



Article

Hydromulching Enhances the Growth of Artichoke (*Cynara cardunculus* var. *scolymus*) Plants Subjected to Drought Stress through Hormonal Regulation of Source–Sink Relationships

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Abstract: Mulching the soil with organic-based formulations (hydromulching) is a sustainable alternative to plastic mulching that is here hypothesized to maintain crop production under drought stress by hormonal and metabolic regulation of source–sink relationships. To test this hypothesis, artichoke plants were grown on non-mulched soil and on soil mulched with polyethylene and three different organic mixtures, and subjected to optimal and reduced irrigation regimes. Under drought stress, the growth parameters were higher in plants grown with the different mulching treatments compared to non-mulched plants, which was related to a higher photosynthetic rate and water-use efficiency. Importantly, mulching-associated growth improvement under stress was explained by higher sucrolytic activity in the leaves that was accompanied by a decline in the active cytokinins. Besides this, salicylic acid decreased in the leaves, and abscisic acid and the ethylene precursor 1-aminocyclopropane-1-carboxylic acid were impaired in the artichoke heads, which is associated with better regulation of photoassimilate partitioning. Taken together, these results help to explain the hydromulching-associated growth improvement of artichokes under water stress through the hormonal regulation of sucrose metabolism, which could be very useful in future breeding programs for drought tolerance.

Keywords: hydromulching; artichoke; water stress; source-sink relationships; sucrolytic activity; plant hormones



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1. Introduction

The reduction in freshwater resources in arid and semiarid areas is one of the main constraining factors that affect both growth and crop productivity. Climate change might exacerbate this situation due to the increase in drought conditions and hydroclimatic variability, especially in the Mediterranean basin [1,2]. Some crop species are especially susceptible to drought stress, such as artichoke, due to their high transpiration rate, which limits photosynthesis, and other metabolic processes that reduce crop yield and quality [3,4]. Different agronomic strategies have been developed to cope with drought stress in order to improve crop productivity [5,6]. The use of plastic mulching in horticultural crops is a very common practice to compensate for the scarcity of water resources [6]. Mulching with polyethylene films reduces crop-field evaporation, thus improving water-use efficiency and productivity to maintain the food supply. However, the intensive use of plastic mulching in agriculture has provoked significant environmental problems through the generation of enormous amounts of non-degradable and difficult-to-recycle wastes, along with microplastic residues [7]. Therefore, research needs to focus on the search for sustainable and

environmentally friendly alternatives to plastic films that guarantee both crop production and quality. In this regard, hydromulching, which is based on liquid formulations from vegetable residues, is an innovative and organic mulching technology for preventing water evaporation from the soil and increasing crop productivity due to its intrinsic characteristics [8–10]. The effect of organic and living mulches on soil quality characteristics and the growth of horticultural crops has been shown in several studies (reviewed in [7]). The economic viability of hydromulching [10] as well as its effectiveness in the improvement of the growth and productivity of escarole under water stress [11] have been recently stated. Even though it has been proven that the regulation of the hormonal balance plays a key role in controlling growth responses under water stress associated with the use of hydromulching [11], the physiological mechanism that explains the maintenance of the activity of source leaves and sink organs need to be elucidated.

Source and sink relationships are highly sensitive to environmental changes and notably susceptible to drought conditions [12]. Under water stress, the competition for carbon between different physiological processes and sink organs deeply affects plant growth and crop yield [13–15]. The depletion of crop yield is caused by first decreasing growth and the number of assimilate-consuming sink organs, and then by reducing assimilate production in photosynthetically active source tissues [16–18]. Invertases are key enzymes for energy supply to sink organs that catalyze the cleavage of the glycosidic bond of sucrose (reviewed in [19]), and have been found to play important roles in biotic and abiotic stress responses, especially cell-wall invertase [15,20]. Indeed, several studies have reported that, under water stress, differences in carbohydrate accumulation were correlated with differences in sugar profiles, the expression of invertase genes, and levels of fructan biosynthesis (reviewed in [21]).

