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EFFECTS OF SALINITY AND THE INTERACTION BETWEEN *THYMUS VULGARIS* AND *LAVANDULA ANGUSTIFOLIA* ON GROWTH, ETHYLENE PRODUCTION AND ESSENTIAL OIL CONTENTS

M. Pilar Cordovilla,[1] Milagros Bueno,[1] Carolina Aparicio,[1] and Miguel Urrestarazu[2]

[1]*Departamento de Biología Animal, B. Vegetal y Ecología, Facultad de Ciencias Experimentales, Universidad de Jaén, Jaén, Spain*
[2]*Departamento de Producción Vegetal, Escuela Superior de Ingeniería, Universidad de Almería, Almería, Spain*

□ *This study evaluated the effects of salinity on thyme (*Thymus vulgaris*) and lavender (*Lavandula angustifolia*) plants grown alone and in combination with each other. After transplanting, two-month-old plants received nutrient solutions supplemented with 0, 50, and 100 mM sodium chloride (NaCl) for 21 d. Thyme and lavender grown alone were each more tolerant to salt stress than thyme and lavender grown together. In the 100 mM NaCl treatment, all lavender plants grown with thyme died. In thyme, the carbon (C) and nitrogen (N) contents of the roots increased. Ethylene production in thyme was stimulated by salinity only in plants that interacted with lavender. However, in lavender, ethylene production was not influenced by the presence of thyme. The production of essential oils (EOs) was increased by salinity in thyme plants, whereas the EO production of lavender plants depended on the presence of thyme.*

Keywords: C content, lavender, N content, interaction, salt stress, thyme

INTRODUCTION

Water scarcity in the Mediterranean basin is one of the main factors limiting agricultural development, particularly in the period of 2000–2025 (Chartzoulakis et al., 2002). To overcome water shortages and satisfy the increasing water demand for agricultural development, the use of water of

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Address correspondence to M. Pilar Cordovilla, Departamento de Biología Animal, B. Vegetal y Ecología, Facultad de Ciencias Experimentales, Universidad de Jaén, Campus Las Lagunillas s/n, E-23071, Jaén, Spain. E-mail: mpilar@ujaen.es

marginal quality (brackish, reclaimed, and drainage) will become necessary in many countries (Hamdi et al., 1995; Correia, 1999). However, the use of saline water for irrigation requires an adequate understanding of how salts affect plant performance.

The effects of salinity on plants are evidenced by a moderate to severe reduction in plant growth and yield, and plant death may occur if saline conditions persist (Storey and Walker, 1999; Parida and Das, 2005). Osmotic stress and ion toxicity have been identified as probable causes of salinity toxicity. Osmotic stress is associated with the lack of cell wall extension and cell expansion, which leads to the cessation of growth. The ionic effect interferes with nutrient imbalance, nitrogen uptake, and the transport of essential ions within the plant as well as lowers net photosynthetic rates in the affected plants (Greenway and Munns, 1980). The molecular mechanisms of signal transduction and the physiological consequences of altered gene expression in plant salt tolerance (e.g., osmolyte biosynthesis, osmolyte function, and transport of ions for maintenance and re-establishment of homeostasis) are well understood (Hasegawa et al., 2000; Munns, 2005).

Ethylene is involved in plant responses to a variety of biotic and abiotic stresses (Morgan and Drew, 1997). This hormone may modulate the physiological effects induced by salinity (Gómez-Cárdenas et al., 1998). Many steps in ethylene biosynthesis can be altered by stress. However, it is unclear if an increased level of ethylene causes some of the symptoms of stress or induces acclimation processes that aid in plant survival (Petruzzelli et al.,2000).

The biosynthesis of secondary metabolites is strongly affected by environmental factors, even though it is genetically controlled (Foyer et al., 1994). In nature, secondary metabolites produced by one species can affect the development of other species (Heisey and Heisey, 2003; Jasicka-Misiak et al., 2005). Essential oils (EOs) are among the most studied plant secondary metabolites. Mono- and sesquiterpenes affect physiological processes in weeds, including photosynthesis and chlorophyll synthesis. The cytoplasmic accumulation of lipid globules and the reduction of organelles (mitochondria and nuclei) due to membrane organelle disruption have also been reported (Weston and Duke, 2003; Azirak and Karaman, 2007).

