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# Morphological and physiological response of hemp to different levels of water availability and salinity

Valeria Cafaro [a,*], Laura Siracusa [b], Luana Pulvirenti [b], Giorgio Testa [c], Antonella Iurato [c], Salvatore L. Cosentino [c], Cristina Patanè [a]

[a] CNR-Istituto per la BioEconomia (IBE), Sede Secondaria di Catania, Via P. Gaifami 18, Catania 95126, Italy
[b] Consiglio Nazionale delle Ricerche-Istituto di Chimica Biomolecolare (CNR-ICB), Via Paolo Gaifami 18, Catania 95126, Italy
[c] Dipartimento di Agricoltura, Alimentazione e Ambiente, Università degli Studi di Catania, via Santa Sofia 100, Catania 95123, Italy

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ABSTRACT

A study was conducted to assess the plant morphological and physiological response of hemp grown under LED light to different levels of water availability and salinity. Chlorophyll, fluorescence, and flavonoids were measured at 15 and 24 days after transplant (DAT). Plants were harvested at 25 DAT, when they were at full flowering stage, and the number of leaves per plant, stem height, and plant fresh weight were measured, and laboratory analysis were carried out for malondialdehyde (MDA), proline, and cannabidiol (CBD) content measurement. Moderate water replenishment (60 % ETc, I60) had negligible effects on morphological traits, whereas a low level of water replenishment (30 % ETc, I30) exerted a significant depressive effect. Salinity negatively affected all morphological traits already at mild level (−0.2 MPa water potential). MDA was higher under moderate (+24 % in I60) and low (+26 % in I30) water replenishment, and picked at 17.4 μmol $g^{-1}$ FW at the highest level of salinity (−0.4 MPa water potential, +41 %). Proline content was maximized under restricted water conditions (30 % ETc), and at the highest level of salinity (−0.4 MPa). Water limitation significantly increased CBD only at the highest level (30 % ETc, +45.6 % of CBD), whilst salinity induced a strong raise in CBD at both levels (+31.3 and +36.4 % at −0.2 and −0.4 MPa, respectively). Overall, hemp resulted more sensitive to salinity than water scarcity.

## 1. Introduction

In the last decades, the world has witnessed significant transformation, and it will face different challenges in the years to come. Climate change represents one of the biggest issues to solve, influencing crops, livestock, water resources, and the overall population. It is crucial to note that the continuous rise in the average global temperature is expected to reach 2°C by 2100 and a significant 4.2°C by 2400 (Malhi et al., 2021). The Mediterranean area is facing a great decline in mean precipitation and a rise in the variability during the dry season, which cause a strong area aridification (Straffelini and Tarolli, 2023). This trend, together with a strong increase in $CO_2$ concentration, salinization, and heightened flooding, will lead to severe agricultural losses on a global scale (Khondoker et al., 2023).

The agronomic research plays an important role in identifying alternative crops that can meet the significant challenges of the new millennium. In this regard, hemp may represent a promising candidate for cultivation on marginal lands, offering potential for utilization and exploitation.

Industrial hemp (*Cannabis sativa* L.) is a plant belonging to the Cannabaceae family, originating from Central Asia (Chandra et al., 2017). It adapts well to temperate areas of Europe and America, and nowadays it is spread across the globe.

In the past, hemp was primarily used in the textile industry. Today, being a multi-functional crop, hemp production has grown exponentially as raw material for industries (*i.e.,* textiles, construction, bioplastics) (Ahmed et al., 2022), but also for oil and secondary metabolites production, such as cannabinoids and terpenes (Visković et al., 2023). The high biomass production and energy yield make hemp an appealing choice for bioenergy production (Kołodziej et al., 2023). Its products can be converted into different forms of bioenergy such as bioethanol (from biomass) and biodiesel (from seed oil), which are more environmentally

* Corresponding author.
*E-mail addresses:* valeria.cafaro@ibe.cnr.it (V. Cafaro), laura.siracusa@icb.cnr.it (L. Siracusa), l.pulvirenti@icb.cnr.it (L. Pulvirenti), gtesta@unict.it (G. Testa), antonella.iurato@unict.it (A. Iurato), cosentin@unict.it (S.L. Cosentino), cristinamaria.patane@cnr.it (C. Patanè).

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friendly than fossil fuels. This would not only address the growing demand for renewable energy, but also would make it feasible the use of marginal lands where non-food crops can be easily introduced (Blandinières and Amaducci, 2022).

Hemp plants produce at least 120 different cannabinoids, synthetized within basal disk cells and subsequently stored in the secretory cavity of glandular trichomes. Flower tissues have the highest concentration of glandular trichomes, which lead to the highest amount of cannabinoids in these tissues, *i.e.*, carboxylic acids such as tetrahydrocannabinolic acid (THCA) and cannabidiolic acid (CBDA), which decarboxylate into neutral cannabinoids like tetrahydrocannabinol (THC) and cannabidiol (CBD) during storage and heating (Di Mola et al., 2021). As in all plants, the content of secondary metabolites in hemp is mainly genetically driven, although external factors, *e.g.,* photoperiod, light intensity, and light quality can also influence them (Siracusa et al., 2023). Additionally, it appears that the production of secondary metabolites is a defense mechanism against abiotic stresses (Siracusa, 2023).

At present, the validity of introducing hemp into cropping systems of semi-arid cultivation areas in the Mediterranean regions is under consideration (Cosentino et al., 2013), particularly in light of the environmental challenges posed by water scarcity and soil salinity. Recent studies under controlled-environmental conditions demonstrated that water-deficit stress can induce metabolic reprogramming in *Cannabis*. This phenomenon enhances the accumulation of secondary metabolites by altering the redox balance and redirecting carbon allocation toward highly reduced compounds (Dimopoulos et al., 2025). Furthermore, irrigation experiments with increasing levels of NaCl salinity indicated that changes in biomass were closely related to salinity levels. Additionally, alterations in the phytocannabinoid profiles were revealed, suggesting that hemp exhibits varying physiological and secondary metabolic responses to salt stress (Formisano et al., 2024). However, the extent of these effects varies according to the severity of the stress and the developmental stage of the plant (Cappello Fusaro et al., 2025; Sharma et al., 2025). As a matter of fact, drought and salt stress represent significant environmental constraints on plant growth and productivity on a global scale. The responses of plants to these stressors are characterized by a high level of complexity, involving numerous interconnected signaling pathways that function across various regulatory levels (Ma et al., 2020). This complexity hinders the ability of predicting the plant responses in the face of stress conditions.

