

Magnesium which is the second most abundant cation in plant living cells after potassium (Kobayashi and Tanoi, 2015) is an essential nutrient playing many physiological and biochemical functions in plants (Marschner, 2012; Verbruggen and Hermans, 2013; Chen et al., 2018). Mg is crucial for chlorophyll synthesis since up to 35% of the total Mg is present in chloroplast and is associated with chlorophyll molecules ensuring light absorption and contributing to the fixation and assimilation of carbon dioxide during the photosynthesis process (Cakmak and Yazici, 2010; Gerendás and Führs, 2013; Hauer-Jákli and Tränkner, 2019; Jia et al., 2021). Furthermore, protein synthesis and enzyme activities depend greatly on Mg. This later is considered as a cofactor of more than 300 enzymes, such as ATPases, phosphatases, carboxylases, and RNA polymerases (Farhat et al., 2016) and ensures the long transport of carbohydrates from source-to-sink organs (Farhat et al., 2016). Besides, it is involved in maintaining ribosome structure (Akanuma et al., 2018). As shown for K, in spite of its abundance in the soil, the availability of Mg for plants is very low since the substantial proportion is incorporated in the crystal lattice structure of minerals that is why it is not directly available for plants (Senbayram et al., 2015). Actually, Mg^{2+} deficiency is very common constraint because of its easy loss from the soil (Wang et al., 2023).

In the rhizosphere, nutrients are in continuous interaction thus, affecting the uptake, transport, or assimilation of each other (Kumar et al., 2021). Some elements are absorbed in synergy while others are taken up in antagonism leading to problems of nutrient imbalance in plants. Synergistic and antagonistic effects between nutrients can occur during their uptake from the soil or their transport from roots to shoots and their distribution within the plant (Xie et al., 2021). Such interaction was evidenced since when a given nutrient is not available for the plant, this later increases the uptake of other nutrients. This is due to an overexpression of nonspecific transporters aimed at improving the uptake of the deficient nutrient (Maillard et al., 2016). For instance, a competitive relationship was described between K and Mg because generally high K concentrations induce Mg deficiency in many agricultural systems (Xie et al, 2021). It has been reported that Mg can partially substitute K in some processes including nitrate reduction, ammonium assimilation, photosynthesis and carbohydrate allocation (Ding et al., 2006; Xie et al., 2021). This competitive effect is attributed to the existence of nonselective ion channels (NSCC) responsible for Mg uptake by plant roots which are also permeable to K (Shabala and Hariadi, 2005). Recently, it has been demonstrated that OsHAK1(i.e. a high-affinity K transporter gene) was up-regulated in rice plants under Mg deficiency. On the other hand, the expression of OsMGT (i.e. an Mg transporter gene) was significantly up-regulated by K shortage (Hermans et al., 2013). Interaction between N and P was also evidenced given that the availability of N can modulate several responses induced by P deficiency (Medici et al., 2019). Nitrate (NO_3) uptake was regulated either by Mg or K since both elements were shown to modulate the activity of enzymes involved in NO_3 metabolism (i.e. nitrate reductase and glutathione synthase) and transport (i.e. NRT2) (Li et al., 2017; Peng et al., 2020; Xu et al., 2020).

Halophytes represent excellent models to study plant response to abiotic stresses known to be intensified in the future because of the current climate change. Besides, in the scenario of the current climate change characterized by an increase of several abiotic stresses, the use of halophytes with potential to be nutritious crops is of great significance since many species were shown to be used as functional foods (Agudelo et al., 2021; Srivarathan et al., 2023). For those raisons, the domestication of halophytes is actually encouraged. Nevertheless, wild species are different from field crop plants and their domestication involves a better understanding of their nutrient needs in order to establish an efficient fertilization system for its commercial cultivation since cultivated soils are generally deficient in one or more nutrient especially Mg and K (Guo et al., 2016; Cui and Tcherkez, 2021). More interestingly, it is well known that the morphological and physiological adaptations of plants to the variations in mineral availability has received actually worth attention (Xiao et al., 2015; Bichara et al., 2021; Kumari et al., 2022). Nevertheless, information regarding halophytes remained scare. This lack of information encouraged us to study the effects of both Mg and K supplies on the halophyte *C. maritima* widely used in human consumption (i.e. salads and generally incorporated in flours to make bread) and characterized by its high tolerance to multiple abiotic stressors including salinity (Houmani et al., 2016) and nutrient deficiencies (Houmani et al., 2022). To the best of our knowledge, limited information is available about *C. maritima* response towards different Mg and K supplement levels. Hence, it is of great interest to evaluate the optimal supplement level of potassium and magnesium for *C. maritima* growth *via* investigating the effects of both elements on several morphological and physiological attributes including shoot length, leaf number, leaf, stem and root growth, chlorophyll content, malondialdehyde, electrolyte leakage, and several K and Mg stress tolerance indices. We hypothesize that *C. maritima* as a halophyte does not require high amount of Mg and K to sustain its growth and development.

