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COMPREHENSIVE EVALUATION OF ABIOTIC STRESS RESPONSES AND BIOSTIMULANT MODULATION IN *Thymus* spp.

Doctoral (Ph.D.) Thesis

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1 Introduction

Medicinal and aromatic plants represent an important source of bioactive compounds used in traditional and modern medicine (Baruah et al., 2024; Islam, 2019). Within this context, the genus *Thymus* is a member of the Lamiaceae family and includes approximately 250 taxa, comprising 214 species and 36 subspecies, distributed in Eurasia and Northwest Africa, mainly in the Mediterranean region, particularly northwest Africa and the Iberian Peninsula (Iftikhar et al., 2023; Stahl-Biskup & Venskutonis, 2012). *Thymus* species are widely recognised for their aromatic and medicinal value due to their rich content of bioactive secondary metabolites.

Although *Thymus vulgaris* is the most thoroughly studied species because of its high thymol and carvacrol content and its extensive use in medicine, cosmetics, and food applications, other species such as *Thymus pannonicus* All., *Thymus* × *citriodorus* (Pers.) Schreb., and *Thymus capitatus* (L.) Hoffmanns. & Link, have recently gained scientific attention. These species present different essential oil chemical profiles while maintaining comparable biological activities, making them promising candidates for pharmaceutical, nutraceutical, and aromatic applications. The phytochemical composition of *Thymus* species includes major terpenoid compounds in the essential oil such as thymol, carvacrol, geraniol, linalool, camphor and β-caryophyllene, which are associated with antimicrobial, anti-inflammatory, antioxidant and anticancer properties (Anwar et al., 2024; Ghasemi Pirbalouti et al., 2015; Marković et al., 2020; Mazulin et al., 2024).

However, *Thymus* species performance is strongly influenced by environmental conditions. Under climate change scenarios, drought and salinity stress are expected to become more frequent and severe, particularly in the Mediterranean and North African regions (Knippertz et al., 2003). These abiotic stresses negatively affect water uptake, photosynthesis, and biomass accumulation in *Thymus* species (Da Silva et al., 2025; Kramer et al., 2025).

In natural environments, plants are rarely exposed to a single stress factor. Drought and salinity often occur simultaneously, producing more severe effects than individual stresses (Mittler, 2006). Therefore, sustainable strategies are needed to improve plant stress tolerance. In this context, seaweed extract-based biostimulants have gained attention as eco-friendly tools to enhance plant performance under abiotic stress. Brown seaweed extracts, such as *Ascophyllum nodosum* extract (ANE) and *Cystoseira barbata*, have been reported to stimulate root growth, improve nutrient uptake efficiency, and enhance stress tolerance in plants (Cardozo et al., 2007; Hassan et al., 2021; Hussain et al., 2021; Mukherjee & Patel, 2020; Staykov et al., 2025).

Within this framework, this study aims to evaluate the responses of *T. pannonicus*, *T.* × *citriodorus* and *T. capitatus* to drought and salinity stresses applied individually and in combination, and to assess the mitigating role of seaweed biostimulant application.

2 Objectives

- To evaluate the effects of drought (40% Soil water capacity [SWC]) and progressively increasing salinity (60, 90 and 120 mM NaCl), applied individually and in combination, on morphological, physiological, and biochemical responses of *T. pannonicus*, *T.* × *citriodorus* and *T. capitatus*.
- To assess the suitability of *Ascophyllum nodosum* seaweed extract to mitigate drought, salinity, and combined stress effects in the studied *Thymus* species.
- To compare species-specific physiological and biochemical responses of *Thymus* species under drought and salinity, highlighting their phenotypic and metabolic diversity and adaptive tendencies.
- To evaluate the phenotypic plasticity of the three *Thymus* species under increasing stress intensity.
- To investigate the balance between growth performance and secondary metabolite accumulation under stress conditions and the modulatory role of seaweed extract in this trade-off.

3 Materials and methods

3.1 Experimental design and procedures

All experiments were conducted under greenhouse conditions at the Buda Campus of the Hungarian University of Agriculture and Life Sciences (Budapest).

Seven experiments were performed over a three-year period (2003-2025). *T. pannonicus* was propagated by division/offshoot isolation from mother plants maintained in the open-field collection of the Medicinal Plant Unit (Budapest-Soroksár). *T.* × *citriodorus* plants were initially obtained from a commercial source, and subsequent experiments were established using rooted cuttings. *T. capitatus* was developed from seeds collected from wild populations in northern Tunisia. After germination under controlled conditions, seedlings were grown in pots and later transferred to the greenhouse for experimentation. Plants were also propagated by cuttings for subsequent trials.

The first four experiments included four treatments: control (70 % SWC), drought (40 % SWC), salinity (70 % SWC + NaCl), and combined stress (40 % SWC + NaCl). In the final three experiments, the same treatments were applied with and without *A. nodosum* extract. The overall experimental structure, stress levels, and biostimulant treatments are summarised in Table 1.

Before each experiment, plants were acclimatised to greenhouse conditions. Uniform 2 L pots were used throughout the study. All plants were grown in a homogeneous substrate composed of 50 % peat moss, 30 % potting soil, 15 % perlite, and 5 % sand. The soil water capacity of the mixture was determined gravimetrically using the Reynolds (1970) method, enabling precise regulation of soil moisture during the experiments.

Table 1. Summary of experimental design, species, treatments, and stress conditions applied (Budapest, 2023–2025).

