Variations in the growth, oil quantity and quality, and mineral nutrients of chamomile genotypes under salinity stress

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Abstract

Understanding how plants respond to salinity, which severely restricts plant growth, productivity, and survival, is highly important in agriculture. Using three genotypes of *Matricaria recutita* L. (Shiraz, Ahvaz, and Isfahan) with different sensitivity to NaCl, the effect of long-term (about 110 days) NaCl treatments (2.5, 6, 9, and 12 $dS^{*}m^{-1}$) on crop growth, oil quality and quantity, and nutrient variations were investigated to underpin its agricultural management in the future. The adaptation strategy and plant responses were influenced by salinity level, genotype, and genotype × salinity interactions. With higher productivity compared to the Isfahan genotype, the Shiraz and Ahvaz genotypes had efficient Na^{+} exclusion at root surface as an avoidance strategy; however, under higher NaCl concentration, their higher performance were mainly attributed to the Na^{+} sequestration in root vacuoles and higher Ca^{2+}/Na^{+}, Mg^{2+}/Na^{+}, and root/shoot ratios as tolerance strategies. The higher oil yield and chamazulene percentage in the Isfahan genotype were not affected by salinity level and were only genotype dependent. Under 12 $dS*m^{-1}$ NaCl, roots of the Shiraz and Ahvaz genotypes accumulated markedly higher Ca^{2+} (2.5% and 1.5% respectively) and Mg^{2+} (1.6% and 1.3% respectively), required for membrane stability and chlorophyll synthesis, respectively, more than the Isfahan genotype (0.2% Ca and 0.1% Mg^{2+}) and considerably more than the control plants to keep low concentrations of ion toxicity of Na^{2+} and Cl^{-} in shoots. Overall, greater salt tolerance found in the Shiraz and Ahvaz genotypes could be due to a variety of mechanisms, including higher efficiency of nutrient uptake (Ca^{2+}, Mg^{2+}, and Zn^{2+}), utilization (N, P, Ca^{2+}, and Mg^{2+}), compartmentation (Na in roots), and maintenance of higher root/shoot ratios. Taking flower and oil yield as well as chamazulene percentage into consideration, the findings recommended cultivation of the Ahvaz genotype in the absence of salt stress (by 1.18 $g*plant^{-1}$, 6.25 $kg*ha^{-1}$, and 12.54% respectively), the Isfahan genotype under 6 $dS*m^{-1}$ NaCl (by 0.73 $g*plant^{-1}$, 4.84 $kg*ha^{-1}$, and 11.66% respectively), and the Shiraz genotype under high salinity of 9 and 12 $dS*m^{-1}$ NaCl (by 0.68 $g*plant^{-1}$, 5.20 $kg*ha^{-1}$, and 13.46% respectively under 12 $dS*m^{-1}$ NaCl).

Keywords: genetic variation, German chamomile, nutrient composition, salt stress, salt tolerance mechanisms

Introduction

Salinity is a major agro-environmental constraint on crop production, affecting at least 50% (45 million hectares) of all irrigated lands worldwide (Abbasi et al., 2016; Nedjimi, 2016), limiting growth and productivity of plants (Baghalian et al., 2008; Ben Hamed et al., 2014). The area of saline lands is expected to increase due to global climate changes and as a consequence of many irrigation practices (Nedjimi, 2016). A saline soil can be defined as those having a high electrical conductivity of the saturated paste extract (EC) of 4 $dS*m^{-1}$ (4 $dS*m^{-1}$ ≈ 40 mM NaCl) or more. Salt stress causes many adverse effects on crops because plants may suffer high damage due to osmotically induced water stress, specific ion toxicity, ion imbalance, and oxidative stress, i.e., production of reactive oxygen species (ROS), interfering with hormonal control and signalization, cell expansion, differentiation, division, and structure (e.g. chloroplast and cell wall), metabolism (e.g. membrane chemistry and enzyme activity), ion homeostasis, photosynthesis, photorespiration, and transpiration. Salt-induced ROS are highly reactive and toxic to plants and can lead to cell death by causing damage to proteins, membrane lipids, and nucleic acids (Munns et al., 2006; Kaymakanova et al., 2008; Miller et al., 2010; Abbasi et al, 2016). Accumulation of excess Na^+ may perturb metabolic processes where low Na^+ and high K^+ or Ca^{2+} are required for optimum function. For example, a decrease in nitrate reductase activity, inhibition of photosystem II, and chlorophyll breakdown are all associated with increased Na^+ concentrations. Thus, the regulation of Na^+ uptake by cells and long distance Na^+ transport is considered to be a crucial adaptation of plants to salt stress (Munns et al., 2006). Understanding plant responses to salt stress, employing precise agricultural managements, and selecting salt-tolerant crops can help to minimize the negative impact of salinity on crop production and increase agricultural performance. In salty arid and semi-arid regions, where salinity and water scarcity can impose a serious negative impact on agriculture, selection of tolerant genotypes would be an efficient strategy to utilize land resources (Abbasi et al., 2016; Nedjimi, 2016).