2. MATERIAL AND METHODS

2.1. Plant material and growth conditions

Seeds of *C. maritima* were collected in October 2013 at Raoued, a Tunisian city locally close to the Mediterranean coast (20 km from the north of Tunis). Seeds were germinated in petri dishes for 7 days. The germinated seeds were transferred to hydroponic medium containing ½ Hoagland solution. Vigorous seedlings were then subjected to different potassium and Mg supply using a wide range of Mg and K concentrations according to previous studies conducted in our laboratory (Unpublished data). Based on the results obtained in our preliminary study, three concentrations for each element were chosen to investigate some physiological and biochemical responses of *C. maritima* to low (0.01 mM Mg or K), moderate (0.05 mM Mg or K) and high (0.25 mM for Mg or 1 mM for K) Mg or K supply. Adequate concentrations of $NH_4H_2PO_4$, $NaNO_3$ and Na_2SO_4 were added to maintain the concentrations of PO_4, NO_3 and SO_4 when Mg and K were omitted from the nutrient solution.

The experiment was carried out in a greenhouse under sunlight conditions at 23/25 °C in the Center of Biotechnology of Borj Cedria (North-East of Tunisia, 36°42′32.9″N, 10°25′40.9″E).

2.2. Photosynthetic pigment analysis

Chlorophyll concentration was assayed according to Lichtenthaler method (1987). 100 mg of fresh leaves were extracted in 5 ml of 80% (v/v) acetone. Absorbances were read at 663 and 647 nm for chlorophyll a and chlorophyll b, respectively.

2.3. Chlorophyll stability index

Chlorophyll stability index (CSI) was determined according to the method of Sairam et al. (1997) and calculated using the following equation:

$$CSI = (\text{Total chlorophyll of stressed plants} / \text{Total chlorophyll of control plants}) \times 100$$

2.4. Relative electrolyte leakage (EL)

The electrolyte leakage (EL) was determined using an electrical conductivity meter as described previously by Sairam and Srivastava (2002). Fresh Leaf samples were placed in 10 mL of deionized water and incubated in a water bath at 25°C for 2 h. The initial electrical conductivity C1 was read. Then, samples were kept in the same solution and the temperature was raised to 100ºC. After 30 mn, samples were cooled at 25°C and the final electrical conductivity C2 was measured. EL was quantified using the following equation:

EL = (C1/C2) × 100

2.5. Membrane stability index (MSI)

Membrane stability index was calculated using the following equation:

MSI = (1-C1/C2) × 100

2.6. Lipid peroxidation

The quantification of malondialdehyde (MDA), the final product of lipid peroxidation was determined to assess the oxidative stress-induced degradation of unstable lipid peroxides using the thiobarbituric acid method (Draper and Hadley, 1990). Briefly, leaf samples were homogenized in trichloroacetitic acid (TCA, 0.1%) and then, centrifuged at 15,000g for 10 min. The supernatant was collected, mixed with thiobarbituric acid (TBA, 0.5%) prepared in 20% TCA, and the obtained mixture was heated at 95°C for 30 min. The samples were cooled in an ice bath and then, centrifuged at 10.000g for 10 min at 4°C. Finally, the absorbance was read at 532 nm and 600 nm. MDA content was calculated using the molar extinction coefficient of MDA (155 mM^{-1} cm^{-1}).

