

## Review article

# Mild abiotic stresses improve essential oils yield and composition of Mediterranean medicinal and aromatic plants with minimal impact on plant growth: A systematic literature review

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## ABSTRACT

Medicinal and Aromatic Plants (MAPs) are industrially relevant crops primarily valued for their production of bioactive secondary metabolites used across the pharmaceutical, cosmetic, and food sectors, and many species also exhibit good adaptability to marginal environments. Their ability to synthesize many bioactive compounds, such as essential oils (EOs; singular: EO), underlines their strategic importance in pharmaceutical, cosmetic, flavor, and food industries. The Mediterranean Basin, home to a wide variety of MAPs, is increasingly affected by drought and land degradation due to climate change. One major challenge lies in optimizing the yield, qualitative characters and quantitative composition of plant extracts, while ensuring sustainable and resilient cropping systems. Specifically, MAPs often increase the production of active compounds under abiotic stress. Exploiting this feature represents an opportunity for enhancing both yield and composition of EOs and cultivating MAPs in marginal areas, though outcomes depend on multiple factors. This systematic review evaluates the potential of applying mild abiotic stress to enhance EO yield and composition and examines the underlying hypothesis that mild stress can stimulate their biosynthesis. We critically analyzed a total of forty-nine articles identified through Web of Science and Scopus, following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines. Findings show that mild stress can influence EO content and profile, while maintaining plant growth and highlighting the adaptability of MAPs to Mediterranean conditions. We outlined that MAPs interact with the environment, affecting secondary metabolism and EOs production. Further research is needed to clarify the relationships between abiotic stress, compound synthesis, and environmental factors, aiming to stabilize EOs for industrial applications. Enhancing the adaptation of MAPs to marginal lands may offer sustainable solutions for climate-resilient agriculture and natural product industries.

## 1. Introduction

The Mediterranean basin, one of the world's eight Vavilov's Centers of Origin of Crop Plants, is a region of great interest for preserving biodiversity (Loskutov et al., 2023). This area hosts numerous plant species that have evolved to thrive in its unique climate and soil conditions. The plant biodiversity includes Medicinal and Aromatic Plants (MAPs) belonging to several botanical families such as *Abietaceae*,

*Apiaceae*, *Asteraceae*, *Cupressaceae*, *Lamiaceae*, *Lauraceae*, *Myrtaceae*, and *Rutaceae* (Napoli et al., 2020). Medicinal and Aromatic Plants are a category of industrial crops with sensory, biological, and pharmacological properties. Their ability to produce secondary metabolites, particularly terpenoids, phenolic compounds, and alkaloids, distinguishes them from staple field crops such as cereals and legumes (Napoli et al., 2020). These plants can be used fresh or processed, with extraction methods selected according to the target compounds and end-use (e.g.,

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hydrodistillation/steam distillation, solvent or supercritical CO<sub>2</sub> extraction) (Mahajan et al., 2020; Yeshe et al., 2022). Active ingredients extracted from MAPs are employed in cosmetics, pharmaceuticals, fragrances, cleaning products, functional foods, bioherbicides, bio-insecticides, and flavoring industries (Yeshe et al., 2022). Terpenoid compounds are widely used for their antimicrobial, antifungal, and antioxidant activities, helping extend shelf life and enabling natural preservative formulations (Bolouri et al., 2022). In cosmetic and pharmaceutical applications, these ingredients provide both fragrance and functional benefits; reported examples include hair-care effects (rosemary and chamomile in shampoos; peppermint oil for hair growth) and antiacne activity via inhibition of *Cutibacterium acnes* (e.g., citronella extracts) (Bolouri et al., 2022). Secondary metabolites also underpin bioherbicidal uses: several volatile compounds exhibit phytotoxicity that inhibits seed germination and seedling growth, supporting their potential in weed management (Verdeguer et al., 2020). Numerous MAPs species, including rosemary (*Salvia rosmarinus* Spenn.), lavender (*Lavandula* spp.), sage (*Salvia* spp.), and mint (*Mentha* spp.), have a long history of traditional uses due to their production of active molecules. Their effectiveness belongs to bioactive compounds like terpenes, alkaloids, and phenolic compounds, which have analgesic, anticancer, anti-inflammatory, and muscle-relaxant properties (Uritu et al., 2018). The biosynthesis of active compounds depends on a complex of metabolic activities influenced by the interaction between plant species and their growing environment (Punetha et al., 2022). Indeed, these active compounds are produced when a plant responds to various external environmental factors, including temperature, salinity, air moisture levels, soil water content, heavy metals, and nutrient content. The secondary-metabolite biosynthesis can increase or decrease essential-oil yield and alter aromatic profile. Whether these changes are desirable depends on the target application, while from the plant perspective, some shifts may support stress tolerance but can trade off with biomass accumulation (Avasiloaiei et al., 2023). Medicinal and Aromatic Plants show a peculiarity due to their ability to react under stressful conditions; they adapt their metabolism to environmental conditions, which can help enhance the value of marginal lands, i.e., areas at the margin of crop productivity and/or subject to biophysical constraints (poor soil quality, salinity, water scarcity, slope) that limit conventional yields (Peterson and Galbraith, 1932; Mahajan et al., 2020).

Among secondary metabolites, essential oils (EOs; singular: EO) are mainly demanded by industry, particularly in the cosmetic and pharmaceutical industries, and are derived from a complex of terpenes, terpenoids, phenylpropanoids, and other volatile and low molecular weight compounds (Nazari et al., 2023). Essential oils are synthesized and stored in specialized secretory structures (e.g., glandular trichomes, internal resin ducts, and secretory glands). Depending on the species, EOs can be extracted from leaves, flowers/bracts, bark/wood, peels/fruits, seeds, roots, or whole plants, and their synthesis, storage, and emission can differ among organs bearing secretory structures (Aqeel et al., 2023). These dynamics can support defense against biotic and abiotic stressors and pollinator attraction (Verdeguer et al., 2020). Essential oils are derived from a complex of enzymatic reactions between terpenoids and phenylpropanoids, which are responsible for the aroma and flavor (Aqeel et al., 2023). Specifically, the most frequent constituents of plant EOs are isoprenoids, starting with mevalonate (MVA) and 2-C-methyl-D-erythritol-4-phosphate (MEP). Thus, producing active ingredients involves complex biochemical reactions regulated by the interaction of external factors, including climate change, which directly affects plant behavior (Punetha et al., 2022).

In recent years, a new strategy has been developed and assessed. This strategy involves applying mild stress to plants during precise stages of their growth cycle to boost the production of certain compounds without negatively impacting their growth (Niinemets, 2010). Mild abiotic stress is defined as exposure to an environmental factor below the damage threshold. In this case, the plant's response is reversible, dominated by physiological plasticity and adaptation rather than an irreversible

condition (Biswas et al., 2023). From a physiological standpoint, a key distinction between mild and severe stress lies in the reversibility and plasticity of the plant response (Martínez-Ferri et al., 2019). Mild abiotic stress refers exclusively to non-biological drivers (e.g., water deficit, salinity, temperature, light/UV) operating within a sub-threshold zone where the signal is perceived but does not exceed the plant's homeostatic capacity (Niinemets, 2010; Formica et al., 2024). Under these conditions, core functions such as photosynthesis, water balance, and primary metabolism remain largely functional, while signaling cascades activate targeted adjustments, including the selective modulation of gene expression, antioxidant defenses, and secondary metabolic pathways. In contrast, severe stress leads to systemic damage, loss of metabolic control, and often a shutdown of energy-intensive processes, including growth and reproduction (Niinemets, 2010). This can be particularly beneficial for growing MAPs in marginal agricultural areas, where water availability is limited and poses a significant constraint on cultivating high-input-demanding crops (Kulak, 2020; Yeshe et al., 2022). In this context, mild drought stress can be seen not only as an inevitable limit but also as a feasible stimulus that can enhance plant quality traits (Niinemets, 2010). Indeed, understanding the physiological threshold between mild and severe abiotic stress is crucial. Severe drought causes metabolic disruption and reduced yields, but mild stress can stimulate secondary metabolism synthesis without significantly impairing crop development. However, the increase in the concentration of EOs or key bioactive constituents is often associated with a reduction in fresh leaf and flower biomass per unit area (Selmar and Kleinwächter, 2013; Abouzeid et al., 2022). Furthermore, recognizing how genotype, environment, and intensity of stress can influence the composition of EOs is crucial. (Nemeth-Zambori et al., 2016; Nazari et al., 2023). Punetha et al. (2022) reported that mild drought altered the EOs composition of common sage (*Salvia officinalis* L.), with changes in the relative abundance of key constituents depending on the stress regime. Similarly, in common thyme (*Thymus vulgaris* L.), mild drought has been associated with increased concentrations of thymol, carvacrol,  $\gamma$ -terpinene, and p-cymene, depending on stress severity and elicitation conditions. Different stress levels can lead to distinct metabolic responses; however, many studies agree that mild stress can promote the synthesis of EO without substantial reductions in biomass production (Paraskevopoulou et al., 2020; Kumlay et al., 2022; Delfine et al., 2024; Araniti et al., 2024). This aspect allows the cultivation of MAPs in marginal areas with limited environmental growth conditions, such as high salt levels or low water availability due to drought (Radwan et al., 2017).

The stressors that most affect the quality and yield of EOs are mainly thermic, drought, salt, and light stresses, which all affect the photosynthetic process (Patni et al., 2022; Aqeel et al., 2023). This review addresses the current lack of an integrated perspective by defining mild or moderate abiotic stress, and synthesizing when and to what extent it can enhance EOs yield and composition without compromising plant growth, offering a clear framework for research and practice. To address this gap, we conducted a PRISMA-guided systematic review to synthesize evidence on how mild abiotic stresses influence EOs yield and composition in Mediterranean MAPs. This review highlights the potential of MAPs to tolerate controlled abiotic stress conditions while maintaining growth and modulating EOs production, supporting the development of innovative and sustainable cropping strategies for marginal lands. Ultimately, our findings underline the strategic role of MAPs as industrial crops capable of supplying high-value raw materials for the cosmetic, pharmaceutical, and agri-food sectors under climate-constrained conditions.

## 2. Methodology

The systematic literature review (SLR) was conducted following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Moher et al., 2015). The PRISMA methodology

provides a checklist and a flow diagram to document study identification, screening, eligibility, and inclusion, thereby improving transparency and reproducibility of evidence syntheses, and it is increasingly used in environmental and agricultural research (Wezel et al., 2025). After screening, 49 studies were included. The aim was to collect and analyse scientific evidence on the effects of controlled abiotic stress on Mediterranean MAPs, with particular attention to EOs yield and quality. Studies involving biostimulants, microbial consortia, or other biological agents were excluded to maintain a clear focus on abiotic factors.

The literature research utilized two major bibliographic databases, Web of Science (WoS) and Scopus, which comprehensively cover high-impact scientific literature (Do et al., 2021).

The search strategy was designed to align with the review objectives. Consistent with the PRISMA standard, a pre-specified temporal filter (2014–2024) was applied to include the most relevant and up-to-date studies, while maintaining methodological comparability across analyses. The following keywords were used in the search string to ensure the focus on abiotic stress factors while excluding studies involving microorganisms, bacteria, arbuscular mycorrhizae, proline, and other biostimulant products.