German chamomile (*Matricaria recutita* L. also known as *Matricaria chamomilla* L. from Asteraceae family) is a moderately salt-tolerant medicinal plant and a promising candidate for water saving on arid lands with a reasonable performance (Baghalian et al., 2011). Due to genetic diversity and adaptation to different edaphoclimatic conditions in Iran, chamomile has a wide range of genotype distribution (Solouki et al., 2008; Salehi and Nazarian Firouzabadi 2013). According to El Sahhar and Zanati (1981), on the fine-textured soils, *M. recutita* can tolerate salinity levels up to 13 EC and grow better under the sodicity level of 31.8 exchangeable sodium percentage (ESP). Afzali et al. (2011) showed that external application of NaCl up to 4 $dS*m^{-1}$ resulted in improving chamomile growth, while the higher concentration caused a severe negative impact. A review of the pertinent literature reveals that the plant resistance to salinity is mainly associated with the maintenance of higher K^+/Na^+ and Ca^{2+}/Na^+ ratios both in roots and shoots, accumulation of compatible solutes such as proline in leaves, compartmentation of Na^+ in roots, and high root/shoot ratios (Ashraf and Orooj, 2006; Wen-Bo et al., 2008; Abbasi et al., 2016; Nedjimi, 2016; Dhar et al., 2016).

World-widely cultivated for many centuries, chamomile has been used as an alternative medicine because of its healing and pharmacological properties and consumed as functional foods and herbal tea (Wang et al 2005; Srivastava et al., 2010; Sing et al., 2011). Due to a growing demand from the pharmaceutical, cosmetic, food, and hygienic industries for high-quality herbal raw materials, chamomile cultivation has received considerable attention lately (Beier and Ehlert 2014). In spite of conducting many studies on responses of few chamomile genotypes to salinity and drought stresses in recent years, the knowledge about endemic genotype responses on sodic and saline soils is still elusive. Plant responses to specific toxin ions differ and depend on the type of species and genotypes (Abbasi et al., 2016). It is therefore necessary to understand genotype responses to different salinity levels to find out the required managements for their cultivation. So, this study was undertaken to 1) investigate uptake, partitioning, and transportation of nutrients of three endemic chamomile genotypes under four salinity levels 2) find the most salt-tolerant genotype 3) evaluate the interaction effects of genotypes and salinity on plant nutrient composition 4) determine the nutritional value of crops 5) find the correlations between plant nutrient elements of different parts 6) assess the effect of salt-stress on growth, yield, oil production, and chamazulene percentage of different genotypes. The soil tests and plant analysis were performed to improve agricultural management and soil fertilization in the future.

Materials and methods

Seedling preparation

Kabootar-Abad Agricultural Research Station of Isfahan provided seeds, which were sown by hand in a cold frame at 27±5 ˚C and 65±10% RH on 6 October, 2012.

Experimental design and plant preparation

The 6-month-old seedlings having 5 cm height were transplanted on 5 March, 2013 on lines with a length of 10 cm distance within-row and 25 cm between-row spacing. The field experiment was conducted on 36 plots spacing 3 m × 3 m on each side (1579 m above sea level, latitude of 32˚ 36″ north, and longitude of 51˚ 34″ east), during 2012-2013. The soil properties of the location are presented in Table 1. Chamomile has a continuous flowering habit for 2 months, starting from 21 April, 2013 with 10 to16-day harvest intervals. Accordingly, all plants were hand harvested three times at 10-day intervals.

Irrigation with saline water

One month after the seedling transplantation, chamomile genotypes were subjected to different salinity levels, including 2 (control), 6, 9, and 12 $dS*m^{-1}$ NaCl, when field capacity reduced to 50% (about 2 weeks interval on the soil moisture of 2.3 TDR; from 5 April, 2013 to 21 June, 2013). The adjustment of the salinity levels was carried out by adding appropriate amounts of NaCl to water and monitored by a portable EC meter instrument (model AZ8351, China).

Plant growth and yield assessment

The evaluated growth parameters were flower dry weight (g*plant^{-1}) and root dry weight (g*plant^{-1}).

Plant nutrient analysis

The sampling was repeated every 10 days. 5 plants per each plot were hand-harvested for each sample and subsequently separated into roots and flowers (anthodia attached to approximately one cm flower-stalk). Roots were carefully washed with 1% (v/v) HCl to get rid of all the adhering particles and then rinsed several times with distilled water. After oven-drying of the roots at 70 ˚C for 48 hours and air-drying of shoots, samples were grounded in an agate mortar grinder for nutrient analysis. The amounts of P, K^+, Ca^{2+}, Na^{2+}, Cu^{2+}, Zn^{2+}, Fe^{3+}, and Mg^{2+} were determined after the dry ashing method at 550 ˚C for 4 hours (Plank, 1992). The content of N was determined by the conventional Kjeldahl method (Bremner and Mulvaney, 1982). The P content was determined spectrophotometrically at 860 nm (Olsen and Sommers 1982). The concentrations of Na^{2+} and K^+ were determined by flame photometer apparatus (Knudsen et al., 1982). Finally, the amounts of Zn^{2+}, Cu^{2+}, Fe^{3+}, Ca^{2+}, and Mg^{2+} were determined by atomic absorption spectrometer, (Watson et al., 1990).

