



# Multidimensional assessment of drought and salinity tolerance in six Lamiaceae species from the Mediterranean basin (El Tarf, Algeria) under climate change

Louiza Smichette, Nadia Nawel Azizi, Nesrine Hacini, Radia Djelloul, Mohamed Nejib EL Melki

## Correspondence

Louiza Smichette<sup>1</sup>, Nadia Nawel Azizi<sup>1</sup>, Nesrine Hacini<sup>1</sup>, Radia Djelloul<sup>1</sup>, Mohamed Nejib EL Melki<sup>2\*</sup>

<sup>1</sup>Laboratory of Functional and Evolutionary Ecology Research, Faculty of Nature and Life Sciences, Chadli Bendjedid University of El Tarf, PB 73, El-Tarf 36000, Algeria

<sup>2\*</sup>Higher School of Engineers of Medjez El Bab, Department of Mechanical and Agro-Industrial Engineering, University of Jendouba, Jendouba 8189, Tunisia

\*Corresponding Author: mohamed.najib.melki@gmail.com

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## Research

### Abstract

**Background:** The Mediterranean Basin, a biodiversity hotspot, faces intensified abiotic stresses, such as drought and salinity, owing to climate change. These conditions pose significant challenges to the sustainable production of medicinal and aromatic plants (MAPs). These plants, especially those in the Lamiaceae family, are vital for traditional knowledge and high-value essential oil (EOs) production. Their production and composition are strongly influenced by environmental factors. Therefore, understanding how MAPs adapt to stress is essential for optimizing cultivation practices and ensuring a reliable supply.

**Methods:** This study evaluated the comparative tolerance of six Lamiaceae species (*Lavandula angustifolia*, *Mentha piperita*, *Origanum vulgare*, *Ocimum basilicum*, *Rosmarinus officinalis*, and *Salvia officinalis*) to progressive drought and salinity stress. Experiments were conducted under controlled conditions, and species selection was guided by ethnobotanical criteria in the El Tarf region of northeastern Algeria, as previously described. Quantitative tolerance indices (Stress Tolerance Index, Tolerance, Yield Stability Index) and the Phenotypic Plasticity Index were used, along with multivariate analyses (PCA) to assess species performance. These tools helped identify critical stress thresholds based on the EO yield and biomass.

**Results:** *Origanum vulgare* and *Rosmarinus officinalis* emerged as the most drought-tolerant species, maintaining 98–99% and 97–106% of the control EO yields, respectively, and showing minimal biomass reduction (less than 19%) under moderate drought (50% FC). *Lavandula angustifolia* exhibited superior salinity tolerance, maintaining 74% of control EO production and surviving as the only species at severe salinity (150 mM NaCl), whereas all other species showed 100% mortality. Conversely, *Ocimum basilicum* and *Mentha piperita* were highly sensitive to both stresses, with EO yields dropping to 0% under moderate drought (50% FC) and severe salinity (150 mM NaCl) conditions. Mild stress (75% FC drought, 50 mM NaCl salinity) sometimes induced hormetic responses, with EO accumulation increasing by up to 14.3% in *Salvia officinalis*. Distinct critical thresholds were identified, including 60–65% FC for drought and 75 mM NaCl for salinity, beyond which EO production sharply declined.

**Conclusions:** This study ranked six Lamiaceae species according to their tolerance to drought and salinity. *Origanum vulgare* and *Rosmarinus officinalis* were identified as optimal candidates for cultivation in water-limited environments, whereas *Lavandula angustifolia* showed the highest potential under saline conditions. These findings provide essential benchmarks for precision agriculture and support strategic water management and cultivar selection to enhance the resilience and productivity of MAPs under climate change conditions.

**Keywords:** Ethnobotany; Lamiaceae; Drought stress; Salinity stress; Essential oil; Tolerance indices; Phenotypic plasticity; Climate change

## Background

The Mediterranean Basin, with its exceptional plant biodiversity and climate characterized by hot, dry summers and mild, wet winters, is particularly vulnerable to climate change impacts, including reduced rainfall and increased soil salinization (IPCC, 2021). This region, the cradle of many MAP species, constitutes a natural laboratory for studying plant adaptation to increasingly harsh environmental conditions. In North Africa, especially Algeria and Tunisia, Lamiaceae cultivation holds ecological, economic, and cultural importance, supporting both traditional knowledge and the production of high-value essential oils (EOs) (Said-Al Ahl *et al.* 2009).

The El Tarf valley in northeastern Algeria represents an ecosystem rich in plant biodiversity, where protected wetlands coexist with agricultural lands under anthropogenic pressure. This environmental diversity and the cultural importance of MAPs motivated a study combining ethnobotanical, physiological, and phytochemical approaches to evaluate the resilience of six flagship Lamiaceae species (*Lavandula angustifolia*, *Mentha piperita*, *Origanum vulgare*, *Ocimum basilicum*, *Rosmarinus officinalis*, and *Salvia officinalis*) to drought and salinity stress in this context (Bettaieb *et al.* 2011; Said-Al Ahl *et al.* 2009).

The six Lamiaceae species selected for this study are key medicinal plants in Mediterranean and North African traditional medicine, with deep cultural significance in the El Tarf region. *Lavandula angustifolia* has been used for centuries to alleviate anxiety, insomnia, depression, and various nervous disorders, and its applications in wound healing and skin conditions are well documented (Neves *et al.* 2009; Khabbach *et al.* 2012). Its calming and sedative properties have made it a cornerstone of traditional aromatherapy and folk remedies throughout Algeria and the wider Mediterranean basin.

*Origanum vulgare* holds a central place in traditional medicinal practices for treating respiratory ailments such as cough, bronchitis, and the common cold, as well as digestive disorders including indigestion and diarrhea (Neves *et al.* 2009; Bouasla & Bouasla, 2017). It is also used for headaches, pruritus, and as an external remedy for wounds and toothaches. In certain traditional practices, its flowering branches are even applied directly to fracture sites (Bellakhdar, 1997). Preparations of *Mentha piperita* have long been recognized for their analgesic and anti-inflammatory properties (Benabdallah *et al.* 2016; Lahsissene *et al.* 2009), as well as for their beneficial effects on digestive discomfort and relaxation, in addition to their widespread use in medicinal teas and culinary applications.

*Ocimum basilicum* is among the most widely used plants in Algerian traditional medicine (Miara *et al.* 2018; Doudach *et al.* 2021). It is employed to treat headaches, cough, kidney disorders, intestinal parasitosis, and as an antispasmodic agent, with well-established antibacterial and anti-inflammatory applications in traditional pharmacopeia. *Rosmarinus officinalis* is one of the most valued medicinal plants in Algeria, with remarkably high use values (UV = 0.80) reported in the southwest of the country (Miara *et al.* 2018; Bouasla & Bouasla, 2017). Traditionally, it is used to treat various respiratory conditions (cough, influenza, cold), as well as rheumatism, muscle spasms, cholelithiasis, and fever (Bouasla & Bouasla, 2017). More broadly in Algerian traditional medicine, rosemary is cited for its antidiabetic, antitumoral, antihypertensive, and hepatoprotective properties (Doudach *et al.* 2021). Known locally as “Klil” or “Lazir,” it is widespread across the Mediterranean basin and the Algerian Sahara and commonly used in culinary traditions as an aromatic herb (Lograda *et al.* 2013; Allali *et al.* 2008).

*Salvia officinalis* (sage) is well recognized for its high content of rosmarinic acid and its wide range of medicinal properties, including antioxidant, anti-inflammatory, antibacterial, antiviral, antidepressant, and anticancer activities (Bahmani *et al.* 2015). In Mediterranean traditional medicine, sage is incorporated into complex herbal formulations used to treat cognitive dysfunction, psychological disorders, and various infections (Khabbach *et al.* 2012). The convergence between these traditional uses and findings from modern phytochemical and pharmacological research reinforces the relevance of ethnobotanical knowledge for identifying species with strong stress resilience and high adaptive potential. This

ethnobotanical background highlights the cultural, medicinal, and socio-economic importance of these species, reinforcing the relevance of evaluating their drought and salinity tolerance to support their conservation, sustainable use, and resilience under climate change.