Therefore, it is necessary to investigate the effects that water scarcity and salinity exert on plant morphology and physiology, in order to evaluate the threshold above which its production is altered.

On this basis, a study was conducted in a controlled environment to limit the impact of external atmospheric factors on a cultivar of hemp under LED light (light – emitting diode), to assess the plant morphological and physiological response to different levels of soil water availability and salinity of irrigation water.

## 2. Materials and methods

### 2.1. Controlled chamber experiment

The experiment was carried out at the Department of Agriculture, Food and Environment, University of Catania (Italy), using the monoecious cultivar 'Tygra' of industrial hemp (*Cannabis sativa* L.). In a completely randomized design, the following experimental factors were studied: water availability (100, 60, 30 % of evapotranspiration-ETc restoration), and salinity levels (0, −0.2, −0.4 MPa water potential). Eight pots (*i.e.*, eight replicates) were used for each experimental treatment. Seeds were provided by a commercial company (Canapuglia, Bari, Italy). Before the start of the experiment, the seeds were surface-sterilized with 1 % sodium hypochlorite (NaClO) (Sigma-Aldrich s.r.l., Milano, Italy), placed in Petri dishes on a single paper filter moistened with 5 mL of distilled water, and incubated in the dark at 25°C for germination.

When the seed radicle was approx. 5 mm long, germinated seeds were sown in a cell plug tray filled with commercial soil mixture (Geolia soil, Italy), and placed in a controlled growth chamber at constant 25°C under light conditions and a RH of 50–60 %. When the emerged seedlings were at the 2-true leaf stage (approx. 25 days later), plantlets were transplanted in pots 12 cm high and having a 14 cm diameter (total volume of pot approx. 615 $cm^3$). Pots were filled with soil collected from a cultivated area of eastern Sicily (clay 28.3 %, sand 49.3 %, loam 22.4 %, organic matter 1.4 %) and plantlets were left to grow in growth chamber, under LED light conditions (Bilberry Ltd., Lodz, Poland), at a photon flux density (PPFD) of 300 μmol $m^{-2}$ $s^{-1}$, a 12/12 h photoperiod, and a temperature of 25 ± 1°C.

#### 2.1.1. Water availability experiment

At transplant, all pots were fulfilled with deionized water to soil capacity. To this end, water was supplied until the soil appeared water-saturated, allowing the exceeding water to percolate (up to approximately field capacity), then pots were weighed (*i.e.,* pot weight at soil field capacity). Afterwards, in order to monitor soil water content and define the irrigation time, all pots were weighed daily. The available soil water content (ASWC, %) was calculated each day as follows:

ASWC (%) = [(PFC-P/(PFC-PWP)) x 100]

where PFC is the weight of the pot at soil field capacity (g), P is the daily weight of the pot (g), PWP is the weight of the pot at soil wilting point (this last estimated as 11 % of soil water content). When ASWC dropped to its 33 % (*i.e.*, 66 % of ASWC was lost by evapotranspiration, measured by weighing the pots), water was supplied according to water treatment. Three levels of water replenishment were compared: I100 (fully irrigated control, 100 % ETc restoration), I60 (moderate level of water replenishment, 60 % ETc restoration), and I30 (low level of water replenishment, 30 % ETc restoration). Pots in I100 were irrigated to fully restore the water lost by ETc, those in I60 were irrigated with a volume of water corresponding to 60 % of that in I100, those in I30 were irrigated with a volume of water corresponding to 30 % of that in I100.

After the first irrigation, equal for all treatments, water was supplied weekly with different amounts of water according to water treatments, for a total of 3 irrigations.

#### 2.1.2. Salinity experiment

Three levels of salinity were considered in this experiment. Salt solutions were prepared by dissolving 0, 69 and 110 mM NaCl in deionized water. These solutions had water potentials (ψ) of 0 (control, no salinity), −0.2 and −0.4 MPa, and electric conductivity (*EC*) of 0, 6.2 and 9.0 dS $m^{-1}$, respectively. EC was measured in a portable conductivity meter (Mod. CyberScan CON 400/410). Irrigations were applied according to I100 treatment described in paragraph 2.1.1 (Water availability experiment). In this experiment, the same control of water availability experiment (I100) was considered as the control.

### 2.2. Measurements

During the experiment, non-destructive measurements of chlorophyll, fluorescence, and flavonoids were carried out at 15 and 24 days after transplant (DAT), on 3 fully expanded leaves per plant, using a MPM-100 multi-pigment-meter (ADC BioScientific Ltd, UK) (Cerovic et al., 2008).

Plants were harvested at the full flowering stage (25 DAT). At harvest, number of leaves per plant, stem height, plant fresh weight, as total and partitioned in stem, leaves and inflorescence, were measured. A fresh leaf sample from each plant was stored at −20°C until malondialdehyde (MDA) and proline content were analysed. Inflorescences were air dried and stored in paper bags until analysis of cannabidiolic acid (CBDA) and cannabidiol (CBD).

#### 2.2.1. MDA content

To determine the lipid peroxidation under salinity and water shortage in hemp leaves, the malondialdehyde (MDA) was measured according to Li et al. (2010) modified. Freeze leaf samples (0.2 g) were extracted in 5 mL of trichloroacetic acid (TCA) (0.1 %) (w/v), then the extract was centrifuged at 5000 *g* for 10' at 5 °C. Surnatant (1 mL) was added to 4 mL of 20 % trichloroacetic acid (TCA) containing 0.5 % of thiobarbituric acid (TBA). The mixture was heated at 95°C for 30 min, followed by a quick immersion in an ice bath, and then centrifuged at 5000 *g* for 15' at 5 °C. Absorbance (A) was read in a spectrophotometer (ONDA UV-31 Scan Spectrophotomer, ONDA Spectrophotometers Service, Carpi (MO), Italy) at 450, 532, and 600 nm. The MDA content was calculated as follows (Raziq et al., 2022):

$$\text{MDA } (\mu\text{mol L}^{-1}) = 6.45 \text{ x } (A_{532} - A_{600}) - 0.56 \text{ x } A_{450}$$

The results were expressed as μmol $g^{-1}$ FW (fresh weight).