2.7. Physiological stress tolerance indices

Several indices of stress tolerance were evaluated as described by Kausar et al. (2012) and Majeed et al. (2018) using the following equations:

Shoot fresh weight stress tolerance index (SFSI) = (Shoot fresh weights of stressed plants / Shoot fresh weights of control plants) x 100

Root fresh weight stress tolerance index (RFSI) = (Root fresh weights of stressed plants / Root fresh weights of control plants) x 100

Shoot dry weight stress tolerance index (SDSI) = (Shoot dry weights of stressed plants / Shoot dry weights of control plants) x 100

Root dry weight stress tolerance index (RDSI) = (Root dry weights of stressed plants / Root dry weights of control plants) × 100

Plant dry matter stress tolerance index (DMSI) = (Dry matter of stressed plants / Dry matter of control plants) × 100

2.8. Statistical analysis

Two experiments were carried out to study the effect of three K and Mg levels; 0.01, 0.05 and 1 or 0.25 mM on *C. maritima* seedlings. 1 and 0.25 mM were chosen as optimal concentrations for K and Mg, respectively based on our preliminary study (unpublished data). Eight and four replicates were used for physiological parameters evaluation and biochemical analysis, respectively. Samples were collected after one month of treatment and measurements were made separately for each experiment. The data were analyzed statistically using one-way ANOVA (SPSS, Statgraphics program). Means were statistically compared by Duncan's test at $P < 0.05$ level. Different letters denoted significant differences between the treatments.

3. RESULTS & DISCUSSION

3.1. Effect of K and Mg supply on *C. maritima* growth parameters, leaf number and shoot length

3.1.1. Leaf number and shoot length

To investigate the effect of K and Mg supply on *C. maritima* growth, several attributes were evaluated including shoot height, leaf number and leaf, stem and root biomass production. Our data demonstrated that leaf number was significantly reduced by low K and Mg supply (0.01 mM) (Fig. 1A). The reduction was about 33% upon low K supply while medium K supply (0.05 mM) improved this parameter and values are relatively closed to the control (Fig. 1A). By contrast, low and medium Mg supply declined significantly leaf number with a noticeable effect recorded at low Mg concentration (-48.3%, Fig. 1A). Shoot length was not affected by K supply (Fig. 1B), but, was significantly diminished by low and moderate Mg supply. Reductions were about 30% in both cases (Fig. 1B).

3.1.2. Leaf, stem and root plant growth

The growth of the main plant organs was also evaluated under low, moderate and optimal K or Mg supply. Our data demonstrated that both deficiencies (0.01 mM) reduced significantly leaf, stem ad root fresh weight (Fig. 2).

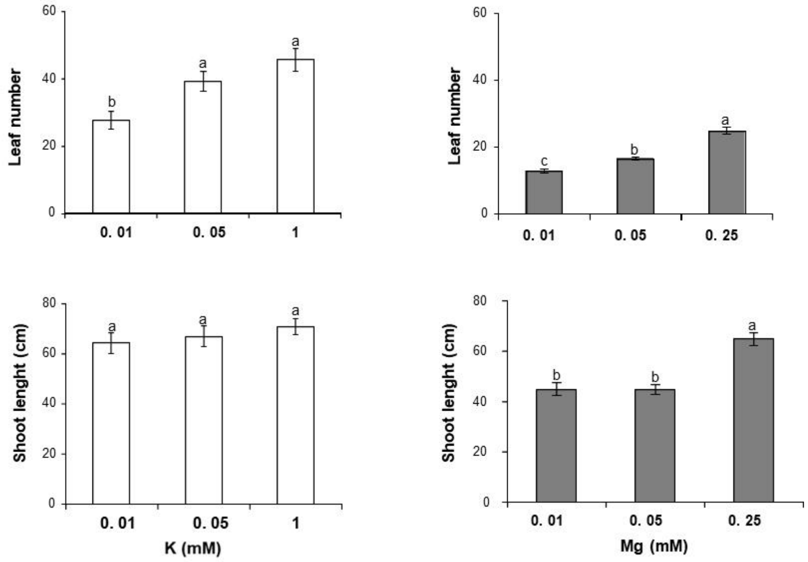

Fig. 1. Effect of different Mg and K supply on leaf number and shoot length. Values are means of 8 replicates. Means followed by the different letters are significantly different at P ≤ 0.05 according to the Duncan's test.