The hormonal regulation of sucrose metabolism is currently attracting much attention because of its practical implications for crop physiology and productivity [22,23]. In this regard, several studies have demonstrated the hormonal control of plant growth through the regulation of sink strength and photoassimilate partitioning. For example, a direct interaction has been shown between plant hormones in sink-related processes and their effects on invertase gene expression [23]. Trouverie et al. [24] observed a strong correlation of vacuolar invertase activity with xylem sap abscisic acid (ABA) concentrations that induce stomatal closure in maize plants to reduce transpiration under water deficit. Furthermore, studies performed on rice and wheat have stated that the overexpression of ABA biosynthesis and signaling regulators augmented source and sink capacity, thus maintaining photosynthetic efficiency and improving yield and drought tolerance [12,23,25]. Importantly, Albacete et al. [26] discovered an integrated mechanism of dehydration avoidance in tomato plants overexpressing the cell-wall invertase gene *CIN1* through hormonal and stress-signal regulation. These authors found that drought resistance was associated with the increase in the senescence-delaying hormones cytokinins (CKs) and the depletion of the senescence-inducing ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC). Besides this, the expression of the genes *CIN1* in the fruit or *IPT*, key in CK biosynthesis, in the root recovered tomato yield under osmotic stress through the enhancement of sucrolytic activities and CK concentration and the reduction in ACC levels in the reproductive tissues [27]. Overall, integrating metabolic, hormonal, and stress signals provides a novel strategy to overcome drought-induced limitations to crop yield. Therefore, we hypothesized that hydromulching-mediated improvement of artichoke growth and yield under water limitations is associated with the hormonal regulation of source–sink relationships.

2. Materials and Methods

2.1. Plant Material and Experimental Design

The experimental site was situated in Murcia, southeastern Spain (latitude: 37°45' N; longitude: 0°59' W). The mean annual temperature and precipitation are 19.5 °C and 216 mm, respectively. Most of the precipitation occurs between September and December.

The soil in which the experiment was performed is classified as Haplic Calcisol. Artichoke seed-grown plants (*Cynara cardunculus* var. *scolymus* L.) cv. Symphony (Nunhens-BASF) were cultivated in the field with a crop density of 0.5 plants per m². Three randomized cultivation blocks with 10 plants per treatment were established. The hydromulching treatments consisted of three ecological formulations, composed of a common mixture of three additives, recycled paper pulp, powdered gypsum, and kraft pulp from *Pinus radiata*, plus a specific crop residue: wheat straw (WS), rice hulls (RH), and a substrate used for mushroom cultivation (MS). Hydromulches were applied as a liquid heterogeneous paste that became a solid layer of 2 cm due to water evaporation after 2–3 days. Two control treatments were established: the first control consisted of low-density transparent polyethylene (PE) and the second consisted of bare soil without any mulching cover (BS). The irrigation consisted of a standard Hoagland solution that was applied by an underground drip irrigation system at a depth of 5 cm, with emitters of 4 L·h^{−1}. Two weeks after transplanting, the plants were separated into two homogenous groups and grown under two water regimes (WR): well-watered (control), where plants were irrigated to field capacity, and low-watered (water stress), where plants received 70% of the volume of water necessary to saturate the soil. Soil moisture was monitored at a depth of 15 cm during the whole experimental period using ECH₂O moisture sensors (Decagon Devices, Pullman, WA, USA).

2.2. Plant-Growth- and Water-Related Parameters

Plant-growth-related parameters (plant height, plant diameter, number of leaves, and edible part fresh weight) were recorded at the end of the experiment in 5 plants per irrigation and mulching treatment. Plant height and plant diameter were determined with a measuring tape. Two water-related parameters were also measured: osmotic potential (Ψ_s) and relative water content (RWC). Ψ_s was analyzed in leaf extracts with an osmometer (model Vapro 5520, Wescor Inc., South Logan, UT, USA). The RWC was measured using leaf discs of 1 cm² and calculated according to the following equation:

$$RWC = \left[\frac{FW - DW}{TW - DW} \right] \cdot 100$$

where FW is the fresh weight recorded during collection, TW is the turgid weight, and DW is the oven-dry weight (60 °C until constant weight). To determine TW, disc leaves were kept in distilled water in darkness at 4 °C to minimize respiration losses until they reached a constant weight (full turgor), typically after 24 h.