TITLE-ABS-KEY ( ( "medicinal and aromatic plants" OR "MAPs" OR "mediterranean medicinal and aromatic plants") OR ( "rosemary" OR "Rosmarinus officinalis" OR "Salvia rosmarinus") OR ( "thyme" OR "Thymus vulgaris" OR "Thymus capitatum" OR "Thymbra capitata") OR ( "sage" OR "Salvia officinalis") OR ( "oregano" OR "Origanum vulgare") OR ( "fennel" OR "Foeniculum vulgare") OR ( "Calendula officinalis" OR "marigold") OR ( "coriander" OR "Coriandrum sativum") OR ( "mint" OR "Mentha") OR ( "lavender" OR "lavandula" OR "Lavandula angustifolia") AND ( "abiotic stress" OR "water stress" OR "drought stress" OR "salinity" OR "salt stress" OR "light stress" OR "thermal stress") AND ( "essential oil quality" OR "essential oil yield" OR "EOs" OR "essential oil") AND NOT ( "microorganism" OR "bacteria" OR "arbuscular mycorrhizae" OR "proline" OR "jasmonic acid" OR "salicylic acid" OR "jasmonate" OR "gallic acid" OR "biostimulants" OR "biofertilizer" OR "nanoparticle" OR "foliar" OR "penconazole" OR "gene expression" OR "genetics" OR "band" OR "fertility") ) AND PUBYEAR > 2013 AND PUBYEAR < 2025 AND ( LIMITTO ( DOCTYPE, "ar" ) )

The bibliographic outputs from WoS and Scopus were combined to maximize the likelihood of capturing all significant scientific contributions and achieving the highest level of search and selection accuracy. The selection process was conducted systematically following PRISMA guidelines (Page et al., 2021), applying predefined inclusion and exclusion criteria to assess the eligibility of each study. Specifically, the following criteria were used:

1. Only scientific articles written in English were considered.
2. Papers published in book chapters and conference records were not reviewed, as it is difficult to access and extrapolate them from the literature.
3. The authors defined a final list of articles, eliminating the duplication of papers reported in both databases.
4. The authors read the abstract of each paper to determine whether the topic fit with the review's aim, selecting only papers focused on mild abiotic stress application to MAPs' chosen species.
5. Only papers meeting the above criteria were selected, and their full texts were thoroughly considered according to the review's objectives.

The query yielded 188 records, of which 36 were removed as duplicates. In the initial screening phase, titles and abstracts were reviewed to ensure alignment with the inclusion criteria, leaving 152 studies for further assessment. After these studies underwent a comprehensive evaluation to determine their eligibility, 57 articles were excluded for various reasons: being of the wrong type (e.g., literature reviews), irrelevant to the topic, or focusing solely on the quality and antimicrobial properties of EOs without examining abiotic stress.

This process resulted in 95 papers entering the eligibility stage. Of these, 46 studies were further excluded due to a focus on abiotic stress concerning microorganism applications (14), targeting soil fertility improvement rather than directly enhancing EOs concentration (8), or investigating non-target MAPs (24). Ultimately, 49 articles were selected for inclusion in the results and discussion of this SLR, as illustrated in Fig. 1.

After screening the articles, a VOSviewer diagram was generated using VOSviewer software version 1.6.20. The VOSviewer diagram was implemented to analyze the co-occurrence of keywords from papers included in the review. It was based on keywords that appeared with a minimum frequency of 5 in the articles selected (Van Eck and Waltman, 2007).

### 3. Results and discussion

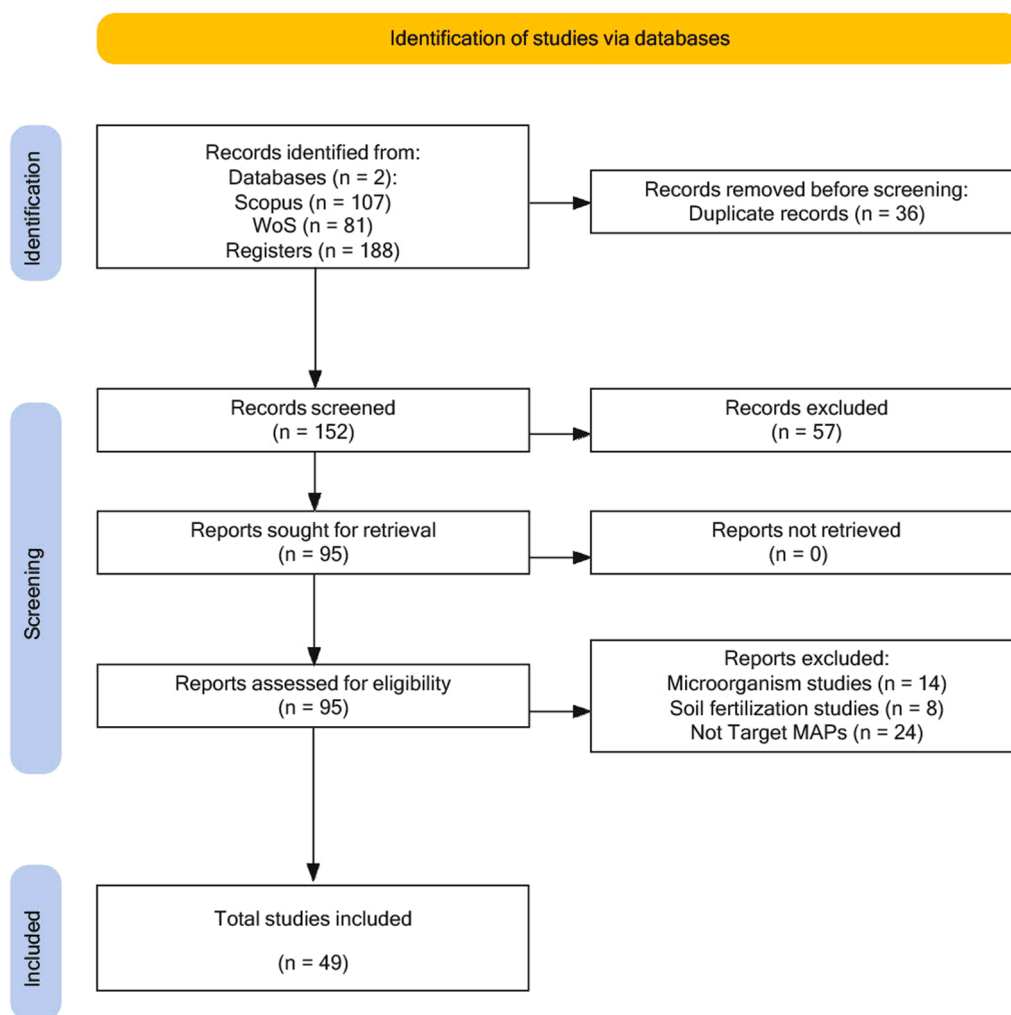
Based on the research string query, 49 scientific papers were found. Abiotic stresses include drought, light, high and low temperatures, and salt stress, which have been documented for their influence on plant growth, physiological aspects, and modulation of essential-oil biosynthesis, yield, and the constituent profile of volatiles. Most articles focused on *Lamiaceae* species, and a few explored *Asteraceae* and *Apiaceae* botanical families. The selected articles were published in the following journals: *Industrial Crops and Products*, *Journal of Essential Oil Research*, *Journal of Ethnopharmacology*, *International Journal of Agronomy, Water (Switzerland)*, *European Food Research and Technology*, *Biochemical Systematics and Ecology*, etc. (Table 1 – Supporting Materials). This indicates a topic of interest across various scientific domains, including agronomy, environmental science, plant physiology, and natural products chemistry.

The VOSviewer diagram provides a visualization of the research landscape concerning the effects of abiotic stress on MAPs and EOs production (Fig. 2). This network reveals several distinct thematic clusters (Van Eck and Waltman, 2010). The green cluster encompasses drought stress and its impact on EOs production and plant physiology. Terms like “drought stress”, “soil moisture”, “irrigation”, and “crops” underscore research focused on the challenges posed by water scarcity and potential mitigation strategies. This diagram outlines the key research areas related to EOs and plant stress, highlighting current trends and possible opportunities for future investigation. Most studies focus on drought and salinity stress, while light and temperature variations have received comparatively less attention over the past decade.

The following paragraphs will explore the effects of various physiological stresses, such as drought, shading, extreme temperatures, and high soil salinity.

#### 3.1. Effects of drought stress

The Mediterranean climate is characterized by hot, dry summers and mild, wet winters, with most precipitation occurring between October and March (Peel et al., 2007). Consequently, rainfall during summer is typically scarce, often resulting in prolonged droughts and potential water shortages. In the Mediterranean regions under consideration, mean monthly summer rainfall rarely exceeds 20–30 mm, whereas winter months often reach 80–100 mm (Peel et al., 2007). This marked seasonality places considerable pressure on water resources, inducing drought conditions when even the wet season may not sufficiently replenish water reserves (Tramblay et al., 2020). Drought stress is one of the most frequent and damaging abiotic stresses that MAPs face. Nevertheless, MAPs have adapted to drought conditions by employing strategies such as adjusting stomatal conductance to minimize water loss through transpiration while maintaining photosynthetic efficiency to optimize energy use (Radwan et al., 2017). Morphological adaptations include reduced leaf area and deep root systems to enhance water uptake (Punetha et al., 2022). Drought also reduces canopy height and width, root growth, and biomass (Formica et al., 2024).



**Fig. 1.** PRISMA Flowchart of the SRL performed. The diagram summarizes the stepwise process, record identification in Scopus and Web of Science, de-duplication, title/abstract screening, full-text assessment, and quality appraisal, used to select studies for this review. Eligibility focused on Mediterranean MAPs exposed to mild (non-lethal) abiotic stress with essential-oil outcomes (yield and/or composition).

At the biochemical level, water stress initiates the production of stress-related proteins and antioxidant enzymes, the activation of signal transduction pathways, and the synthesis of active compounds as part of the plant's defense mechanisms (Nemeth-Zambori et al., 2016).

Table 1 summarizes the effects of drought stress reported by the authors of the reviewed articles, while sub-Sections 3.1.1–3.1.6 discuss the results for each species in detail.

### 3.1.1. *Lavandula angustifolia* Mill.

The lavender (*Lavandula angustifolia* Mill.), a member of the *Lamiaceae* family, is a MAP species that exhibits susceptibility to drought stress. According to the findings of Gorgini Shabankareh et al. (2021), drought conditions considerably impair the growth of lavender. Drought stress was applied at 80–70 %, 60–50 %, and 40–30 % FC. The lowest fresh and dry biomass yields were observed at 40–30 % FC. It was observed that a reduction in water supply leads to a decrease in the leaf surface area, concurrently resulting in a diminished yield of EOs from the fresh aerial parts. Additionally, proline content, a physiological indicator of drought stress, increased progressively as FC levels declined. Concerning the EO composition under drought stress, there was a shift in chemical composition toward a predominance of sesquiterpenes over monoterpenes, specifically, lavandulyl-acetate and  $\gamma$ -cadinene attained their peak concentrations at mild stress levels within the range of 40–30 % FC. The same species was studied by Kumlay et al. (2022)

yielding similar results for 11, 17, and 28 days of drought. Furthermore, increasing stress intensity in this study negatively affected fresh and dry weight and leaf length. Notably, following 17 days of stress, there was an increase in the yield of EOs compounds, including camphene, delta-3-carene, D-limonene, and camphor. Conversely, other compounds such as endoborneol and eucalyptol exhibited minimal variation, with no reductions detected. A similar trend was recorded for rosmarinic acid, ascorbic acid, quercetin, and kaempferol, which enhanced content under stress conditions. Chrysargyris et al. (2016) emphasized that the intensity of stress significantly influences chemical composition, consistent with Hasibi and Abdossi (2022), observing a positive result under moderate drought stress in a pot-based experiment. Still, the chemical composition of certain compounds was minimally reduced, such as  $\alpha$ -pinene, sabinene,  $\beta$ -pinene, D-limonene, and  $\alpha$ -terpineol. The 1,8-cineole and borneol levels significantly increased at more intense stress (25 % FC), from 74.44 to 76.39 % and 3.41–3.95 %, respectively.