Essential oil yield and chamazulene percentage

Each flower sample (100 g in triplicate) was subjected to hydro-distillation using a Clevenger-type apparatus for 4 hours according to the method described in the current European Pharmacopoeia Commission (EP) (2010) for determination of oil yield (kg*ha^{-1}). The oils were dried over anhydrous sodium sulphate and kept in a refrigerator at 4˚C in sealed brown vials until they were analyzed. Chamazulene content (%) was then determined spectrophotometrically at 603 nm by using dichloromethane for calibration (Ahmadi-Golsefidi and Soleimani, 2006).

Statistical analysis

Analysis of variance was performed using SAS statistical software (version 9.4) based on the split-plot design arranged in a randomized complete-block trial consisted of four salinity levels as main plots and three genotypes as subplots in triplicate. Using the statistical package MSTAT-C, mean comparisons were performed by Duncan's multiple range test and correlation coefficient between nutrient contents was estimated by Pearson's test ($P \leq 0.05$).

Results and discussion

Soil characteristics

Some physical and chemical properties of the soil are shown in Table 1. The soil was sodic (pH=7.5) and non-saline (EC=2.5 dS*m^{-1}). The soil texture was silty clay loam. Soil organic carbon content was low (0.5%) and the values of available K^+ and P

were 114 and 33.66 mg*kg^{-1}, respectively. The soil had a field capacity volumetric water content of about 22.5% and a permanent wilting point of about 10.1% (Table 1). The effects of salinity on P, K^+, EC, and pH are shown in Table 2.

Table 1. Soil chemical and physical characteristics of the experimental field before chamomile cultivation.

Analysis	Soil depth 0-30 cm
Electrical conductivity (EC)	2.5 dS*m^{-1}
pH	7.5
Field capacity (FC)	22.5%
Permanent Wilting Point (PWP)	10.1%
Saturation percentage (SP)	38.5%
Clay	32%
Silt	50%
Sand	18%
Texture	Silty clay loam
Organic Carbon (OC)	0.5%
Total N	0.04%
Available K^+	110 mg*kg^{-1}
Available P	33 mg*kg^{-1}

Table 2. Soil chemical analysis:
After the first treatment

Salinity treatment (dS*m^{-1})	Available P (mg*kg^{-1})	Available K (mg*kg^{-1})	EC (dS*m^{-1})	pH
Control	33.66	114	1.8	7.5
6	61.83	110	5.5	7.5
9	23.59	114	7.5	7.5
12	30.76	126	11.6	7.5
After the last treatment				
Control	27.12	122	2.2	7.5
6	20.14	104	7.1	7.5
9	31.55	140	9.7	7.6
12	29.70	108	12.2	7.6

Differential responses of genotypes to salinity levels and nutrient variations

Water stress in its broadest sense encompasses both drought and salt stress. Because cell-signaling controls plant responses and adaptation to water stress, scientists believe that resistant plants have more or less similar resistance patterns under both saline and drought stress (Baghalian et al., 2011). Consistent with the findings of the present study, numerous studies show that the interaction among the different parts of a plant is a key factor in genotype to phenotype association (Faccioli et al., 2009). As shown in Table 3, salinity had a significant influence on all mineral nutrients except for the Ca^{2+} and Mg^{2+} in roots. Genotype had a strong influence on

the amounts of N, P, and Mg^{2+} in both roots and flowers and Ca^{2+} in roots, which plays a crucial role in plant responses to environmental stress. Amounts of N and Na^{2+} in roots and flowers and the amounts of K^{+}, Cu^{2+}, Zn^{+}, Ca^{2+}, and Mg^{2+} in roots were considerably influenced by genotype × salinity interactions (Table 3). Salinity reduces photosynthesis primarily by reducing the diffusion of CO_2 to the chloroplast, both by stomatal closure and by changes in mesophyll structure which decreases the conductance to CO_2 diffusion in the leaf. Salt stress can reduce the amounts of Ca^{2+} and Mg^{2+} and, consequently, deteriorate membrane stability and chlorophyll synthesis, respectively (Delfine et al., 1998). Na^{+} ion compete with Ca^{2+} ion for binding sites under salinity and thus crops that have the potential to keep calcium levels high under stress condition can ameliorate the negative effects of Na^{+} toxicity on plant growth and development (Khayyat et al., 2009). Intracellular release of Ca^{2+} ions belongs to the earliest events in signal perception in eukaryotes (Hashimoto et al., 2012). Ca^{2+}-sensor Calcineurin B-like protein (CBL) (Beck et al., 2007) and Ca^{2+}-sensing proteins Calmodulin (CaM) (Virdi et al., 2015) play a crucial role in sensing and signaling involved in a myriad of cellular processes and responses to biotic and abiotic stressors, all of which are important for plant survival under stress conditions (Virdi et al., 2015). Additionally, physiological processes like stomata movement and root hair elongation are accompanied by distinct spatio-temporal changes in Ca^{2+} concentration (Scholz et al., 2015). CBL-interacting protein kinases complexes are crucially involved in relaying plant responses to many environmental signals and in regulating ion fluxes (Hashimoto et al., 2012). Expression profile of CaCBL genes in response to different abiotic stresses and hormones related to development and stresses (abscisic acid, auxin, cytokinin, salicylic acid, and jasmonic acid) at different time intervals suggests their diverse roles in development and plant defense in addition to abiotic stress tolerance (Meena et al., 2015). Consequently, the higher growth and tolerance level of the Shiraz and Ahvaz genotypes might have been attributed to their genotype-specific protection mechanisms and ion homeostasis capacity to maintain particularly higher concentrations of the Ca^{2+} and Mg^{2+} under high salinity levels up to 12 $dS*m^{-1}$ NaCl, strongly more than the concentrations under normal condition (Tables 3, 4, and 6). Compared to the Isfahan genotype, the Shiraz and Ahvaz genotypes, respectively, accumulated more amounts of Na^{+}, Ca^{2+}, Mg^{2+}, and Zn^{2+} in roots under 12 $dS^{*}m^{-1}$ NaCl to the most extent as an adaptation strategy for improving water absorption, nutrient uptake, and ion homeostasis (Table 4).