2.3. Leaf Gas Exchange

Gas exchange was monitored in fully expanded leaves at the plant vegetative stage. Measurements were carried out after starting the hydric stress condition. Net CO₂ fixation rate (A_{max} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance to water vapor (g_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), and transpiration rate (E , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were measured in a steady state under conditions of saturating light (800 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and 400 ppm CO₂ with a LI-6400 equipment (LI-COR, Lincoln, NE, USA). The intrinsic water-use efficiency (WUEi) was calculated from the gas exchange data as A_{max}/E .

2.4. Chlorophyll Concentrations

Chlorophylls were extracted from 1 g of frozen artichoke leaves (−80 °C) with 25 mL of acetone solvent. Samples were homogenized and centrifuged at 5000 × g for 6 min and 4 °C. Subsequently, the optical density of the supernatant was measured spectrophotometrically at wavelengths of 663 and 645 nm. The analysis was carried out in four replicates. The contents of chlorophyll a and b were calculated according to the Nagata and Yamashita equations [28]:

$$\text{Chlorophyll a (mg} \cdot 100 \text{ mL}^{-1}) = 0.999 \cdot A_{663} - 0.0989 \cdot A_{645}$$

$$\text{Chlorophyll b (mg} \cdot 100 \text{ mL}^{-1}) = -0.328 \cdot A_{663} + 1.77 \cdot A_{645}$$

2.5. Leaf Mineral Content

The youngest fully-sized leaves of each plant were freeze-dried for 72 h at -55°C (Christ Alpha 1-2 LDplus, Osterode am Harz, Germany). Anions were extracted with bidistilled water and were subsequently measured with an ion chromatograph (METROHM 861 Advanced Compact IC; Metrohm, Herisau, Switzerland), using a METROHM Metrosep CARB1 150/4.0 mm column. The cations were extracted from freeze-dried leaves (0.1 g) by acid digestion, using an ETHOSONE microwave digestion system (Milestone Inc., Shelton, CT, USA) and analyzed by inductively-coupled plasma optical emission spectrometry (ICP-OES, Varian Vista MPX, Palo Alto, CA, USA). The total nitrogen was analyzed in freeze-dried leaves using a combustion nitrogen determinator (LECO FP-528, Leco Corp., St. Joseph, MI, USA).

2.6. Sugar Content

The concentrations of sugars (glucose, fructose, and sucrose) were determined using the methodology described by Albacete et al. [26] with some modifications. Briefly, 1 mL of extraction buffer (methanol/water, 80/20, *v/v*) was added to 50 mg of previously freeze-dried and ground sample. The samples were homogenized and incubated at 4°C for 30 min, with shaking. After incubation, they were centrifuged at $20,000 \times g$ and 4°C for 15 min. The supernatant was passed through C18 solid-phase extraction columns (C18 Sep-Pak, Waters, Milford, MA, USA) to remove interfering macromolecules. The analysis was carried out by ion chromatography using an 817 Bioscan (Metrohm, Herisau, Switzerland) system equipped with a pulsed amperometric detector (PAD) and a gold electrode. The column used was a METROHM Metrosep Carb 1-150 IC column (4.6×250 mm), which was heated to 32°C .

2.7. Sucrolytic Activities

Sucrolytic activities were assayed by determining the NADH delivered in a coupled enzymatic reaction using specific substrates/enzymes depending on the target enzyme, based on the protocol described by Balibrea et al. [29] with some modifications. Briefly, 50 mg of freeze-dried ground sample were resuspended in 1 mL homogenization buffer (200 mM HEPES, 3 mM MgCl_2 , 1 mM EDTA, 2% glycerol, 0.1 mM PMSF, 1 mM benzamidine). The homogenate was mixed for 20 min at 4°C and centrifuged for 15 min at $10,500 \times g$ and 4°C . The supernatant was used for soluble invertase activity determination. The pellet was used for cell-wall invertase activity preparation by washing the insoluble extract three times with bidistilled water and re-suspending it in 200 mM HEPES, 3 mM MgCl_2 , 15 mM EDTA, 2% glycerol, 0.1 mM PMSF, 1 mM benzamidine, and 1 M NaCl. The NADH released in the micro-assays was determined spectrophotometrically at a wavelength of 340 nm. The proteins were analyzed with Bradford reagent using BSA as standard and also determined spectrophotometrically at a wavelength of 595 nm. The sucrolytic activities were determined as the sum of the soluble invertase activity and cell-wall invertase activity and expressed on a protein-content basis.