Essential oils (EOs), complex secondary metabolites produced by many MAPs, play a central role in the therapeutic and commercial values of these plants. Their biosynthesis and accumulation are strongly influenced by environmental factors, including abiotic stress (Khalid, 2006; Zheljazkov *et al.* 2008). Stress modulates secondary metabolism, altering both the overall EO yield and chemical composition, which can profoundly impact their biological properties and market value (Bettaieb *et al.* 2009; Taarit *et al.* 2012). Despite extensive research on the effects of individual stressors, significant knowledge gaps persist regarding the comparative impacts of drought and salinity on essential oil production in Mediterranean Lamiaceae species (Bistgani *et al.* 2024; Mansinhos *et al.* 2024). From a physiological perspective, the differential regulation of terpene synthase genes and volatile biosynthetic pathways under water deficit versus ionic stress remains poorly characterized, particularly for non-model aromatic species (Nazari *et al.* 2023; Nicolas-Espinosa *et al.* 2023; Perez-Gil *et al.* 2024). These modifications result from adjustments in metabolic pathways, such as the mevalonate and methylerythritol phosphate pathways, which are responsible for terpene synthesis, major compounds of essential oils (Vranová *et al.* 2013).

Phytochemically, although previous studies have reported stress-induced changes in monoterpene and sesquiterpene profiles in isolated experiments, there is a lack of comprehensive comparative analyses quantifying how drought and salinity differentially influence the full spectrum of volatile compounds across multiple Lamiaceae genera (Karalija *et al.* 2022; Laftouhi *et al.* 2023). Moreover, the critical stress thresholds at which plants shift from growth-prioritizing strategies to the accumulation of defense-related secondary metabolites remain poorly defined for most aromatic species (Mansinhos *et al.* 2024; Caser *et al.* 2019).

Plant responses to abiotic stresses are complex and multidimensional, involving coordinated morphological, physiological, biochemical, and epigenetic adaptations (Chaves *et al.* 2003; Ashraf & Foolad, 2007; Crisp *et al.* 2016). Stress tolerance varies considerably between species and even between genotypes within the same species, reflecting contrasting ecological strategies and unequal phenotypic plasticity (Chapin *et al.* 1993; Valladares *et al.* 2006; Nicotra *et al.* 2010). From an ecological standpoint, the adaptive trade-offs between biomass production and essential oil synthesis under resource-limited conditions remain insufficiently explored, particularly in co-occurring Mediterranean species exhibiting contrasting life-history strategies (Moshrefi-Araghi *et al.* 2023; Abdali *et al.* 2023). A deeper understanding of these ecophysiological compromises is essential for predicting how climate change-induced stress alters the chemical ecology, resilience, and commercial potential of both wild and cultivated aromatic plant populations (Alhailoul *et al.* 2020; Szekely-Varga *et al.* 2020). Some "stress-avoidant" species thrive under favorable conditions but collapse under stress, while others, "stress-tolerant," maintain their functionality at the expense of rapid growth (Munns & Tester, 2008). This interspecific variability is an asset for selecting species adapted to constrained environments and for the sustainable valorization of MAPs.

Moreover, the nature of the stress determines adaptive responses. Salinity stress, in particular, combines an osmotic effect common to drought with an ionic effect due to toxic accumulation of Na<sup>+</sup> and Cl<sup>-</sup> ions, which disrupts cellular and enzymatic processes (Parida & Das, 2005; Flowers & Colmer, 2008). This dual constraint triggers distinct adjustments, such as the accumulation of osmoprotectants (proline, glycine betaine), regulation of ion transporters, and stimulation of antioxidant defenses (Munns & Tester, 2008; Acosta-Motos *et al.* 2017). Therefore, a comparative analysis of MAP responses to drought and salinity is essential to identify the most resilient species and define adapted cultivation strategies.

Despite the economic importance of essential oil crops in Mediterranean agriculture, evidence-based irrigation strategies and stress management protocols that optimize both biomass yield and essential oil quality under water-limited conditions remain insufficiently developed (García-Caparrós *et al.* 2019; Chiappero *et al.* 2022). The integration of quantitative tolerance indices with detailed phytochemical profiling to inform cultivar selection and guide precision irrigation scheduling represents a major gap in the development of sustainable MAP production systems (Farouk *et al.* 2020; Al-Fraihat *et al.* 2023). Moreover, the scalability of laboratory-based stress tolerance assessments to real field conditions, where multiple abiotic stressors typically interact, remains uncertain and requires validation through multi-site agronomic trials (García-Caparrós *et al.* 2019; Chiappero *et al.* 2022).

In this context, the present study aims to comparatively evaluate the tolerance to drought and salinity of six Lamiaceae species (*Lavandula angustifolia*, *Mentha piperita*, *Origanum vulgare*, *Ocimum basilicum*, *Rosmarinus officinalis*, and *Salvia officinalis*), identify critical stress thresholds, and characterize the underlying adaptation strategies. Relying on an

## Materials and Methods

This study was conducted in El Tarf Province (36°30'–37°00'N, 7°45'–8°45'E), northeastern Algeria, covering approximately 2,900 km<sup>2</sup>. The region encompasses coastal wetlands (e.g., Lac des Oiseaux and Garaet El Tarf), fertile plains, and forested hills dominated by cork oak (*Quercus suber*) and maritime pine (*Pinus pinaster*). El Tarf is recognized as a biodiversity hotspot with ~1,200 vascular plant species and Ramsar-listed wetlands, providing an ideal environment for studying the resilience of medicinal and aromatic plants (MAP) to abiotic stress.

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### Selection of Species and Ethnobotanical Criteria

Species selection was guided by three well-established quantitative ethnobotanical indicators: Relative Citation Frequency (RCF), Use Value (UV), and Informant Consensus Factor (ICF). The RCF (%) measures the proportion of informants who mentioned a given species in relation to the total number of respondents and is defined as:

$$RCF = (S / N) \times 100 \quad (1)$$

where S is the number of informants citing the species and N is the total number of informants (Tardío & Pardo-de-Santayana, 2008; Vitalini *et al.* 2013). This index measures the cultural significance and local recognition of each species, with higher values indicating broader community knowledge and utilization (Albuquerque *et al.* 2019). The Use Value (UV) quantifies the versatility of each plant species and was computed as:

$$UV = \Sigma(U_i) / N \quad (2)$$

where  $U_i$  corresponds to the number of uses mentioned by the  $i$ th informant (Phillips & Gentry, 1993; Vitalini *et al.* 2013). The UV index reflects the relative cultural and functional importance of each species by integrating its versatility across multiple use categories, including medicinal, culinary, cosmetic and ritual applications. Higher UV values indicate a broader multipurpose utility and stronger ethnobotanical relevance within local communities (Albuquerque *et al.* 2019; Molina *et al.* 2022). The Informant Consensus Factor (ICF) reflects the degree of agreement among informants regarding plant use for specific ailment categories and is expressed as:

$$ICF = (n_{ur} - n_t) / (n_{ur} - 1) \quad (3)$$

where  $n_{ur}$  represents the total number of citations for a particular disease category, and  $n_t$  is the number of taxa associated with that category (Heinrich *et al.* 1998; Ugulu, 2021). ICF values ranged from 0 to 1, with values close to 1 indicating strong agreement among informants regarding the preferred plant species for treating specific health conditions. Such a high consensus reflects well-established, culturally embedded therapeutic practices and reinforces the reliability of traditional medicinal knowledge (Gazzaneo *et al.* 2005; Abbasi *et al.* 2013).