#### 2.2.2. Proline content

Proline content was determined according to Bates et al. (1973) modified. Freeze leaf samples (0.1 g) were extracted in 10 mL of 3 % sulfosalicylic acid (w/v), and centrifuged for 30' at 5000 *g*. Aliquots of 1 mL of the extract were mixed with 1 mL of acetic acid 99 % and 1 mL of acid ninhydrin solution (2.5 g ninhydrin dissolved in a 100 $mL^{-1}$ solution of acetic acid, deionized water, and orthophosphoric acid 85 % in a volume of 6:3:1), and placed in a heated bath at 90°C for 1 h. Then, the samples were cooled in ice bath for 5' to stop the reaction. Four mL of toluene were added and the samples were vigorously vortexed for 20'' to allow the separation of the mixture. The upper layer of the separation extract was used for measurements. Absorbance was read spectrophotometrically at 520 nm, using proline as standard curve ($R^2 = 0.99$). Toluene was used as blank. Proline content was reported as μmol $g^{-1}$ FW.

#### 2.2.3. Identification and quantification of CBDA/CBD levels in hemp inflorescences via HPLC/Uv-vis-DAD analyses

All chemicals and solvents were of analytical grade and used without further purification. Pure reference standards cannabidiol (CBD) and cannabidiolic acid (CBDA) were purchased from Supelco (VWR, Milan, Italy) as 1 mL of 1 mg $mL^{-1}$ methanolic solutions (CBD: code C6395; CBDA: code C-1445). HPLC grade water and acetonitrile were also from VWR (Milan, Italy). A set of preliminary experiments was carried out to find the most performing extraction solvent/mixture in terms of cannabinoids yield (data not shown). As a result, a 70 % aq. EtOH (EtOH: $H_2O$ 70:30 v/v) solution was used. Hemp inflorescences were powdered with a mortar and pestle, accurately weighed, and small aliquots (ca. 50 mg) were put in 8 mL vials and suspended in 3 mL of the extraction mixture. The resulting heterogeneous suspensions were left stirring overnight on a magnetic plate in the dark at room temperature, then filtered over standard laboratory filter paper. The so obtained greenish solutions were put in HPLC 2 mL amber vials and immediately analysed. Chromatographic analyses were carried out on an Ultimate3000 UHPLC focused instrument equipped with a binary high pressure pump, a Photodiode Array detector, a Thermostatted Column Compartment and an Automated Sample Injector (Thermo Fisher Scientific, Inc., Milan, Italy). Collected data were processed through a Chromeleon Chromatography Information Management System v. 6.80. Analytical runs were performed using a reverse-phase column (Gemini $C_{18}$, 250 ×4.6 mm, 5 μm particle size, Phenomenex Italia s.r.l., Bologna, Italy) equipped with a guard column (Gemini $C_{18}$ 4 ×3.0 mm, 5 μm particle size, Phenomenex Italia s.r.l., Bologna, Italy). Hemp cannabinoids were eluted with a gradient developed according to Brighenti et al. (2017). The solvent flow rate was 1 mL/min, the temperature was kept at 25°C and the injector volume selected was 20 μL. Quantification was carried out at 280 nm using CBD ($R^2 = 0.9999$) and CBDA ($R^2 = 0.9998$) as external standards. For each plant/replicate, analyses were performed in triplicate.

### 2.3. Statistical analysis

Data of all traits were subjected to a one-way analysis of variance (ANOVA), using CoStat version 6.003 (CoHort Software). When "F" ratios were significant, means were separated by Tukey's test ($p \leq 0.05$).

## 3. Results

### 3.1. Soil water content

Soil water content was measured during the experiment (Figs. 1, 2). Under no stress conditions (I100/0 MPa), after the first irrigation soil water content progressively decreased down to the threshold for irrigation (*i.e.*, 33 % of ASWC). After that, the soil was refilled to 100 % ASWC. The same trend was followed after each irrigation until harvest. A similar ASWC trend was followed in I60 and I30, but at each irrigation, soil was never fulfilled, and water content was kept below 65 %, in I60, and 50 %, in I30. In some cases, ASWC in both I60 and I30 dropped below the threshold for irrigation. In particular, in I30, plants were overstressed from 14 DAT onwards, because ASWC was always kept below 33 %, even after irrigation. This result indicates that plants in I30 were able to extract water from soil at low water potentials.

The course of soil water content in the three salt treatments almost overlapped during the experiment, progressively decreasing down to the threshold for irrigation, and then quickly approaching field capacity after irrigation. However, when −0.2 and −0.4 MPa water potential solutions were used for irrigation, soil water content did not reach 100 %, except at the last irrigation.

### 3.2. Plant morphological traits

Water limitation affected *plant height* only at the highest level, and plants in I30 were 34 % smaller than those in I100 ($p < 0.05$) (Fig. 3). Conversely, moderate water shortage in I60 did not depress plant height. Differently, salinity affected plant elongation at all levels, and a final height 23 and 64 % lower than that in unstressed plants, was measured at −0.2 and −0.4 MPa, respectively.

The effect of water availability on the number of leaves was significantly evident only at the lowest level, and plants in I30 had five leaves less than plants in I100 ($p < 0.01$) (Fig. 4). Differently than that observed for plant height, salinity did not affect this trait at a mild level (−0.2 MPa), but at the highest level it significantly reduced the number of leaves from 11 (at 0 MPa) to 9 (at −0.4 MPa, $p < 0.001$).

As mentioned for plant height and number of leaves per plant, plant weight was significantly influenced by both water limitation and salinity ($p < 0.001$). A progressive 28 % and 66 % weight reduction over the control was measured, respectively, in plants of I60 and I30.

The effect of salinity on plant weight was more pronounced than that of water availability, and 33 and 80 % total weight reductions were measured at −0.2 and −0.4 MPa, respectively, over the unstressed control (Fig. 5).

Overall, water limitation exerted a depressive effect upon all plant components, but did not much influence the relative contribution to total plant weight. Differently, the negative effect of salinity was clearer upon the weight of inflorescence (-83 % at −0.4 MPa) compared to the unstressed control.