2.8. Hormone Extraction and Analysis

Cytokinins (*trans*-zeatin, tZ, zeatin riboside, ZR, and isopentenyl adenine, iP), gibberellins (GA1, GA3, and GA4), indole-3-acetic acid (IAA), abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) were analyzed according to Albacete et al. [26] and Großkinsky et al. [30] with some modifications. Briefly, 50 mg of freeze-dried samples were extracted using a methanolic buffer and Sep-Pak Plus C18 cartridges (SepPak Plus, Waters, Milford, MA, USA). The filtered extracts were analyzed in a U-HPLC-HRMS system (Accela-Exactive, ThermoFisher Scientific, Waltham, MA, USA).

2.9. Statistical Analyses

The data were tested first for homogeneity of variance and normality of distribution. The significance of the treatment effects was determined by analysis of variance (ANOVA). The significance ($p < 0.05$) of the differences between mean values was tested by Tukey's honest significant difference (HSD). Principal component analyses (PCA) and heat maps were also performed to evaluate general patterns. The Varimax rotation method was used for loading-PCA while score-PCA was graphically plotted as a Bi-Plot score. All statistical analyses were performed using the SPSS software (version 25.0, Chicago, IL, USA).

3. Results

3.1. Growth- and Water-Related Parameters

The mulching treatment increased the number of leaves under both control and drought-stress conditions. This increment was particularly important in plants hydromulched with MS and WS under water-stress conditions (by 65% with respect to BS, Table 1). Plant height also increased in all mulching treatments under both control and water-stress conditions. Plants grown in soils covered with PE and MS presented the greatest plant height under water stress (by 70% higher than BS). The same trend was observed under drought conditions for plant diameter, with PE- and MS-treated plants presenting the highest diameter (Table 1). Finally, the fresh weight (FW) of the globe artichoke edible part also improved in all mulching treatments under well- and little-watered regimes, presenting RH- and WS-treated plants the highest FW under drought stress (superior by 30% to BS plants).

Table 1. Osmotic potential (Ψ_s), relative water content (RWC), and the growth-related parameters, number of leaves, plant height, plant diameter, and fresh weight (FW) of edible part measured in artichoke plants (cv. Symphony) cultivated under different mulching and irrigation conditions.