### 3.1.2. *Salvia rosmarinus* Spenn.

Bidgoli (2018) investigated drought stress in rosemary and observed increased EOs concentration with negligible effects on biomass. Under mild drought (50–70 % FC), stem fresh weight showed a transient increase followed by a decline at lower FC, while root fresh and dry weight consistently increased, suggesting stimulation of root development

**Table 1**  
Drought stress in MAPs: experimental conditions and EOs responses.

| Species                                     | Experimental Conditions  | Effects on EOs Yield and Composition  |  | Reference                         |
|---|--|---|--|-----------------------------------|
| <i>Lavandula angustifolia</i> Mill.         | On field experiment conducted over the course of two years, with four levels of drought stress (Irrigation Regime) as follows: I1: 90–100 % field capacity (FC); I2: 70–80 % FC; I3: 50–60 % FC; and I4: 30–40 % FC.                             | EO yield increased with FC of 30–40 %; fresh and dry biomass weight decreased under drought.  | Lavandulyl acetate and $\gamma$ -cadinene attained their peak concentrations at moderate stress levels.  | Gorgini Shabankareh et al. (2021) |
| <i>Lavandula angustifolia</i> Mill.         | The experiment was carried out on pots in a mix of perlite, soil and peat. 100 % (adequate irrigation; 50 mL/pot/daily), 50 % (moderate water deficit; 50 mL/pot/3 days) and 25 % (severe water deficit; 50 mL/pot/week) of field capacity (FC). | Moderate drought (50 % FC) increased EOs yield.   | Moderate drought enhanced the concentration 1,8 cineole and borneol (74.44 % to 76.39 %; 3.41–3.95 %).   | Chrysargyris et al. (2016)        |
| <i>Lavandula angustifolia</i> Mill.         | In a pot experiment using a soil/peat/perlite mixture. The plants were grown under the following conditions: 14-h photoperiod; mean temperature: 26–30 °C in the day, 16–20 °C in the night; and relative humidity: 60–70 %.                     | Generally, EOs yield increased under mild stress.   | Moderate stress preferentially elevated camphene, 8-3-carene, D-limonene, and camphor, with endoborneol and 1,8 cineole exhibiting negligible variation.   | Kumlay et al. (2022)              |
| <i>Salvia rosmarinus</i> Spenn.             | In a pot experiment, the irrigation treatment used in this study was D1 = 100 % FC, D2 = 85 % FC, D3 = 70 % FC, D4 = 55 % FC and D5 = 40 % FC (D - Drought treatment)  | Increased EO yield under mild stress (55–70 % FC).  | Increase in camphor, camphene, borneol, myrcene, and 1,8-cineol; decrease in linalool, $\alpha$ -pinene, and sabinene; camphor synthesis peaked at 40 % FC.  | Bidgoli (2018)                    |
| <i>Salvia rosmarinus</i> Spenn.             | A field experiment in open air and a complementary greenhouse experiment was conducted.  | Highest EO yield at 50 % FC; positive response with secondary metabolite increases.           | Decrease of $\alpha$ -pinene (8.34 %), camphene (4.14 %), Increase of 1,8-cineole (55.36 %) and borneol (2.44 %) under mild conditions.  | Laftouhi et al. (2023)            |
| <i>Salvia rosmarinus</i> Spenn.             | In a field experiment, at the blooming stage three different water treatments were applied, including water stress and salt water stress.  | Drought at 50–70 % of FC did not negatively affected EOs synthesis.                           | Linalool, 1–3-cyclopentadiene, and limonene were synthesized only when drought stress occurred.  | Sarmoum et al. (2019)             |
| <i>Salvia rosmarinus</i> Spenn.             | In a field experiment, rosemary was grown in four rows: two rows received full irrigation, and two rows were subjected to controlled drought stress applied three weeks before harvest (balsamic period).  | Stressed plant exhibited higher EO yield by 30 % under drought stress.                        | $\alpha$ -pinene was considerably reduced by moderate drought; bornyl-acetate and E-caryophyllene showed an increase; 3-octanone, $\alpha$ -humulene, and $\gamma$ -terpinene significantly increased. | Formica et al., (2024)            |
| <i>Salvia officinalis</i> L.                | During the field experimentation, maximum temperatures never exceeded 30 °C, while minimum temperatures averaged 18 °C. Drought stress was applied according to the available water supply.  | Increased EOs yield under moderate conditions, especially at third harvest (42 days).         | Aromatic profile favorable under rainfed conditions, with elevated levels of $\alpha$ -thujone, camphor, 1,8-cineole, and $\beta$ -thujone.  | Delfine et al. (2024)             |
| <i>Salvia officinalis</i> L.                | By decreasing the daily water supply, evapotranspiration of the experimental plants was adjusted to 70–80 % of that of the well-watered controls.  | Lower EOs yields under well-watered conditions.   | Biosynthesis of cineole, camphor, and $\alpha/\beta$ -thujone upregulated due to key enzyme activation (cineole synthase, etc.).   | Radwan et al. (2017)              |
| <i>Salvia officinalis</i> L.                | In a pot experiment, plants were watered with tap water twice a week to 100 % (control, C) or 50 % (moderate water deficit, MWD) of field water capacity for three months (March–May 2016).  | EOs were not significantly affected.  | $\alpha$ -thujene, $\alpha$ -pinene, and camphor were reduced under drought; sesquiterpene compounds slight increased.   | Grisafi et al. (2017)             |
| <i>Salvia sclarea</i> L.                    | In a field experiment, two irrigation levels were defined based on the difference between reference evapotranspiration (ET <sub>0</sub> ) and rainfall.  | EOs content decreased from 27.68 mL/kg under optimal irrigation to 13.05 mL/kg under drought. | Quality analysis not detected.   | García-Caparrós et al. (2019)     |
| <i>Salvia sclarea</i> L.                    | In a field experiment, full irrigation (FI) received 100 % of the irrigation demand, whereas regulated deficit irrigation treatments RDI85, RDI70, RDI55 and RDI40 received 85 %, 70 %, 55 % and 40 % of FI, respectively.                       | EOs content peaked at 0.05 % under drought stress.  | Quality analysis not detected.   | Abbaszadeh et al. (2017)          |
| <i>Salvia fruticosa</i> Mill.               | In a pot experiment with a soil/peat/perlite mixture, plants were grown under the following conditions: 14-h photoperiod; mean temperatures of 26–30 °C during the day and 16–20 °C at night; and relative humidity of 60–70 %.                  | EO synthesis per unit of biomass increased.   | Increased D-limonene, 1,8-cineole, sabinene, $\alpha$ -thujone, $\beta$ -caryophyllene, and camphor under drought.   | Chrysargyris et al. (2016)        |
| <i>Thymus daenensis</i> Celak               | In a field experiment conducted in open air, the experimental factors were soil water content at three levels: 100 % of field capacity (FC, control), 67 % FC and 33 % FC.   | Increased EO yield under 67 % FC when combined with manure application.                       | Highest thymol content under mild stress.  | Askary et al. (2018)              |
| <i>Thymus x citriodorus</i> (Pers.) Schreb. | Greenhouse experiment: polyethylene glycol (PEG-6000) was used as a drought agent and was added to theirrigation water in three different concentrations: 0 (control), 2 % (moderated drought), and 4 % (high drought stress)                    | Increase of EOs yield under mild stress.  | Increased thymol (+4.4 %) and carvacrol (+31.7 %) under drought stress.  | Tátrai et al. (2016)              |
| <i>Thymus capitatus</i> L.                  | In a field experiment, two irrigation levels were defined based on the difference between reference evapotranspiration (ET <sub>0</sub> ) and rainfall.  | EO content remained stable under drought.   | Quality analysis not detected.   | García-Caparrós et al. (2019)     |

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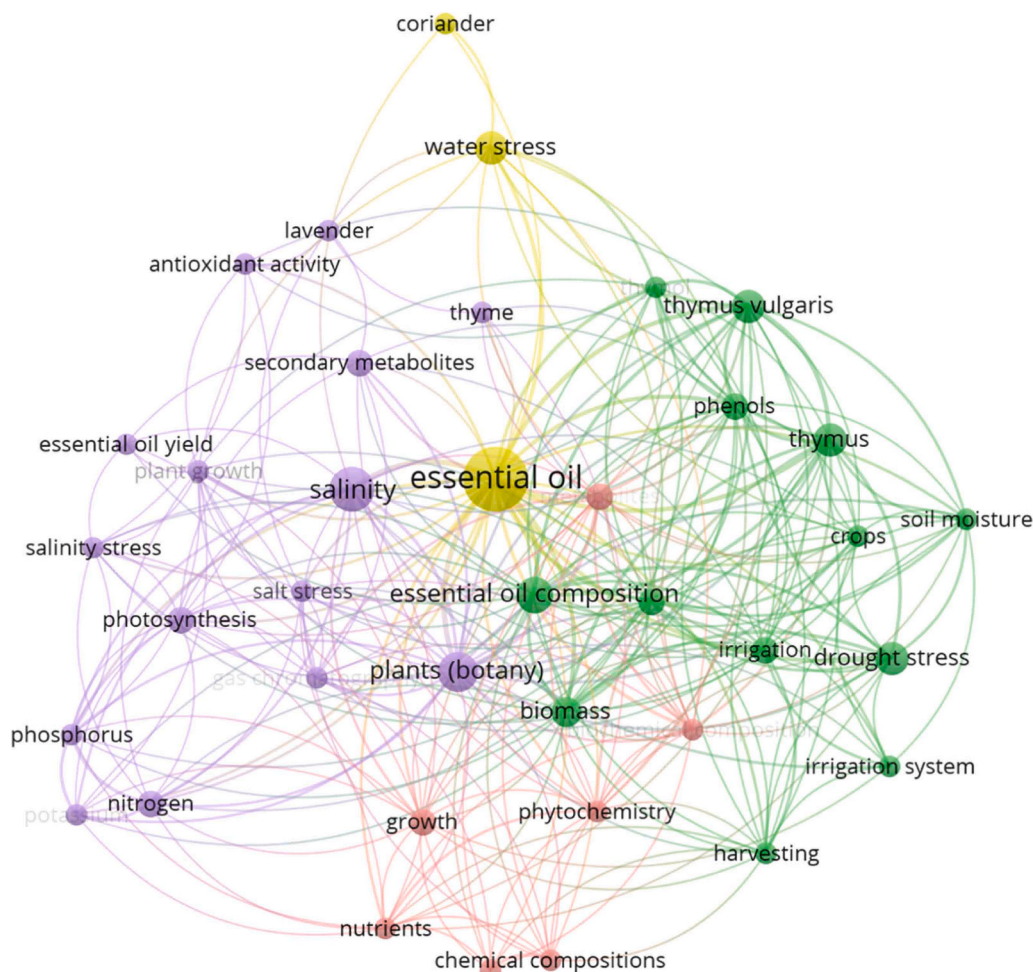
Table 1 (continued)