The lower Na^{+} accumulation of the Shiraz and Ahvaz genotypes under normal condition (Table 4) could be ascribed to the higher capacity and differences in Na^{+} exclusion at the root surface associated with a lower passive sodium permeability of the plasmalemma of epidermal and root cortex cells (Schubert et ., 1990). The adaptation strategy, however, altered under higher salinity levels. Under higher salinity levels both genotypes employed tolerance strategy instead of avoidance strategy by sodium compartmentation in roots, which was evident for the Ahvaz genotype under 9 and Shiraz genotype under 12 $dS*m^{-1}$ NaCl (Table 4). Recent studies indicate that under high salinity levels the capacity for regulation of membrane proteins (ATP-binding cassette transporters for compatible solutes, Na^{+}-dependent transporters, and cell motility proteins) in tolerant plants may provide a major protection strategy against hyperosmotic stress to counteract higher salinity effects (Zhang et al., 2015). Genetic differences in Na^{+} exclusion are highly

correlated with the differences in salinity tolerance. From these results, it can be inferred that under high salinity levels Na^+ transporters of the Shiraz and Ahvaz genotypes avoided shoot Na^+ over-accumulation by mediating Na^+ exclusion from xylem vessels, and subsequently Na^+ retention and sequestration into the root vacuoles to balance the intracellular osmotic status of cells in the presence of a large amount of Na^+ without toxic ion accumulation in the cytosol thereby protecting cells and areal parts of the plant before reaching the toxicity level (Table 4). Energy-dependent Na^+ transport (i.e. against a concentration gradient) across plant cell membranes (plasmalemma and tonoplast) is usually coupled to the proton (H^+) electrochemical potential established by H^+-translocating pumps. The vacuolar Na^+/H^+ antiporter and H^+-pyrophosphatase pump (H^+-PPase) are genotype dependent and confer tolerance to salinity (Goel et al., 2010; Bhaskaran et al., 2011). Additionally, resistant crops benefit from the higher capacity of K^+ - Na^+ homeostasis. Na^+ competes with K^+ in plant uptake specifically through high-affinity potassium transporters and nonselective cation channels. Membrane depolarization caused by Na^+ makes it difficult for K^+ to be taken up by K^+ inward-rectifying channels and increases K^+ leakage from the cell by activating potassium outward-rectifying channels. Minimizing Na^+ uptake and preventing K^+ losses from the cell may help to maintain a K^+ : Na^+ ratio optimum for plant metabolism in the cytoplasm under salt-stress conditions. Besides, K^+ removal by high-yielding crops is exacerbated under sodic or saline-sodic soil conditions as a consequence of K^+-Na^+ antagonism (Wakeel, 2013). Shortage of Ca^{2+} and high Na^+/Ca^{2+} ratio contribute to a general collapse of membrane and cell wall structure, membrane dysfunction and consequently root growth suppression (Ashraf and Wu 1994). Excessive level of Na^+ causes nutrient imbalance, membrane disorganization, growth suppression, inhibition of cell division and expansion (Flowers et al., 1977; Hu and Schmidhalter, 1997) and exerts a profound negative impact on Ca^{2+} mobility and distribution within certain plant organs (Grattan and Grieve, 1998). On the other hand, Ca^{2+} metabolism contributes to preservation and stabilization of cell wall membrane structure, regulation of cell wall enzyme activity, ion ex-change capacity as well as ion transport and selectivity (Marschner 1995; Rengel 1992). Accordingly, the higher yield of the Shiraz and Ahvaz genotypes in addition to their higher root to shoot ratios than the Isfahan genotype under the high salinity levels of 9 and 12 $dS*m^{-1}$ NaCl could be mediated by their superior salt tolerance mechanisms, improved water absorption, nutrient uptake, partitioning, and balance (Tables 3, 4, 5, and 6). However, the severity of the salt stress under 6 $dS*m^{-1}$ NaCl was less pronounced in the Isfahan genotype, by 0.73 $g*plant^{-1}$ dry flower weight compared to the Shiraz and Ahvaz genotypes by 0.44 and 0.37 $g*plant^{-1}$ dry flower weight respectively. Because the differences among nutrient elements were less pronounced under 6 $dS*m^{-1}$ NaCl, the higher flower yield of the Isfahan genotype at this level might have been attributed to the substantial higher peroxidase enzyme activity of this genotype more than other genotypes under all ranges of salinity levels up to 12 $dS*m^{-1}$ NaCl reported by Askari-Khorasgani and coworkers (2017) to protect cells against harmful concentrations of hydroperoxides and ROS (Askari-Khorasgani et al., 2017). Compared to 6 $dS*m^{-1}$ NaCl, 9 and 12 $dS*m^{-1}$ NaCl had less negative impact on root and shoot biomass of the Shiraz and Ahvaz genotypes, which could be ascribed to their tolerance mechanism to maintain higher ion homeostasis, particularly higher Ca^{2+}/Na^+, Mg^{2+}/Na^+ ratios, and higher root/shoot ratios (Tables 4 and 6). In contrast to biomass