Experiment	Species	Labels	Date	Total number of plants	Drought level	Salinity level	*A. nodosum* concentration	Treatments
1	*T. pannonicus*	TP1	24/05/2023–30/06/2023 (36 days)	100	**70 % SWC**: Control, salinity stress, control with ANE, salinity stress with ANE. **40 % SWC**: Drought stress, combined stress, drought stress with ANE, combined stress with ANE.	60 mM NaCl	Not applied	4 treatments: 1/Control 2/Drought stress 3/Salinity stress 4/Combined stress
2	*T. pannonicus*	TP2	27/05/2024–08/07/2024 (41 days)	80		90 mM NaCl		
3	*T. × citriodorus*	TL1	23/04/2024–03/06/2024 (41 days)	60		120 mM NaCl		
4	*T. capitatus*	TC1	10/06/2024–21/07/2024 (41 days)	80		90 mM NaCl		
5	*T. pannonicus*	TP3	30/05/2025–23/07/2025 (53 days)	80		120 mM NaCl	8 ml ANE L^{-1} water	8 treatments: 1/Control 2/Drought stress 3/Salinity 4/Combined stress 5/Control + ANE 6/Drought stress + ANE 7/Salinity stress + ANE 8/Combined stress + ANE
6	*T. × citriodorus*	TL2	23/05/2025–16/07/2025 (53 days)	80				
7	*T. capitatus*	TC2	07/06/2025–30/07/2025 (53 days)	80				

SWC: Soil water capacity; ANE: *Ascophyllum nodosum* extract.

Irrigation was performed twice weekly using tap water (baseline NaCl: 1.037 mM). Salinity stress was imposed by adding NaCl to the irrigation water (50 mL per irrigation) and was applied progressively to avoid osmotic shock. Depending on the experiment, final salinity levels reached 60, 90, or 120 mM NaCl, as described in Table 1. Pots were individually weighed at each irrigation to maintain precise moisture levels.

The *A. nodosum* extract (Terra Aquatica, France) was applied at 8 mL L^{-1} (100 mL per plant) every two weeks in the final three experiments. In combined treatments, the extract was applied prior to saline irrigation, and soil moisture was subsequently adjusted to the target SWC.

3.2 Determination of morphological parameters and masses

3.2.1 Shoot growth parameters and masses

One day before harvest, morphological parameters were recorded. Shoot length was measured from the soil surface at the base of the stem to the apical tip of the longest shoot, and the number of shoots per plant was counted. At the end of each experiment, plants were harvested, and their shoot fresh weight was recorded individually. Samples were then air-dried in a shaded area until constant weight was reached, and shoot dry weight was subsequently determined.

3.2.2 Root growth parameters and masses

For root-related measurements, five plants per treatment were randomly selected on the harvest day. Roots were carefully separated from the substrate, washed gently with tap water to remove adhering soil particles, and lightly blotted to remove excess moisture. Root length and root fresh weight were recorded immediately. Afterwards, the roots were air-dried naturally until reaching a constant weight to determine their dry weight.

3.3 Determination of physiological parameters

3.3.1 Photosynthetic pigments contents

Chlorophyll a, chlorophyll b, and carotenoid content were determined according to Lichtenthaler and Wellburn (1983) and Mackinney (1941). Fresh leaf samples (0.1 g) from five biological replicates per treatment were homogenised in 80 % acetone and centrifuged (1000 × g, 3 min).
The absorbance of the supernatant was measured at 480, 644, and 663 nm using a spectrophotometer, with 80 % acetone as blank. Pigment concentrations were calculated using standard equations based on absorbance values and expressed per unit fresh weight.

3.3.2 Relative water content (RWC)

The RWC was determined according to Orsini et al. (2010). For each treatment, five plants were randomly selected, and 20 leaves per plant were collected as biological replicates. Fresh weight (FW) was recorded, leaves were hydrated in distilled water at 4 °C for 24 h to obtain saturated weight (SWt), and then oven-dried at 105 °C for 48 h to determine dry weight (DW). Finally, the RWC was calculated as follow: RWC (%)= [(FW – DW) / (SWt – DW)] × 100.

3.3.3 Proline content

Proline content was determined according to Bates et al. (1973). In the final week of the experiment, four plants per treatment were randomly selected, and 0.5 g of fresh tissue was homogenised in 3 % sulfosalicylic acid. The homogenate was filtered, and the filtrate was reacted with acid ninhydrin and glacial acetic acid. The mixture was incubated in a boiling water bath for 1 h, cooled on ice, and extracted with toluene. The absorbance of the upper phase was measured at 520 nm using a spectrophotometer, with toluene as blank. Proline concentration (μmol g^{-1} FW) was calculated from a standard curve prepared with L-proline.

3.3.4 Soluble sugar content

Soluble sugars were determined according to Trevelyan and Harrison (1952). Fresh tissue (0.4 g) from four biological replicates per treatment was homogenised in 95 % ethanol and incubated at 85 °C for 20 min. After centrifugation, the extraction was repeated twice, and the supernatants were combined for analysis. For colour development, the extract was reacted with anthrone reagent, heated in a boiling water bath, and rapidly cooled to stabilise the colour. Absorbance was measured at 620 nm using a spectrophotometer. Soluble sugar content (mg glucose g^{-1} FW) was calculated from a glucose standard curve.

3.4 Determination of biochemical parameters

3.4.1 Essential oil content (EOC)

For each treatment, four bulk samples (incl. four plants per bulk) were prepared as biological replicates and homogenised. Approximately 10–15 g of dried material were subjected to hydrodistillation for 2 h using a Clevenger-type apparatus according to the Hungarian Pharmacopoeia (2004) procedure. Essential oil content was calculated on a dry weight basis (mL 100 g^{-1} DW) after moisture correction. Essential oils were stored at 4 °C until GC–MS analysis and evaluated according to the European Pharmacopoeia (2023) standard for *Serpylli herba* (≥ 0.3 mL 100 g^{-1} DW).