Thyme (*Thymus vulgaris* L.) and lavender (*Lavandula angustifolia* Mill.) belong to the Lamiaceae family, and they are aromatic and medical plants of increasing economic importance. Thyme volatile phenolic oil has been reported to be among the top 10 EOs with antibacterial, antimycotic, intoxicative, natural food preservative and mammalian age-delaying properties (Jackson and Hay, 1994; Letchamo et al., 1995). The EO components of thyme are thymol, carvacrol and p-cymene (Inouye et al., 2001). The main constituents of lavender oil are linalool, linalyl acetate, 1,8-cineole, β-ocimene, terpinen-4-ol and camphor (Cavanagh and Wilkinson, 2002).

The aim of the present work was to study the effect of salt [sodium chloride (NaCl)] stress on growth, ethylene production, and yield in thyme and lavender plants. An additional aim was to determine the importance of the interaction between thyme and lavender in their tolerance to salt stress.

MATERIALS AND METHODS

Plant Material and Growth Conditions

The experiment was conducted with thyme (*Thymus vulgaris* cv. 'Compacta') and lavender (*Lavandula angustifolia* Mill.). Two-month-old rooted plants were purchased from a commercial nursery, and they were transplanted (two per pot) into plastic pots (11 cm in diameter and 8.5 cm high) containing a white sphagnum/coconut fiber mixture (2:1; v/v). Fifty plants of each species were removed from the substrate and washed with distilled water for the determination of increases in biomass (W0). A $2 \times 3 \times 3$ factorial experimental design was used as follows: two species x three types of interactions (thyme/thyme, TT; thyme/lavender, TL; and lavender/lavender, LL) x three salt treatments (0, 50, and 100 mM NaCl). Fifty replicate plants were subjected to each treatment using a completely random design in a growth chamber with a 16–8 h light-dark cycle, 25–20°C day-night temperature, 55–75% relative humidity and 500 μmol·m^2 s^1 photosynthetic photon flux density (400–700 nm) supplied by Sylvania Cool White (Osram Sylvania Inc., Danvers, MA, USA) (F48T12/CW/WHO/LT.115W) and Osram Dulux Superstar (Osram Sylvania Inc., Danvers, MA, USA) (8W/627.65 mA and 60/80 Hz) lamps. The solutions were prepared by adding 50 or 100 mM NaCl to half-strength Hoagland's solution (Hoagland and Arnon, 1950), and the non-salinized control (0 mM) received only nutrient solution. The electrical conductivity (EC) values of the 0, 50, and 100 mM NaCl solutions were 1.23, 6.10, and 10.56 dS·m^{-1}, respectively. Plants were irrigated three times per week with 100 ml of solution, which was sufficient to drain from the bottom of all pots. Salinity treatments were continued for three weeks. After the salinity treatment, the plants were irrigated with nutrient solution without additional salt for five weeks, and the experiment ended when the plants were 4 months old growth parameters, carbon content, and nitrogen content

At the end of the experiment, fifty plants per species, interaction type and salinity level were harvested for biomass determinations. The plants were gently removed from the substrate, the roots were washed with distilled water, and the plants were partitioned into different organs. After the measurement of fresh weight (FW), the dry weight (DW) of the roots, stems and leaves was determined after drying at 75°C for 48 h in a forced-air oven at the beginning of the experiment when the plants were two months old.

The root mass ratio (RMR; root biomass per total plant biomass), stem mass ratio (SMR; stem biomass per total plant biomass), leaf mass ratio (LMR; leaf biomass per total plant) and root/aerial part (stem + leaves) ratio (RAPR) were calculated. The biomass increase was determined with the following equation:

$$\text{Biomass increase}(\%) = [(\text{W100} - \text{W0})/\text{W0}] \cdot 100$$

where W0 is the initial biomass at the beginning of the experiment and W100 is the final biomass at the end of experiment (Liu et al., 2011). During the period of plant growth, the visual symptoms of salinity toxicity (necrosis or chlorosis) in the leaves were assessed.