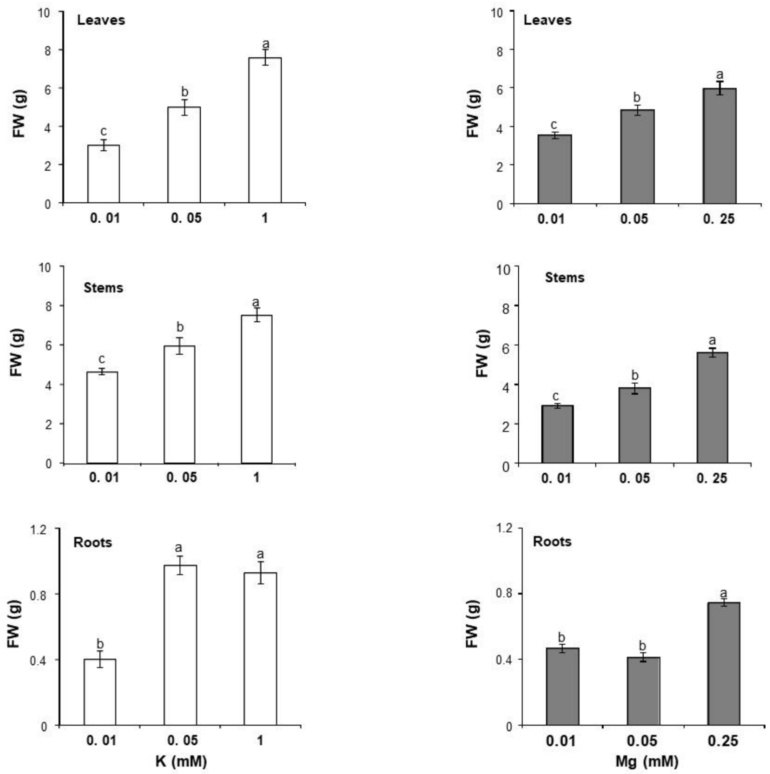

Fig. 2. Effect of different Mg and K supply on leaf, stem and root fresh weight (FW). Values are means of 8 replicates. Means followed by the different letters are significantly different at P ≤ 0.05 according to the Duncan's test.

Low and moderate K supply reduced leaf fresh weight by 60% and 34.2%, respectively (Fig. 2). Stem fresh weight was reduced by 37.2% and 20.3% in plants supplemented by 0.01 and 0.05 mM, respectively (Fig. 2) while root fresh weight was affected only by severe K deficiency (0.01 mM K, Fig. 2).

The growth of the main organs of *C. maritima* was also affected by Mg bioavailability in the external medium. Under Mg deficiency stress, leaf fresh weight was reduced by 40.8% while a slight decrease (-19%) was noted under moderate Mg supply (Fig. 2). Stem fresh weight was also reduced by low Mg supply (-48%) and to less extend by medium Mg concentration (-32%). Mg availability impacted the root biomass production as root fresh weight was decreased by 37.4% and 44.4% under low and moderate Mg supply, respectively (Fig. 2).

3.2. Effect of K and Mg supply on some stress tolerance index

To assess the effect of different K and Mg levels on *C. maritma* growth, some physiological traits were evaluated (Table 1). The data regarding SFSI, RFSI, SDSI and RDSI revealed that at all levels of K and Mg this parameter was reduced but to a less extended at moderate concentration of both elements.

Table 1. Effect of different K and Mg supply on SFSI, RFSI, SDSI, RDSI and DMSI. Values are means of 8 replicates. Means followed by the different letters are significantly different at P ≤ 0.05 according to the Duncan's test.