To ensure rigorous selection, the following thresholds were applied:  $RCF \geq 20\%$ ,  $UV > 0.5$ , and  $ICF \geq 0.7$ , thereby retaining species that are most culturally valued and broadly recognized for their therapeutic efficacy. Application of these criteria emphasized the predominance of the Lamiaceae family, with six species emerging as the most representative: *Lavandula angustifolia* Mill., *Mentha piperita* L., *Origanum vulgare* L., *Ocimum basilicum* L., *Rosmarinus officinalis* L., and *Salvia officinalis* L. These taxa are widely documented for their rich essential oil content and pharmacological potential in the Mediterranean and North African traditions (Figueiredo *et al.* 2008; Mansinhos *et al.* 2024). Nonetheless, the analysis accounted for potential limitations inherent to ethnobotanical surveys, including the “shifting baseline syndrome,” wherein inter-generational knowledge loss or modernization may lead to under representation of lesser-known or endangered species. Recognizing such biases strengthens the reliability of the selected species for subsequent experimental assessment.

#### Plant Material and Ethnobotanical Selection

At the end of the stress period, the aerial parts were harvested early in the morning to minimize essential oil volatilization. Fresh biomass was measured immediately, and the samples were air-dried at room temperature (25 °C) in a shaded, ventilated area until a constant weight was reached. Dry biomass was used for essential oil extraction and chemical analysis. Biomass accumulation was defined as the total mass (fresh or dry) produced by the aerial parts under each treatment, whereas dry matter content (DM) was calculated as the ratio of dry biomass to fresh biomass, expressed as a percentage according to established plant physiology protocols.

Essential oils were extracted by hydrodistillation using a Clevenger-type apparatus for 3 h, following the standard method of the European Pharmacopoeia. The extracted oils were dried over anhydrous sodium sulfate and stored at 4 °C in amber glass vials until further analysis. The essential oil yield was calculated as a percentage of the dry biomass (v/w). Gas chromatography–mass spectrometry (GC–MS) analysis was performed to identify the major volatile components using a Shimadzu GCMS-QP2020 equipped with an RTX-5MS capillary column (30 m × 0.25 mm, 0.25 µm film thickness).

To quantitatively assess species tolerance and adaptation to stress conditions, several widely used stress tolerance indices were calculated based on essential oil yields under control and stress conditions (Fernandez, 1992; Fischer and Maurer, 1978). The Stress Tolerance Index (STI) was determined using the equation:

$$STI = (Y_s \times Y_p) / (\bar{Y}_p)^2 \quad (4)$$

where  $Y_s$  is the yield under stress,  $Y_p$  the yield under control conditions, and  $\bar{Y}_p$  the mean yield of all genotypes under control conditions. The Tolerance index (TOL) was calculated as:

$$TOL = Y_p - Y_s \quad (5)$$

The Yield Stability Index ( $Y_{SI}$ ) was computed using the relation:

$$Y_{SI} = Y_s / Y_p \quad (6)$$

These indices have been extensively used in stress physiology research to distinguish between stress-tolerant and stress-sensitive genotypes (Bettaieb *et al.* 2011; Taarit *et al.* 2012). Stress treatments were clearly defined as follows: T0 corresponded to the control at 100% field capacity (FC) without added NaCl; T1 and T2 represented drought stress levels at 60% and 40% FC, respectively; S0 indicated no salinity (0 mM NaCl), while S1, S2, and S3 corresponded to increasing salinity levels of 50 mM, 100 mM, and 150 mM NaCl, respectively. Field capacity (FC) was defined as the maximum water content retained by the soil after excess gravitational water had drained, expressed in % (v/v), and NaCl concentrations were expressed in millimolar (mM). All percentage-based parameters, including biomass traits, dry matter content, and essential oil yield, were expressed in either w/w or v/w depending on the measurement. They provide complementary information on different aspects of stress response and are valuable tools for identifying genotypes with superior adaptability and stability under varying environmental conditions.

### Statistical Analysis

All data are expressed as mean  $\pm$  standard deviation (SD). Statistical analyses were performed using SPSS version 25.0 (IBM Corp., Armonk, NY, USA). One-way ANOVA was used to test the effect of stress treatments, followed by Tukey's HSD post hoc test ( $p < 0.05$ ) for mean separation of the data. Pearson's correlation analysis was applied to assess the relationships among biomass, essential oil yield, and tolerance indices. The statistical procedures followed standard guidelines for biological and agronomic experiments as described by Gomez & Gomez (2010) and Montgomery (2017).

## Results

### Differential Essential Oil Production Under Drought Stress

The imposition of progressive drought stress significantly affected essential oil production across all six medicinal plant species ( $F = 48.73$ ,  $p < 0.001$ ), although the magnitude and pattern of the response varied considerably among taxa (Table 1, Figure 2). Under control conditions (T0, 100% field capacity), baseline EO yields ranged from 0.82% in *Lavandula angustifolia* to 1.05% in *Mentha piperita*. Mild water stress (T1, 75% FC) stimulated EO accumulation in four of the six species examined. *Salvia officinalis* exhibited the most pronounced enhancement, with EO yield increasing by 14.3% relative to control (from 0.98% to 1.12%,  $p < 0.01$ ), followed by *Ocimum basilicum* (+26.2%, reaching 1.06%), *Mentha piperita* (stable at 1.05%), and *Lavandula angustifolia* (+8.5% to 0.89%).

Moderate drought stress (T2, 50% FC) represented a critical threshold that differentiated stress-tolerant and stress-sensitive genotypes. *Rosmarinus officinalis* emerged as the most resilient species, maintaining EO production at 106% of the control level (1.06%). *Origanum vulgare* maintained near-optimal performance at 99% of the control (0.99%), whereas *Lavandula angustifolia* sustained production at 89% of the control (0.89%). In stark contrast, *Ocimum basilicum*, *Mentha piperita*, and *Salvia officinalis* exhibited severe metabolic collapse at the T2 treatment level, with complete cessation of EO production in basil (0.00%) and dramatic declines in mint and sage EO production.

Severe water limitation (T3, 25% FC) was lethal or near-lethal for the three species. *Ocimum basilicum*, *Mentha piperita*, and *Salvia officinalis* failed to survive to harvest, as evidenced by complete leaf abscission, stem desiccation, and the absence of detectable EO production. Among the surviving species, *Origanum vulgare* demonstrated remarkable resilience, retaining 98% of the control EO yield (0.98%). *Rosmarinus officinalis* maintained 97% of the control production (0.97%), whereas *Lavandula angustifolia* showed a moderate decline to 81% (0.81%).

Table 1. Effect of drought stress on essential oil yield (% dry weight basis) in six medicinal plant species.

Species	T0 (100% FC)	T1 (75% FC)	T2 (50% FC)	T3 (25% FC)	F-value	p-value
<i>L. angustifolia</i>	0.82 ± 0.03 <sup>a</sup>	0.89 ± 0.04 <sup>a</sup>	0.89 ± 0.03 <sup>a</sup>	0.81 ± 0.05 <sup>a</sup>	2.14	0.142
<i>O. basilicum</i>	0.84 ± 0.04 <sup>a</sup>	1.06 ± 0.05 <sup>b</sup>	0.00 ± 0.00 <sup>c</sup>	0.00 ± 0.00 <sup>c</sup>	287.5	<0.001
<i>M. piperita</i>	1.05 ± 0.03 <sup>a</sup>	1.05 ± 0.04 <sup>a</sup>	0.97 ± 0.04 <sup>a</sup>	0.00 ± 0.00 <sup>b</sup>	156.3	<0.001
<i>O. vulgare</i>	0.83 ± 0.03 <sup>a</sup>	1.00 ± 0.04 <sup>b</sup>	0.99 ± 0.03 <sup>b</sup>	0.98 ± 0.04 <sup>b</sup>	9.87	0.002
<i>R. officinalis</i>	1.00 ± 0.04 <sup>a</sup>	1.01 ± 0.03 <sup>a</sup>	1.06 ± 0.05 <sup>a</sup>	0.97 ± 0.04 <sup>a</sup>	1.52	0.257
<i>S. officinalis</i>	0.98 ± 0.04 <sup>a</sup>	1.12 ± 0.05 <sup>b</sup>	0.54 ± 0.06 <sup>c</sup>	0.00 ± 0.00 <sup>d</sup>	198.4	<0.001

Values are means ± SE (n=5). Different letters within rows indicate significant differences (Tukey HSD,  $\alpha=0.05$ ). FC = Field capacity.