| Species   | Experimental Conditions  | Effects on EOs Yield and Composition  |   | Reference                                  |
|---|--|---|---|--|
| <i>Thymus vulgaris</i> L.                               | In a pot experiment, two water-supply levels were used to ensure 40 % (stressed, S) and 70 % (control, C) saturation of soil water capacity (SWC).   | EOs yield decreased significantly at 40 % SWC due to stomatal closure.  | Reduced thymol content; increased $\gamma$ -terpinene and p-cymene levels.  | Nemeth-Zambori et al. (2016)               |
| <i>Thymus vulgaris</i> L.                               | In a field experiment, sample 1 was cultivated under usual seasonal mean temperature and precipitation, whereas samples 2 and 3 were cultivated at temperatures 5 °C and 10 °C above normal, respectively, and with 50 % and 75 % reductions in water availability, respectively, within a confined environment. | Highest EOs yield recorded under moderate drought and 5 °C temperature increase.  | Carvacrol peaked under moderate stress (83.3 %).  | Laftouhi et al. (2024)                     |
| <i>Thymus vulgaris</i> L.                               | In a pot experiment, one month after transplantation, irrigation-interval treatments (4, 8, 12 and 16 days) were initiated by applying 2 L of water per pot at each irrigation.  | Increase in EOs concentration under drought.  | Changes in thymol and p-cymene levels.  | Said-Al Ahl et al. (2019)                  |
| <i>Thymus vulgaris</i> L.                               | In a field experiment conducted in open air, the experimental factors were soil water content at three levels: 100 % FC (control), 67 % FC and 33 % FC.  | Reduced EO yield under severe water stress (33 % FC).   | Significant variation in aromatic profile; thymol peaked under severe stress.   | Askary et al. (2018)                       |
| <i>Thymus vulgaris</i> L. chemotype rich in 1,8-cineole | The sampling was carried out in two moments related to the most representative phenological stages: full flowering, at the first week of May 2013 and post fruiting stage, in the most dry period (first week of August 2013).   | Drought enhanced the EOs yield.   | Increased 1,8-cineole levels variability in linalool, camphor, and $\alpha$ -cadinol across populations.  | Llorens-Molina and Vacas (2017)            |
| <i>Mentha longifolia</i> L.                             | A field experiment was conducted during the summer season over two years, arranged as a split-split-plot design with two irrigation levels (100 % and 60 % of field capacity, FC) as water-stress treatments.  | 'Hormozgan' cv. maintained higher yields (5.12 % oil content).  | Reduction in limonene and p-carvone content under drought stress.   | Moshrefi Araghi et al. (2019)              |
| <i>Mentha spicata</i> L.                                | The experiment was done using a randomized design with four replications, each consisting of 1 pot with six plants, two treatments [watered (C) and drought-stressed (T)] and two-time cycles (T1 and T2).   | Increase of terpenes synthesis.   | Increase of trans-carvel acetate, p-menth-8-en-2-ol, bornyl acetate, bisabolene, and valencene.   | Araniti et al. (2024)                      |
| <i>Mentha x piperita</i> L.                             | Field experiments were carried out: irrigation treatments comprised full irrigation (FI) that received 100 % of irrigation demand; regulated deficit irrigation treatments received 85 %, 70 %, 55 % and 40 % of the full irrigation treatment.  | Increment of EOs yield by 2.45 % and 2.38 % observed in PRD <sub>55</sub> .   | Quality analysis not detected.  | Akbarzadeh et al. (2022)                   |
| <i>Mentha x piperita</i> L.                             | Greenhouse experiment: Then peppermint plant were subjected to water stress at FC (field capacity), mild stress (60 $\pm$ 5 % FC), and severe stress (40 $\pm$ 5 % FC).  | Increased EO yield under mild stress (60 % FC).   | Menthofuran increased under moderate stress; menthol and neomenthol proportions higher drought.   | Abdi et al. (2019)                         |
| <i>Melissa officinalis</i> L.                           | Greenhouse experiment: peppermint plant were subjected to water stress at FC (field capacity), mild stress (60 $\pm$ 5 % FC), and severe stress (40 $\pm$ 5 % FC).   | EOs yield decreased by 65 % in 'Lemona' cv. under mild drought stress; increased by 58 % in 'Soroksár' cv.              | Citral decreased under stress, while $\beta$ -caryophyllene and germacrene-D increased in 'Soroksár' cv. indicating selective biosynthesis stimulation. | Szabó et al. (2017)                        |
| <i>Origanum vulgare</i> L. subsp. <i>hirtum</i>         | In a greenhouse pot experiment, irrigation treatments corresponded to 40 %, 60 %, 80 % and 100 % of the soil water-holding capacity.   | EOs yield was positively affected under stress conditions.  | Quality analysis not detected.  | Ninou et al. (2017)                        |
| <i>Calendula officinalis</i> L.                         | In a pot experiment, soil moisture was maintained at a gravimetric water content corresponding to a volumetric water content between 75 % of field capacity (-78 kPa) and field capacity (-33 kPa).  | Flower yield reduced by 70 % under drought; EOs doubled in second harvest.  | Moderate stress was associated with an increase in $\alpha$ -pinene.  | Anderson et al. (2016)                     |
| <i>Calendula officinalis</i> L.                         | In a field experiment, treatments included four irrigation regimes with irrigation applied after 5, 10, 15 and 20 days, respectively.  | Grain yield and flower dry weight reduced as irrigation intervals increased; EO yield highest under mild stress levels. | Quality analysis not detected.  | Pirmani et al. (2022)                      |
| <i>Coriandrum sativum</i> L.                            | In a field experiment, water stress was created by replacing 100 %, 75 %, 50 % or 25 % of the water depleted from field capacity.  | Under moderate stress, biomass, height, and EOs yield decreased.  | Linalool remained stable despite stress.  | Unlukara et al. (2016); Hani et al. (2015) |

under drought (Bidgoli, 2018). In the same study, drought also altered EOs composition, increasing camphor, camphene, borneol, myrcene, and 1,8-cineole, while decreasing linalool,  $\alpha$ -pinene, and sabinene. The authors further reported that camphor peaked at 40 % FC, and the greatest variability in key oil components occurred at 50 % FC, corresponding to the highest yield (Bidgoli, 2018).

Sarmoum et al. (2019) examined the impact of mild drought (50–70 % FC) on EOs production and observed a negative effect on the concentrations of  $\alpha$ -pinene, 1,8-cineole, camphene, borneol, D-verbenone, and bornyl acetate. In contrast, other compounds, such as linalool,

1–3-cyclopentadiene, and limonene, were synthesized only during drought. In their study, Formica et al. (2024) examined the impact of drought stress on rosemary during its balsamic period in both autumn and spring. This investigation involved an exploration of rosemary growth and EOs synthesis. Under drought, the woody and leaf components exhibited signs of impairment. Concurrently, a 30 % augmentation in EO concentration was detected in plants exhibiting signs of stress. Furthermore, regarding chemical composition, several compounds were more concentrated in stressed plants, such as bornyl acetate, E-caryophyllene, camphor, and  $\gamma$ -terpinene, indicating that drought stress



**Fig. 2.** The VOSviewer network diagram based on research string output and PRISMA screening. Each color represents a different cluster of closely related keywords, indicating thematic groupings in the literature. The size of each node (point) is proportional to the frequency of keyword occurrence in the dataset, with larger nodes indicating more frequently mentioned terms. The thickness and density of the lines represent the strength of the co-occurrence relationships between keywords.

modulated secondary metabolite biosynthesis.

Laftouhi et al. (2023) examined how the interaction of drought and heat stress impacts rosemary, applying conditions of 50 % FC drought stress combined with a 5°C rise, and 75 % FC drought stress with a 10°C increase. The findings indicate a positive response of rosemary to drought stress, which is correlated with an increased concentration of secondary metabolites. However, it is observed that as temperatures rise, the content of these metabolites tends to decrease. This observation highlights the interactions between abiotic factors such as drought and elevated temperatures. Regarding EOs, the mild drought stress level of 50 % FC determined the highest yield, showcasing an aromatic profile with  $\alpha$ -pinene at 8.34 %, camphene at 21.44 %, borneol at 2.44 %, and 1,8-cineole at 55.36 %.

### 3.1.3. *Salvia officinalis* L.

A further drought-tolerant species frequently investigated is *Salvia officinalis* L., which shows a response pattern different from rosemary: biomass yield generally decreases under non-irrigated conditions, while monoterpene production increases under drought (Radwan et al., 2017; Delfine et al., 2024). Under mild drought (50 % FC), sage showed a marked change in leaf morphology. Leaf length decreased by approximately 50 %, whereas EOs yield was not significantly affected (Grisafi et al., 2017). These morphological adjustments under drought conditions, particularly the reduction in leaf area, are likely adaptive responses to reduce water loss through transpiration. The drought affected monoterpene synthase expression, showing significant pattern

differences (Ramezani et al., 2020). Specifically, it was found that key compounds such as  $\alpha$ -thujene,  $\alpha$ -pinene, and camphor were reduced under drought deficit. However, sesquiterpene compounds, known for their therapeutic properties, displayed resilience or even slight increases (Grisafi et al., 2017).

Radwan et al. (2017) stated that the enhancement of secondary metabolites in sage subjected to drought stress can be attributed to a passive reallocation of biosynthesis and an active upregulation of the enzymes that govern the respective biosynthetic pathways. Drought stress significantly modulates the biosynthesis of crucial terpenes in sage, particularly cineole, camphor, and  $\alpha/\beta$ -thujone, which collectively represent over 95 % of the plant's total monoterpene content. Under mild drought conditions, the biosynthetic pathways for these compounds may be upregulated as a response mechanism, potentially driven by the activation of key enzymes such as cineole synthase, (+)-bornyl diphosphate synthase, and sabinene synthase. These enzymes catalyze critical steps in cineole, camphor, and thujone production, respectively. Thus, mild drought stress could enhance terpene concentration by intensifying the activity of these pathways.

Delfine et al. (2024) examined the effects of different drought stress levels and harvest timing on common sage during its balsamic period. Their study involved two irrigation treatments: well-watered and rain-fed conditions. Samples were collected at two distinct harvest times. The highest dry biomass and relative water content were recorded under well-watered conditions. Conversely, under severe drought, lower soil water availability led to reduced stomatal conductance, limiting

transpiration and gas exchange. The highest EOs yield was obtained under rainfed conditions at the third harvest (42 days after the onset of flowering), yielding 1.5 % of dry weight. Under well-watered conditions, EOs yields across all three harvest periods (0, 21, and 42 days after the onset of flowering) were lower than those observed under rainfed conditions. The variability in EOs composition in drought-stressed plants was notably higher, with 33 compounds identified. At 21 days after the onset of flowering under rainfed conditions (mild water stress), the aromatic profile was most favorable, characterized by elevated levels of  $\alpha$ -thujone, camphor, 1,8-cineole, and  $\beta$ -thujone. Most bioactive compounds of interest were found under rainfed conditions, suggesting that mild water stress positively impacts EOs composition despite moderately affecting physiology and plant growth.

### 3.1.4. *Thymus vulgaris* L.

Studies on common thyme (*Thymus vulgaris* L.) have revealed that water scarcity influences biomass production and EOs production (Nemeth-Zambori et al., 2016; Laftouhi et al., 2024). Indeed, Said-Al Ahl et al. (2019) in a greenhouse pot study tested irrigation interval of 4, 8, 12, and 16 days across six harvests, showing a clear trade-off: as intervals lengthened, fresh biomass and EOs yield declined, whereas EOs content rose. Within the mild drought window (4–8 days), biomass already decreased relative to 4 days, but EOs content increased, and the constituent profile shifted toward thymol.