3.4.2 Essential oil composition

The chemical composition of essential oils was analysed using gas chromatography–mass spectrometry (GC–MS) on an Agilent 6890N GC system coupled with an Agilent 5975 inert mass selective detector. Separation was performed using an HP-5 capillary column under a temperature program starting at 60 °C and increasing to 240 °C. Helium was used as the carrier gas at a flow rate of 1 mL min^{-1}. Samples (0.2 μL of 1 % essential oil in n-hexane) were injected in split mode (30:1). The mass spectrometer operated in electron ionisation mode at 70 eV, scanning m/z 50–550.

Compound identification was based on comparison of mass spectra and linear retention indices (LRIs) with literature data, NIST and Wiley libraries, and an in-house database. Relative compound abundance was determined using peak area normalisation.

3.4.3 Total polyphenol content (TPC)

The remaining portion of the bulk samples was ground, sieved, and 0.5 g was extracted in boiling distilled water (50 mL) for 24 h at room temperature. Extracts were filtered, stored at −20 °C, and a subsample was evaporated to determine extract dry weight. Total polyphenol content was determined using the Folin–Ciocalteu method (Singleton & Rossi, 1965). Aliquots of the extracts were reacted with Folin–Ciocalteu reagent and sodium carbonate, incubated for colour development, and absorbance was measured at 760 nm using a spectrophotometer. Results were expressed as mg gallic acid equivalents per g dry weight (mg GAE g^{-1} DW) based on a gallic acid standard curve.

3.4.4 Antioxidant capacity (AOC)

The FRAP assay was used to determine antioxidant capacity following Benzie and Strain (1996). Three extract replicates were analysed, and FRAP reagent was prepared from acetate buffer, TPTZ solution, and ferric chloride solution. The reagent was mixed with distilled water and plant extract samples, and the reaction was allowed to develop before measuring absorbance at 593 nm using a spectrophotometer. Antioxidant capacity was expressed as mg ascorbic acid equivalents per g dry weight (mg AAE g^{-1} DW) based on an ascorbic acid standard calibration curve.

3.4.5 Hydrogen peroxide (H_2O_2) content

Hydrogen peroxide content was determined according to Patterson et al. (1984). Four plants per treatment were randomly selected as biological replicates, and 1 g of fresh tissue was homogenised in cold acetone. The homogenate was centrifuged, and the supernatant was reacted with titanium reagent and ammonia to form a precipitate. The pellet was washed, dissolved in sulfuric acid, and absorbance was measured at 410 nm using a spectrophotometer. Hydrogen peroxide concentration (μmol H_2O_2 g^{-1} FW) was calculated using a standard calibration curve.

3.5 Determination of stress indexes

Stress susceptibility index (SSI) and stress tolerance index (STI) were calculated to evaluate plant performance under stress. SSI was determined according to Fischer and Maurer (1978) to measure how strongly plant performance is affected by stress compared with its growth under optimal conditions. Stress tolerance was evaluated using the STI proposed by Fernandez (1993), which identifies treatments maintaining high productivity under stress relative to control conditions. SSI and STI were calculated using plant biomass data following the corresponding standard formulas.

3.6 Statistical analysis

All experiments were conducted using a completely randomised design (CRD). Data were analysed using one-way ANOVA to evaluate stress effects in the first four experiments, and two-way ANOVA to evaluate the effects of stress and *A. nodosum* extract and their interactions in the last three experiments. Post-hoc comparisons were performed using Tukey's HSD or Games–Howell tests at a significance level of $p \leq 0.05$. Normality and variance homogeneity were verified prior to analysis. Statistical analyses were performed using IBM SPSS, while RStudio was used to generate the clustered heatmaps and principal component analyses.

4 Results and discussion

4.1 Morphological and production biological stress responses of *Thymus* spp.

All three *Thymus* species showed growth inhibition under drought, salinity, and combined stress, with species-specific sensitivity patterns. In *T. pannonicus*, drought was the dominant factor limiting aerial growth, reducing shoot number, shoot length, and biomass. Moderate salinity (60–90 mM) showed limited effects, while high salinity (120 mM) and combined stress produced stronger reductions like in the fresh shoot weight by 24 % and 51 % respectively in TP3, indicating additive negative effects of osmotic and ionic stress. Root growth followed similar trends, with combined stress causing the strongest reductions in root length and biomass.

In *T.* × *citriodorus*, growth traits were relatively stable under single stress treatments, but combined drought and high salinity produced marked reductions in shoot biomass, suggesting a synergistic stress interaction. Root length was less affected in TL2 than root biomass, which decreased by 25 % and 35 % respectively for the fresh and dry root weights in combined stress, indicating structural rather than functional growth adjustment under stress.

T. capitatus showed higher sensitivity to stress, with significant reductions in both shoot and root traits under drought, salinity, and especially combined stress, suggesting limited tolerance to simultaneous osmotic and ionic constraints (Figure 1).

Overall, growth reductions under stress are associated with physiological disturbances caused by salinity-induced ionic toxicity and drought-induced water deficit. These stresses reduce cell expansion, photosynthetic pigment content, and nutrient uptake efficiency, ultimately limiting biomass accumulation. When combined, drought and salinity exert stronger inhibitory effects due to simultaneous osmotic and ionic pressures on plant metabolism.

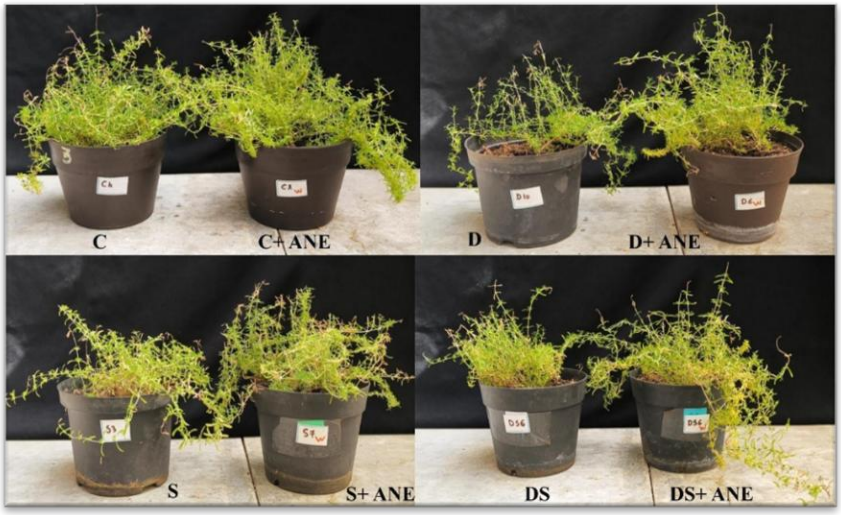

Figure 1. *T. capitatus* plants in TC2 under different treatments applied. C: control; D: drought stress; S: salinity stress (120 mM NaCl); DS: combined stress; ANE: *Ascophyllum nodosum* extract.