Plant water content (PWC) values were also calculated from fresh mass (FW) and dry mass (DW) measurements with the following equation:

$$\text{PWC}(\%) = [(\text{FW} - \text{DW})/\text{FW}] \cdot 100.$$

The carbon and nitrogen contents of the leaves, stems and roots were estimated by elemental analysis using a Thermo Finnigan CHN elemental analyzer (Model Flash EA 1112, Milan, Italy).

The percentage of EO in the air-dried leaves from each treatment was determined by hydrodistillation according to Tibaldi et al. (2010). Aliquots of fresh and dry material (approximately 500 g) were steam distilled using glass distillation equipment composed of the following components: an electrical heating mantel (500 Watts-Thermo Scientific Electro Thermal, Waltham, MA, USA), a 2-L Pyrex glass balloon filled with 1.5 L of deionized water with an overlying 4-L modified Pyrex glass balloon filled with the herb material, a cooling column operating in co-current and a graded burette. Every distillation cycle lasted for approximately 105 min, with 45 min of steam produced by the boiling water in the glass balloon. The distillation time of 45 min started when the first drop of liquid condensed in the cooling column and dripped into the graded burette. The EO production was calculated as the weight ratio (w/w) of the cold oil collected from the burette to the original material.

Statistical Analysis

Data were subjected to a two-way analysis of variance (ANOVA) to determine differences among interactions and the saline treatment for each variable. The significant differences between the means were determined by Tukey's test at $P \leq 0.05$, which was performed among three saline treatments for each species and among interactions (TT, TL, or LL) under the same saline treatment. Statistical tests were performed with Statgraphics Centurion XVI (University of Jaén, Jaén, Spain).

TABLE 1 Biomass, biomass increase and plant water content (PWC) in thyme and lavender plants grown alone or together and treated with 0, 50 and 100 mM NaCl (means ± S.E, $n = 50$)

Species	Interactions	NaCl (mM)		
		0	50	100
		Biomass (g)		
Thyme	TT	0.48 ± 0.03ab, A	0.24 ± 0.02b, B	0.20 ± 0.02b, B
	TL	0.48 ± 0.05ab, A	0.25 ± 0.03b, B	0.13 ± 0.01c, C
Lavender	TL	0.37 ± 0.03b, A	0.34 ± 0.01a, A	—
	LL	0.60 ± 0.04a, A	0.38 ± 0.03a, B	0.27 ± 0.02a, B
		Biomass increase (%)		
Thyme	TT	510.71 ± 41.05a, A	304.47 ± 28.94a, B	227.02 ± 19.12a, B
	TL	477.67 ± 24.85a, A	391.09 ± 27.81a, B	125.42 ± 5.64b, C
Lavender	TL	112.68 ± 7.86b, A	79.48 ± 4.72b, B	—
	LL	215.90 ± 16.46b, A	97.50 ± 6.80b, B	44.32 ± 3.95c, B
		Plant water content (%)		
Thyme	TT	78.08 ± 0.64b, A	75.48 ± 1.23a, A	76.67 ± 1.87a, A
	TL	79.65 ± 0.55ab, A	77.97 ± 1.15a, A	62.18 ± 2.59b, B
Lavender	TL	80.85 ± 1.74ab, A	82.87 ± 0.96a, A	—
	LL	83.63 ± 0.62a, A	81.28 ± 1.43a, A	75.78 ± 2.97a, B

Lowercase letters in the same column denote significant differences among interactions, while different uppercase letters in the same row denote significant differences among three salinity treatment ($P<0.05$, according Tukey's test). TT or LL denote thyme and lavender plants growing alone in container, while TL and LT denote thyme and lavender on the same container.