### 3.3. Physiological traits

#### 3.3.1. Malondialdehyde (MDA)

MDA significantly differed with the level of water scarcity ($p < 0.01$) and salinity ($p < 0.001$) (Fig. 6). MDA content was minimized in the control (< 9 μmol $g^{-1}$ FW). Both moderate and severe water shortage induced a significant increase in MDA of leaves (> 11 μmol $g^{-1}$ FW) with

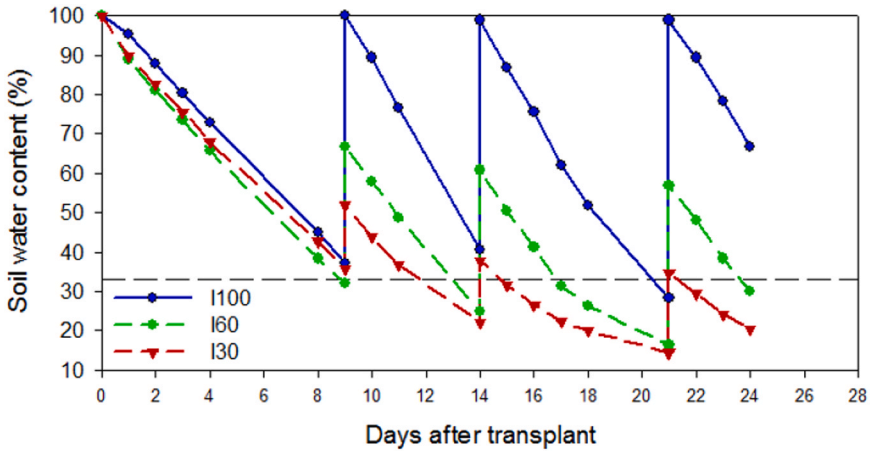


**Fig. 1.** Soil water content measured at three levels of water restoration (I100, I60, I30). The constant horizontal short dashed lines indicate the empirical minimum threshold for irrigation.

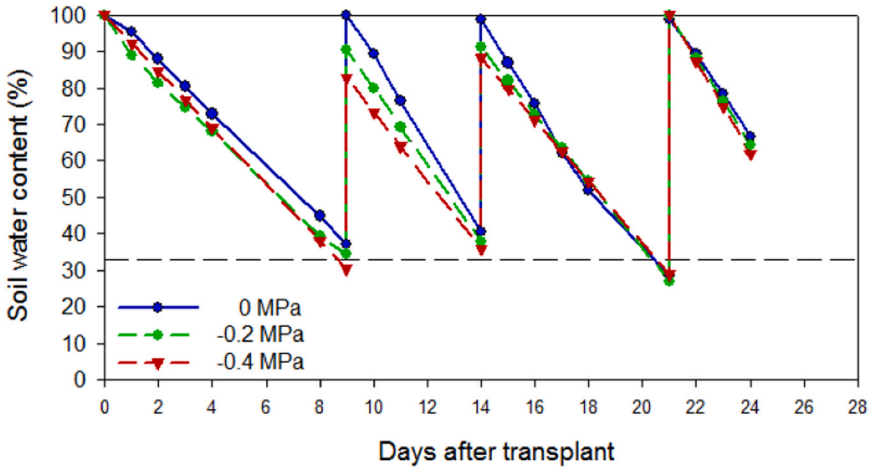


**Fig. 2.** Soil water content measured at three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl. The constant horizontal short dashed lines indicate the empirical minimum threshold for irrigation.

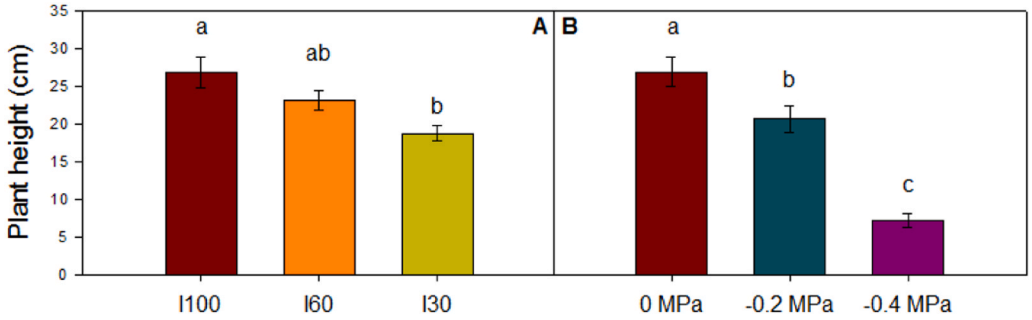


**Fig. 3.** Plant height (cm) measured at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

no differences between the two levels of water availability.

Differently, a mild salinity (−0.2 MPa) did not affect MDA content, but a great rise in this last (> 17 μmol $g^{-1}$ FW) occurred under the highest level of salinity (−0.4 MPa).

### 3.3.2. Proline content

A low content of proline (< 1.6 μmol $g^{-1}$ FW) was accumulated in leaves under unstressed conditions (Fig. 7). A moderate level of water replenishment in I60 did not induce any significant change in proline content. This last, however, steeply increased under water shortage in I30 (> 12 μmol $g^{-1}$ in I30).

Differently than what observed for MDA content, salinity caused a significant increase in proline content already at −0.2 MPa (7.6 μmol $g^{-1}$ FW), and at −0.4 MPa, proline content approached 14 μmol $g^{-1}$ FW.

### 3.3.3. CBDA and CBD

CBDA (cannabidiolic acid) is the precursor of cannabidiol (CBD). It was statistically affected by both water and salt stress ($p < 0.05$).

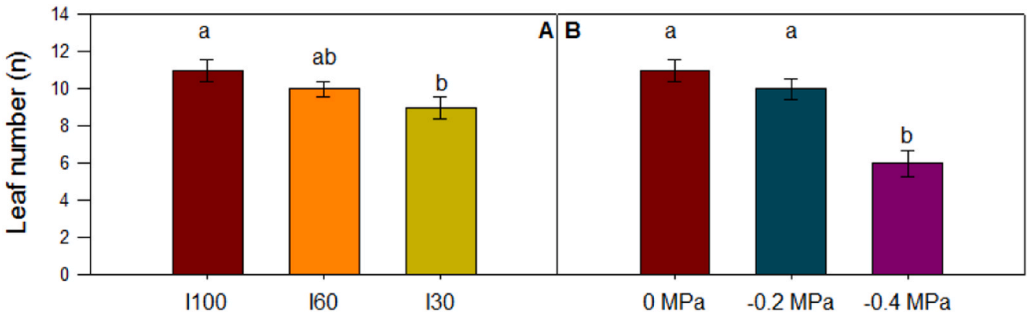


**Fig. 4.** Number of leaves per plant (n) measured at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

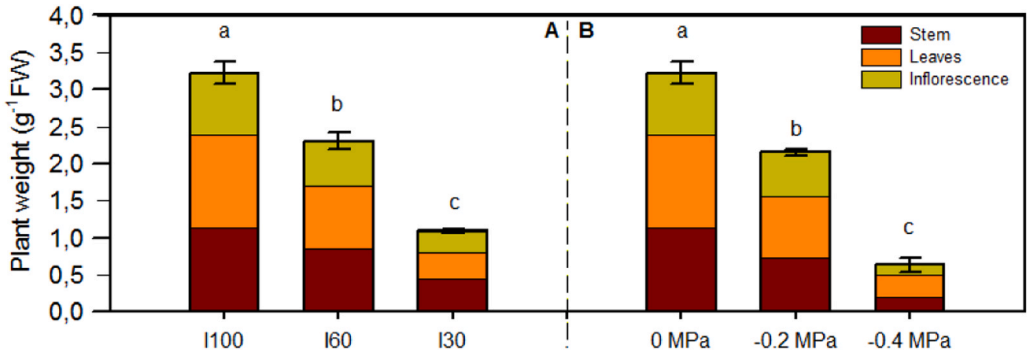


**Fig. 5.** Plant weight ($g^{-1}$ FW) measured at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Letters and standard error (ES) refer to the total plant weight. Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