production, oil yield and chamazulene percentage were only genotype dependent and were not influenced by salinity so that the Isfahan genotype had superior oil traits under all salinity levels, but without significant differences with the Ahvaz genotype under 2.5 and 6 $dS*m^{-1}$ NaCl and the Shiraz genotype under 6, 9, and 12 $dS*m^{-1}$ NaCl (Tables 5 and 6). Under 12 $dS*m^{-1}$ NaCl, the Shiraz genotype maintained a higher K^+/Na^+ ratio in shoots (Table 4) most likely as a tolerance mechanism to prevent Na^+ and Cl^- levels reaching too high, because the higher K^+/Na^+ and Ca^{2+}/Na^+ ratios in the shoot segment generates lower stress damage (Dasgan et al., 2002; Lambers et al., 2008; Tuteja et al., 2012). The Na^+ translocation from xylem sap of shoot back to root by phloem and subsequently sequestration into the root vacuoles of the Shiraz and Ahvaz genotypes appear to be the main contributory factors for the higher protection strategy against high salinity levels. It can be concluded that the Isfahan genotype had lower capacity to exclude Na^+ ion from shoots, accumulating 3005 ppm Na^+ in shoots under 12 $dS*m^{-1}$ NaCl, while the Shiraz and Ahvaz genotypes respectively accumulated 2490 and 2817 ppm Na^+ (Table 4). From these results, it can be inferred that higher Ca^{2+} and Mg^{2+} uptake and Na^+ retention in roots of the Shiraz and Ahvaz genotypes under 12 $dS*m^{-1}$ NaCl were responsible for creation of the positive charges and increment of the electrochemical gradient (lower potential in cytosol than outer solution) in root rectifying or selective channels to restrict Na^+ and Cl^- uptake and transport to shoots, similar to the findings described by Barker and Pilbeam (2015). Prevention of Cl^- transport from root to shoot has also been reported in the roots containing a relatively high amount of phosphatidylcholine and phosphatidylethanolamine lipid fractions in their membranes as opposed to the root membranes rich in glycolipids (Kuiper 1968). Cl^- transport from root to shoot was strongly restricted in all genotypes most likely as a strategy to escape from the ion toxicity (data not shown).

Nitrogen accumulation was influenced by genotype, salinity, and genotype × salinity interactions (Table 3). Root nutrient analysis showed that the Shiraz and Isfahan genotypes exposed to 12 $dS*m^{-1}$ NaCl and the Shiraz genotype under 2.5 $dS*m^{-1}$ NaCl had the highest N concentration (Table 4). Polyamines are a number of nitrogen containing compounds (NCC) that accumulate in plants exposed to different environmental stresses such as salinity. Osmotic adjustment, protection of cellular macromolecules, storage form of nitrogen, maintaining cellular pH, detoxification of the cells, and scavenging of free radicals are proposed functions for these compounds under stress conditions. NCC accumulation is usually correlated with plant salt tolerance (Mansour, 2000). Polyamines exert their functions through complex interactions with metabolic networks, diverse-signaling pathways, and intricate hormonal cross-talks (Alcázar et al., 2010; Sequera-Mutiozabal et al., 2016). In addition to the salt composition (Abdelgadir et al., 2005), the N form might also affect the plant sensitivity to salinity (Speer and Kaiser 1994). At the whole-plant level, the effect of stress is usually perceived as a decrease in photosynthesis and growth, and it is associated with alterations in C and N metabolism (García-Mata and Lamattina, 2001).

Table 3. Analysis of variance of mineral nutrients of different *M. recutita* genotypes under different salinity levels.