4.2 Physiological stress responses of *Thymus* spp.

In *T. pannonicus*, photosynthetic pigments remained relatively stable under moderate salinity (60 mM) but declined significantly under drought, higher salinity (from 90 mM) in TP2, and especially combined stress, indicating progressive impairment of the photosynthetic apparatus under severe osmotic and ionic pressure. In *T.* × *citriodorus*, drought had limited effects, whereas high salinity (120 mM) and combined stress caused marked reductions in chlorophyll a, chlorophyll b and carotenoids (by 27 %, 19 % and 29 % respectively for the salinity), suggesting reduced light-absorbing and photoprotective capacity. *T. capitatus* showed also a strong pigment reduction under drought, salinity (from 90 mM), and combined stress (1335.51 in the control to 645.19 µg g^{-1} FW in combined stress for total chlorophyll in TC2), indicating inhibition of pigment biosynthesis and photosynthetic efficiency. These responses are probably associated with oxidative stress induced by excess reactive oxygen species (ROS) production, which can degrade chlorophyll, damage thylakoid membranes, and impair electron transport and carbon assimilation.

In *T. pannonicus*, RWC decreased primarily by drought and combined stress, while maintained relatively stable hydration under moderate salinity (up to 90 mM) but higher level of salinity like in TP3 (120 mM), mainly under combined stress, could severely reduced leaf water status by 13.61 %. *T.* × *citriodorus* exhibited a progressive decline in RWC from control to drought, salinity, and combined stress, indicating increasing disruption of water uptake and tissue hydration. *T. capitatus* showed partial tolerance under individual stresses but significant RWC decline under combined stress (by 11.34 % in TC2), confirming the additive effect of osmotic and ionic stress on plant water balance. These changes reflect reduced soil water availability under drought and ionic toxicity effects of Na^+ and Cl^- under salinity.

Stress-related metabolites increased in response to stress intensity in all species. In *T. pannonicus*, proline, soluble sugars, and H_2O_2 increased under severe stress, indicating activation of osmotic adjustment and oxidative stress signalling mechanisms. Similar trends were observed in *T.* × *citriodorus,* where the highest metabolite accumulation occurred under combined stress (by 367 %, 111 % and 182 % respectively in TL2). *T. capitatus* showed the highest biochemical stress response, with very strong accumulation of osmolytes and H_2O_2 under combined stress, suggesting activation of defence mechanisms to maintain cellular homeostasis.

Overall, physiological responses indicate that drought and salinity disrupt photosynthetic processes, water balance, and metabolic homeostasis through ionic toxicity, osmotic stress, and oxidative damage. The accumulation of osmolytes and H_2O_2 suggests coordinated protective responses involving ROS signalling, membrane protection, and osmotic regulation to improve stress tolerance.

4.3 Biochemical stress responses and stress indices of *Thymus* spp.

Across the three experiments, *T. pannonicus* showed a marked decline in essential oil content under drought, salinity (from 90 mM), and especially under combined stress (up to 57 % in TP3) as presented in Figure 2. In addition to reducing total EO yield, stress induced compound-specific changes: thymol remained relatively stable under single stress but decreased under combined stress

(by 5 % in TP3); p-cymene increased under moderate salinity but declined as stress intensified, suggesting that stress does not uniformly suppress secondary metabolism but rather redirects metabolic pathways toward specific compounds under adverse conditions.