K (mM)	**0.01**	**0.05**
SFSI	47.58 b	69.35 a
RFSI	43.25 b	101.35 a
SDSI	53.61 b	67.78 a
RDSI	43.02 b	99.51 a
DMSI	52.89 b	73.48 a
Mg (mM)	**0.01**	**0.05**
SFSI	55.06 b	72.82 a
RFSI	62.46 a	56.36 a
SDSI	52.68 b	64.76 a
RDSI	51.46 a	52.9 a
DMSI	51.79 b	63.99 a

Under low K concentration SFSI and RFSI were reduced by 52.4% and 56.7% as compared to plants adequately supplied with K. SFSI was reduced by only 30.6% at moderate K concentration while RFSI was unaffected. SDSI and RDSI decreased by 46.4%and 63.8%, respectively under low K supplementation. Moderate K concentration reduced both parameters only by 32% and 16.4%. SDSI declined by 47.9% in plants suffering severe K deficiency and 27.6% in plants receiving moderate K supply.

Mg supply affected differently the studied physiological indices. Low Mg concentration decreased SFSI and RFSI by 44.9% and 37.5% (Table 1) while moderate Mg supply reduced both parameters by 27% and 43.6%, respectively. SDSI and RDSI decreased by 47.3% and 48.5%, respectively under low Mg supplementation. Moderate Mg concentration reduced both parameters by 35.2% and 47%. SDSI declined by 48% in plants suffering severe Mg deficiency and 36% in plants receiving moderate Mg supply.

3.3. Effect of K and Mg supply on photosynthetic pigments of fully expanded *C. maritima* leaves

Photosynthetic pigments are an integral and vital part of photosynthesis. Their evaluation under stress conditions is an indicator of the integrity of the photosynthetic machinery. Under our experimental design, the quantification of the photosynthetic pigments in the fully expanded leaves of *C. maritima* revealed that chlorophyll *a* (Chl*a*), chlorophyll *b* (Chl*b*) and chlorophyll (*a*+*b*) decreased significantly either by severe K or Mg deficiency (0.01 mM) (Table 2).

Under K deficiency, decreases about 69.4%, b 67.9% and 69% were recorded for Chl*a*, Chl*b* and Chl(*a*+*b*), respectively (Table 2) resulting in a decrease in chlorophyll stability index (CSI, -68.9%). The increase of K concentration in the external medium promoted chlorophyll synthesis as reflected by the significant increase of Chl*a*, Chl*b* and total chlorophyll (Table 2). In fact, Chl*a*, Chl*b*, Chl (*a*+*b*) and CSI increased by 1.9 fold in plants subjected to 0.05 mM K as compared to those receiving 0.01 mM K.

Mg deficiency (0.01 mM) hampers Chl*a*, Chl*b*, Chl (*a*+*b*) content and CSI since reductions of about 70% were recorded under such conditions (Table 2). Increasing Mg bioavailability improved the photosynthetic attributes as plants supplied with 0.05 mM Mg displayed an intermediate behavior as compared to plants receiving 0.01 mM Mg and 0.25 mM Mg (Table 2).

Table 2. Changes in Chla, Chlb, Chl (a+b), and CSI in C. maritima exposed to different K and Mg supply. Values are means of 4 replicates. Means followed by the different letters are significantly different at $P \leqslant 0.05$ according to the Duncan’s test.

K (mM)	**0.01**	**0.05**	**1**
Chl*a* (mg g^{-1} FW)	0.12 c	0.25 b	0.42 a
Chl*b* (mg g^{-1} FW)	0.055 b	0.10 a	0.17 a
Chl(*a*+*b*) (mg g^{-1} FW)	0.18 c	0.35 b	0.59 a
CSI (%)	31.05 c	59.46 b	100.00 a
Mg (mM)	**0.01**	**0.05**	**0.25**
Chl*a* (mg g^{-1} FW)	0.076 c	0.112 b	0.26 a
Chl*b* (mg g^{-1} FW)	0.041 b	0.056 b	0.13 a
Chl(*a*+*b*) (mg g^{-1} FW)	0.12 c	0.168 b	0.39 a
CSI (%)	30.18 c	43.26 b	100.00 a