RESULTS

The interaction type (TT, TL, or LL) significantly affected the growth parameters ($P \leq 0.05$). In the control plants (0 mM NaCl), lavender had a 38% reduction in biomass when grown with thyme (TL) after 56 ds of the experiment, indicating less vigorous growth when grown with thyme. For thyme, however, there was no significant difference in biomass when grown with lavender (Table 1). With 50 mM NaCl, the biomass was the same in the two types of interactions (TT or TL for thyme; TL or LL for lavender) for both species. For thyme treated with 100 mM NaCl, there was a 35% reduction in biomass for the TL interaction compared to the TT interaction. In the TL interaction with 100 mM NaCl, all of the lavender plants died. Therefore, lavender was at a disadvantage in the TL interaction compared to thyme. Biomass was significantly reduced by salinity (Table 1). In the TT interaction, thyme plants treated with 50 and 100 mM NaCl showed a 54.17% inhibition of growth with respect to the control (0 mM NaCl). Similarly, when lavender was grown without thyme (LL), the same growth inhibition occurred with 50 and 100 mM NaCl (45.83%). In the TL interaction, growth of thyme was inhibited by 47.96 and 72.92% with the 50 and 100 mM NaCl treatments, respectively.

Thyme plants exhibited a greater biomass increase than lavender plants in all cases (Table 1). With 100 mM NaCl, thyme plants showed a 44%

inhibition of biomass increase in the TL interaction compared to the TT interaction. Moreover, in the TT interaction, salt (50 and 100 mM NaCl) caused a 47.96% reduction in the thyme plant biomass increase compared to the control. In the TL interaction, thyme biomass increase was reduced by 18.12 and 73.74% compared to the control when the plants were treated with 50 and 100 mM NaCl, respectively. Compared to thyme, the biomass increase of lavender showed greater inhibition by salinity. In the TL interaction, lavender had a 29.46% reduction in biomass increase at 50 mM NaCl. In the LL interaction, growth inhibitions of 54.84 and 79.47% were observed for lavender treated with 50 and 100 mM NaCl, respectively. Therefore, the interaction between thyme and lavender reduced the salinity tolerance of both species.

With 100 mM NaCl treatment, thyme plants showed an 18.90% inhibition in plant water content in the TL interaction compared to the TT interaction. In the TL interaction, high salinity (100 mM NaCl) caused a significant decrease in the water content of thyme plants (21.93% decrease compared to 0 mM NaCl) (Table 1). In the LL interaction, a 9.38% plant water inhibition was observed with 100 mM NaCl for lavender.

The leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR) and root/aerial part ratio (RAPR) values are presented in Table 2. In control plants, thyme had lower LMR values than lavender. With 100 mM NaCl, the LMR values for thyme significantly decreased with respect to the control (30.64%) in the TL interaction. In the TT interaction with 50 mM NaCl, the LMR and SMR values were increased by 1.57-fold and 2.05-fold, respectively. In the TL interaction with 50 mM NaCl, the RMR value of thyme significantly increased. Significant effects of the interaction type (TT, TL, or LL) and salinity were observed in the RAPR values for thyme. An increase in RPAR values was detected in thyme plants treated with 100 mM NaCl in the TT interaction and in plants treated with 50 mM NaCl in the TL interaction, with RAPR value increases of 29.76 and 59.84%, respectively.

Leaf, stem and root macronutrients [nitrogen (N) and carbon (C)] of thyme and lavender were affected by salinity. In the 100 mM NaCl treatment, the leaf and stem C contents of thyme diminished (Table 3), and the root C content of thyme increased by 2.50%. In thyme stems, the inhibition of macronutrients was 1.66 times higher in plants grown with lavender. In lavender, the plants grown with NaCl had decreased C content only in the leaves. This inhibition was 1.70 times higher in the TL interaction than in the LL interaction (50 mM NaCl). For all of the organs in the control plants, the C contents were lower in the lavender plants.