Irrigation Regime	Mulch	Ψ_s (MPa)	RWC (%)	Leaf Number	Plant Height (cm)	Plant Diameter (cm)	Edible Part FW (g)
Control	BS	-1.57 ± 0.05 Aa	87.25 ± 0.55 Aa	47.40 ± 4.34 Ac	95.20 ± 1.89 Ab	212.60 ± 3.54 Ab	57.55 ± 2.42 Ab
	PE	-1.59 ± 0.07 Aa	91.00 ± 2.59 Aa	74.40 ± 7.42 Ab	116.80 ± 3.37 Aa	251.00 ± 6.89 Aa	73.48 ± 5.93 Aa
	MS	-1.40 ± 0.09 Aa	87.52 ± 0.44 Aa	85.00 ± 1.93 Aab	122.20 ± 2.63 Aa	267.80 ± 3.60 Aa	67.91 ± 1.89 Aab
	RH	-1.57 ± 0.05 Aa	88.15 ± 1.47 Aa	69.00 ± 3.35 Abc	115.80 ± 1.76 Aa	251.80 ± 6.47 Aa	66.29 ± 2.69 Aab
	WS	-1.39 ± 0.09 Aa	87.35 ± 2.19 Aa	87.75 ± 4.13 Aa	124.75 ± 4.21 Aa	258.00 ± 5.18 Aa	66.34 ± 3.47 Aab
Water stress	BS	-1.76 ± 0.08 Aa	85.17 ± 1.07 Aa	42.20 ± 2.60 Ab	73.40 ± 1.93 Ab	212.00 ± 8.56 Ab	47.95 ± 7.84 Ab
	PE	-1.60 ± 0.03 Aa	85.26 ± 0.60 Aa	69.20 ± 1.96 Ba	126.40 ± 3.37 Aa	251.60 ± 4.37 Aa	59.57 ± 2.51 Aab
	MS	-1.77 ± 0.04 Ba	82.91 ± 0.66 Aa	69.00 ± 4.43 Ba	125.60 ± 2.93 Aa	254.40 ± 4.63 Aa	59.22 ± 0.52 Bab
	RH	-1.70 ± 0.04 Aa	84.12 ± 0.86 Aa	59.40 ± 3.57 Ba	118.20 ± 2.75 Aa	250.80 ± 5.62 Aa	60.24 ± 1.80 Aab
	WS	-1.67 ± 0.12 Aa	84.10 ± 0.63 Aa	70.67 ± 2.35 Aa	117.33 ± 3.30 Ba	271.17 ± 4.50 Aa	63.67 ± 3.91 Aa

Within a column, the different capital letters indicate significant differences due to the irrigation treatment, while the different small letters indicate significant differences among the mulching treatments for the same irrigation regime ($p \leq 0.05$, HSD Tukey test). Abbreviations used: bare soil (BS), polyethylene (PE), mushroom substrate (MS), rice husk (RH), and wheat straw (WS).

Surprisingly, water-related parameters were not affected, in general, by the mulching or water-stress treatments (Table 1). Indeed, although the osmotic potential increased with drought in all mulching treatments, it was significant only in MS-mulched plants. Furthermore, the relative water content decreased with drought, but this reduction was not significant, neither for the drought treatment nor for the mulching treatment (Table 1).

3.2. Leaf Gas Exchange Measurements

In general, all leaf gas-exchange-related parameters were affected by the drought stress and/or the use of different mulching formulations (Figure 1). Under control conditions, mulched plants had higher photosynthesis, measured as net CO_2 assimilation, than plants grown in BS (Figure 1a). Water depletion strongly decreased photosynthesis, but PE-, MS-, and RH-treated plants were able to maintain levels significantly higher than non-covered plants (by 50%). Stomatal conductance did not significantly vary among mulching treatments under either control or water-stress conditions, whereas the water stress reduced

stomatal conductance significantly in all mulching treatments, except for PE (Figure 1b). Regarding the transpiration rate, it was significantly reduced in MS- and RH-covered plants under control and water-stress conditions, respectively, compared to non-covered plants (Figure 1c). However, no significant effect of the water shortage on transpiration rate was observed in any mulching treatment, except for WS treatment. Importantly, intrinsic WUEi, calculated as the ratio between photosynthetic and transpiration rates, significantly increased in all mulching treatments with respect to BS under control conditions (by 30% on average, Figure 1d). Although water stress reduced WUEi significantly in all mulching treatments, it was maintained at a significantly higher level in PE-, MS-, and RH-covered plants compared to plants grown on BS (by 60% on average).