3.4. Effect of K and Mg supply on some indicators of oxidative damage

Electrolyte leakage and malondialdehyde content are two potential biochemical indicators of oxidative stress. Their evaluation leads to assess the oxidative damage caused by abiotic stresses. EL was enhanced by 36% upon low K availability while it remained unaffected under moderate K concentration (Fig. 3). Likewise, MSI was reduced by 29.8% in plants subjected to K deficiency stress and restored by moderate K supply (Fig. 3). Leaf MDA concentration was stimulated in leaves of *C. maritima* plants suffering severe K stress (+81.8%) (Fig. 3). Moderate K supply enhanced also this parameter but at less extend compared to low K supply (+51.3%) (Fig. 3). Similar findings were obtained under different Mg supply. Inadequate Mg increased EL by 58.5% and 41.5%, respectively in plants cultivated in presence of 0.01 and 0.05 mM Mg. MSI was reduced by 51.6% and, 36.6% under low and moderate supply of Mg (Fig. 3). MDA content was higher in plants lacking Mg reaching the highest value under severe Mg deficiency (+147.8%) (Fig. 3).

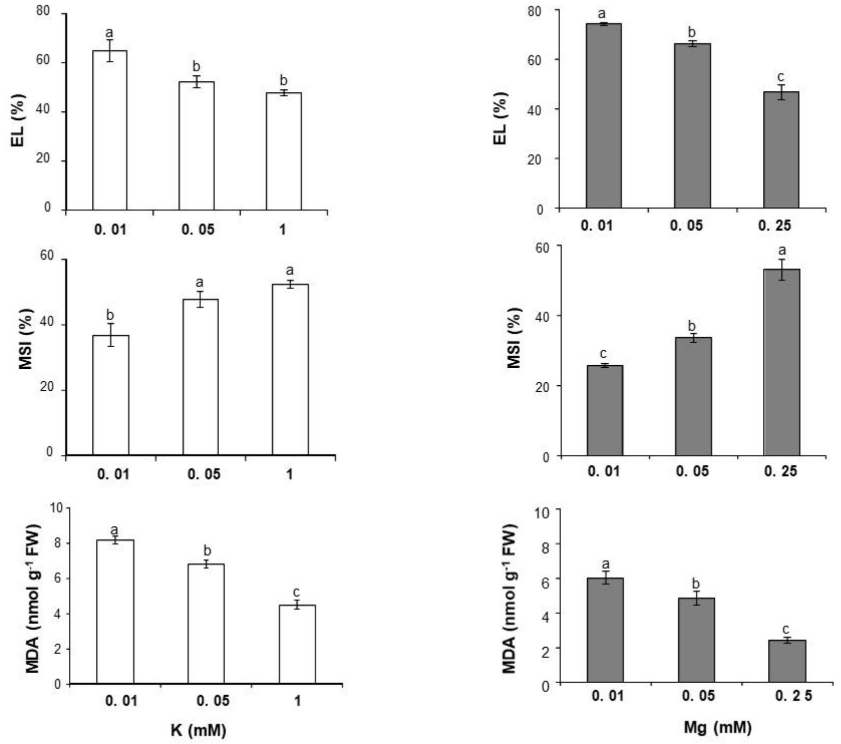

Fig. 3. Effect of different Mg and K supply on electrolyte leakage (EL), membrane stability index (MSI) and malondialdehyde content (MDA). Values are means of 4 replicates. Means followed by the different letters are significantly different at $P \leq 0.05$ according to the Duncan’s test.