SOV	DF	Means of square									
		N		P		K		Na		Cu	
		Flower	Root	Flower	Root	Flower	Root	Flower	Root	Root	Flower
Replication	2	0.011	0.003	0.005	4569.893	0.058	21719.4	292125.7	129620.2	7.194	6.756
Salinity	3	0.307**	0.019**	0.078**	38759.182**	0.360**	0.3**	6580236.1**	1593053.6**	106.851**	32.395**
Salinity error	6	0.001	0.003	0.002	8855.879	0.051	1365383	159437.8	26633.5	3.018	4.340
Genotype	2	0.087**	0.042**	0.006*	13122.865*	0.024	39905.5	101459.3	41647.2	6.048	2.965
Genotype×Salinity	6	0.037**	0.028**	0.001	2265.286	0.003	422904.8**	216987.4**	700913.1**	6.594	10937*
Experiment error	16	0.003	0.001	0.001	3386.232	0.009	42854.8	38320.1	40434.5	9.854	3.392
CV (%)		4.225	8.004	13.516	22.414	13.114	21.256	11.165	19.890	25.225	21.217

Contd…		Zn		Fe		Ca		Mg	
		Flower	Root	Flower	Root	Flower	Root	Flower	Root
Replication	2	17.062	3.812	533.527	7.155	46.719	0.017	1.731	0.195
Salinity	3	655.435**	34.155**	14927.574**	78.831**	2775.069**	0.414	31.687**	0.317
Salinity error	6	47.525	1.932	945.046	12.733	98.780	0.074	3.026	0.100
Genotype	2	25.520	7.270	81.590	6.490	147.952	7.700**	4.100*	1.592**
Genotype×Salinity	6	19.039	23.724**	560.525	1.916	186.535	2.897**	2.308	1.443**
Experiment error	16	14.430	3.100	631.447	4.009	130.325	0.342	1.127	0.146
CV (%)		12.027	17.682	15.716	36.847	19.119	41.130	31.840	43.631

*Significant at 5% level; **Significant at 1% level; SOV: Source of variations; DF: Degree of freedom; CV: Coefficient of variation.

Table 4. Interaction effects of salinity levels and genotypes on mineral nutrients of three Iranian *M. recutita* genotypes.

Salinity levels ($dS*m^{-1}$)	Genotype	N		P		K		Na		Cu	
		Flower (%)	Root (%)	Flower (%)	Root (ppm)	Flower (%)	Root (ppm)	Flower (ppm)	Root (ppm)	Flower (ppm)	Root (ppm)
Control	Isfahan	1.376ef	0.553b	0.274b	166.7b	0.731bc	1945a	1163e	967cd	15.17a	9.67abc
	Ahvaz	1.703b	0.490c	0.266b	186.9b	0.780abc	1120bcd	1594d	574ef	11.67abc	8.00bcd
	Shiraz	1.693b	0.670a	0.339a	262.9ab	0.770abc	1021cde	1098e	563ef	15.67a	11.17ab
6	Isfahan	1.316f	0.396d	0.138d	182.3b	0.413d	541fg	799e	577ef	8.83bcd	7.17cd
	Ahvaz	1.330f	0.523bc	0.150d	177.0b	0.483d	535g	850e	516f	5.50d	5.33d
	Shiraz	1.126g	0.536bc	0.175cd	241.7ab	0.470d	645efg	903e	697def	7.50cd	6.17cd
9	Isfahan	1.440de	0.536bc	0.368a	255.4ab	0.893ab	1453b	1751d	1436b	14.50cd	8.00bcd
	Ahvaz	1.516cd	0.576b	0.382a	346.3a	0.950a	1308bc	2164c	1867a	14.83ab	10.83ab
	Shiraz	1.370ef	0.546bc	0.388a	337.1a	0.953a	903def	2400c	925cde	13.50ab	13.00a
12	Isfahan	1.610bc	0.670a	0.215bc	301.4a	0.690c	808def	3005a	809c-f	14ab	8.50bcd
	Ahvaz	1.813a	0.403d	0.269b	329.8a	0.803c	823def	2817ab	1125bc	14.8ab	9.67abc
	Shiraz	1.616b	0.710a	0.272b	328.1a	0.866abc	763def	2490bc	2070a	13.3abc	6.67cd

Contd… Salinity levels ($dS*m^{-1}$)	Genotype	Zn		Fe		Ca		Mg	
		Flower (ppm)	Root (ppm)	Flower (ppm)	Root (ppm)	Flower (%)	Root (%)	Flower (%)	Root (%)
Control	Isfahan	30.0c	13.5ab	158a	6.21ab	6.1b	2.333a	3.535b	1.708a
	Ahvaz	32.0bc	10.2cde	188a	8.29a	5.9b	0.175c	6.286a	0.107d
	Shiraz	33.0bc	8.2cde	170a	7.54a	8.4a	0.894bc	4.580ab	0.766bcd
6	Isfahan	23.7d	7.5e	92b	0.17c	3.1c	1.651ab	0.076c	0.901bc
	Ahvaz	15.2e	7.8de	111a	0.25c	3.8c	0.215c	0.620c	0.241cd
	Shiraz	20.9de	7.5e	95b	2.64bc	3.3c	2.460a	1.145c	0.728bcd
9	Isfahan	35.2abc	9.7cde	192a	6.31ab	6.3ab	2.498a	3.449b	1.389ab
	Ahvaz	37.5ab	7.5e	173a	6.78a	6.8ab	0.164c	3.727b	0.114d
	Shiraz	36.7abc	11bcd	172a	6.51a	6.5b	2.299a	3.708b	1.380ab
12	Isfahan	38.5ab	8.7cde	197a	6.08ab	7.6ab	0.287c	3.629b	0.131d
	Ahvaz	35.9abc	11.5bc	176a	6.62a	6.6ab	1.526ab	3.581b	1.379ab
	Shiraz	41.7a	16.5a	191a	7.86a	7.3ab	2.555a	5.682a	1.675a

Values followed by the same letter in each column are not significantly different at 5% probability level by Duncan's multiple range test.