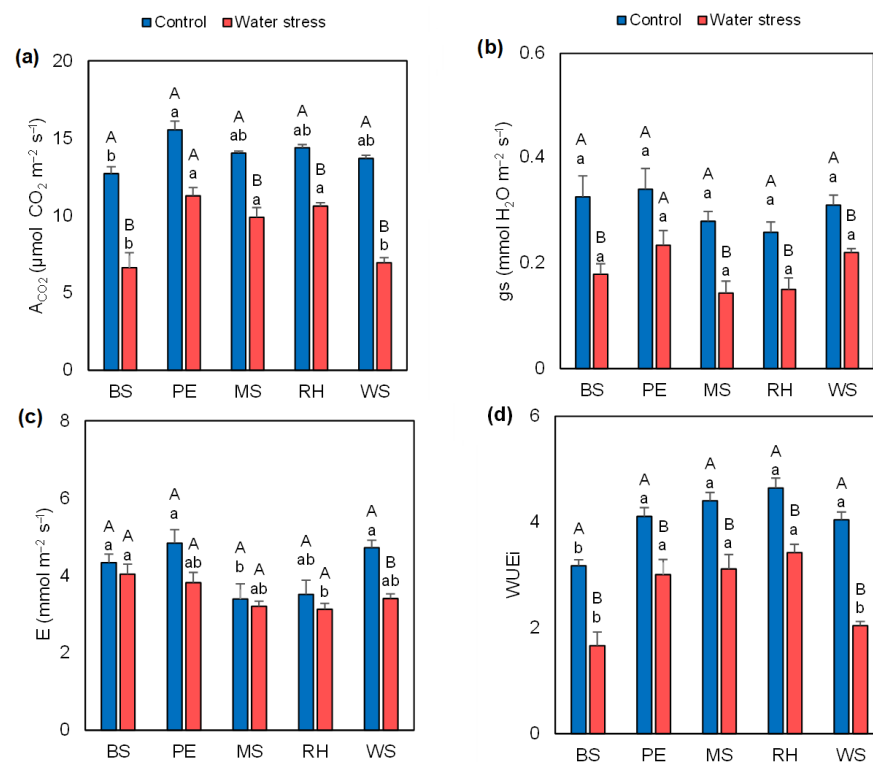


Figure 1. (a) Net CO₂ fixation rate (A_{max}), (b) stomatal conductance (g_s), (c) transpiration rate (E), and (d) water-use efficiency (WUE_i) in artichoke plants of the commercial Symphony variety non-mulched or subjected to different mulching treatments and cultivated under control (well-watered) and water-stress (70% ETC) conditions. Bars show the means of five plants \pm standard error. Different capital letters indicate significant differences due to the water-stress treatment, while different small letters show significant differences among mulching treatments according to Tukey's test ($p \leq 0.05$). Abbreviations used: bare soil (BS), polyethylene mulch (PE), mushroom-substrate-based hydromulch (MS), rice-hull-based hydromulch (RH), and wheat-straw-based hydromulch (WS).

3.3. Chlorophyll Content

The concentrations of chlorophyll a were not significantly affected by either the mulching treatment or the drought stress (Table 2). Even though chlorophyll b was not significantly affected by the use of mulch under control conditions, non-mulched plants showed the lowest concentration of chlorophyll b. Moreover, the water depletion caused a marked decrease in chlorophyll b, which was significant in plants grown under PE and RH treatments (Table 2). Therefore, total chlorophyll concentrations, calculated as the sum of chlorophyll a and chlorophyll b concentrations, were also reduced by drought in PE- and RH-covered plants. Notably, although no effect of the mulching treatment was observed in total chlorophyll concentrations under both control and water-stress conditions, mulched

plants presented higher total chlorophyll concentrations than non-mulched plants under the well-watered regime (Table 2).

Table 2. Chlorophyll content in leaves of artichoke plants (cv. Symphony) cultivated under different mulching and irrigation conditions.

Irrigation Regime	Mulch	Chlorophyll a (mg 100 mL ⁻¹ g ⁻¹ FW)	Chlorophyll b (mg 100 mL ⁻¹ g ⁻¹ FW)	Total Chlorophylls (mg 100 mL ⁻¹ g ⁻¹ FW)
Control	BS	2.18 ± 0.05 Aa	1.26 ± 0.11 Aa	3.43 ± 0.24 Aa
	PE	2.20 ± 0.03 Aa	1.59 ± 0.05 Aa	3.79 ± 0.03 Aa
	MS	2.23 ± 0.20 Aa	1.62 ± 0.22 Aa	3.85 ± 0.27 Aa
	RH	2.23 ± 0.04 Aa	1.73 ± 0.18 Aa	3.96 ± 0.19 Aa
	WS	2.24 ± 0.10 Aa	1.40 ± 0.09 Aa	3.64 ± 0.11 Aa
Stress	BS	2.08 ± 0.04 Aa	1.06 ± 0.11 Aa	3.14 ± 0.14 Aa
	PE	2.10 ± 0.03 Aa	1.14 ± 0.05 Ba	3.25 ± 0.07 Ba
	MS	1.97 ± 0.17 Aa	1.15 ± 0.22 Aa	3.12 ± 0.39 Aa
	RH	2.00 ± 0.05 Aa	0.88 ± 0.02 Ba	2.88 ± 0.05 Ba
	WS	2.16 ± 0.01 Aa	1.20 ± 0.09 Aa	3.36 ± 0.10 Aa