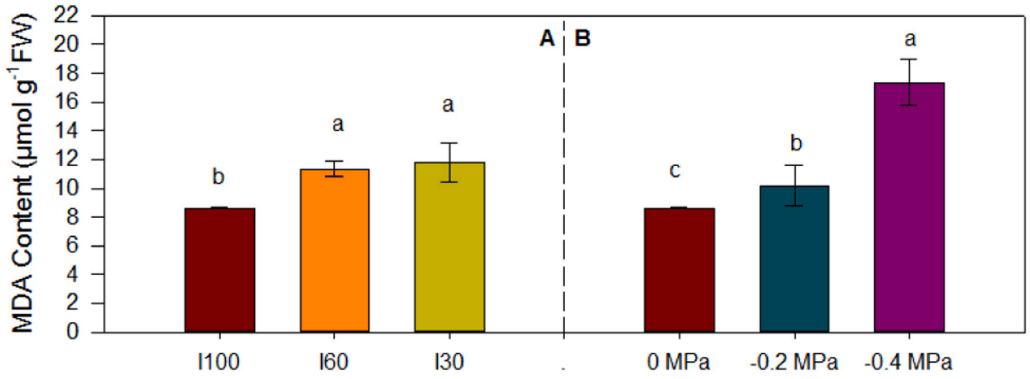


**Fig. 6.** MDA measured at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error (n = 8).

A moderate water replenishment in I60 did not affect the content of CBDA. However, a strong water shortage in I30 significantly decreased the CBDA by 46 % respect to well-irrigated control (Fig. 8). Differently, CBDA was significantly reduced by salinity at both levels (−16 and −42 %, at −0.2 and −0.4 MPa, respectively).

The CBD (cannabidiol) was statistically affected by both water availability and salinity ($p < 0.05$). Irrigation at a 60 % ETc rate did not change CBD content that, conversely, significantly increased under a very high level of water scarcity (+ 45.6 % over the control in I30) (Fig. 9).

Differently, mild and moderate levels of salinity strongly affected CBD, which was significantly increased by 31.3 and 36.4 %, at −0.2 and −0.4 MPa, respectively.

### 3.3.4. *Chlorophyll content*

Chlorophyll content was measured in hemp leaves at 15 and 24 DAT. Water scarcity at mild level (I60) did not affect chlorophyll content at 15 DAT, but later on (24 DAT), the content was significantly increased at both mild and severe levels (+20 and +30 %, in I60 and I30, respectively).

In salt stress treatments, at 15 DAT, plants in the control and those at −0.2 MPa showed chlorophyll content that were not significantly different (0.44 and 0.41, respectively) (Fig. 10). A severe stress at −0.4 MPa increased the content to 0.61, which was significantly higher than that measured in the control. A similar trend was observed at 24 DAT, where chlorophyll gradually and significantly increased with the level of salinity (+23 and +116 %, at −0.2 and −0.4 MPa, respectively).

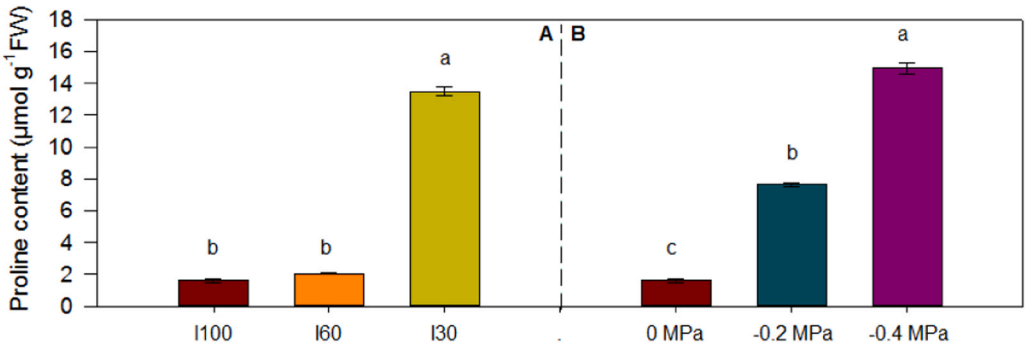


**Fig. 7.** Proline content at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

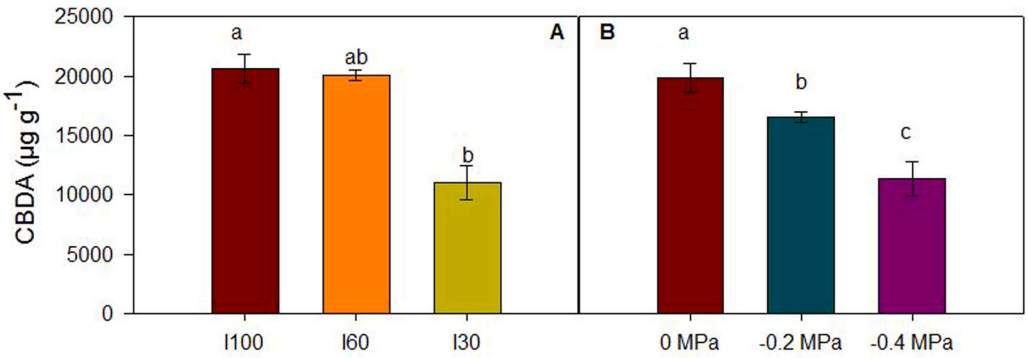


**Fig. 8.** CBDA measured at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

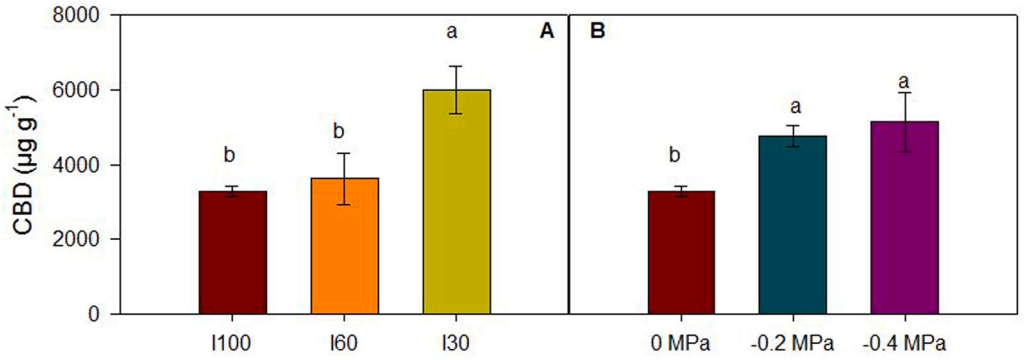


**Fig. 9.** CBD measured at three levels of water restoration (I100, I60, I30) (**A**) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (**B**). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