Table 5. Analysis of variance of the physiological and phytochemical traits of three *M. recutita* genotypes under salinity stress.

SOV	DF	Means of square			
		FDW	RDW	Oil yield	Chamazulene
Replication	2	0.05	0.0003	0.34	3.355
Salinity	3	0.59**	0.0006*	3.57	18.286
Salinity Error	6	0.032	0.0004	1.6	23.159
Genotype	2	0.17**	0.0019**	7.77**	100.935**
Genotype× Salinity	6	0.14**	0.001**	2.15	12.063
Total Error	16	0.012	0.0001	1.1996	18.274
CV%		15.19	18.87	21.13	34.59

*Significant at 5% level; **Significant at 1% level; SOV: Source of variations; DF: Degree of freedom; CV: Coefficient of variation; FDW: Flower dry weight; RDW: Root dry weight.

Table 6. Interaction of salinity levels and genotypes on morpho-physiological and phytochemical traits of *M. recutita*.

Salinity levels $dS*m^{-1}$	Genotype	FDW ($g*plant^{-1}$)	RDW ($g*plant^{-1}$)	Oil yield ($kg*ha^{-1}$)	Chamazulene (%)
Control	Isfahan	0.78c	0.06bcd	6.95a	17.83a
	Ahvaz	1.18a	0.05cd	6.25abc	12.54abc
	Shiraz	1.32a	0.08b	4.62b-e	9.90bc
6	Isfahan	0.73c	0.06bcd	4.84a-e	11.66abc
	Ahvaz	0.44e	0.07bc	4.13cde	8.79bc
	Shiraz	0.37e	0.05cd	4.55b-e	10.32abc
9	Isfahan	0.45de	0.04d	6.47ab	15.84abc
	Ahvaz	0.72c	0.08b	4.08de	9.31bc
	Shiraz	0.98b	0.11a	5.68a-d	13.21abc
12	Isfahan	0.44e	0.04d	5.95a-d	16.75ab
	Ahvaz	0.64cd	0.07bc	3.41e	8.66c
	Shiraz	0.68c	0.07bc	5.20a-e	13.46abc

Values followed by the same letter in each column are not significantly different (Duncan's multiple range test, at %5 probability level); FDW: Flower dry weight; RDW: Root dry weight.

It has been found that organic fertilization and mineral elements such as phosphorus and nitrogen can regulate plant drought stress responses by maintaining a higher relative water content, lower malondialdehyde, and promoting antioxidant enzyme activity such as superoxide dismutases and peroxidase (Li-Ping et al., 2006). N uptake and metabolism affect plant nutrient composition (Kováčik et al., 2012), contributing to nutrient balance and plant resistance to salt-stress (Mahmood and Kaiser 2003; Abdelgadir et al., 2005). Therefore, application of appropriate N fertilizer rate and source is a requirement of good agricultural practices in chamomile, which can affect not only quantitative traits but also its qualitative traits such as pharmaceutical properties and nutritional values (Andrzejewska and Woropaj-Janczak 2014).

Growth, oil content, and chamazulene percentage

Duncan results indicated that dry flower weight and dry root weight were highly affected by salinity, genotype, and genotype × salinity interactions (Table 5). By contrast, Baghalian and coworkers' (2008) results showed that the salinity levels had no significant effect on dry flower weight. The plant's responses to salinity was dependent on genotype, environmental conditions (soil type, soil fertilisation, agricultural practices, composition of ions, and climate), and genotype-environment interactions (Baghalian et al., 2008), indicating the importance of conducting this study before cultivation on a large-scale. In this study, oil yield and chamazulene percentage were only affected by genotype and not by salinity or genotype × salinity interactions; however, the negative impact of sodium ions on oil content and composition have been reported by Ram et al. (1999) and Prasad et al. (2006).

Studies indicate that phenotype expressions are under the influence of multiple gene interactions whose expression is often dependent on environmental conditions and developmental stage. These results will be useful for pyramiding of quantitative trait locus and microarray analysis in chamomile breeding programs (Gosal et al., 2010). Studies show that different responses of chamomile genotypes to salt and drought stresses (Baghalian et al., 2008) could have been attributed to the genotype-by-environmental interactions.

The experiment concluded that chamomile can represent high agronomic performance with sufficient medicinal properties through proper genotype selection and agricultural management. Consistently, Baghalian and coworkers showed that saline irrigation water and drought had no significant effect on oil quantity, oil quality, and apigenin content of chamomile (Baghalian et al., 2008; Baghalian et al., 2011). Therefore, cultivation of chamomile on a large scale can be successfully accomplished on saline water, where cultivation of field crops irrigated with fresh water is not possible.