Within a column, the different capital letters indicate significant differences due to the irrigation treatment, while the different small letters indicate significant differences among the mulching treatments for the same irrigation regime ($p \leq 0.05$, HSD Tukey test). Abbreviations used: bare soil (BS), polyethylene (PE), mushroom substrate (MS), rice husk (RH) and wheat straw (WS).

3.4. Leaf Mineral Content

Table 3 exhibits the concentrations of mineral nutrients in artichoke leaves. Under control conditions, P concentrations presented significant differences among mulching treatments, being significantly higher in plants grown with MS treatment (Table 3). Mulching did not have any effect on total N, K, Mg, Ca, and SO_4^{2-} concentrations under control conditions; however, under drought conditions, mulched plants presented significantly higher K and SO_4^{2-} concentrations than non-mulched plants. Regarding micronutrients overall, the mulching treatment did not affect their concentrations. In contrast, drought stress increased Mn, B, and Na concentrations, while decreasing Zn concentrations, but, in general, these changes were not significant (Table 3).

3.5. Sugar Concentrations

Under control conditions, the concentrations of the hexoses, glucose and fructose, in the leaves were similar in all mulching treatments (Figure 2a). The water stress provoked an increase in leaf hexose concentrations, which were significant in PE-, MS-, and WS-covered plants, whereas no effect of the mulching treatment was observed under stress conditions. In contrast, water stress provoked a significant decrease in the hexose concentrations of artichoke heads (Figure 2b). Importantly, under water stress, the MS and RH hydromulching treatments significantly decreased the hexose concentrations of artichoke heads compared to the BS treatment (by 70%). Leaf sucrose concentrations were not affected by the mulching treatment under control conditions (Figure 2c). Drought stress provoked a significant reduction in leaf sucrose concentrations in all mulching treatments except for MS treatment. Indeed, MS-covered plants presented significantly higher leaf sucrose concentrations than non-covered plants under stress (by 55%, Figure 2c). In artichoke heads, despite sucrose increasing significantly with drought in all mulching treatments, hydromulched plants tended to decrease sucrose concentrations (Figure 2d).

3.6. Sucrolytic Activity

Under control conditions, the leaf sucrolytic activity in all mulching treatments was higher in comparison with BS (Figure 3a). Importantly, this augmentation was significant in plants grown with MS treatment, with a fourfold increase in comparison with BS treatment. Drought stress produced a significant increase in sucrolytic activity in artichoke leaves, except for MS treatment, which presented a non-significant reduction of 38% (Figure 3a). Concerning the artichoke heads, drought conditions did not affect sucrolytic

activity (Figure 3b). Notably, sucrolytic activity was significantly augmented in the MS-treated plants grown under both optimal and drought stress conditions (3.8- and 4.4-fold, respectively) in comparison with BS treatment.

Table 3. Mineral nutrient concentrations in leaves of artichoke plants (cv. Symphony) cultivated under different mulching and irrigation conditions.