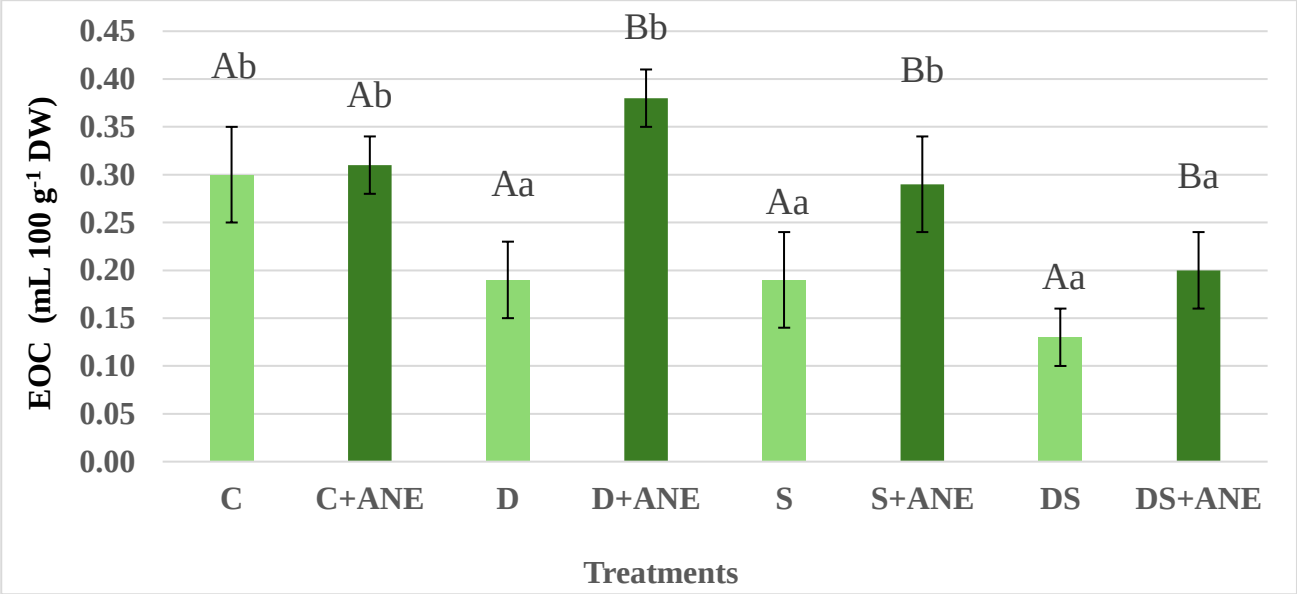

Figure 2. Essential oil content of *T. pannonicus* in TP3 (2025, 120 mM salinity), under the different stress and *A. nodosum* extract treatments, evaluated by two-way ANOVA. Means ± SD are displayed for the data. Different lowercase letters between bars indicate significant differences among treatment categories (C, D, S, DS) for the same *A. nodosum* extract application (without or with ANE), whereas different uppercase letters indicate significant differences between *A. nodosum* extract applications within the same treatment category ($p \leq 0.05$). EOC: essential oil content; DW: Dry weight; C: control; D: drought stress; S: salinity stress; DS: combined stress; ANE: *Ascophyllum nodosum* extract.

In *T.* × *citriodorus*, drought, salinity, and especially their combination reduced essential oil content, with the strongest decline under combined stress (up to 31 % in TL2), indicating limited maintenance of secondary metabolism under severe stress conditions. Stress also altered oil composition: geraniol decreased (by 12 % under combined stress in TL2), while geranial, neral, and β-bisabolene increased, shifting the oil profile toward citral-type aldehydes and sesquiterpenes, which may contribute to stress adaptation and cellular protection.

In *T. capitatus*, responses differed between experiments, partly reflecting differences in plant age and biomass structure. Older plants, characterised by a higher proportion of woody tissues relative to leaves, showed more stable essential oil levels (TC2) compared with younger plants with leaf-dominated biomass (TC1), which may help to explain the different response patterns observed between experiments, although other minor factors may also contribute. In TC1, drought, 90 mM salinity, and combined stress caused strong reductions in essential oil content (up to 34 % under combined stress). In contrast, TC2 showed greater stability in oil yield under stress. Stress also modified oil composition in a compound-specific manner: carvacrol increased (by 6.45 % under combined stress in TC2), whereas p-cymene and γ-terpinene generally declined, while β-caryophyllene accumulated under dual stress. These shifts suggest a stress-responsive

reprogramming of secondary metabolism that favours compounds associated with stress defence and cellular protection.

Total polyphenol content and antioxidant capacity showed species-dependent responses to stress intensity. In *T. pannonicus* and *T.* × *citriodorus*, phenolic content generally decreased under severe salinity (120 mM) and combined stress (21–46 %), suggesting that phenolic biosynthesis may be inhibited or that phenolic compounds are consumed in ROS scavenging. In contrast, *T. capitatus* showed increased phenolic accumulation under combined stress, indicating activation of phenolic biosynthetic pathways as a defence response. Antioxidant capacity declined under salinity and especially under combined drought–salinity stress in all three *Thymus* species. In *T. pannonicus*, antioxidant capacity decreased by 41 % under salinity (120 mM), and 3 % under combined stress, indicating that high ionic stress was the main driver of oxidative imbalance, while drought alone had minor effects. In *T.* × *citriodorus*, antioxidant activity was even more severely affected, with reductions reaching up to 58 % under salinity and combined stress in TL1, whereas drought caused only slight changes. In *T. capitatus*, antioxidant capacity declined by 24 % under salinity (90 mM) and 29 % under combined stress. Notably, even where total phenolics and carvacrol increased under combined stress in *T. capitatus*, this was insufficient to prevent the overall decline in antioxidant capacity, while in the other species total polyphenol decreased under stress, suggesting that enzymatic antioxidant systems such as superoxide dismutase, catalase, and ascorbate peroxidase may become overwhelmed under severe conditions, highlighting the necessity of coordinated biochemical and enzymatic defences to maintain cellular protection.

Regarding stress susceptibility and tolerance indices, our results confirmed that combined drought–salinity stress was the most damaging treatment across species. *T. pannonicus* showed relatively higher drought tolerance but remained highly sensitive to high salinity and combined stress. *T.* × *citriodorus* showed moderate tolerance to individual stresses but high susceptibility to combined stress. *T. capitatus* showed comparatively better stress tolerance but still experienced significant productivity losses under dual stress conditions, confirming that simultaneous osmotic and ionic stress imposes the highest physiological cost on plant growth and metabolism.

4.4 *A. nodosum* extract biostimulant-mediated stress mitigation

The application of *A. nodosum* extract improved stress tolerance in all three *Thymus* species, although the magnitude of response was species- and trait-dependent. Overall, *A. nodosum* showed the greatest effectiveness under severe combined drought–salinity stress, indicating that its protective role is most pronounced under high environmental pressure.

In *T. pannonicus*, ANE mainly improved biomass production and root system functionality under severe stress conditions. Root traits responded more strongly than shoot traits, suggesting that ANE supports water and nutrient acquisition under adverse environments. The extract also helped stabilise photosynthetic pigments under high stress intensity, indicating improved photoprotection and maintenance of photosynthetic efficiency, although effects on relative water content were limited.