Laftouhi et al. (2024) investigated combined heat and drought effects in common thyme under three regimes: (i) control/optimal conditions, (ii) mild combined stress (+5 °C relative to control with 50 % water reduction), and (iii) severe combined stress (+10 °C with 75 % water reduction). Under the moderate combined stress treatment (+5 °C and 50 % water reduction), the aromatic profile varied significantly among samples, with the highest carvacrol content (83.3 %). Thymol was also detected and reached its highest concentration under the severe stress treatment.

Nemeth-Zambori et al. (2016) studied four *Lamiaceae* species: *Origanum majorana* (L.), *Melissa officinalis* (L.), *Mentha × piperita* (L.), and thyme, focusing on drought stress effects on thyme at different soil water capacities (SWC). They used a control group at 70 % SWC and a stressed group at 40 % SWC. Focusing on the thyme species, drought stress reduced fresh and dry biomass by 3.30 times in the stressed group compared to the control. Essential oil yield also fell significantly at 40 % SWC, likely due to reduced photosynthesis from stomatal closure. While EO yield decreased, drought stress changed thyme's oil composition, lowering thymol but raising  $\gamma$ -terpinene and p-cymene levels. Furthermore, the study by Askary et al. (2018) investigated the effects of drought stress and manure application on the EO yield and composition in two thyme species, *Thymus daenensis* Čelak and common thyme. Utilizing a factorial experiment within a randomized complete block design, the research spanned two years and included three water stress levels (100 %, 67 %, and 33 % FC). Results indicated that moderate water stress (67 % FC) increased EOs yield in *T. daenensis*. In common thyme, thymol content was highest under mild stress, while severe water stress reduced EOs yield, underscoring the importance of balanced water availability for optimal oil production (Table 1).

A study by Lorens-Molina and Vacas (2017) regarding the effects of drought stress on the EOs composition of common thyme focused on the chemotype high in 1,8-cineole. Researchers studied wild populations in the Eastern Iberian Peninsula, comparing EOs profiles during flowering (May) and post-fruiting (August) under Mediterranean drought conditions. Results showed significant qualitative and quantitative changes in EOs composition. Specifically, 1,8-cineole levels increased from a range of 21.8 %–43.2 % recorded in May to a range of 42.6 %–68.5 % observed in August. Other compounds, including linalool, camphor, and certain sesquiterpenoids, showed population-specific variability, demonstrating the influence of genetic and environmental factors.

### 3.1.5. *Mentha* spp.

Moshrefi Araghi et al. (2019) conducted a study in which 20 different *Mentha longifolia* (L.) L. genotypes were tested under two irrigation levels (100 % FC as control and 60 % FC as drought stress). The study emphasized the importance of the genotype component to stress response; indeed, the EO yield decreased under drought for most genotypes, but the 'Hormozgan' cultivar maintained higher yields under stress, positioning itself as a promising cultivar candidate for cultivation in Mediterranean areas frequently affected by extreme drought.

Araniti et al. (2024) applied cyclic mild drought to spearmint (*Mentha spicata* L.) by intermittently withholding water until soil tension reached –300 mbar. The treatment reduced stomatal conductance, transpiration rate, and net photosynthesis, but did not significantly affect overall biomass. Mild drought also altered the EOs' terpene profile: among the 55 identified compounds, eight showed a significant increase. Besides carvone, the treatment promoted the accumulation of trans-carvyl acetate, p-menth-8-en-2-ol, bornyl acetate, bisabolene, and valencene, compounds of interest for the perfume and fragrance industry (Bhatia et al., 2008). Consistently, Batista et al. (2024) reported that drought did not negatively affect terpene synthesis in spearmint.

Another study in peppermint (*Mentha × piperita* L.) by Akbarzadeh et al. (2022) demonstrated the impact of regulated deficit irrigation (RDI) in RDI<sub>85</sub>, RDI<sub>70</sub>, RDI<sub>55</sub>, and RDI<sub>40</sub> levels and partial root-zone drying (PRD) in PRD<sub>70</sub>, PRD<sub>55</sub>, and PRD<sub>40</sub>, both on fresh herbage yield and EOs production. The maximum fresh herbage yield (9427 kg ha<sup>-1</sup>) was achieved under full irrigation (FI), while the lowest yield was recorded with RDI<sub>40</sub> treatment (5729 kg ha<sup>-1</sup>). Essential oils ratios remained similar between full and deficit irrigation treatments, with the highest values of 2.45 % and 2.38 % observed in PRD<sub>55</sub> and PRD<sub>70</sub>, respectively. Another study by Abdi et al. (2019) on peppermint showed that drought stress significantly influences EO content and composition across different growth stages. Peppermint increased EOs yield under mild stress (60 % FC), while severe stress (40 % FC) led to a noticeable reduction. Additionally, monoterpene and sesquiterpene profiles varied with stress intensity and plant maturity. Compounds such as menthofuran increased under moderate stress, whereas menthol and neomenthol showed higher proportions as the plants matured under mild stress.

### 3.1.6. Other species

A study conducted on lemon balm (*Melissa officinalis* L.) by Szabó et al. (2017) assessed the effects of drought stress on five cultivars, applying controlled soil moisture levels (40 % SWC for drought, 70 % SWC for optimal conditions) with gravimetric monitoring. Drought significantly reduced plant growth, with declines in height, canopy diameter, and fresh and dry biomass in both roots and aerial parts, with the cultivar 'Soroksár' showing higher sensitivity. Essential oils yield exhibited cultivar-specific responses: for instance, the cultivar 'Lemona' showed a 65 % reduction under stress, whereas 'Soroksár' showed a 58 % increase, highlighting genotype-dependent variability. Essential oils composition was also affected, with citral decreasing under stress, while  $\beta$ -caryophyllene and germacrene-D increased in specific cultivars (e.g., 'Soroksár'), suggesting selective stimulation of biosynthetic pathways.

Drought stress has been observed in Greek sage (*Salvia fruticosa* Mill.) by Chrysargyris et al. (2016). In Greek sage, drought stress reduced the LAI and canopy height while significantly increasing the percentage of EOs. Consequently, drought stress significantly increased the EOs synthesis rate per biomass unit. The composition differed between irrigated and non-irrigated plants; under moderate stress, the concentrations of compounds such as D-limonene, 1,8-cineole, sab-inene,  $\alpha$ -thujone,  $\beta$ -caryophyllene, and camphor notably increased (Table 1).

Abbaszadeh et al. (2017) demonstrated that clary sage (*Salvia sclarea* L.) responds variably to different irrigation intervals, impacting growth and EO production. Under frequent irrigation (every 3 days), clary sage showed relatively high values for shoot yield (2880 kg ha<sup>-1</sup>), leaf yield

(2025 kg ha<sup>-1</sup>), and petiole yield (854.2 kg ha<sup>-1</sup>), indicating that sufficient water availability supports robust biomass production. In contrast, the biomass metrics decreased significantly under the most prolonged irrigation interval (every 9 days) and without nitrogen supplementation, with shoot yield at 2705 kg ha<sup>-1</sup>, leaf yield at 1956 kg ha<sup>-1</sup>, and petiole yield at 748.4 kg ha<sup>-1</sup>. Interestingly, the EOs concentration peaked at 0.05 % under these water-stressed conditions, the highest across all treatments, suggesting that water deficit may induce metabolic shifts that concentrate EO components.

A study conducted by Ninou et al. (2017) on various genotypes of Greek oregano genotypes revealed that genotype selection and water availability play significant roles in influencing both dry matter and EOs yield during drought conditions. The 'Pelion' and 'Kissavos' cultivars produced higher dry matter and EOs yields than the 'Olympus' cultivar, underscoring the adaptability of specific genotypes to water scarcity. Dry matter production varied with irrigation levels, with 'Olympus' thriving at 60 % water availability, while 'Pelion' and 'Kissavos' thrived at 80 % water capacity.

Tátrai et al. (2016) studied the effects of drought stress on lemon thyme. Under reduced water availability, the plant responded with morphological and physiological adaptations. The growth was limited due to stomatal closure, which diminished transpiration and restricted carbon dioxide assimilation, reducing photosynthetic rate. Concerning the yield and the composition of EO, drought conditions induced substantial alterations in the profile of volatile compounds. For instance, thymol exhibited an increase of 4.4 % under heightened drought stress despite being present only in trace amounts in well-watered plants. Additionally, carvacrol demonstrated a remarkable growth of 31.7 % under drought stress.

García-Caparrós et al. (2019) investigated the effect of drought on *Thymus capitatus* L. (= *Thymbra capitata* (L.) Cav.) and *Salvia sclarea* L. under two water treatments: 100 % evapotranspiration demand (ET<sub>0</sub>) and 70 % ET<sub>0</sub>. Plants were cultivated in an experimental plot and subjected to these irrigation regimens, simulating optimal and drought conditions. *Salvia sclarea* L., exhibited no significant changes in fresh biomass under drought conditions, maintaining values of 0.71 kg m<sup>-2</sup> at 100 % ET<sub>0</sub> and 0.70 kg m<sup>-2</sup> at 70 % ET<sub>0</sub> while EOs content per dry weight decreased significantly, from 27.68 mL kg<sup>-1</sup> under optimal irrigation to 13.05 mL kg<sup>-1</sup> under drought stress, indicating a notable reduction in oil production under limited water availability. It is important to note that differences in EOs yield under drought conditions may not only depend on the species, as in the case of *S. sclarea*, but also on how the drought stress has been imposed. For instance, in *S. sclarea*, Abbaszadeh et al. (2017) applied stress by adjusting irrigation frequency, whereas García-Caparrós et al. (2019) used a percentage of ET<sub>0</sub> restitution. These distinct methodologies may lead to different plant physiology responses and EOs synthesis, potentially explaining the divergent results observed across studies. In the same study, García-Caparrós et al. (2019) also found that *T. capitatus* showed a decline in fresh weight (from 1.57 to 1.08 kg m<sup>-2</sup>) and water content (from 66.34 % to 53.64 %), while EO content remained relatively stable (46.36 mL kg<sup>-1</sup> at 100 % ET<sub>0</sub> vs 44.65 mL kg<sup>-1</sup> at 70 % ET<sub>0</sub>), suggesting notable resilience.

Moving to the *Asteraceae* family, pot marigold (*Calendula officinalis* L.), is another herbaceous MAP that grows in the Mediterranean basin and produces EOs known for their pharmaceutically active compounds. Anderson et al. (2016) studied the effect of drought stress on marigold growth and EOs extracted from flowers. Leaf Area Index (LAI) was one of the parameters most reduced by drought stress, like flower weight and diameters. The flower yield was reduced by 70 % under drought conditions (40 % FC), but active ingredients were nearly double in concentration in the secondary flowers. Furthermore, Anderson et al. (2016) illustrated the significant influence of drought stress on the EOs yield in different types of flowers. Primary flowers consistently produced more total oil than secondary flowers, though plants were drought stressed. These results underscore the complex relationship

between resource availability and terpenes synthesis, highlighting how environmental factors may differently impact yield flowers on the same plant. The primary compound defining calendula's profile is  $\alpha$ -pinene, whose levels increased during drought in the first and secondary flowers.