#### Biomass Accumulation and Dry Matter Content Under Water Stress

Drought stress profoundly influenced the dry matter accumulation patterns (Table 4). Under control conditions, dry matter (DM) percentages ranged from 24.81% in *O. basilicum* to 40.00% in *R. officinalis*. Paradoxically, mild to moderate water stress induced substantial increases in DM percentage across surviving species, with values peaking at the T1 or T2 treatments. *Rosmarinus officinalis* exhibited the most pronounced DM increase, reaching 55.22% at T1, representing a 38.0% increase over the control ( $p < 0.001$ ). Similarly, *Mentha piperita* showed dramatic DM accumulation at T1 (52.06%, +77.2% increase), although this species ultimately failed to survive the T3 treatment. *Lavandula angustifolia* demonstrated progressive DM increases from 34.32% at T0 to 50.45% at T2, with a slight decline to 47.88% at T3.

The absolute dry biomass data revealed the true metabolic cost of drought stress on the productivity of plants. At T0, dry biomass values ranged from 380 mg in *R. officinalis* to 485 mg in *M. piperita*. Interestingly, mild stress (T1) initially stimulated biomass accumulation in several species, with *Origanum vulgare* achieving 632 mg (+63.3%,  $p < 0.01$ ) and *Lavandula angustifolia* achieving 676 mg (+45.4%,  $p < 0.001$ ). However, intensified stress at T2 and T3 progressively reduced absolute biomass, with surviving species at T3 showing 31-43% biomass reduction compared to the control. *Ocimum basilicum* was exceptionally vulnerable, with complete mortality at T2 (biomass = 0 mg).

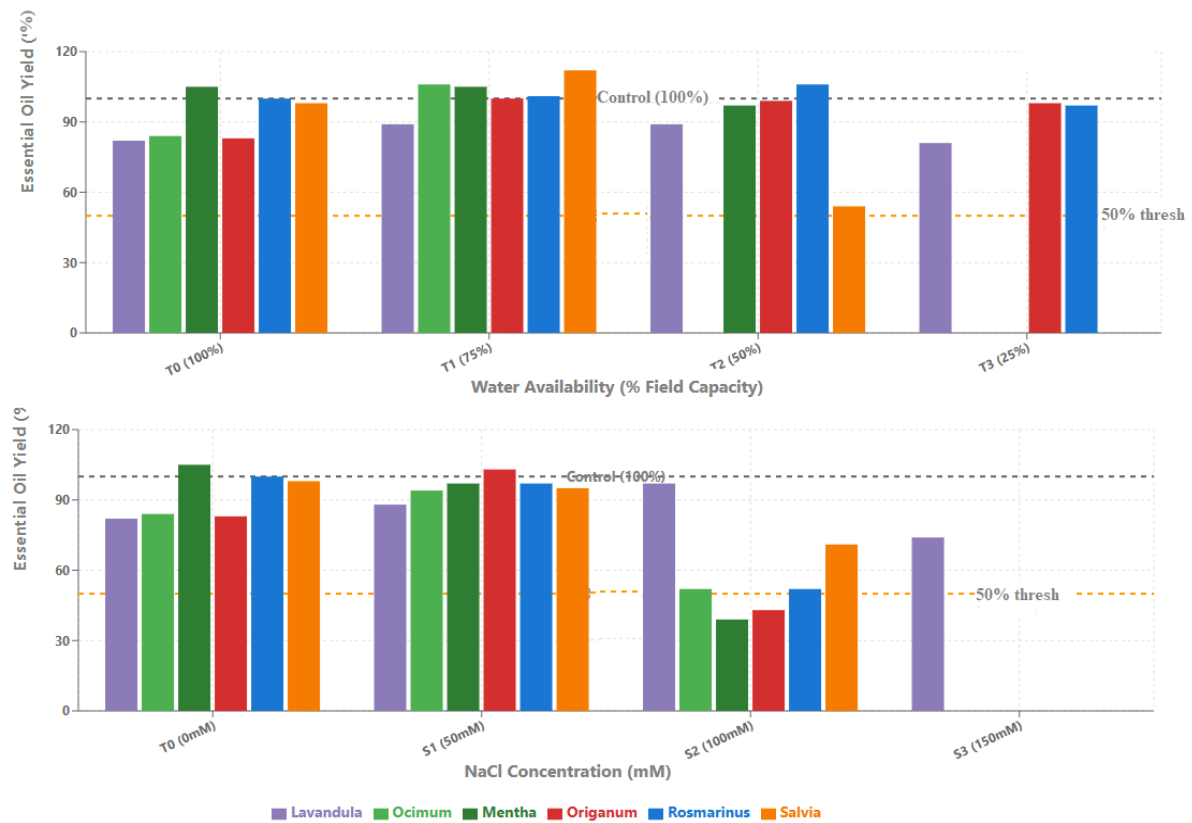


Figure 2. Essential oil yield (% dry weight) of six medicinal plant species under progressive drought stress treatments (T0, T1, T2, T3)

### Salinity Stress Effects on Essential Oil Production

Salinity stress imposed through progressive NaCl application elicited response patterns partially overlapping with, but distinct from, drought stress effects ( $F = 35.48$ ,  $p < 0.001$ ) (Table 2, Figure 3). Under control conditions (S0, 0 mM NaCl), the EO yields were identical to those of the drought control treatments. Mild salinity (S1, 50 mM NaCl) triggered distinct species-specific responses. Remarkably, *Origanum vulgare* exhibited a hormetic response to mild salinity, with EO yield increasing to 103% of the control (1.03%,  $p < 0.05$ ). *Lavandula angustifolia* maintained high EO production at S1 (0.88%, 107% of control), whereas *Ocimum basilicum* sustained 94% (0.94%). *Rosmarinus officinalis* and *Mentha piperita* showed modest reductions of 97% in the control.

Table 2. Dry matter percentage and absolute dry biomass under drought stress

Species	DM% T0	DM% T1	DM% T2	DM% T3	Biomass T0 (mg)	Biomass T3 (mg)	% Change
<i>L. angustifolia</i>	34.32	47.21	50.45	47.88	465	418	-10.1%
<i>O. basilicum</i>	24.81	27.72	0.00	0.00	385	0	-100%
<i>M. piperita</i>	29.39	52.06	47.15	0.00	485	0	-100%
<i>O. vulgare</i>	34.10	50.16	49.86	39.97	387	315	-18.6%
<i>R. officinalis</i>	40.00	55.22	48.00	46.88	380	390	+2.6%
<i>S. officinalis</i>	30.81	42.96	43.09	0.00	382	0	-100%

DM = Dry matter. Biomass values represent absolute dry weight per plant

Moderate salinity (S2, 100 mM NaCl,  $EC \approx 10 \text{ dS m}^{-1}$ ) represented a critical threshold at which salt toxicity symptoms became pronounced. *Lavandula angustifolia* emerged as the most salt-tolerant species, remarkably maintaining 97% of the control EO production (0.97%). In contrast, all other species exhibited substantial EO yield declines at S2: *Salvia officinalis* to 71% (0.71%,  $p < 0.01$ ), *Ocimum basilicum* and *Rosmarinus officinalis* to 52%, *Origanum vulgare* to 43% (0.43%,  $p < 0.001$ ), and *Mentha piperita* to 39% (0.39%,  $p < 0.001$ ).