In *T.* × *citriodorus*, ANE acted mainly as a stress buffer, particularly under combined stress conditions. The extract helped maintain shoot biomass and canopy stability, while root responses were relatively weaker. ANE also partially protected photosynthetic pigments and improved water status under severe stress, indicating enhanced protection of the photosynthetic apparatus and better cellular stability under osmotic and ionic constraints.

In *T. capitatus*, ANE supported both shoot and root performance, although responses were more pronounced under combined stress. The extract helped stabilise photosynthetic pigments and partially improved relative water content under drought conditions. However, its effect under single stress treatments was weaker, suggesting that ANE mainly enhances stress resilience under complex stress environments rather than under mild stress conditions.

A. nodosum extract also reduced stress-induced accumulation of proline and soluble sugars in *T. pannonicus* and *T.* × *citriodorus*, suggesting reduced physiological stress perception and lower reliance on osmotic adjustment mechanisms. Hydrogen peroxide levels were also partially reduced, indicating improved oxidative stress regulation. In *T. capitatus*, ANE effects were more selective, mainly reducing oxidative pressure under combined stress while having limited effects on osmolyte metabolism. Overall, *A. nodosum* extract enhanced stress tolerance mainly through physiological and metabolic regulation rather than direct growth stimulation. It improved photosynthetic stability, reduced oxidative stress, and supported metabolic balance, with the strongest effects observed under severe stress, highlighting its potential as a sustainable tool for improving plant performance under climate-related stress conditions.

In *T. pannonicus*, *A. nodosum* significantly improved essential oil yield under stress, increasing EOC from 0.19 to 0.38 ml 100 g^{-1} DW under drought, from 0.19 to 0.29 under salinity, and from 0.13 to 0.20 under combined stress, approaching the control level (0.31 ml 100 g^{-1} DW), while no effect was observed under non-stressed conditions. In terms of composition, ANE increased thymol under combined stress from 23.18 % to 26.17 %, with partial numerical increases under other stress treatments, indicating restoration toward control-like levels; p-cymene also tended to recover under ANE application. Under severe combined stress, ANE further enhanced total polyphenol content by approximately 45 % and restored antioxidant capacity from 110.14 to 153.86 mg AAE g^{-1} DW, bringing antioxidant capacity close to control values. These results indicate that ANE mitigates severe oxidative stress and supports both essential oil yield and quality mainly under high stress intensity rather than under optimal conditions.

In *T.* × *citriodorus,* ANE improved essential oil stability under stress, increasing EOC by 18 % under drought and 21 % under combined stress. Regarding oil composition, ANE increased geraniol only under combined stress (+8.49 %), while significantly decreasing geranial in the salinity and combined stress treatments and reducing neral in all stressed treatments, resulting in more uniform terpene proportions across treatments. ANE also stimulated phenolic metabolism, raising total polyphenol by 23% under drought stress, 26 % under salinity stress, and 8.42 % under combined stress, with stronger accumulation under single stresses. Antioxidant capacity showed a pronounced enhancement,

increasing by 54 % under drought stress, 83 % under salinity stress, and 92 % under combined stress, indicating the role of *A. nodosum* in enhancing redox balance and metabolic stability rather than fully suppressing stress responses.

In *T. capitatus*, ANE increased EOC significantly under non-stressed conditions (from 1.54 to 2.11 ml 100 g^{-1} DW), while under stress reached values comparable to control with the seaweed and remained consistently higher than untreated plants. ANE did not significantly affect carvacrol, but enhanced p-cymene and γ-terpinene under salinity, indicating partial stabilisation of the terpenoid profile. Total polypehnols content was strongly restored under individual stresses, rising from 175.43 to 210.29 mg GAE g^{-1} DW in drought stress treatments and from 153.67 to 210.43 mg GAE g^{-1} DW in salinity stress treatment. Antioxidant capacity was also markedly improved, particularly under combined stress (from 134.99 to177.79 mg AAE g^{-1} DW), the latter exceeding all other ANE-treated groups, confirming that ANE primarily enhanced redox balance and metabolic stability, especially under saline and combined stress conditions.

Across species, ANE improved stress tolerance indices, particularly under drought and salinity stress. This biostimulant improved physiological performance by enhancing water relations, supporting osmotic adjustment, and strengthening antioxidant defence systems. The greatest benefits were observed under combined stress conditions, where overlapping osmotic and oxidative constraints created greater potential for biostimulant-mediated protection. The protective effects of ANE are linked to its bioactive compounds (polysaccharides, phytohormones, and minerals), which act as signalling modulators activating ROS- and calcium-related stress pathways and stress-responsive gene expression. It enhances photosynthetic stability by supporting chlorophyll synthesis and limiting pigment degradation, thereby improving carbon assimilation under stress. ANE also promotes root development through hormonal modulation (auxin–cytokinin balance), improving water and nutrient uptake. Functioning mainly as a priming agent rather than a nutrient source, ANE strengthens stress preparedness with limited impact under optimal conditions, making it a sustainable tool for enhancing *Thymus* resilience under multifactorial climate-related stress.

4.5 The phenotypic and metabolic diversity among *Thymus* spp. under various stress conditions

The three *Thymus* species exhibited clear phenotypic and metabolic differentiation under drought and salinity stress, reflecting species-specific adaptive strategies. Among physiological traits, *T. capitatus* showed the highest stability, particularly in maintaining photosynthetic pigment integrity under severe stress, suggesting intrinsic protective mechanisms that reduce damage to the photosynthetic apparatus. In contrast, *T. pannonicus* and *T.* × *citriodorus* were more sensitive to stress, showing stronger declines in pigment content under salinity and combined stress conditions.

Stress metabolite profiles further supported interspecific differentiation. Proline accumulation patterns suggested that *T. capitatus* relies less on osmotic adjustment through proline synthesis compared with the other species, indicating alternative intrinsic tolerance mechanisms that reduce the

need for strong metabolic reprogramming. In contrast, *T.* × *citriodorus* showed the highest metabolic stress responses, reflecting stronger physiological sensitivity to osmotic and ionic constraints.