The response of N content to salinity was different in the leaf, stem and root (Table 4). In thyme, N content decreased in the leaf and increased in the stem and root. The highest increases were observed in the stem in the 100 mM NaCl treatment with 14.05 and 16.77% increases found in the TT and TL interactions, respectively. In lavender, the N contents of the three

TABLE 2 Leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR), and root/part aerial ratio (RAPR) in thyme and lavender plants grown alone or together and treated with 0, 50 and 100 mM NaCl (means ± S.E, $n = 50$)

Species	Interactions	NaCl (mM)		
		0	50	100
		Leaf mass ratio (%)		
Thyme	TT	48.81 ± 4.09a, B	76.69 ± 6.84a, A	52.52 ± 4.96a, AB
	TL	55.44 ± 4.99a, A	58.86 ± 5.42a, A	38.45 ± 2.62b, B
Lavender	TL	72.67 ± 1.16b, A	69.91 ± 0.44a, A	—
	LL	73.26 ± 0.99b, A	73.49 ± 1.94a, A	70.09 ± 0.51a, A
		Stem mass ratio (%)		
Thyme	TT	42.83 ± 4.03a, B	87.62 ± 8.36a, A	69.55 ± 6.01a, AB
	TL	46.32 ± 2.63a, A	49.69 ± 3.47ab, A	53.67 ± 2.31a, A
Lavender	TL	9.84 ± 0.28b, A	10.17 ± 0.13b, A	—
	LL	11.09 ± 0.57b, A	10.54 ± 0.95b, A	13.29 ± 0.46b, A
		Root mass ratio (%)		
Thyme	TT	17.51 ± 0.65a, A	18.97 ± 1.57a, A	19.29 ± 0.73a, A
	TL	11.67 ± 0.64b, B	19.83 ± 1.46a, A	12.17 ± 0.64b, B
Lavender	TL	17.59 ± 0.76a, A	19.91 ± 0.33a, A	—
	LL	15.64 ± 0.62a, A	15.97 ± 0.96a, A	16.62 ± 0.45a, A
		Root/aerial part ratio (%)		
Thyme	TT	13.24 ± 0.69b, B	12.88 ± 0.78c, B	17.18 ± 1.13a, A
	TL	11.13 ± 1.09b, B	17.79 ± 1.35b, A	12.75 ± 0.87b, B
Lavender	TL	21.90 ± 1.60a, A	24.88 ± 0.52a, A	—
	LL	18.86 ± 1.36a, A	19.19 ± 1.80ab, A	20.00 ± 1.40a, A

Lowercase letters in the same column denote significant differences among interactions, while different uppercase letters in the same row denote significant differences among three salinity treatment ($P<0.05$, according Tukey's test). TT or LL denote thyme and lavender plants growing alone on container, while TL and LT denote thyme and lavender on the same container.

organs were decreased by salinity. In the LL interaction with 100 mM NaCl, N content inhibitions of 14.72, 13.17, and 10.95% were detected in the leaf, stem and root, respectively.

Due to salinity, the C/N ratio increased in all three organs in lavender, and the C/N ratio increased in the leaf and decreased in the stem and root in thyme.

In general, the production of ethylene was higher in thyme than in lavender (Table 5). Thyme plants grown with lavender (TL) had lower levels of ethylene production in the 0 mM NaCl (control) treatment and higher levels of ethylene production in the 100 mM NaCl treatment compared to plants grown without lavender (TT). The ethylene production response to the NaCl treatment contrasted between the two species. Thyme plants grown without lavender showed the same reduction in ethylene production with 50 and 100 mM NaCl (41.92% on average), and thyme plants grown with lavender showed an increase in ethylene production with 100 mM NaCl (63.48%). Ethylene production increased in lavender plants grown

TABLE 3 Carbon content percentage in leaf, stem and root of thyme and lavender plants grown alone or together and treated with 0, 50 and 100 mM NaCl (means ± S.E., $n = 50$)