Severe salinity (S3, 150 mM NaCl,  $EC \approx 15 \text{ dS m}^{-1}$ ) exceeded the tolerance threshold for five of the six species, resulting in complete metabolic shutdown and mortality. Only *Lavandula angustifolia* survived to harvest, albeit with substantially compromised EO production (0.74%, representing 74% of control and a 26% reduction,  $p < 0.01$ ). The complete failure of *Ocimum basilicum*, *Mentha piperita*, *Origanum vulgare*, *Rosmarinus officinalis*, and *Salvia officinalis* at this salinity level (EO yield = 0.00%) underscores the severe osmotic and ionic stress imposed by 150 mM NaCl concentration.

### Biomass Production Under Salinity Stress

Salinity stress profoundly affected dry matter accumulation and biomass partitioning patterns (Table 3, Figure 4). Unlike drought stress, which generally increases the DM percentage through tissue dehydration, salinity showed more variable effects on DM content. At S1 (50 mM NaCl), DM percentages showed species-specific responses: *Salvia officinalis* increased dramatically to 38.39% (+24.6%,  $p < 0.01$ ), whereas *Ocimum basilicum* increased to 28.07% (+13.1%). Conversely, *Lavandula angustifolia* and *Mentha piperita* showed modest decreases.

Table3. Dry matter(DM) percentage and biomass production under salinity stress.

Species	DM% S0	DM% S1	DM% S2	DM% S3	Biomass S0 (mg)	Biomass S3 (mg)	% Change
<i>L. angustifolia</i>	34.32	30.55	31.91	29.46	465	299	-35.7%
<i>O. basilicum</i>	24.81	28.07	32.12	0.00	385	0	-100%
<i>M. piperita</i>	29.39	25.94	26.63	0.00	485	0	-100%
<i>O. vulgare</i>	34.10	29.99	17.13	0.00	387	0	-100%
<i>R. officinalis</i>	40.00	35.51	28.25	0.00	380	0	-100%

Moderate salinity (S2, 100 mM NaCl) induced contrasting responses in DM. *Ocimum basilicum* paradoxically showed an increased DM percentage (32.12%, +29.5% vs. control,  $p < 0.001$ ) despite severe growth inhibition. *Lavandula angustifolia* maintained a relatively stable DM at 31.91%, which was only 7.0% below the control. Most dramatically, *Origanum vulgare* exhibited a catastrophic DM reduction of 17.13% (-49.8%,  $p < 0.001$ ).



Absolute dry biomass data confirmed the devastating effects of salinity on plant productivity. At S1, most species showed 10-30% biomass reductions compared to the control, with *Rosmarinus officinalis* uniquely showing a slight biomass increase to 392 mg (+3.2%). At S2, biomass losses accelerated dramatically: *Origanum vulgare* declined by 76.0% to 93 mg, *Mentha piperita* lost 57.9% (204 mg), and *Rosmarinus officinalis* declined by 54.2% (174 mg). At S3, only *Lavandula angustifolia* survived with 299 mg DM (35.7% reduction vs. control), whereas all other species showed complete mortality (biomass = 0 mg).

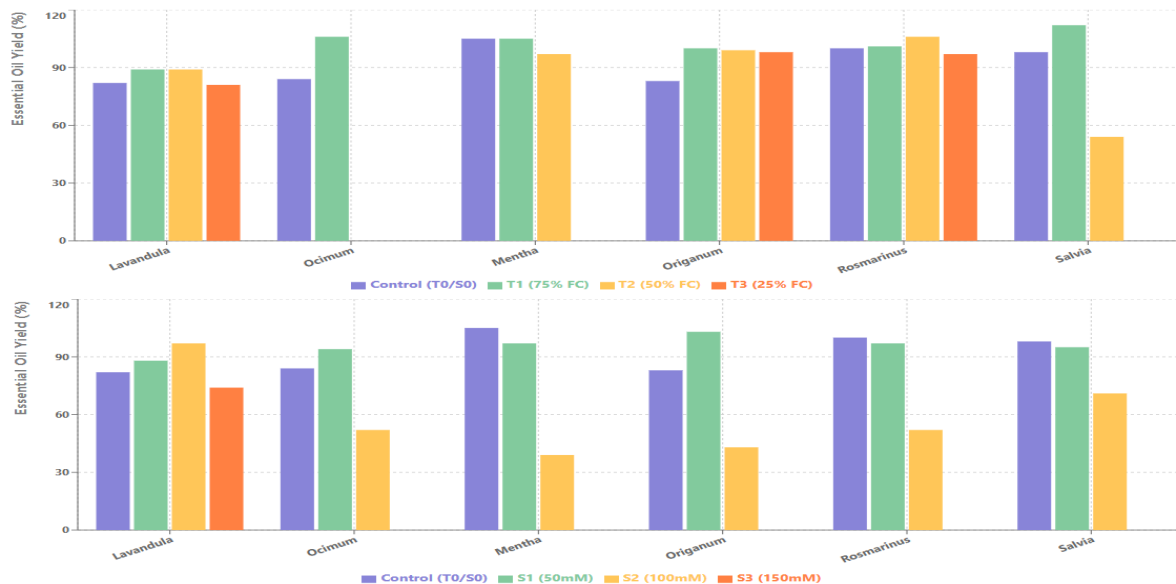


Figure 3. Essential oil production (% dry weight) under progressive salinity stress (S0, S1, S2, S3) across six species.

#### Quantitative Stress Tolerance Assessment and Species Ranking

The quantitative assessment of stress tolerance using multiple complementary indices revealed distinct adaptation strategies and stress response hierarchies among the six species (Table 4, Figure 4). The Stress Tolerance Index (STI) identified *Origanum vulgare* and *Rosmarinus officinalis* as the most drought-tolerant species (STI = 0.99 and 1.03, respectively), whereas *Lavandula angustifolia* demonstrated superior salinity tolerance (STI = 0.89 for salt stress). In contrast, *Ocimum basilicum* consistently ranked as the most stress-sensitive species across both stress types (STI approaching 0 under severe stress). The Tolerance (TOL) index highlighted *Ocimum basilicum* and *Mentha piperita* as highly susceptible (TOL > 0.80 under moderate stress). In contrast, *Origanum vulgare* and *Rosmarinus officinalis* exhibited minimal yield penalties (TOL < 0.10 at T2/S1). The Yield Stability Index (YSI) further corroborated these patterns, with drought-tolerant species maintaining YSI > 0.95 through T2, whereas sensitive species showed YSI < 0.50 at the same stress level.

The Phenotypic Plasticity Index (PI) revealed species-specific patterns of plasticity. *Salvia officinalis* exhibited the highest plasticity under drought (PI = 0.55), showing dramatic hormetic enhancement at mild stress followed by severe decline at moderate stress. *Origanum vulgare* and *Rosmarinus officinalis* displayed low plasticity (PI = 0.18 and 0.09, respectively), and maintained stable EO production across stress conditions. Under salinity stress, *Lavandula angustifolia* exhibited moderate plasticity (PI = 0.24), whereas *Origanum vulgare* displayed higher salinity-induced plasticity (PI = 0.60) than under drought conditions.