Pirmani et al. (2022) also studied the drought effects on pot marigold for different irrigation intervals (5, 10, 15, and 20 days). They recorded that the growth and physiological parameters were negatively affected under increasing water stress (longer irrigation intervals). At the shortest irrigation interval (5 days), plants reached a height of 28.78 cm, with a flower number of 283.97 per m<sup>2</sup>, a flower dry weight of 5.53 g m<sup>-2</sup>, and a biological yield of 11283 kg ha<sup>-1</sup>. However, as the irrigation interval extended to 20 days, these values declined markedly: plant height reduced to 30.53 cm, flower number to 121.68 per m<sup>2</sup>, flower dry weight to 3.85 g m<sup>-2</sup>, and biological yield to 8867 kg ha<sup>-1</sup>. The grain yield and EOs yield were highest with the 5-day interval (2596.4 kg ha<sup>-1</sup> and 10.61 kg ha<sup>-1</sup>, respectively) but dropped substantially under the 20-day interval (990.1 kg ha<sup>-1</sup> and 8.11 kg ha<sup>-1</sup>, respectively). As expected, these results indicate that water stress restricts both the growth and EOs production of marigold, with reductions in plant biomass and yield components, underscoring the sensitivity of these parameters to water availability.

Coriander (*Coriandrum sativum* L.) is a green herb from the Mediterranean that belongs to the *Apiaceae* family and is used medicinally for anxiety, indigestion, convulsion, and rheumatism. A study by Unlukara et al. (2016) indicated that coriander is sensitive to varying irrigation levels in semi-arid climates. Reducing water availability significantly decreased biomass, plant height, seed yield, and EOs content. Interestingly, despite yield impacts, the primary component of EOs, linalool, remained stable across irrigation treatments. This suggests that drought stress can reduce biomass and yield, whereas EOs composition (e.g., linalool) may be comparatively less affected under reduced water availability (Hani et al., 2015). These species demonstrate the importance of selecting genotypes and tailoring stress applications to optimize EOs production for industrial uses.

### 3.2. Effects of salt stress

Salinity stress significantly affects semi-arid and arid regions due to high evapotranspiration, elevated temperatures, and infrequent rainfall. It can result from natural soil characteristics (primary salinization) or human activities, such as using saline irrigation water and fertilizers (secondary salinization) (Hanin et al., 2016). Poor irrigation practices and high groundwater levels exacerbate salinity issues, challenging agriculture (Kulak et al., 2020). Excess salts, including chlorides and sodium sulfates, potassium, magnesium, and calcium, modify soil structure and water retention, negatively affecting plant development (Eynard et al., 2005). Increased salinity limits water and nutrient uptake, disrupts metabolic processes, causes stomatal closure, and hinders CO<sub>2</sub> assimilation by photosynthesis (Hanin et al., 2016). High salt levels generate osmotic pressure that disrupts water absorption, reducing water availability for roots due to the presence of ions (Wouters Kuhn et al., 2023). As a defensive response, plants close their stomata to conserve water, leading to decreased cellular turgor and a limitation in synthesizing sugars and other primary metabolites (Tounekti and Khemira, 2015; Hanin et al., 2016). This reduction in photosynthetic efficiency creates a complex physiological response, as salinity imposes cellular and metabolic constraints that vary with plant development and growth (Chaves et al., 2009).

Medicinal and Aromatic Plants employ strategies such as efficient water management, ion expulsion, and osmolyte accumulation (e.g. proline) to stabilize membranes and maintain rubisco activity under stress (Cordovilla et al., 2014). Salinity stress alters the availability of metabolic precursors, shifting carbon flow towards secondary metabolite synthesis instead of growth compounds. This stress response likely activates key enzymes, such as terpene synthases, enhancing terpene

accumulation, which may act as osmoprotectants or antioxidants, improving resilience against salinity effects on cellular integrity and physiological function (El-Din et al., 2009; Göçer et al., 2021; Nazari et al., 2023).

Table 2 summarizes the effects of salt stress reported by the authors of the reviewed articles, while sub-Sections 3.2.1–3.2.5 discuss the results for each species in detail.

### 3.2.1. *Salvia officinalis* L.

Kulak et al. (2020) investigated the effects of different salt compounds (NaCl, KCl, MgSO<sub>4</sub>, MgCl<sub>2</sub>, Na<sub>2</sub>SO<sub>4</sub>, and CaCl<sub>2</sub>) at concentrations from 0 to 200 mM on the growth of common sage under controlled conditions. Salt concentrations above 100 mM severely impacted plant growth, with 200 mM NaCl causing the most significant reduction in leaf biomass. Conversely, moderate levels, such as 100 mM KCl, increased dry biomass. The highest EOs yield was observed at 100 mM MgCl<sub>2</sub>. The study identified 22 EO compounds, with  $\alpha$ -pinene and camphor generally increasing across salinity treatments, while others, like 1,8-cineole, showed different responses. Notably, 1,8-cineole peaked under 200 mM MgSO<sub>4</sub>, and  $\beta$ -thujone increased at 150 and 200 mM KCl.

Subsequent research conducted by Yaldiz and Camlica (2021) on common sage involved various salt interactions with selenium as a micronutrient for the purpose of circumventing deleterious stress consequences. The results showed a significant reduction in growth because of elevated salt concentrations (100 mM NaCl). While the dry biomass yield remained unaffected by salt stress, the number of branches per

plant increased in response to higher salt levels. Furthermore, increasing concentrations of NaCl did not influence the production of EOs, presumably due to the resilience of sage. The highest levels of camphor and camphene were identified at moderate salt stress (50 mM NaCl).

### 3.2.2. *Lavandula* spp.

Paraskevopoulou et al. (2020) investigated the impact of different salinity levels on four lavender species (*Lavandula angustifolia* Mill., *L. dentata* var. *dentata*, and *L. stoechas*). Plants were grown in pots under greenhouse conditions and irrigated with NaCl solutions at 0 (control), 25, 50, 100, and 200-mM concentrations. The findings underscored the significant impact of salinity stress on plant height, shoot canopy diameter, and growth index, all substantially reduced at higher NaCl concentrations (100–200 mM). Notably, *L. angustifolia* exhibited the smallest height and growth index but showed resilience in shoot dry weight reduction, contrasting with *L. dentata* var. *dentata* and *L. dentata* var. *candicans*, which displayed higher overall growth.

Despite the negative impact on growth, Chrysargyris et al. (2018) documented a significant increase at 100 mM MgCl<sub>2</sub>, resembling mild salt stress, which suggests that moderate salinity may augment oil concentration. The composition of the EOs fluctuated with notable compounds such as  $\alpha$ -pinene and camphor, generally experiencing an increase. The most pronounced alterations were observed at elevated NaCl concentrations, implying that salt stress can modify secondary metabolites' biosynthetic pathways, potentially enhancing specific aromatic qualities.

**Table 2**  
Salt stress in MAPs: experimental conditions and EOs responses.

| Species  | Experimental Conditions  | Effects on EOs Yield and Composition   |  | Reference                  |
|--|--|--|--|----------------------------|
| <i>Salvia officinalis</i> L.                     | In a field experiment, salt compounds (NaCl, KCl, MgSO <sub>4</sub> , MgCl <sub>2</sub> , Na <sub>2</sub> SO <sub>4</sub> and CaCl <sub>2</sub> ) were applied at five concentrations: 0, 50, 100, 150 and 200 mM).  | EOs yield increased under MgCl <sub>2</sub> stress.  | $\alpha$ -pinene and camphor increased across treatments; 1,8-cineole peaked under 200 mM MgSO <sub>4</sub> ; $\beta$ -thujone increased at 150–200 mM KCl.                | Kulak et al. (2020)        |
| <i>Salvia officinalis</i> L.                     | In pot and climate-chamber experiments, NaCl treatments (25–100 mM) were prepared by dissolving NaCl in distilled water.   | EO yield remained stable under mild salt stress (50 mM/L).   | Highest camphor and camphene levels under moderate salt stress; linalool concentration increased with varying stress intensities.  | Yaldiz and Camlica (2021)  |
| <i>Lavandula angustifolia</i> Mill.              | In a pot experiment, plants were exposed for up to 60 days to four saline treatments: 0, 25, 50 and 100 mM NaCl.   | Increase of EOs under mild salinity stress (50 mM NaCl).   | as $\alpha$ -pinene and camphor generally increased.   | Chrysargyris et al. (2018) |
| <i>Salvia rosmarinus</i> Spenn.                  | In a field experiment, at the blooming stage, salt treatments were applied using a saline solution containing 4.2 g NaCl L <sup>-1</sup> .   | EO yield is reduced under saltwater irrigation but is enhanced under drought.  | The key components ( $\alpha$ -pinene, camphene, and borneol) were found at different concentrations. In general, the concentrations were higher under drought conditions. | Sarmoum et al. (2019)      |
| <i>Salvia rosmarinus</i> Spenn.                  | In a field experiment, plants were irrigated with graded saline solutions, starting at 25 mmol L <sup>-1</sup> and increasing to 50 and 100 mmol L <sup>-1</sup> for each treatment group.   | Higher EOs yield under saline stress.  | Saline stress enhanced the composition of EOs. Many compounds were found in samples that were moderately stressed.   | Besher et al. (2024)       |
| <i>Mentha x piperita</i> L.                      | In a pot experiment, four salinity levels were applied: 0 (control), 2.5, 5.0 and 7.5 dS m <sup>-1</sup> .   | Reduced EOs content under high salinity levels (7.5 dS m <sup>-1</sup> ); retained higher RWC, indicating salt tolerance.            | Quality analysis not detected.   | Hosseini et al. (2023)     |
| <i>Mentha spicata</i> L.                         | In a pot experiment, four salinity levels were tested: T0, 0 mM NaCl (control); T1, 50 mM NaCl; T2, 100 mM NaCl; and T3, 150 mM NaCl.  | The EO yield dropped from 32.9 mL (control) to 10.1 mL under severe stress (150 mM NaCl), but remained stable under mild conditions. | Menthol content increased under moderate salinity (50–100 mM NaCl).  | Kumar et al. (2023)        |
| <i>Coriandrum sativum</i> L.                     | In a pot experiment, 30 days after sowing, NaCl was added to the nutrient solution at 25, 50, 75 and 100 mM.   | High salt levels negatively affected the EOs yield. However, coriander was able to withstand moderate stress.                        | Quality analysis not detected.   | Okkaoglu et al. (2015)     |
| <i>Origanum vulgare</i> L. subsp. <i>gracile</i> | In a pot experiment, four salinity treatments were applied: control (0 mM), 25 mM, 50 mM and 100 mM NaCl.  | EO content initially increased at 25 mM NaCl but declined at 50 and 100 mM NaCl.   | Lower carvacrol content under salinity stress compared to subsp. <i>vulgare</i> .  | Azimzadeh et al. (2023)    |
| <i>Origanum vulgare</i> L.                       | In a pot experiment, four salinity treatments were applied: control (0 mM), 25 mM, 50 mM and 100 mM NaCl.  | EOs content declined only at higher salinity levels.   | Carvacrol content increased with rising salinity levels.   | Azimzadeh et al. (2023)    |
| <i>Origanum onites</i> L.                        | The experiment was realized in lysimeters: there were eight irrigation waters with different electrical conductivities (EC <sub>w</sub> ) including S1 = 0.54 (tap water as a control), S2 = 1.2, S3 = 1.8, S4 = 2.5, S5 = 3.5, S6 = 5.0, S7 = 7.0 and S8 = 10.0 dS/m. | EO yield decreased by up to 78 % under severe salinity stress (>5 dS/m).   | Higher salinity resulted in increased carvacrol, $\beta$ -cymene, and $\gamma$ -terpinene, while linalool reached its peak at moderate salinity.                           | Hancioglu et al. (2019)    |

### 3.2.3. *Salvia rosmarinus* Spenn.

The study by Sarmoum et al. (2019) explored the effects of different irrigation regimes on rosemary, including irrigation with saltwater. Plants exposed to saltwater (70 mM NaCl) showed a substantial reduction in fresh and dry biomass compared to those irrigated with high-quality irrigation water. The salt stress caused osmotic imbalances, impairing water uptake and plant health. Salt stress ( $0.33 \text{ mL m}^{-2}$ ) led to the lowest EO yield, highlighting its adverse effects on oil production. The qualitative components of the EO were also altered, with fewer identified compounds than in other treatments, suggesting that salinity may suppress specific secondary metabolite pathways. However, key components like  $\alpha$ -pinene, camphene, and borneol showed stable concentrations also under altered conditions. The study by Beshar et al. (2024) documented that saline stress stimulates the production of EO only in mild conditions (from 50 mM to 100 mM). In their experiment, mildly stressed plants produced a higher EOs yield and a more complex chemical composition.