Species	Interactions	NaCl (mM) 0	50	100
		Leaf		
Thyme	TT	44.66 ± 0.14a, A	41.92 ± 0.01a, B	41.26 ± 0.02a, B
	TL	43.96 ± 0.12a, A	42.35 ± 0.18a, A	40.40 ± 0.38a, B
Lavender	TL	41.35 ± 0.28b, A	38.89 ± 0.10b, B	—
	LL	41.52 ± 0.12b, A	37.34 ± 0.17c, B	39.59 ± 0.90a, B
		Stem		
Thyme	TT	44.15 ± 0.02a, A	41.40 ± 0.09b, B	40.98 ± 0.04a, C
	TL	44.13 ± 0.06a, A	43.21 ± 0.03a, B	38.88 ± 0.14c, C
Lavender	TL	40.89 ± 0.06b, A	41.00 ± 0.09b, A	—
	LL	40.33 ± 0.25b, A	39.90 ± 0.25c, A	39.98 ± 0.15b, A
		Root		
Thyme	TT	40.73 ± 0.11a, B	39.88 ± 0.35b, B	41.77 ± 0.07a, A
	TL	40.97 ± 0.09a, B	41.16 ± 0.17a, B	41.97 ± 0.11a, A
Lavender	TL	40.81 ± 0.18a, A	40.50 ± 0.04ab, A	—
	LL	39.84 ± 0.14b, A	41.13 ± 0.02a, A	41.39 ± 0.06b, A

Lowercase letters in the same column denote significant differences among interactions, while different uppercase letters in the same row denote significant differences among three salinity treatment ($P < 0.05$, according Tukey's test). TT or LL denote thyme and lavender plants growing alone on container, while TL and LT denote thyme and lavender on the same container.

TABLE 4 Nitrogen content percentage in leaf, stem and root of thyme and lavender plants grown alone or together and treated with 0, 50 and 100 mM NaCl (means ± S.E, $n = 50$)

Species	Interactions	NaCl (mM) 0	50	100
		Leaf		
Thyme	TT	3.70 ± 0.04a, A	3.56 ± 0.02a, A	3.08 ± 0.05b, B
	TL	3.66 ± 0.04a, A	3.35 ± 0.08b, B	3.42 ± 0.03a, B
Lavender	TL	2.44 ± 0.04b, A	2.26 ± 0.02c, B	—
	LL	2.31 ± 0.05b, A	2.05 ± 0.04*d*, *B*	1, 97 ± 0.02c, B
		Stem		
Thyme	TT	1.57 ± 0.01c, B	1.77 ± 0.01a, A	1.79 ± 0.01b, A
	TL	1.67 ± 0.01b, C	1.78 ± 0.01a, B	1.95 ± 0.01a, A
Lavender	TL	1.85 ± 0.02a, A	1.40 ± 0.01b, b	—
	LL	1.67 ± 0.02b, A	1.82 ± 0.08a, A	1.45 ± 0.02c, B
		Root		
Thyme	TT	1.96 ± 0.03c, B	2.27 ± 0.07b, A	2.21 ± 0.03b, A
	TL	2.20 ± 0.02b, A	1.86 ± 0.03c, B	2.26 ± 0.05b, A
Lavender	TL	2.66 ± 0.05a, A	3.05 ± 0.03a, B	—
	LL	2.83 ± 0.06a, B	3.00 ± 0.01a, A	2.52 ± 0.02a, C

Lowercase letters in the same column denote significant differences among interactions, while different uppercase letters in the same row denote significant differences among three salinity treatment ($P < 0.05$, according Tukey's test). TT or LL denote thyme and lavender plants growing alone on container, while TL and LT denote thyme and lavender on the same container.

TABLE 5 Ethylene production (nl g^{-1} FW h^{-1}) in leaf of thyme and lavender plants grown alone or together and treated with 0, 50 and 100 mM NaCl (means ± S.E, $n = 50$)

Species	Interactions	NaCl (mM)		
		0	50	100
Thyme Lavender	TT	30.09 ± 2.81a, A	17.65 ± 1.49a, B	17.30 ± 1.20b, B
	TL	14.98 ± 1.16b, B	18.19 ± 0.30a, B	24.49 ± 1.60a, A
	TL	4.76 ± 0.26c, B	6.66 ± 0.40b, A	—
	LL	3.47 ± 0.37c, B	8.22 ± 0.47b, A	3.88 ± 0.30c, B

Lowercase letters in the same column denote significant differences among interactions, while different uppercase letters in the same row denote significant differences among three salinity treatment ($P < 0.05$, according Tukey's test). TT or LL denote thyme and lavender plants growing alone on container, while TL and LT denote thyme and lavender on the same container.

with 50 mM NaCl when they were grown with thyme (39.91%) and without thyme (136.89%).