### 3.3.5. *Fluorescence*

Fluorescence, which indicates the level of functioning of the photosynthetic system, decreased with time in all treatments, according to plant senescence (Fig. 11).

At 15 DAT, irrigation at moderate (I60) and low rate (I30) slightly but significantly reduced the leaf fluorescence. Interestingly, later on (at 24 DAT), leaves under water limitation became more fluorescent than those of the control (+10 and 22 % in I60 and I30, respectively).

At 15 and 24 DAT, plants irrigated with −0.2 MPa saline water kept stable levels of leaf fluorescence. In contrast, those at the highest level of salinity (−0.4 MPa) experienced a drastic decline in fluorescence, with values of 0.64 and 0.42 at 15 and 24 DAT, respectively.

### 3.3.6. *Flavonoids content*

Flavonoids in leaves increased throughout the plant growth, as confirmed by higher contents measured at 24 DAT respect to those at 15 DAT, irrespective of water or salt treatment.

After a couple of weeks from transplant, plants irrigated at 60 and 30 % rates accumulated more flavonoids than the control (+35 and +39 %, respectively in I60 and I30) (Fig. 12). Later on (24 DAT), these differences became less evident, but they were still kept significant (+4 % in I60 and +8 % in I30).

Differently from water scarcity, salinity induced an increase in flavonoids only at the highest levels (−0.4 MPa, +64 %).

## 4. Discussion

This study examined the effects of drought and salinity on the morphological and physiological traits of a hemp cultivar. Overall, the effects of salinity were more pronounced than those of water deficiency.

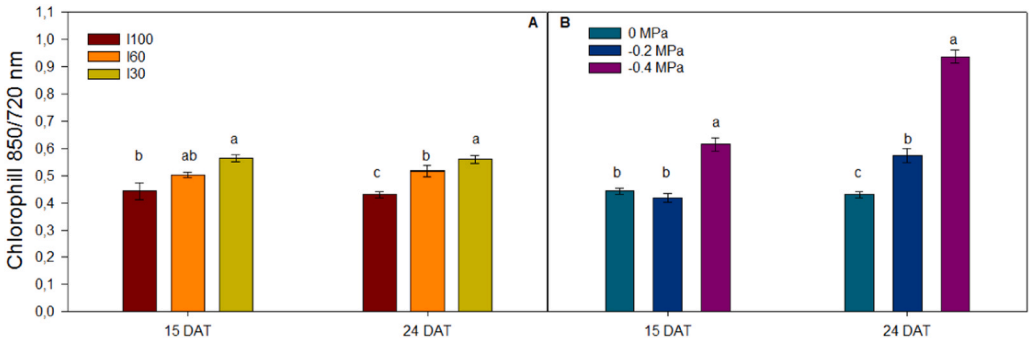


**Fig. 10.** Chlorophyll content measured at three levels of water restoration (I100, I60, I30) (A) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (B) at 15 and 24 days after transplant (DAT). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

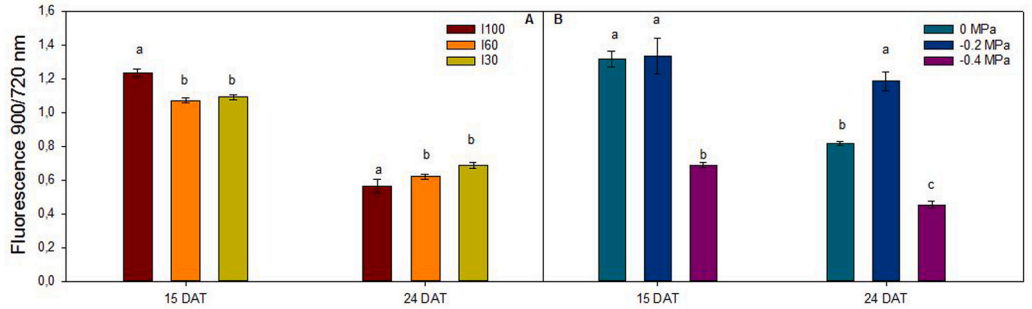


**Fig. 11.** Fluorescence content measured at three levels of water restoration (I100, I60, I30) (A) and three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (B) at 15 and 24 days after transplant (DAT). Different letters indicate significance at $p \leq 0.05$ (Tuckey's test). Small black vertical bars indicate the standard error ($n = 8$).

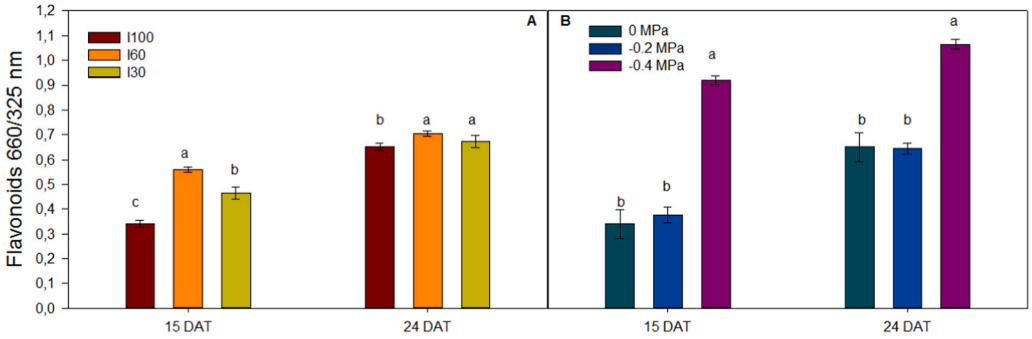


**Fig. 12.** Flavonoids content measured at three levels of water restoration (I100, I60, I30) (A) and at three levels of water potential (ψ) (0, −0.2, −0.4 MPa) in NaCl (B) at 15 and 24 days after transplant (DAT). Different letters indicate significance at p ≤ 0.05 (Tuckey's test). Small black vertical bars indicate the standard error (n = 8).