Correlation between nutrient elements

As described earlier, the significant correlations among the Zn^{2+} and Mg^{2+}, Fe^{3+}, and Ca^{2+} pointed toward their synergistic effects on improving nutrient utilization and crop performance. The results indicate that the correlations among N, P, and Cu^{2+} in relation to Na^{+} content may lead to a better nutrient uptake and Na^{+} compartmentation in roots (Tables 6 and 7). Thus, chamomile, particularly the Isfahan genotype, may benefit from the application of fertilizers containing N, P, Zn^{2+} and Mg^{2+}, Ca^{2+}, and Fe^{3+}. Consistently, Nasiri et al. (2010) findings corroborated the beneficial impact of foliar application of ferrous sulphate and zinc sulphate at both stem elongation and flowering stages of chamomile on improving flower yield and oil content. The positive influence of Fe^{3+}, Zn^{2+}, Mn^{2+} and Cu^{2+} nutrients compensate their deficiency in arid- and semi-arid regions by regulating metabolism and synthesis of enzymes and proteins and stabilization of cell and membrane structures (Nasiri et al., 2010), hence conferring stress tolerance through better perception, signal transduction, modification of metabolite pathways and consequently osmotic regulation, and detoxification (Tuteja et al., 2012).

Table 7. Simple correlation coefficient of flower and root nutrient composition of *M. recutita* genotypes under different salinity levels.

Characteristics		Flower N	Root N	Flower P	Root P	Flower K	Root K	Flower Na	Root Na	Flower Cu	Root Cu
Flower	N	1									
Root	N	0.169	1								
Flower	P	0.345	0.301	1							
Root	P	0.3942	0.358	0.577*	1						
Flower	K	0.037	0.082	0.404	0.398	1					
Root	K	-0.056	-0.094	0.393	-0.062	0.258	1				
Flower	Na	0.589*	0.270	0.416	0.812**	0.162	0.179	1			
Root	Na	0.214	0.358	0.509	0.636*	0.515	0.404	0.532	1		
Flower	Cu	0.625*	0.349	0.778*	0.524	0.224	0.438	0.578*	0.468	1	
Root	Cu	0.317	0.107	0.782**	0.499	0.300	0.212	0.377	0.111	0.730**	1

Contd…

Characteristics		Flower Zn	Root Zn	Flower Fe	Root Fe	Flower Ca	Root Ca	Flower Mg	Root Mg	Root Cl
Flower	Zn	1								
Root	Zn	0.518	1							
Flower	Fe	0.896**	0.475	1						
Root	Fe	0.868**	0.513	0.904**	1					
Flower	Ca	0.860**	0.393	0.896**	0.873**	1				
Root	Ca	0.098	0.514	-0.103	0.014	-0.118	1			
Flower	Mg	0.788*	0.568	0.873**	0.957**	0.802**	-0.076	1		
Root	Mg	0.271	0.721**	0.121	0.194	0.143	0.884**	0.113	1	
Root	Cl	-0.121	-0.117	0.329	-0.312	-0.312	0.149	-0.289	0.137	1

*Significant at 5% level; **Significant at 1% level.

Sufficient amounts of micronutrients contribute to metabolism changes (e.g. saccharide) (Nasiri et al., 2010), hydraulic conductivity associated with hormonal regulation (e.g. cytokinin, abscisic acid, and ethylene) (Ehlert et al., 2011), nutrient availability, (Ehlert et al., 2009), maintenance of photosynthesis, cell wall extensibility (Ehlert et al., 2011), and finally cell division and expansion (Nasiri et al., 2010; Dosio et al., 2011). As recommend by recent findings, agricultural performance of chamomile can be improved by applying vermicompost (20 ton*ha^{-1}) and foliar spraying of amino acids at both budding and flowering stages (Hadi et al., 2011). Mycorrhizal inoculation can also be applied as another efficient agricultural practice to promote plant growth and tolerance exposed to stressors by improving water use efficiency and nutrient uptake such as P, Zn^{2+}, K, Ca^{2+}, and Mg^{2+} concentrations and Ca^{2+}/Na^{+}, and Mg^{2+}/Na^{+} ratios (Wu et al., 2009).

Conclusions

Taken together, a higher nutrient uptake and balance associated with higher salt resistance were evident in the Shiraz and Ahvaz genotypes, respectively, while the Isfahan genotype was less tolerant. A higher root to shoot ratio, and capacity for sodium retention in root were regarded as the main morpho-physiological and biochemical adaptations to salinity, leading to the higher productivity and resistance of the Shiraz and Ahvaz genotypes to high salinity levels up to 12 dS*m^{-1}. The results provide the motivation for conducting further studies to alleviate the negative effects of salt and water stress on chamomile by mycorrhizal inoculation, fertilization and foliar application of Ca^{2+}, Mg^{2+}, K^{+}, Fe^{3+}, and Zn^{2+}. Additionally, high-throughput screening techniques such as DNA microarrays and quantitative trait locus analysis can be employed for the evolution of superior chamomile genotypes in the future.

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