Similar to ethylene production, EO production in response to the NaCl treatment contrasted between the two species (Table 6). In thyme plants, EO production increased in the 100 mM NaCl treatment compared to control plants. This increase was significant only in thyme plants grown with lavender (TL) (49.58%). With respect to lavender, the EO production response depended on the presence of thyme. In the TL interaction, EO production increased with salinity by 16.11%, while in the LL interaction, EO production decreased with salinity by 38.89%.

DISCUSSION

The effect of salinity on non-halophytes consists of a reduction in growth and yield (Mass and Hoffman, 1997). We demonstrated a significant effect of NaCl salinity on biomass and biomass increase in thyme and lavender plants. Similar results have been described by other authors for *Thymus*

TABLE 6 Essential oil (EO) percentage (v/w) in leaf of thyme and lavender plants grown alone or together and treated with 0, 50 and 100 mM NaCl (means ± S.E, $n = 50$)

Species	Interactions	NaCl (mM)		
		0	50	100
Thyme	TT	4.08 ± 0.26ab, AB	3.61 ± 0.24ab, B	4.71 ± 0.23a, A
	TL	3.55 ± 0.39b, B	3.47 ± 0.27ab, B	5.31 ± 0.59a, A
Lavender	TL	3.91 ± 0.05ab, B	4.54 ± 0.27a, A	—
	LL	4.95 ± 0.37a, A	2.90 ± 0.22b, B	3.15 ± 0.37b, B

Lowercase letters in the same column denote significant differences among interactions, while different uppercase letters in the same row denote significant differences among three salinity treatment ($P < 0.05$, according Tukey's test). TT or LL denote thyme and lavender plants growing alone on container, while TL and LT denote thyme and lavender on the same container.

vulgaris (Koocheki et al., 2008; Ezz El-Din et al., 2009: Urrestarazu et al., 2011) and other medicinal plants (Abdul-Jaleel et al., 2008; Bazihizina et al., 2009). Zidan et al. (1990) reported that salt stress may directly or indirectly inhibit cell division and/or cell elongation in growing tissues of roots, stems and leaves. However, the interaction between the thyme and lavender plants adversely affected the growth of plants treated with high levels of NaCl (100 mM). The effect of 100 mM NaCl on biomass was greater when the thyme and lavender plants were grown together than when grown alone. Moreover, all lavender plants grown with thyme died when subjected to high levels of NaCl. This negative interaction of thyme and lavender plants was generally consistent with results obtained for other species (Armas and Pugnaire, 2009; Armas et al., 2010).

The effect of salinity on leaf growth (LMR) was significant in thyme plants grown with lavender plants. Furthermore, leaf abscission occurred under these conditions. The decline in leaf growth is the earliest response of glycophytes exposed to salt stress (Munns and Termaat, 1986; Chartzoulakis et al., 2002).

In lavender for all levels of NaCl and for both interactions (LL and TL) and in thyme with moderate levels of NaCl (50 mM) and no interaction with lavender (TT), the reduction in the aerial part dry weight was comparable to that of the root indicating that the shoot and root were equally sensitive to salinity. At high salinity (100 mM NaCl), root growth of thyme plants was less affected than shoot growth, resulting in an increase in the RAPR. Therefore, high NaCl salinity in thyme may alter the pattern of dry matter distribution, favoring the root. Similar findings have been reported for beans (Seemann and Critchley, 1985), kiwifruit (Chartzoulakis et al., 1995), peas and fava beans (Cordovilla et al., 1999). In contrast to this trend, Belaqziz et al. (2009) reported that the aerial parts of thyme seedlings are more affected by salinity than the roots. According to Nelson et al. (2004) and Xu and Zhou (2005), improvement of the ratio of roots to aerial parts may play an important role in adaptation of plants to stress.