### 3.2.4. *Mentha* spp.

The study by Kumar et al. (2023) explored the effects of varying levels of salinity (0, 50, 100, and 150 mM NaCl) on the growth, oil yield, and physiological parameters of three mint species, including *Mentha spicata* L., *M. × piperita* L., and *M. arvensis* L. Salt stress had a different impact on EOs yield and composition. Increasing salinity reduced EOs content, although the pattern varied by species and salinity level. For *M. spicata* L., the EOs yield significantly decreased from 32.9 mL in control conditions to 10.1 mL under the highest salinity (150 mM NaCl). However, some compounds, such as menthol, increased under stress, suggesting that moderate salinity (50–100 mM) had a positive effect, boosting the production of some valuable compounds. With increasing NaCl concentrations, especially at 160 mM and above, there was a marked reduction in plant height, leaf area, and dry weight. This growth suppression is likely due to osmotic stress and ionic toxicity, which restrict water and nutrient uptake, reducing cellular expansion and biomass accumulation.

Hosseini et al., (2023) studied the effect of salt stress on 18 mint ecotypes among the following species: *Mentha longifolia* (L.), *M. pulegium* (L.), *M. spicata* (L.) and *M. × piperita*. These ecotypes were chosen to explore diverse responses to NaCl levels, especially regarding chlorophyll fluorescence, relative water content (RWC), and EOs yield. Firstly, they observed a decrease in RWC with salinity, further confirming the detrimental impact of salt stress on cellular hydration. All mint ecotypes showed varied tolerance, with some retaining higher RWC at elevated salinity levels; in fact, principal component and cluster analyses (PCA and CA) revealed distinct groupings based on species responses to salinity, highlighting *M. × piperita*'s close association with traits indicative of salt tolerance, such as high RWC. The EOs content increased with increasing salinity stress for all mint species studied (Table 2).

### 3.2.5. Other species

The effect of salt stress has also been studied in coriander by Okkaoglu et al. (2015). The research investigated how varying salt levels (0, 25, 50, 75, and 100 mM NaCl) affected three coriander cultivars: 'Gürbüz', 'Kudret-K', and 'Pel-Mus'. The findings showed that increasing salinity significantly reduced plant height, number of branches, and overall seed weight per plant. For instance, at 100 mM NaCl, all cultivars experienced substantial growth declines. Essential oil composition changed with salinity, indicating stress impact on aromatic compounds synthesis. Excessive salinity (100 mM) generally reduced oil yield, showing a delicate balance between stress and metabolite production.

Azimzadeh et al. (2023) reported differential responses of *Origanum vulgare* subsp. *gracile* to salinity stress, which emphasizes the importance of genotype in determining stress effects, key information applicable to coriander as well. Salt stress treatments were administered at four concentrations: 0 mM (control), 25 mM, 50 mM, and 100 mM NaCl, under greenhouse conditions. The findings showed that EO content

initially increased at 25 mM NaCl, indicating a potential enhancement of secondary metabolite synthesis under mild stress. However, EOs content declined sharply at higher salinity levels (50 and 100 mM). The *O. vulgare* subsp. *gracile* exhibited higher EO yields than subsp. *vulgare*, highlighting genetic differences in resilience to salinity. In terms of chemical composition, notable differences emerged between the subsp. *vulgare*, demonstrated a unique increase in carvacrol content with rising salinity levels, and the subsp. *gracile* that showed a reduction in carvacrol.

Hancioglu et al. (2019) studied how irrigation water salinity affects oregano (*Origanum onites* L.), finding that increased salinity significantly hindered growth parameters, including plant height, fresh and dry biomass, and dry leaf yield. Essential oil yield also decreased with higher salinity, reaching up to 78 % reductions under severe stress. However, moderate salinity levels (up to 3.5 dS/m) increased total phenolic and flavonoid contents alongside antioxidant activity. Carvacrol,  $\beta$ -cymene, and  $\gamma$ -terpinene showed initial declines at salinity up to 2.5 dS/m but increased under higher salinity levels. Conversely, linalool peaked at moderate salinity and sharply declined at severe stress. Understanding these salt-stress-induced biochemical shifts is essential to identify MAPs suitable for cultivation in saline-prone regions and for consistent industrial EOs production.

## 3.3. Effects of light stress

Light is a crucial environmental factor for plant growth and development, as it enables energy conversion for sugar fixation and metabolite production. In the case of MAPs, light has been demonstrated to influence the synthesis of volatile compounds, the development and orientation of the canopy, and the size and shape of leaves (Yang et al., 2019). Light stress, including excess and low light intensity, alters photosynthesis and agronomic yield by inhibiting physiological and metabolic processes. Under such stress, plants adjust cellular and biochemical mechanisms, relying on adaptation and resistance strategies due to their sessile nature (Yang et al., 2019). Variations in light quality, intensity, and type significantly influence canopy development and metabolite accumulation in MAPs. Additionally, shading modulates light input, thereby affecting temperature, humidity, and gas exchanges, which impact morphometric parameters and yield in MAPs.

Most studies reviewed in the literature focus on experimental research within the *Lamiaceae* family, highlighting that complex adaptive mechanisms govern the response to light stress. These adaptations prompt changes in foliage development, chlorophyll pigment composition, and overall biomass yield. Light is crucial for primary metabolism and significantly influences the synthesis of secondary metabolites. Consequently, whether excessive or insufficient, variations in light intensity indirectly affect the biosynthesis of secondary metabolites, including terpenes and EOs precursors (Ilić and Fallik, 2017; Mahajan et al., 2020). However, most studies have examined only the effects of light stress in controlled conditions, emphasizing the need for future research to explore the combined impact of light reduction with other mild abiotic stresses. Table 3 summarizes the effects of light stress reported by the authors of the reviewed articles, while sub-Sections 3.3.1–3.3.3 discuss the results for each species in detail.

### 3.3.1. *Salvia rosmarinus* Spenn.

Raffo et al. (2020) adopted a factorial scheme of drought and light stress to study the influence of stresses on rosemary EOs production. The results show mild stress increased EOs yield under water and light conditions. Light stress negatively affected the production of fresh and dry biomass compared to drought stress. The fresh weight of the aerial parts reached its lowest value with a severe light reduction corresponding to 25 % of full sunlight, as defined in the original study. Conversely, the highest LAI value was recorded at the lowest light level as an adaptive response of the plant to intercept more light. Under moderate light stress, no significant reductions in fresh and dry biomass

**Table 3**  
Light stress in MAPs: experimental conditions and EOs responses.

| Species                         | Experimental Conditions   | Effects on EOs Yield and Composition   | Reference                       |
|---------------------------------|---|--|---------------------------------|
| <i>Salvia rosmarinus</i> Spenn. | In a field experiment: LI (100 %, 50 % and 25 % of natural sunlight) were applied.  | A 50 % reduction in light yield resulted in an increase in EOs yield, while a 25 % reduction in sunlight led to a decrease in EOs yield. | Raffo et al. (2020)             |
| <i>Salvia rosmarinus</i> Spenn. | In a field experiment: one and a half meter long metal constructions were installed over shading plots and covered by 100 % HDPE (High Density Polyethylene) and 40 % and 75 % shading treatments were applied. | EO yield increased by 31 % under 40 % shade and 27 % under 75 % shade in the first year.   | Şeker et al. (2023)             |
| <i>Thymus vulgaris</i> L.       | A field experiment was conducted in which one shading treatment was used (pearl nets with a shade index of 40 %) and a non-shaded control treatment was used as a comparison in a split-plot design.            | EOs yield varied little between shaded and illuminated plants.   | Lalević et al. (2023)           |
| <i>Thymus vulgaris</i> L.       | In a field experiment with randomized design in a 4 × 2 factorial arrangement (three nets: blue, red, and black).   | Under full sunlight conditions, the EO increased, but decreased under net shading.   | Da Cunha Honorato et al. (2023) |
| <i>Thymus vulgaris</i> L.       | In a pot experiment: several salt stress treatments were applied under shade enclosure conditions.  | EO yield influenced by light and salinity; β-cymene decreased under shade and moderate salt stress.                                      | Zrig et al. (2016)              |
| <i>Origanum onites</i> L.       | In a field experiment, 1.5 m-long metal frames were installed over the shading plots and covered with 100 % HDPE (high-density polyethylene); shading treatments of 40 % and 75 % were applied.                 | Enhanced EOs production under shade.   | Şeker et al. (2023)             |
| <i>Origanum majorana</i> L.     | In a field experiment, combinations of plant-species treatments were replicated three times under 40 % shade and in an un-netted control.   | EOs yield increased under shade compared to full sun.  | Milenković et al. (2021)        |
| <i>Origanum vulgare</i> L.      | In a field experiment, combinations of plant-species treatments were replicated three times under 40 % shade and in an un-netted control.   | The EOs' yield was enhanced by moderate shading.   | Milenković et al. (2021)        |

or the development of aerial parts were observed. However, rosemary reduces its EO yield under a severe decrease in light input (25 % of sunlight). Significant fluctuations in the quantities of α-pinene, camphene, 1,8-cineole, verbenone, myrcene, β-caryophyllene, and β-pinene were observed under moderate light and drought stress. Specifically, the levels of α-pinene, camphene, myrcene, β-caryophyllene, and β-pinene reached their maximum values, expressed as a percentage of EOs composition, with a 50 % reduction in light. These results highlight the importance of further investigating the effects of multiple stress interactions, which may simultaneously modulate various physiological and morphological traits, including biomass allocation, leaf architecture, and secondary metabolism.

Şeker et al. (2023) examined the influence of light on pigment synthesis in rosemary. The authors conducted a two-year field experiment. This study evaluated the effects of varying shading treatments (40 % and 75 %) on several growth and biochemical analyses of this species. The findings reveal that both seasonal and environmental conditions significantly impact EO production, with notably higher yields observed in spring across all shading treatments. Shading treatments (40 % and 75 %) did not significantly alter the relative composition of the rosemary EO constituents. However, EOs content increased by 31 % under 40 % shade and 27 % under 75 % shade in the first year, with similar increases observed in the second year. Under full sunlight, the main EOs components included camphor (23.2 %) and 1.8-cineole (15.9 %) in the first year, and camphor (15.1 %) and α-pinene (13.4 %) in the second year. These results indicate that while shading boosts overall EOs yield, it does not substantially modify the chemical profile of rosemary's EOs, suggesting that rosemary can adapt to shaded conditions without significant changes in its biochemical composition (Table 3).