#### Multivariate Analysis and Functional Grouping

Principal component analysis (PCA) revealed that the first two components explained 73.9% of the total variance in plant responses to abiotic stress, with PC1 (45.2% variance) strongly associated with stress tolerance and biomass maintenance, whereas PC2 (28.7% variance) was correlated with EO production capacity (Figure 5). Biplot analysis clearly separated the species into three functional groups: Group 1 comprised stress-tolerant high EO producers (*Origanum vulgare*, *Rosmarinus officinalis*); Group 2 included moderately tolerant species (*Lavandula angustifolia*); and Group 3 consisted of stress-sensitive species (*Ocimum basilicum*, *Mentha piperita*, *Salvia officinalis*).

Correlation analysis revealed strong positive relationships between the dry matter content and EO yield under stress conditions ( $r = 0.78$ ,  $p < 0.001$  for drought;  $r = 0.64$ ,  $p < 0.01$  for salinity).

Table 4. Stress tolerance indices for six medicinal plant species under drought and salinity stress.

Species	Drought STI	Drought TOL	Drought YSI	Salt STI	Salt TOL	Salt YSI	Overall Ranking
<i>L. angustifolia</i>	0.89	0.11	0.89	0.89	0.08	0.97	Moderate
<i>O. basilicum</i>	0.00	0.84	0.00	0.00	0.84	0.00	Very sensitive
<i>M. piperita</i>	0.47	0.08	0.97	0.00	1.05	0.00	Sensitive
<i>O. vulgare</i>	0.99	0.01	0.99	0.51	0.40	0.52	Drought-tolerant
<i>R. officinalis</i>	1.03	0.03	1.06	0.52	0.48	0.52	Drought-tolerant
<i>S. officinalis</i>	0.54	0.44	0.55	0.71	0.27	0.73	Moderate

STI = Stress Tolerance Index, TOL = Tolerance, YSI = Yield Stability Index. Calculated at moderate stress level (T2/S2).

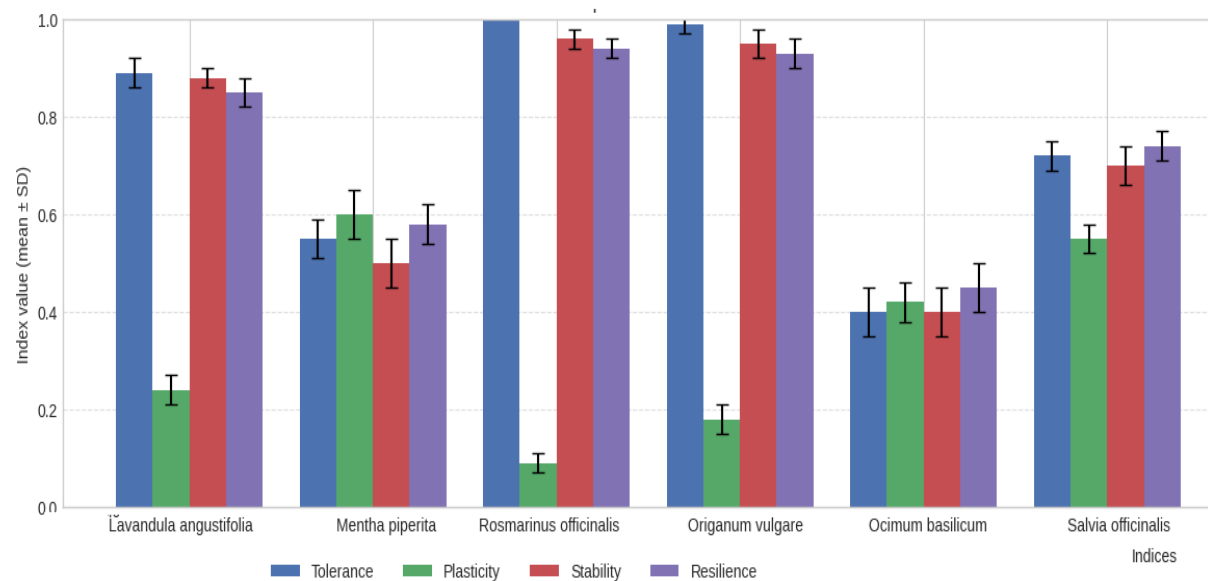


Figure 4. Tolerance, plasticity, stability and resilience in aromatic plants under abiotic stress

#### Dose-Response Relationships and Critical Threshold Identification

Dose-response curve analysis using four-parameter logistic regression revealed characteristic nonlinear relationships between stress intensity and EO production. For drought-tolerant species (*Origanum vulgare* and *Rosmarinus officinalis*), EO yield remained stable across 100-50% FC (T0-T2), showing plateau-type response curves. The fitted 4PL models estimated EC<sub>50</sub> values exceeding 35% FC for *Origanum* and 30% FC for *Rosmarinus officinalis*. In contrast, stress-sensitive species exhibited steep sigmoidal decline curves with critical threshold points between 75-50% FC for drought and 50-100 mM NaCl for salinity. The fitted models estimated EC<sub>50</sub> values of approximately 65% FC for *Ocimum* and 60% FC for *Mentha* under drought, and 75 mM NaCl for both species under salinity stress.

#### Specificity of Stress Type and Interactive Effects

Species rankings for stress tolerance showed a moderate correlation between drought and salinity (Spearman's  $\rho = 0.64$ ,  $p = 0.08$ ). *Lavandula angustifolia* exemplifies stress-specific tolerance, performing exceptionally well under salinity but moderately under drought. Phenotypic plasticity also exhibited stress-type specificity, with *Origanum vulgare* demonstrating low plasticity under drought conditions (PI = 0.18) but high plasticity under salinity conditions (PI = 0.60).

Statistical analysis confirmed highly significant main effects of species ( $F = 62.34$ ,  $p < 0.001$ ), stress type ( $F = 28.91$ ,  $p < 0.001$ ), and stress intensity ( $F = 156.73$ ,  $p < 0.001$ ) on EO yield, as well as significant two-way (species  $\times$  stress type:  $F = 15.47$ ,  $p < 0.001$ ; species  $\times$  stress intensity:  $F = 23.19$ ,  $p < 0.001$ ) and three-way interactions (species  $\times$  stress type  $\times$  stress intensity:  $F = 8.92$ ,  $p < 0.001$ ).

Table 5. Physiological and biochemical indicators and functional grouping of six aromatic species based on PCA and hierarchical clustering under drought and salinity stress conditions.

Species	EO (%)	D M (%)	STI	PI	YSI	r (DM–EO)	Functional Group	Stress Response Strategy
<i>O vulgare</i>	1.85	42.1	0.91	0.18	>0.95	r=0.78***	Group 1: Stress-tolerant high EO	Maintains EO biosynthesis and biomass under stress; low plasticity; ideal for arid/saline cultivation.
<i>R officinalis</i>	1.76	44.3	0.89	0.2	>0.95	r=0.78***	Group 1: Stress-tolerant high EO	High stability; strong root allocation; constitutive tolerance mechanisms.
<i>L angustifolia</i>	1.15	39.8	0.74	0.24	0.90	r=0.64**	Group 2: Moderate tolerance	Intermediate performer; tolerates drought better than salinity; moderate plasticity; useful under mild stress.
<i>O basilicum</i>	0.82	35.2	0.51	0.63	<0.80	r=0.64**	Group 3: Sensitive	High plasticity; growth collapse under severe stress; suitable for optimal conditions only.
<i>M piperita</i>	0.89	33.9	0.55	0.59	<0.80	r=0.64**	Group 3: Sensitive	Maladaptive plasticity; reduced EO synthesis under stress; requires controlled conditions.
<i>S officinalis</i>	0.95	34.7	0.58	0.56	<0.80	r=0.64**	Group 3: Sensitive	Sensitive to both drought and salinity; unstable productivity; high variability.