Previous studies conducted on hemp reported that water deficiency and high soil salinity constrain hemp growth and development (Hameed et al., 2021; Chen et al., 2024).

In this study, no effects upon plant height and leaf number, and a minor reduction in plant weight, occurred under a moderate level of water restoration (60 % ETc), indicating that hemp plant does not suffer from water limitation at low levels of it. However, remarkable plant growth (plant height and weight and leaf number) reduction occurred at very low levels of water availability (*i.e.*, 30 % ETc restoration), revealed that a water stress condition may occur when water availability drops below to a certain threshold. Gill et al. (2022) reported similar results when evaluating the morphological response of industrial hemp to water deficit. According to literature (Chaudhry and Sidhu, 2022), water stress determines a variation in the water balance within the plant; when water is freely available it is easily absorbed by roots, and the cells remain turgid. As water stress rises, plants are no longer able to compensate for the loss of water through transpiration and modulate the stomatal openings, starting to dehydrate. The present study underscores the resilience of cultivar 'Tygra' of hemp to water scarcity. However, a considerable genetic variability in hemp response to drought has been reported in literature (Kousta et al., 2025), highlighting the need of extending the investigation to other cultivars. Nevertheless, this study may provide useful insights on how hemp may behave under water stress conditions.

The morphological changes that occurred in this study under salinity appeared more evident than those observed under water scarcity. Indeed, plant height and weight were reduced by salinity already at mild level of it (−0.2 MPa), revealing a possible major sensitivity of this plant to salinity stress. Sensitivity to salinity may also depend on the cultivar, as documented genotypic variations in stress tolerance exist in hemp

(Dixit, 2022). Hu et al. (2019), as well, evidenced a great sensitivity of hemp to both salt and alkali stress. Yang et al. (2024), applying 140 mM of NaCl (approx. −0.5 MPa) in their study, reported a 34 % reduction in the average plant height and a 26 % decrease in the number of leaves, thereby confirming that hemp subjected to salinity experiences significant growth deficiencies. These outcomes can be ascribed to alterations in the physiological activities of the plant. Salinity prevents plant growth as it limits its ability to supply itself with water (osmotic stress) (Van Zelm et al., 2020). Additionally, it promotes the accumulation of reactive oxygen species (ROS), which can lead to cellular damage. Salinity also determines an increase in the concentration of ions such as Na+ and Cl- inside the cells, which, exceeding certain thresholds, induces phenomena of toxicity (ionic stress). Ionic and osmotic stress reduce cell expansion and determine nutritional imbalances and oxidative stress, which influence the growth, development, and ultimately the survival of the plant (Dzinyela et al., 2023). However, as above mentioned for water scarcity, the results of the current study should be taken cautiously into account, as the observed sensitivity to salinity refers to a single cultivar.

The application of both unfavourable conditions (water limitation and salinity) resulted in decreases in the weight of single components (stem, leaves, inflorescence) of the plant. Among them, the weight of the inflorescence was reduced to a greater extent than that of stem and leaves (up to 83 % less than control) under the highest level of salinity (−0.4 MPa). As indicated by Morgan et al. (2024), the inflorescence is the most stress-sensitive part of the hemp plant. The authors, evaluating the effects of drought on hemp, found that a severe drought led to a significant decrease in yield and flower production. According to Morgan et al. (2024), the decrease in growth and biomass could be related to the negative effects of drought on cell division and elongation, which result in nutrient imbalances, excessive production of ROS, and enzymatic activity inhibition. Cellular components and biological membranes are harmed by these factors, leading to a decrease in biomass production as reported by Kesawat et al. (2023). Similarly, Formisano et al. (2024) by evaluating the effects of different saline irrigations in hemp, noted that a high level of salinity (approx. –0.4 MPa) reduced biomass to an equal extent (49 %) for stems, leaves, and inflorescences.

Lipid peroxidation is measured as malondialdehyde (MDA) content, which is a marker of oxidative damage in cells (Morales and Munné-Bosch, 2019). A consistent increase in MDA can lead to cell death (Dixit, 2022). In this study, MDA increased by 24 % at moderate rate of water replenishment (60 % ETc), with no further increases at lower level of water availability (30 % ETc). Salinity, as well, induced a rise in MDA already at mild level, but at higher level (−0.4 MPa), the increase in MDA became more evident, indicating that a salt stress condition took places. This finding aligns with the one reported by Dixit (2024), who noticed low levels of MDA in hemp exposed to low concentrations of NaCl (50 mM, i.e., approx.- 0.2 MPa), and an increase of 52 % in hemp treated with higher salt concentrations (80 mM, *i.e.*, approx. −0.38 MPa). According to Yang et al. (2024), an increase in the relative electrical conductivity (REC) and MDA levels in plants subjected to stress revealed a high membrane permeability and accelerated lipid peroxidation, indicating an oxidative damage due to the accumulation of ROS. Under unstressing conditions, ROS are regulated by both enzymatic (*e.g.*, superoxide dismutase [SOD] and peroxidase [POD]) and non-enzymatic antioxidant systems. However, when plants experience a salt stress, these defence systems may be overcome, leading to cellular damage that is difficult to counteract. In response to oxidative stress, plants tend to accumulate osmotic compounds such as soluble proteins, soluble carbohydrates, and proline, which promote osmoregulation and enhance the defensive mechanisms against ROS-induced damages (Yang et al., 2024). However, these antioxidative enzymes were not analysed in this study.

The effects of MDA can be reduced by proline, which is a well-known metabolite that accumulates during stress and serves various functions, including osmoregulation, protection of cellular structures, and maintenance of redox balance (Hayat et al., 2012). In the case of water stress, proline accumulates as an adaptive response, promoting water retention and acting as a ROS scavenger to maintain the integrity of cellular membranes (Rezghiyan et al., 2024). Under salt stress, sodium and other ions accumulate in plant tissues, disrupting cellular metabolism. To counteract these imbalances, proline concentration increases, helping to reduce sodium accumulation and detoxify excess ions. In this study, hemp did not osmoregulate under moderate level of water restoration (60 % ETc), as proline was not overproduced respect to control. Contrastingly, a lower water availability (30 % ETc) induced the activation of an osmoregulating mechanism in hemp, as revealed by a steep raise in proline content. Differently, the accumulation that occurred at both levels of salinity could be traced back to salt stress, indicating that hemp activates an osmoregulation mechanism in response to salinity, even at low levels of it.