4. DISCUSSION

Potassium and magnesium deficiencies are two major constraints affecting plant productivity and quality worldwide (Cakmak, 2010; Hauer-Jákli and Tränkner, 2019). In spite of their simultaneous occurrence in the plant biotope, almost the studies treated either the effect of K or Mg deficiency. Information regarding plant and especially halophyte behavior under different macronutrient supply is scare. In order to overcome these issues, elucidating the effect of different Mg and K supplementation in the edible halophyte *C. maritima* opens new perspectives for halophyte domestication since those species are generally low-requiring nutrient plants. In the present investigation, the response of the halophyte *C. maritima* to low, medium and high K or Mg supply was assessed using some physiological and biochemical parameters. Our data revealed that plants fed with low Mg or K supply (0.01 mM) showed low shoot and root biomass, plant heights and leaf numbers compared to plants amended with medium (0.05 mM) or high (0.25 or 1 mM for Mg and K, respectively) Mg or K concentrations. Such findings could be explained by the fact that both elements are key regulators of plant growth and development (Demidchik, 2014; Liu and Liao, 2022) and are two essential components of photosynthesis; the major metabolic process involved in plant biomass accumulation. It has been reported that several developmental pathways notably plant cell expansion, maintenance of the growth regulatory hormones (i.e. auxin) and assimilate transport via the phloem are K-dependent processes (Sustr et al., 2019). Thus, adequate K was shown to increase root length, density, potential of elongation (Xu et al., 2021) as well as the dry weight of adventitious roots (Devi et al., 2012) and its deficiency inhibits root and shoot elongation (Attia et al., 2022). Consequently, an obvious increment in plant growth and yield was observed when supplied with optimal K amount (Xu et al., 2020) which is in concordance with our findings. Likewise, Mg is fundamental for plant growth and development (Gransee and Fuhrs, 2013) and its deficiency hampers plant growth and photosynthesis functioning as reviewed by Hauer-Jákli and Tränkner (2019). Indeed, common consequences of magnesium deficiency are chlorosis, limited growth, and alteration of biomass allocation between shoots and roots (Verbruggen and Hermans, 2013; Hauer-Jákli and Tränkner, 2019). Our results corroborated recent findings documenting the effect of Mg deficiency on plant shoot and root formation, photosynthetic performance, and cellular stress defense mechanisms in various plant species (Farhat et al., 2014; da Silva et al., 2017; Yang et al., 2017; Rehman et al., 2018; Hauer-Jákli and Tränkner, 2019). Interestingly, *C. maritima* does not require high Mg or K for its growth as compared to other glycophyte plant species such as barley (Tränkner et al., 2016) and apple seedlings (Xu et al., 2020) since it exhibited a typical halophytic behaviour, requiring less macroelements to express its growth performance. Generally, halophytes are less macronutrient-requiring since such species absorb and accumulate preferentially Na^+ over some nutrients and are able to use it for several metabolic pathways involved in biomass production particularly Mg and K. As shown by Marschner (1995) and Wang et al. (2012), halophytes require less K^+ for their growth as compared to glycophytes as such species are able to substitute K^+ with Na^+ notably for osmotic potential in vacuoles (Wakeel et al., 2011) and preserve energy used for osmolyte synthesis to improve their growth. Our data are in agreement with those of Farhat et al. (2015, 2016) who subjected the halophyte *Sulla carnosa* to a wide range of Mg and found that this species was able to survive under low Mg availability (0.01 and 0.05 mM Mg) testifying that halophytes need less macronutrient for their growth and establishment. To approve our results, several tolerance stress indexes were evaluated. We found that all parameters were affected by Mg and K availability in the nutrient solution. A general decrease was observed for both elements with some differences between plants subjected to low and medium nutrient deficiency. In the case of Mg, a similar decrease was shown for RFSI, RFSI, SFSI, SDSI and DMSI at both deficiency levels while was improved in plants grown under moderate K and Mg supply. The degree of stress tolerance was increased with increasing Mg and K levels and was higher in plants subjected to 0.05 mM Mg or K as compared to the deficient dose (0.01 mM Mg or K) demonstrating that this concentration improved several physiological traits in the halophyte *C maritima*.

Our results depicted also a significant decrease in chlorophyll content by both deficiencies. In the case of Mg, plants supplied with low or moderate Mg concentrations showed a significant decrease in Chl*a*, Chl*b* and Chl(*a*+*b*) resulting significant decline in CSI. The severe reduction of chlorophyll content in *C. maritima* leaves by Mg deficiency could be due either to a stimulation of enzymes involved in chlorophyll degradation leading to interveinal chlorosis (Chen et al., 2018; Peng et al., 2019) or to an excessive accumulation of sugars or/and ROS in Mg deficient leaves (Cakmak and Kirkby, 2008). It is well recognized that the most commonly known function of Mg in plants is probably its role as the central atom of the chlorophyll molecule in the light-absorbing complex of chloroplasts and its contribution to photosynthetic fixation of carbon dioxide (Cakmak and Yazici, 2010). Thus, upon Mg deficiency, the breakdown of the chlorophyll molecule impaired photosynthesis and consequently the whole plant growth. Similar findings were obtained in other plant species including *Cucumis melo* and *Sulla carnosa* (Pourranjbari Saghaiesh et al., 2019; Farhat et al., 2014). As shown for Mg, low K supply (0.01 mM) reduced chlorophyll synthesis and lowered the capacity of leaves to retain chlorophyll. Interestingly, at 0.05 mM K all the photosynthetic pigments were improved. Indeed, long term K deficiency exposure resulted in chlorosis and necrosis detected in older leaves, a phenomenon related directly to chlorophyll degradation (Liu et al., 2022), as a direct consequence of an over accumulation of ROS or putrescine (Cakmak, 2005; Qi et al., 2019; Cui and Tcherkez, 2021). In our previous study, we demonstrated that subjecting *C. maritima* to K shortage for 15 days resulted in lower chlorophyll content associated to an accumulation of superoxide anion in leaves suggesting the implication of this free radical in the process of chlorophyll breakdown (Houmani et al., 2022). Our data corroborated previous findings focused in many plant species and demonstrating that K deficiency inhibits the main steps of chlorophyll synthesis but stimulates its degradation as the case of the sensitive line of *Zea mays* and *Ocimum basilicum* (Zhao et al., 2016; Attia et al., 2022).