The principal evidence for salt inhibition on the growth of plants is related to the reduction in the capacity to maintain an adequate concentration of essential nutrients (Zidan et al., 1992; Cordovilla et al., 1995). The results of the present study clearly demonstrated that salinity induced changes in the C and N concentrations. In thyme plants, the C content of roots increased, while the C contents of leaves and stems decreased. Foyer et al. (1994) reported that salts also induce water stress. According to Hunt et al. (1996), drought provokes the carbon translocation from a source (e.g., a mature leaf) to a sink (e.g., a root). In contrast, the C content in lavender decreased only in the leaves.

Lewis (1986) showed that excess NaCl interferes with N acquisition and utilization. The results obtained in this study for lavender were in agreement

with this previous assessment. In thyme, however, the N concentration in leaves was significantly decreased by salinity, but salinity increased the N concentration in the stems and roots. Similar results have been described by Cambrollé et al. (2011) in *Glaucium flavum*. Previous studies have shown that NaCl does not modify N content in several plant species (Bartolini et al., 1991) and that N content does not increase with salinity (Zidan et al., 1992). The increase in root N concentration may be ascribed to the accumulation of N-containing compounds, such as amino acids, quaternary ammonium compounds and polyamines, as a stress response to excess salt (Parida and Das, 2005). Therefore, the migration of C and N to the roots of thyme suggests a capacity for adaptation to salinity.

Ethylene is a plant hormone that regulates many processes, from seed germination to organ senescence. Ethylene is also involved in the response of plants to different types of stress (Morgan and Drew, 1997). Other authors have reported an increase in ethylene production in rice and lettuce under conditions of salt stress (Lutts et al., 1996, Zapata et al., 2004) and relate this increase to a greater tolerance to salt stress. In contrast, some authors have described higher levels of ethylene in salt-sensitive cultivars of wheat, corn and soybeans than in cultivars with greater salt tolerance (Datta et al., 1998). In the present study, an increase in ethylene production was evident when the growth of thyme plants was lower (thyme plants grown with lavender and 100 mM NaCl). Moreover, the increase in ethylene production was significant in lavender plants treated with moderate salinity (50 mM NaCl) when grown with thyme or when grown alone.

The response of essential oil (EO) production to salinity was different for thyme and lavender. High salinity (100 mM NaCl) stimulated EO production in thyme, and moderate salinity (50 mM) stimulated EO production in lavender but only in the presence of thyme. The increase in EO production as salinity increased corroborated earlier observations for thyme (Ezz El-Din, et al., 2009) and may be attributed to the function of secondary metabolites, including EOs, as a self-defense component against stress conditions. This increase of EO may be responsible for the death of the lavender plants grown with thyme at high salinity. Similarly, Grosso et al. (2010) reported injuries caused by thyme oils on sweet corn seedlings and dwarf pea seed germination. Tabatabaie and Nazari (2007) reported that the concentration of lemon verbena oil progressively increases as NaCl salinity increases. In contrast, Badaway et al. (1990) found that low salinity results in the highest EO production in *Majorana hortensis* and that EO production decreases as salinity increases. A similar pattern of EO production occurred in the lavender plants grown without thyme in the present study.

In conclusion, plant-plant interactions play a crucial role in the tolerance of thyme and lavender to salinity. The growth of these two species is affected more by salinity when they are grown together. Under this condition,

lavender is more sensitive to salinity than thyme is. In thyme, C and N in the roots increase with salinity, suggesting that thyme can adapt to salinity. In thyme, ethylene production is increased by high salinity when grown together with lavender. Salinity stimulates EO production in thyme, and EO production in lavender is increased when grown together with thyme. Therefore, this study has demonstrated that plant interactions under saline conditions strongly affect the physiological responses of thyme and lavender plants.

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