In hemp, the primary secondary metabolites are phytocannabinoids, specifically tetrahydrocannabinol (THC) and cannabidiol (CBD). These compounds are synthesized in their acidic forms from a common precursor called cannabigerolic acid (CBGA), through the action of two distinct enzymes: THCA synthase (THCAS) and CBDA synthase (CBDAS) (Landi et al., 2019). Environmental conditions contribute to the production and accumulation of cannabinoids, which are greatly influenced by light, temperature, water deficit, heavy metals and soil salinity (Di Mola et al., 2021). In this study, under water limitation, CBDA accumulated to a less extent than control only at the lowest rate of irrigation (30 % ETc) and, under salinity, it accumulated more than control already at mild level of it (−0.2 MPa). Similar declines in CBDA in response to salinity were reported in literature (Formisano et al., 2024). Conversely, some authors indicated that CBDA decline in response to stress, distinguishing its behaviour from that of CBD (Rezghiyan et al., 2024). Yep et al. (2020) reported a rise in CBD under controlled salt stress, which is attributed to enhanced decarboxylation induced by the drying effect associated with osmotic stress and increased light radiation. Caplan et al. (2019) reported a 13 % and 67 % increase in CBDA and CBD concentrations, respectively, through the application of a controlled water stress (-1.5 MPa) at a specific stage of the flowering phase. Lastly, Maravaneh and Davarpanah, (2022) in their research gave interesting insights into the biosynthesis of Transcriptional factors (TF) induced by drought stress.

Photosynthesis is an essential process for energy generation, therefore any disruption to its components can significantly impact plant growth and survival (Pavlovic et al., 2014). Abiotic stress in plants affects the photosystem II (PSII) complex by impairing its function on both the acceptor side (QA) and the donor side (OEC), leading also to the destruction of chlorophyll pigments due to the accumulation of toxic ions. These alterations can be evaluated through chlorophyll fluorescence analysis. Overall, assessing the integrity of the photosynthetic apparatus, particularly the thylakoid membrane, provides a rapid and accurate method for detecting and quantifying plant tolerance to abiotic stresses. In our study, both water deficiency and salinity appeared to cause an increase in the levels of chlorophyll, in particular at a low irrigation rate (30 % ETc) and high level of salinity (−0.4 MPa). This could be an adaptive strategy of plants to maintain or increase photosynthesis, compensating for stressors. Some halophytic or salinity-tolerant plants, such as *Salicornia brachiata* and *Spartina alterniflora* (Siddiqui et al., 2022; Chen et al., 2024) can maintain or even increase the levels of chlorophyll under salt stress as an adaptive mechanism. However, contrary to our findings, other studies on hemp reported that salt stress typically reduces chlorophyll production to limit photosynthetic activity, which becomes less efficient under stress (Yep et al., 2020). The authors reported that an even below −0.2 MPa salinity decreased the plant photosynthetic capacity, resulting in a linear reduction in dry biomass of inflorescences due to lower carbon assimilation and reduced leaf-level gas exchange. Stress also damages thylakoid lipids (Zhang et al., 2018), adversely affecting photosynthetic efficiency and chlorophyll content, leading to slower plant growth rates. Osmotic stress further hampers water absorption, which negatively

impacts photosynthetic parameters, as observed in crops like tomatoes, where damages on photosynthetic enzymes reduced the efficiency of photosystem II (Lovelli et al., 2012). In glycophytic plants, such as hemp, salt ions often accumulate in leaves due to transpiration, exacerbating stress. Shaheen et al. (2013) observed that low NaCl concentrations (50 mM) decreased leaf potassium ($K^+$) and magnesium ($Mg^{2+}$) while increasing sodium ($Na^+$). This ionic imbalance hinders chlorophyll production, as magnesium is crucial for its synthesis. Nutrient supply, *e.g.*, with potassium, may help alleviate salinity stress and mitigate its impact on photosynthesis.

Fluorescence measurements revealed a good capacity of hemp for adaptation under limited water availability. Slight reductions of fluorescence even under strong water limitation (30 % ETc), indicate that hemp maintained a satisfactory level of photosynthetic activity to cope with water scarcity. A similar result was observed at a mild level of salinity (−0.2 MPa), but at the highest level (−0.4 MPa) fluorescence dropped sharply, revealing likely damage to the photosynthesis system. Indeed, as reported by Zuo et al. (2024) during the growth cycle, salt accumulation can compromise membrane permeability and disrupt thylakoid function, leading to reduced chlorophyll levels and fluorescence. In this regard, hemp appears to be tolerant to mild salinity but exhibits sensitivity at higher levels (−0.4 MPa). A further decline in fluorescence observed later in the growth cycle (at 24 DAT) under the highest salinity conditions suggests that a permanent damage may have occurred to the chloroplast structure or photosynthetic membrane function (Hameed et al., 2021). Ultimately, the accumulation of flavonoids in hemp under water limitation and salinity, likely due to the dual osmotic and ionic challenges requiring stronger defence mechanisms, suggested their protective role against abiotic stress, as also suggested by Yuan et al. (2024). Flavonoids serve as antioxidants, helping cells counteract oxidative stress, which is heightened under adverse conditions (Islam et al., 2021).

## 5. Conclusions

The results from this study indicated that hemp exhibited a considerable resistance to water scarcity, making it a valuable crop in arid environments. This resilience to limited water availability makes this crop a good candidate in areas of water scarcity. However, hemp may face significant challenges when it growths in saline soils or it is irrigated with saline water, as revealed by the results from this study. Thus, when exposed to these last conditions, hemp may lose its potential as a sustainable agricultural option. To ensure successful cultivation, it is vital to implement effective management strategies, such as selecting salt-tolerant varieties. It is important to emphasize that these conclusions are based on a single hemp cultivar, and the responses to water and salt stress may vary across different genotypes. Thus, further investigations are recommended to other cultivars of hemp, to strengthen the current findings.

## CRediT authorship contribution statement

**Valeria Cafaro:** Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Laura Siracusa:** Writing – original draft, Investigation. **Luana Pulvirenti:** Writing – original draft, Investigation. **Giorgio Testa:** Writing – review & editing, Validation, Software. **Antonella Iurato:** Visualization, Software. **Salvatore L. Cosentino:** Writing – review & editing, Supervision, Funding acquisition. **Cristina Patanè:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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## 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.

## Data availability

Data will be made available on request.

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