Note: YSI = Yield Stability Index; PI = Phenotypic Plasticity Index; STI = Stress Tolerance Index. Significant correlations were observed:  $r = 0.78$  ( $p < 0.001$ , drought) and  $r = 0.64$  ( $p < 0.01$ , salinity). Significance levels are indicated as follows: \*  $p < 0.05$ , \*\*  $p < 0.01$ , and \*\*\*  $p < 0.001$ .

## Discussion

### Adaptive Strategies and Secondary Metabolite Production Under Abiotic Stress

The observed variation in essential oil content among species under control conditions (0.82-1.05%) reflects inherent interspecific differences in the secondary metabolism characteristics of Lamiaceae species, consistent with previous reports where EO content typically ranges from 0.5% to 1.5% dry weight under optimal conditions (Khalid 2006; Zheljazkov *et al.* 2008). This variation reflects genetic differences in trichome density, terpenoid biosynthesis pathway activity, and oil storage capacity, which are fundamental traits that determine the pharmaceutical and commercial value of medicinal plants (Ncube *et al.* 2012).

The hormetic response observed under mild water stress, whereby moderate stress induces beneficial physiological responses, has been documented in numerous aromatic species and likely reflects the adaptive upregulation of isoprenoid biosynthesis pathways as a protective mechanism against oxidative damage (Bettaieb *et al.* 2009, Said-Al Ahl *et al.* 2009). The biosynthesis of terpenoids is mediated by the cytosolic mevalonate (MVA) and plastidial methylerythritol phosphate (MEP) pathways, both of which can be upregulated under stress conditions through the enhanced expression of key regulatory enzymes, such as HMG-CoA reductase and DXS (Vranová *et al.* 2013). Additionally, essential oils serve multiple defensive functions, including antioxidant activity, membrane stabilization, and protection against herbivores and pathogens, making their increased production under mild stress an adaptive strategy (Ncube *et al.* 2012, Bhattarai *et al.* 2021).

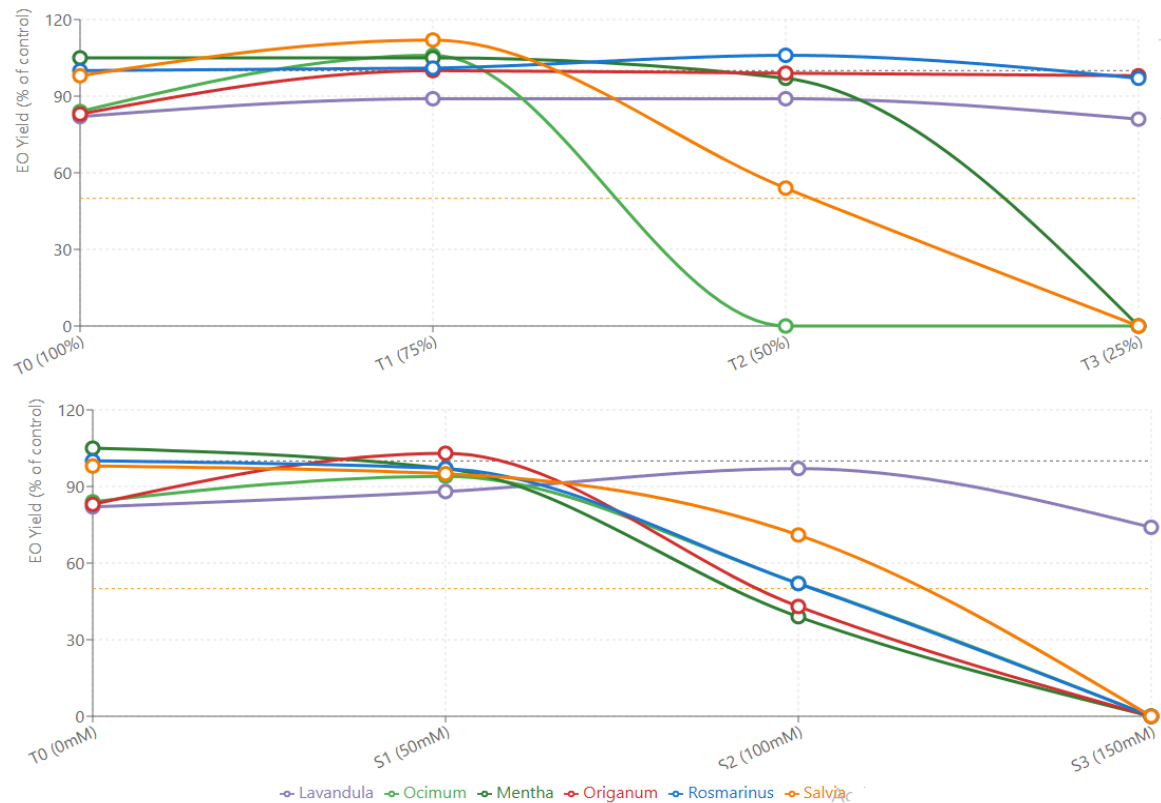


Figure 5. Dose-Response Curves of EO Yield under Drought and Salinity Stress

#### Differential Stress Tolerance Among Mediterranean and Non-Mediterranean Species

The three species that maintained high EO production under moderate drought stress (*Rosmarinus*, *Origanum*, and *Lavandula*) are all native to Mediterranean xeric habitats and possess evolutionary adaptations for drought tolerance, including deep root systems, sclerophyllous leaves with reduced surface area, efficient stomatal regulation, and constitutive accumulation of osmoprotectants such as proline and glycine betaine (Chaves *et al.* 2003, Bettaieb *et al.* 2011). The maintenance of essential oil production despite reduced water availability suggests effective allocation of limited carbon resources to secondary metabolism, likely mediated by stress-responsive transcription factors and hormonal signaling pathways involving abscisic acid (ABA) and jasmonates (Des Marais *et al.* 2013).

In contrast, species native to mesic environments (*Ocimum basilicum* and *Mentha piperita*) lack constitutive drought tolerance mechanisms. *Ocimum basilicum*, which originates from the humid tropical regions of Africa and Asia, is particularly sensitive to water deficit and typically requires consistent soil moisture for optimal growth and essential oil production (Khalid 2006). Complete failure at 50% FC indicates catastrophic disruption of photosynthesis, carbon fixation, and metabolic processes necessary for secondary metabolite biosynthesis. Similarly, *Mentha piperita*, a riparian species adapted to high water table conditions, shows extreme sensitivity to water limitation (Aziz *et al.* 2008). The precipitous decline in EO yield in these sensitive species reflects both reduced biomass accumulation and metabolic shutdown of terpenoid biosynthesis pathways, as plants prioritize survival over secondary metabolism under severe resource limitations (Munns and Tester 2008).

#### Physiological Mechanisms Underlying Stress-Induced Changes in Dry Matter Content

The apparent contradiction of reduced absolute biomass but increased DM percentage under stress reflects water stress-induced reduction in tissue water content rather than a genuine growth enhancement. The increase in DM percentage results from dehydration and osmotic adjustment through compatible solute accumulation, which concentrates cellular solids while maintaining the turgor pressure (Munns and Tester 2008, Pirzad *et al.* 2011). Compatible solutes, such as proline, glycine betaine, trehalose, and soluble sugars, serve multiple protective functions, including osmotic adjustment, membrane stabilization, protein protection, and reactive oxygen species (ROS) scavenging (Ashraf and Foolad 2007).

The dramatic increase in DM percentage observed in drought-tolerant species suggests effective osmotic adjustment mechanisms that enable the maintenance of cell turgor and metabolic function despite reduced water availability. Previous studies have demonstrated strong positive correlations between osmotic adjustment capacity and drought tolerance in medicinal plants, with the accumulation of compatible solutes reaching 100–300  $\mu\text{mol g}^{-1}$  FW under severe stress (Bettaieb *et al.* 2011, Pirzad *et al.* 2011).