### 3.3.2. *Thymus vulgaris* L.

In common thyme harvested in autumn and spring following growth under 50 % colored shade nets (blue, red and black) and full sunlight, Da Cunha Honorato et al. (2023) reported that shading markedly reduced dry biomass compared with full sun. Specifically, total dry weight

(TDW) decreased by 46.8 % under the red net, 53.6 % under the black net, and 82.2 % under the blue net. Across light treatments, spring harvest increased leaf dry weight (LDW), stem dry weight (SDW), root dry weight (RDW), and TDW relative to autumn. From a biochemical perspective, the total phenolic content under the red net was like that observed under full sunlight. This indicates that red light actively promotes the synthesis of phenolic compounds, underscoring the significant influence of light quality on the production of secondary metabolites in thyme. The EOs yield was affected by net shading and ranged from 0.88 % to 1.46 %, with higher levels under full sunlight conditions. Among the compounds, ρ-cymene was synthesized only under full sunlight; the γ-terpinene and thymol increased under shade nets.

Lalević et al. (2023) reported in thyme with a 40 % shading index a low difference in EOs extraction yield between stressed and illuminated plants. After the extraction of the EO, the analysis identified 29–31 compounds, with thymol being the most abundant, accounting for 43.9 % in shaded plants and 44.2 % in illuminated plants. The second primary compound, γ-terpinene, was higher in stressed plants at 18.3 % compared to 16.8 % in illuminated plants, while (*E*)-β-ocimene was found exclusively in shaded plants.

Zrig et al. (2016) also found that light intensity and NaCl soil levels (50 mM) affect EOs and secondary metabolites in thyme. Under increased salinity, open-field plants had higher levels of thymol (24.17) and β-cymene (10.33–38.31 with 150 mM under shading). Shading reduced β-cymene but increased myrcene and other metabolites, indicating that light quality and environmental stressors significantly influence biosynthesis in thyme.

### 3.3.3. *Origanum* spp.

Şeker et al. (2023) investigated the effects of shading (reduced light intensity) on oregano (*Origanum onites* L.) using shade nets that reduced incident light by 40 % and 75 %. In the first year, shading reduced plant height and biomass yield, whereas in the second-year plants grown under shade were taller, suggesting a shade-acclimation response (stem elongation) to enhance light capture. The LAI also increased in shaded

areas to compensate for lower light levels, with some species showing up to 251 % increases. Despite a reduced biomass, the EO content increased under shading by 40 %, with an even more pronounced rise of up to 79 % observed in the second year. Light stress may stimulate the biosynthesis of EOs, potentially increasing the industrial value of these plants for oil extraction under shade. Maximum concentrations of carvacrol, borneol, and verbenone were found at 40 % shading, while significant compounds like  $\beta$ -myrcene,  $\alpha$ -pinene, camphor, and 1,6-cineole were present in higher amounts under full light conditions.

Milenković et al. (2021) evaluated the effects of 40 % shading versus full-sun conditions on oregano (*Origanum vulgare* L.) and marjoram (*O. majorana* L.). In oregano, shading increased EOs yield from 0.27 to 0.32 mL/100 g of air-dried plant material and modified EOs composition: (*E*)-caryophyllene and germacrene D were the dominant constituents, with germacrene D increasing and caryophyllene oxide decreasing under shade. Similarly, in marjoram, EOs yield rose from 0.26 to 0.37 mL/100 g under shade, and the EOs profile shifted toward higher proportions of terpinen-4-ol,  $\gamma$ -terpinene,  $\alpha$ -terpinene, and sabinene, compounds associated with enhanced aromatic quality under reduced light intensity (Table 3).

### 3.4. Effect of thermal stress

Unlike other forms of abiotic stress, such as water, light, or salt, temperature stress encompasses a broader spectrum, classified into heat, cold, and frost stress. Heat stress can severely impair plant physiological processes, leading to reduced germination rates, slower growth, compromised photosynthetic efficiency, and, in extreme cases, plant death (Lee et al., 2024). In response to thermal stress, plants adapt by altering their membrane lipid composition, synthesize secondary metabolites, activate detoxification pathways, regulate gas exchange, and modulate organ development to mitigate damage (Zhao et al., 2017). Temperature fluctuations significantly impact crop productivity, as each plant species has a specific optimal temperature range for growth and reproduction. Deviations from this range can lead to significant declines in fertility, often due to non-viable pollen production, damage to reproductive structures, and impaired fruit setting, leading to substantial yield losses (Chao et al., 2017). Furthermore, extreme heat often enhances the synthesis of phenolic and terpene compound synthesis to mitigate its deleterious effects. Enhancing water-use efficiency becomes critical under combined high temperatures and water. To address these constraints, MAPs increase transpiration rates, a response that not only facilitates cooling but also correlates with an increased synthesis of bioactive secondary metabolites, ultimately boosting the production of valuable compounds (Mahajan et al., 2020; Punetha et al., 2022).

Table 4 summarizes the effects of light stress reported by the authors of the reviewed articles, while sub-Sections 3.4.1–3.4.2 discuss the results for each species in detail.

#### 3.4.1. *Salvia officinalis* L.

Laftouhi et al. (2023) investigated the interaction between thermal

stress and water stress in common sage by applying multiple stress conditions defined in three treatments: 1) baseline conditions, 2) raised temperature by 5°C and water stress by 50 %, and 3) increased temperature by 10°C with 75 % water stress. The authors analyzed physiological responses, including the content of coumarins, alkaloids, flavonoids, tannins, saponins, and EOs. Metabolite distribution varied significantly, highlighting the influence of stressors on compound biosynthesis. In the case of treatment 2, which was identified as moderate stress both for thermal and water stress, the yield of the EO was the highest. The percentage of  $\alpha$ -thujone varied across treatments (0.78 %, 10.44 %, 0.09 %), indicating the compound's sensitivity to combining two stress factors. The highest  $\alpha$ -thujone was noted under mild stress, such as manool and  $\beta$ -caryophyllene, peaking at 13.67 % and 14.01 %, respectively, then declining under severe stress. Fluctuations in viridiflorol and 1,8-cineol across treatments (viridiflorol: 6.54 %, 7.55 %, 6.01 %; 1,8-cineol: 8.71 %, 7.08 %, 9.07 %) suggest complex regulatory mechanisms, possibly involving enzyme activity or precursor availability. This approach demonstrated how interacting environmental factors can jointly influence the secondary metabolism, including the synthesis of EOs.

#### 3.4.2. *Origanum dictamnus* L.

A study by Lianopoulou and Bosabalidis (2014) on dictamnus oregano (*Origanum dictamnus* L.) adaptation to cold or heat temperatures in the Mediterranean basin reported metabolic and morphological changes during winter and summer, studying not only direct stress but also examining its indirect effects. The results showed significant seasonal variations in stomatal density, anatomical structure, and leaf physiological parameters, affecting EOs synthesis. Winter leaves showed higher stomatal density and greater thickness. In contrast, summer leaves exhibited higher gas-exchange performance, specifically higher stomatal conductance ( $g_s$ ) and net photosynthetic rate and, where reported, transpiration, which was positively associated with EOs yield (2.78 % in summer vs. 1.05 % in winter). Qualitative analysis revealed seasonal differences: winter oil featured p-cymene (59.2 %), while the main component of summer oil was carvacrol (42.4 %). These shifts in EO composition result from changes in secondary metabolism, driven by environmental factors like temperature and water availability, which regulate key biosynthesis compounds. These findings highlighted the importance of understanding plant-environment interactions to optimize MAPs cultivation and therapeutic potential under changing climate conditions.

## 4. Conclusion

The SLR shows how mild abiotic stress can enhance EOs production and composition in MAPs, particularly in the *Lamiaceae* family. Plant growth and bioactive compound synthesis remain stable under controlled stress levels. However, severe or prolonged stress harms plant physiology, reducing valuable biomass, especially leaves and flowers. Identifying the optimal stress threshold for each species is crucial for

**Table 4**  
Thermal stress in MAPs: experimental conditions and EOs responses.

| Species                      | Experimental Conditions   | Effects on EOs Yield and Composition                                     | Reference  |                                    |
|------------------------------|---|--|--|------------------------------------|
| <i>Salvia officinalis</i> L. | In a chamber experiment: treat 1 = involved subjecting the samples to typical monthly average temperature and precipitation conditions. treat = the temperature was elevated by 5°C, and water stress was intensified by 50 % within an enclosed chamber. treat 3 = saw a temperature rise of 10°C, coupled with a 75 % escalation in water stress within a closed chamber. | The EOs composition varied significantly under thermal and water stress. | $\alpha$ -thujone decreased from 10.44 % under moderate stress to 0.09 % under severe stress. Meanwhile, manool and $\beta$ -caryophyllene peaked at 13.67 % and 14.01 %, respectively, under moderate stress. | Laftouhi et al. (2023)             |
| <i>Origanum dictamnus</i> L. | Wild plants were sampled. The study focused on winter and summer drought stress.  | Higher EOs yield in summer (2.78 %) compared to winter (1.05 %).         | Seasonal shifts in composition: p-cymene (59.2 %) in winter, carvacrol (42.4 %) in summer, driven by changes in secondary metabolism.  | Lianopoulou and Bosabalidis (2014) |

balancing growth and secondary metabolite production.

Key findings include:

- Drought: When maintained within a moderate range (e.g., 50–70 % FC, depending on species or study), plants often show increases in EOs content alongside reduced shoot growth and root allocation. Beyond this FC range, biomass and EOs yield decline. In drought-tolerant species like rosemary and thyme, compositional shifts frequently involve compounds such as camphene, borneol, 1,8-cineole, or carvacrol/thymol, depending on genotype and timing.
- Salinity: Moderate salinity (e.g., 50–100 mM NaCl) can increase EOs content and adjust profiles (e.g.,  $\alpha$ -pinene, camphor, menthol), whereas higher levels (150–200 mM) typically reduce growth and EOs yield.
- Temperature and light: Evidence is sparser and often confounded by co-occurring stresses. Heat and drought interactions may amplify compositional shifts (e.g., carvacrol in thyme). Shading/light quality can alter specific volatiles (e.g.,  $\alpha$ -pinene, camphene,  $\beta$ -caryophyllene; (*E*)- $\beta$ -ocimene under shade), but responses remain setup-dependent.
- Examining the effects of individual abiotic stresses can be challenging due to the complexity of environmental conditions. The observed responses often result from the combined influence of multiple stressors, such as the interaction between drought and elevated temperatures.

This SLR shows that, in most cases, moderate abiotic stress enhances EOs yield and composition, while keeping plant growth largely stable. Field use must be species and genotype-specific, with stress kept within safe thresholds and aligned to phenology to prevent permanent damage. As a conservative starting point in Mediterranean MAPs, regulated deficit irrigation around 50–70 % FC (and avoiding <40 % FC) and moderate salinity (50–100 mM NaCl) can be piloted in small strips and adjusted by monitoring soil moisture/ET and oil profile. Integrating these approaches into agroecological and low-input systems, we can enhance the consistency of EOs, valorize underutilized lands, and promote climate-resilient value chains for industrial purposes.

#### CRedit authorship contribution statement

**Valentina Formica:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Daniela Romano:** Writing – review & editing, Writing – original draft, Validation, Supervision, Data curation, Conceptualization. **Mercedes Verdeguer:** Writing – review & editing, Visualization, Validation. **Silvia Zingale:** Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Federico Leoni:** Writing – review & editing, Visualization, Validation, Methodology. **Stefano Carlesi:** Writing – review & editing, Visualization, Validation, Methodology. **Paolo Barberi:** Writing – review & editing, Visualization, Validation, Supervision. **Paolo Guarnaccia:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Data curation, Conceptualization.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ijagro.2025.100079](https://doi.org/10.1016/j.ijagro.2025.100079).

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