Inappropriate K or Mg levels may also trigger other stresses which in turn induce oxidative damage to many cellular components. Since Mg is involved in the regulation of chlorophyll metabolism (synthesis and degradation) (Chen et al., 2018; Peng et al., 2019), low Mg availability affects the concentration of chlorophyll in leaves and damaged both photosystem I and II and consequently delayed photosynthetic electron transport (Ye et al., 2019) resulting in an oxidative stress.Indeed, the impairment and/or limitation in the photosynthetic activity as a consequence of a decrease in the rates of CO_2 assimilation (Jezek et al., 2015) results in the formation and accumulation of ROS which are highly toxic and can lethally damage several cell components such as lipids, nucleic acids and proteins (Hauer-Jákli and Tränkner, 2019). Our data demonstrated also that both deficiencies undergo oxidative stress as MDA content, EL and MSI increased under unsuitable supply of Mg and K. The highest values of MDA and EL were found in plants suffering severe Mg or K deficiency (0.01 mM) resulting in low MSI. As a common effect of Mg and K deficiency is the disruption of the electron chain transfer and the generation of free radicals which are harmful for lipids, proteins and nucleic acids causing lipid peroxidation, membrane leakage and protein oxidation and in extreme case DNA damage (Czarnocka and Karpiński, 2018). Similar findings were obtained in *Houttuynia cordata*, and other plant species (Xu et al., 2011; Qi et al., 2019; Ben slima et al., 2022). In our recent study and using the same plant species, we demonstrated that K starvation induced an oxidative stress detected by the excessive accumulation of anion superoxide in leaves associated to an increase in MDA content leading to an activation of the whole anti-oxidative response (Houmani et al., 2022). As for K, Mg shortage is known to increase oxidative damage because electrons and excitation energy are not used in the photosynthetic process leading to an excessive production of ROS in different cell compartments. Similar results were described by Hauer-Jákli and Tränkner (2019) who found that the levels of ROS increased by 31% under Mg deficiency. According to Kobayashi et al. (2018), oxidative stress in Mg deficient leaves may originated from iron toxicity stress as the decrease in Mg concentrations promotes excess iron accumulation and disrupts the main mechanisms involved in the mobilization of toxic iron ions and their storage in vacuoles. Interestingly, moderate Mg or K supply (0.05 mM) mitigated the effects of oxidative stress in *C. maritima* as MDA and El were less important as compared to plants suffering severe Mg or K deficiency. Thus, at this moderate dose the membranes were more stable as reflected by MSI reflecting the role of both elements in maintaining plant membrane stability (Mohamadi et al., 2023).

5. CONCLUSION

In summary our results pointed that *C. maritima* does not require high amount of Mg or K to sustain its growth and development since 0.05 mM of each element was sufficient to promote the biomass production of this halophyte as well as several morphological traits including leaf number, shoot length and to reduce the oxidative damage caused by the lack of both elements in the external medium. Based on these findings, and because the majority of soils are deficient in one or more element, *C. maritima* represents a promising candidate that can be introduced in agriculture since it is an edible plant with low macronutrient requirement.

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