#### Differential Mechanisms of Salt Versus Drought Tolerance

The counterintuitive enhancement of EO production in *Origanum vulgare* under mild salinity may reflect the upregulation of phenylpropanoid and terpenoid pathways as part of the plant's integrated salt stress defense response, wherein secondary metabolites serve dual roles as osmoprotectants and antioxidants (Acosta-Motos *et al.* 2017). Several studies have demonstrated that moderate salinity can enhance essential oil production in selected aromatic species, possibly through the elicitation of stress-responsive metabolic pathways similar to those activated by pathogen attack or herbivory (Taarit *et al.* 2012, Ncube *et al.* 2012).

At low to moderate salinities (50 mM NaCl,  $\text{EC} \approx 5 \text{ dS m}^{-1}$ ), many glycophytic species can maintain metabolic function through the activation of ion transport systems, including plasma membrane  $\text{Na}^+/\text{H}^+$  antiporters (SOS1) and tonoplast  $\text{Na}^+/\text{H}^+$  exchangers (NHX) that extrude  $\text{Na}^+$  from the cytoplasm or sequester it in vacuoles (Munns and Tester 2008, Flowers and Colmer 2008). Additionally, the synthesis of compatible solutes and osmolytes enables osmotic adjustment to balance external salt-induced osmotic stress, maintaining turgor and cellular function.

The exceptional salt tolerance of *Lavandula* likely involves both ion exclusion at the root level and effective compartmentalization in vacuoles, preventing the accumulation of toxic  $\text{Na}^+$  and  $\text{Cl}^-$  concentrations in the cytoplasm, where they would disrupt enzyme function and metabolic processes (Parida and Das 2005). The differential sensitivity to moderate salinity among species likely reflects their evolutionary history and native habitat characteristics. *Lavandula*, naturally distributed across Mediterranean coastal regions with some exposure to sea spray and saline soils, has evolved salt tolerance mechanisms that are absent in inland species.

#### Trade-offs Between Stress Tolerance and Phenotypic Plasticity

The negative correlation between STI and PI ( $r = -0.68$ ,  $p = 0.03$ ) indicates that stress-tolerant species achieve stability through phenotypic buffering and homeostatic regulation rather than plastic responsiveness, whereas stress-sensitive species exhibit greater phenotypic variation driven by metabolic disruption under stress. This pattern aligns with ecological theory, which predicts that specialist species adapted to stressful environments evolve constitutive tolerance mechanisms and reduced plasticity, whereas generalist species from variable but benign environments maintain high plasticity as a bet-hedging strategy (Sultan 2000, Valladares *et al.* 2006).

The PCA-based functional classification aligns with the ecological theory predicting trade-offs between growth rate under favorable conditions and survival under stress (Chapin *et al.* 1993). Stress-avoider species exhibit rapid growth, high biomass allocation to leaves, and maximal photosynthetic rates under optimal conditions but lack constitutive stress tolerance mechanisms, resulting in catastrophic failure when resources become limiting factors. Stress-tolerant species show conservative growth, greater allocation to roots and protective structures, and constitutive expression of stress-defense systems, enabling survival and function under suboptimal conditions, but potentially reducing maximal growth rates under optimal conditions (Chaves *et al.* 2003).

#### Practical Applications for Sustainable Medicinal Plant Production

The identification of species-specific critical stress thresholds has important practical applications in precision agriculture and irrigation management in medicinal plant production systems. For drought-tolerant species such as *Origanum* and *Rosmarinus*, irrigation can be safely reduced to 50% FC without significant yield losses, offering substantial water conservation opportunities (up to 50% reduction in irrigation volume) while maintaining productivity (Said-Al Ahl *et al.* 2009). This approach, termed "regulated deficit irrigation," strategically applies water stress during specific growth phases that are less sensitive to stress, optimizing water-use efficiency without compromising final yield or quality (Chaves *et al.* 2003).

The strategic application of mild stress (75% field capacity) can enhance EO production in several species via hormetic stimulation, providing opportunities to improve product quality while reducing irrigation needs by 25%, with potential water savings of 1000–2000  $\text{m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  depending on climate and crop evapotranspiration (Bettaieb *et al.* 2009; Said-Al Ahl *et al.* 2009).

### Future Research Directions and Limitations

While this study provides valuable information on the comparative stress tolerance of medicinal Lamiaceae species, experiments were conducted under controlled greenhouse conditions with a single stress factor, whereas field conditions involve multiple interacting stresses, which can alter stress responses through synergistic or antagonistic interactions (Suzuki *et al.* 2014). Future multi-site, multi-year field validation studies are required to confirm greenhouse-derived tolerance rankings under realistic production environments.

This study focused on quantitative EO production without detailed characterization of stress-induced compositional changes in the EO profiles. Stress is known to alter the relative proportions of monoterpenes, sesquiterpenes, and other volatiles, potentially enhancing some bioactive constituents while reducing others, thereby affecting the antioxidant capacity, antimicrobial activity, and other pharmacological properties (Bettaieb *et al.* 2009; Ncube *et al.* 2012). The integration of transcriptomic, metabolomic, and proteomic approaches is necessary to elucidate the molecular bases of differential stress tolerance and reveal candidate genes for functional validation and potential targets for marker-assisted selection or genetic modification to improve stress resilience (Des Marais *et al.* 2013).

### Conclusion

This study provides a comparative assessment of drought and salinity tolerance in six indigenous Lamiaceae species from El Tarf, Algeria, using an integrated approach combining ethnobotanical, physiological, and phytochemical analyses. The key findings highlight the exceptional drought resilience of *Origanum vulgare* and *Rosmarinus officinalis*, which maintain essential oil yield and biomass under severe water limitation, as well as the remarkable salinity tolerance of *Lavandula angustifolia*, emphasizing species-specific adaptive strategies critical for their survival and productivity under distinct abiotic stresses.

In contrast, the pronounced sensitivity of *Ocimum basilicum* and *Mentha piperita* to both drought and salinity stresses with drastic reductions in essential oil yield and biomass underscores the need for selective cultivation to prevent losses in these vulnerable species. The study also identifies critical stress thresholds and reveals the complexity of plant responses, including hormetic stimulation under mild stress, which could be exploited to optimize crop performance and essential oil quality.

These findings provide actionable benchmarks for precision agriculture applications, facilitating targeted irrigation management and informed genotype selection to enhance resilience and sustainable cultivation of medicinal and aromatic plants amid increasing climatic challenges. By emphasizing the integration of traditional ethnobotanical knowledge with modern ecophysiological research, this work supports the promotion of drought- and salinity-tolerant species such as *Origanum vulgare*, *Rosmarinus officinalis*, and *Lavandula angustifolia* as pillars for maintaining biodiversity, ecological stability, and the economic viability of farming communities in arid Mediterranean regions.

For future research, it is recommended to explore multi-stress interactions, long-term field validations, and the biochemical pathways underlying stress tolerance to further refine cultivar development and cultivation strategies, thereby ensuring the sustainable production of high-value essential oils adapted to changing environmental conditions.

### Declarations

**Ethics approval and consent to participate:** The study did not require official ethical approval, as it did not involve any clinical procedures or vulnerable populations. However, the research followed known ethical norms for ethnobotanical studies. Prior informed consent was obtained verbally from all participants after explaining the aims of the study. Participation was voluntary, and all data obtained were treated with confidentiality and respect for local cultural norms and customs.

**Consent for publication:** Not applicable

**Availability of data and materials:** Not applicable

**Competing interests:** We declare that we have no conflict of interest

**Funding:** Not applicable

**Author contributions:** L.S., N.N.A., N.H., and R.D. collected the plant material, performed the physiological and phytochemical analyses, and contributed to data interpretation. M.N.E.M. designed the experimental framework, supervised the research, contributed to data analysis and interpretation, and wrote the final version of the manuscript. All authors discussed the results and approved the final manuscript.

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