Essential oil productivity and composition also demonstrated clear species-specific regulation. *T. capitatus* showed high stability of essential oil yield across stress treatments, indicating tight metabolic regulation of secondary metabolism. In contrast, *T. pannonicus* showed strong stress-dependent reductions in oil yield, whereas *T.* × *citriodorus* was mainly affected under combined stress conditions.

Metabolic analysis confirmed strong metabolic diversity within the genus. *T. pannonicus* was characterised by a thymol chemotype, *T.* × *citriodorus* by a geraniol–citral chemotype, and *T. capitatus* by a carvacrol chemotype. Stress conditions induced shifts in secondary metabolite profiles, generally favouring compounds associated with stress defence and oxidative protection. The stability of dominant compounds in *T. capitatus* under stress further suggests stronger chemotype regulation compared with the other species.

Altogether, these findings confirm that phenotypic and metabolic diversity within the *Thymus* genus represents an important adaptive strategy allowing species to maintain metabolic and functional stability under environmental stress. Species-specific metabolic regulation, rather than uniform stress response mechanisms, appears to drive adaptive success under drought and salinity stress.

4.6 Ecological and phenotypic plasticity of *Thymus* spp. under stress conditions

Phenotypic and ecological plasticity reflect the ability of plants to adjust functional traits and maintain performance under environmental fluctuations. This concept is particularly relevant for *Thymus* species, which naturally inhabit stress-prone environments and rely on flexible physiological and metabolic regulation to survive under climatic stress.

Multivariate principal component analysis as shown in Figure 3 revealed clear differences in plasticity patterns among the three species. Drought stress produced relatively small trait displacement from control conditions in all species, indicating that moderate water limitation remained within their adaptive range. However, salinity and especially combined drought–salinity stress caused stronger reorganisation of physiological and biochemical traits. *T. capitatus* showed the highest trait stability and the smallest multivariate displacement, indicating a conservative adaptive strategy characterised by strong resistance to environmental disturbance. In contrast, *T. pannonicus* and *T.* × *citriodorus* showed greater phenotypic shifts, reflecting higher plasticity but also higher sensitivity to environmental stress.

Plasticity patterns were closely linked to species ecological origins of the species. *T. capitatus*, a Mediterranean species naturally adapted to drought-prone habitats, showed strong functional stability under stress, reflecting a conservative survival strategy that prioritises maintenance of core metabolic processes. In contrast, *T. pannonicus*, originating from temperate regions with higher moisture availability, and *T.* × *citriodorus*, a hybrid adapted to moderately warm environments,

showed greater trait reorganisation under stress, indicating more flexible but less stable physiological responses.

Across species, salinity, particularly when combined with drought, represented the strongest constraint on plasticity and performance. These findings suggest that phenotypic plasticity can buffer moderate stress, but severe or combined stress conditions may exceed adaptive physiological limits, leading to stronger metabolic and functional disturbances. Generally, the observed plasticity differences highlight the role of ecological adaptation in shaping stress tolerance strategies within the *Thymus* genus.

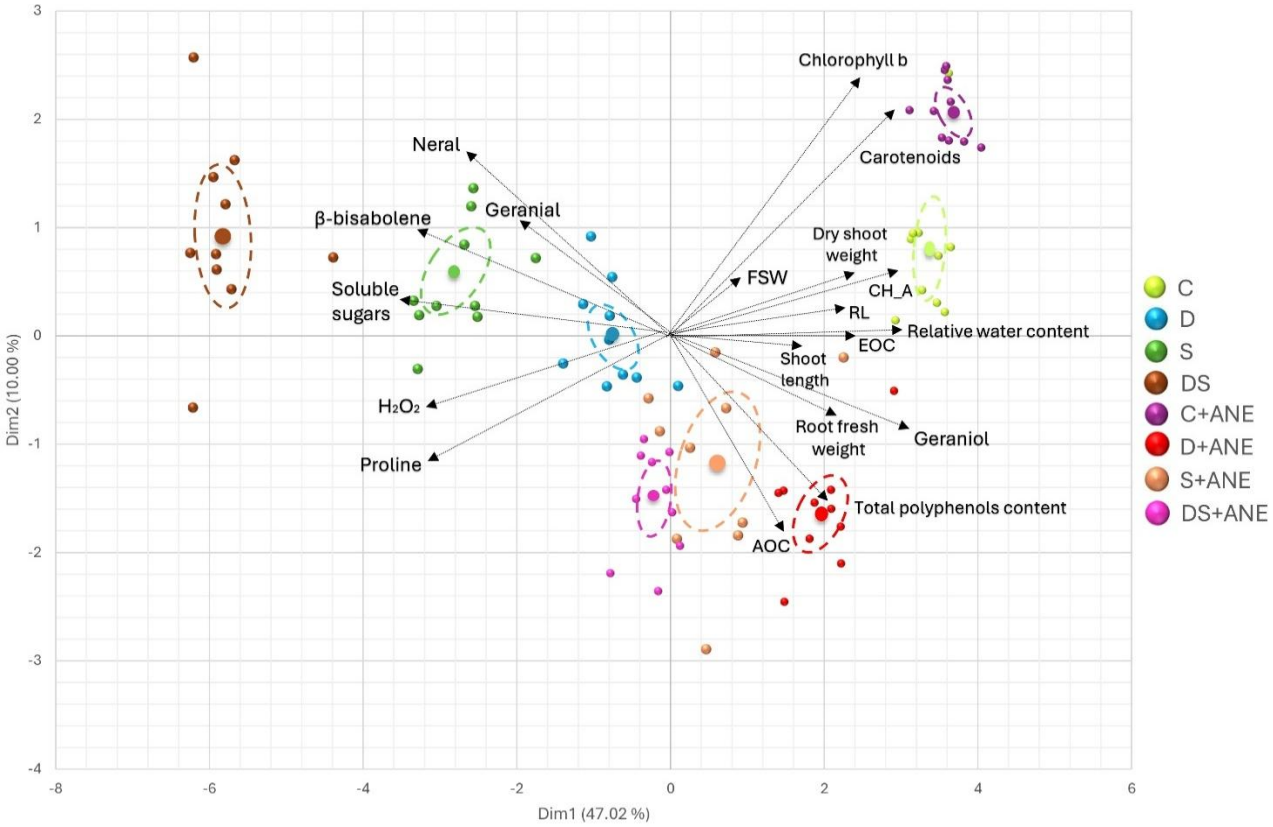

Figure 3. Biplot of principal component analysis illustrating the relationships among the studied parameters of *T.* × *citriodorus* when subjected to various stress and *A. nodosum* extract conditions in TL2. Dim: dimension; C: control; D: drought stress; S: salinity stress; DS: combined stress; ANE: *Ascophyllum nodosum* extract; FSW: fresh shoot weight; EOC: essential oil content; RL: root length; AOC: antioxidant capacity; CH_A: chlorophyll a; H_2O_2: hydrogen peroxide.

4.7 Trade-offs between growth, stress tolerance, and secondary metabolite production in *Thymus* spp.

A clear trade-off between growth and stress defence was observed under drought, salinity, and combined stress conditions (Figure 3). Stress treatments were associated with higher levels of stress markers, while growth-related traits such as biomass, pigments, and RWC declined, indicating that plants redirect resources from growth toward protective metabolic responses.

Abiotic stress also promoted a shift from primary to secondary metabolism, with stress-associated essential oil compounds clustering with stress treatments, while growth and photosynthetic traits

clustered with control conditions. This reflects the energetic cost of stress tolerance in *Thymus* species.

A. nodosum extract partially mitigated this trade-off by improving both physiological performance and secondary metabolism under stress. Rather than eliminating the trade-off, ANE reduced its severity by enhancing stress resilience and metabolic stability under adverse conditions.

5 Conclusion and recommendation

This multi-year study (560 plants across seven experiments, including 240 plants for *A. nodosum* evaluation) demonstrated that drought (40% soil water capacity), salinity (60–120 mM NaCl), and especially their combination significantly attenuate growth, physiology, and metabolism in *Thymus* species. Combined stress at 120 mM NaCl was consistently the most damaging treatment across all species.

T. pannonicus showed good tolerance at 60 mM salinity but progressive sensitivity at 90 mM and clear threshold failure at 120 mM, where salinity effects approached those of combined stress. *T.* × *citriodorus* exhibited a stable response pattern across both trials, with salinity (120 mM) and combined stress being most detrimental, resembling the tolerance profile of *T. pannonicus*. *T. capitatus* displayed comparatively moderate reductions under 90 mM salinity, but stronger deterioration at 120 mM, although treatment differences remained less extreme than in the other species.

Application of *A. nodosum* extract consistently mitigated stress damage, particularly under severe and combined stress, restoring plant performance toward control levels. Its effects were limited under non-stress conditions, confirming that *A. nodosum* functions primarily as a stress-alleviating rather than growth-promoting input.

Future research should focus on enzymatic antioxidants (superoxide dismutase, catalase, peroxidases) and molecular mechanisms underlying *A. nodosum* -induced tolerance. Practically, *A. nodosum* application is recommended as a targeted stress-management strategy for *T. pannonicus* and *T.* × *citriodorus* under increasing drought and salinity risks, particularly in Hungarian production systems, and for *T. capitatus* cultivation in Mediterranean and rainfed regions such as Tunisia, where recurrent abiotic stress limits productivity.

6 NEW SCIENTIFIC RESULTS

1. A concentration-dependent salinity response pattern was demonstrated in *Thymus pannonicus*: low to moderate salinity (60–90 mM) induced only minor changes, whereas high salinity (120 mM) clearly triggered growth reduction and stronger physiological-biochemical adjustments, including increased photosynthetic pigments amounts, relative water content, antioxidant capacity and β-bisabolene percentage. This response pattern confirmed a species-specific salinity tolerance threshold.

2. Metabolic rerouting in *Thymus pannonicus* was proved: stress reduced thymol while increased sesquiterpene and other oxygenated monoterpene levels in the essential oil. These opposite trends indicate compound-specific regulation rather than uniform suppression of essential oil biosynthesis. *Ascophyllum nodosum* extract modulated these pathways differently by enhancing selected biosynthetic branches, indicating regulation at the level of metabolic processes.
3. Stress-related modulation of citral components in *Thymus* × *citriodorus* was verified: Drought and salinity altered the biochemical profile of this species, revealing that stress induced a decline in the geraniol ratio, with a concomitant increase in the geranial and neral percentages, reflecting stress-related metabolic adjustments.
4. Enhanced sensitivity to combined stress in *Thymus capitatus* was validated: while drought or salinity applied individually caused moderate reductions in growth, water status, and pigment levels, their combination exerted a cumulative and more pronounced negative effect across all traits, revealing a higher sensitivity to simultaneous stress than to single stress.
5. Drought tolerance enhancement by *Ascophyllum nodosum* extract in *Thymus capitatus*: it was demonstrated that under drought conditions, the extract markedly improved relative water content, pigment levels, and growth, while oxidative stress remained lower than in untreated plants. Stress tolerance indices shifted from susceptible to strongly tolerant, highlighting a clear protective effect under water deficit.
6. Stress-dependent action of *Ascophyllum nodosum* extract was confirmed: the extract caused only minor or non-significant effects in unstressed *Thymus pannonicus*, *T.* × *citriodorus* and *T. capitatus*, whereas its impact became markedly stronger under drought and salinity. Physiological and biochemical traits responded more prominently under stress conditions, indicating a consistently stress-dependent effect.

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