Irrigation Regime	Mulch	N (mg g ⁻¹ DW)	P ⁵⁺ (mg g ⁻¹ DW)	K ⁺ (mg g ⁻¹ DW)	Mg ²⁺ (mg g ⁻¹ DW)	Ca ²⁺ (mg g ⁻¹ DW)	SO ₄ ²⁻ (mg g ⁻¹ DW)
Control	BS	22.73 Aa	1.51 Ab	23.29 Aa	1.68 Aa	31.26 Aa	3.84 Aa
	PE	21.98 Aa	1.75 Abc	28.03 Aa	1.44 Aa	30.48 Aa	7.11 Aa
	MS	22.82 Aa	2.72 Aa	30.57 Aa	1.45 Aa	25.47 Aa	5.51 Aa
	RH	22.91 Aa	1.87 Abc	26.84 Aa	1.35 Aa	30.12 Ba	6.46 Aa
	WS	22.04 Aa	1.65 Ac	24.63 Aa	1.44 Aa	28.16 Ba	6.83 Aa
Stress	BS	22.69 Aa	1.66 Ba	21.78 Aa	1.11 Ba	27.30 Ab	0.73 Bd
	PE	24.01 Aa	1.57 Aa	22.13 Aa	1.53 Aa	36.74 Aab	2.02 Bcd
	MS	23.78 Aa	1.26 Ba	27.36 Aa	1.27 Aa	29.71 Aab	6.34 Aa
	RH	23.03 Aa	1.46 Ba	20.90 Aa	1.62 Aa	38.76 Aa	4.66 Ab
	WS	23.28 Aa	1.50 Aa	24.78 Aa	1.32 Aa	38.47 Aa	2.89 Bc
Irrigation regime	Mulch	Cu ²⁺ (mg kg ⁻¹ DW)	Mn ²⁺ (mg kg ⁻¹ DW)	Zn ²⁺ (mg kg ⁻¹ DW)	B ³⁺ (mg kg ⁻¹ DW)	Na ⁺ (mg g ⁻¹ DW)	
Control	BS	2.26 Aa	56.36 Aa	16.40 Aa	60.99 Aa	7.99 Aa	
	PE	1.90 Aa	49.69 Aa	15.79 Aa	61.41 Ba	8.84 Aa	
	MS	2.05 Aa	46.10 Aa	16.31 Aa	67.30 Aa	7.96 Ba	
	RH	1.80 Aa	48.77 Ba	13.46 Aa	66.17 Aa	8.65 Aa	
	WS	2.35 Aa	47.23 Aa	23.73 Aa	60.36 Ba	9.14± Aa	
Water stress	BS	1.22 Bbc	56.44 Aa	11.94 Aab	73.59 Aa	10.87 Aa	
	PE	2.86 Aa	61.90 Aa	13.44 Aa	90.34 Aa	8.05 Aa	
	MS	1.55 Ab	51.40 Aa	8.62 Bb	78.38 Aa	9.96 Aa	
	RH	0.81 Bc	66.59 Aa	9.33 Ab	77.95 Aa	6.40 Ba	
	WS	3.15 Aa	61.05 Aa	10.68 Aab	98.85 Aa	8.10 Aa	

Within a column, the different capital letters indicate significant differences due to the irrigation treatment, while the different small letters indicate significant differences among the mulching treatments for the same irrigation regime ($p \leq 0.05$, HSD Tukey test). Abbreviations used: nitrogen (N), phosphate (P), potassium (K), magnesium (Mg), calcium (Ca), sulphate (SO₄²⁻), copper (Cu), manganese (Mn), zinc (Zn), boron (B), sodium (Na), bare soil (BS), polyethylene (PE), mushroom substrate (MS), rice husk (RH), and wheat straw (WS).

3.7. Hormone Profile

Three of the most active CKs in higher plants, tZ, ZR, and iP, were analyzed both in leaves and artichoke heads (Figure 4). Under control conditions, the concentration of tZ in the leaves was lower in the MS- and WS-covered plants than in non-covered plants (Figure 4a). Water stress provoked a significant increase in leaf tZ in all treatments except for RH-treated plants, but hydromulched plants maintained significantly reduced leaf tZ concentrations than the PE- and non-covered plants (lower by 50%). In the artichoke heads, water stress also provoked a significant increase in tZ but no differences were observed among mulching treatments either under control or water-stress conditions (Figure 4b). Regarding ZR, the mulching treatment did not affect leaf ZR concentrations under control conditions (Figure 4c). Water stress increased leaf ZR in PE- and non-covered plants, while decreasing its concentration in hydromulched plants. Indeed, leaf ZR concentrations were significantly lower in the hydromulched plants than in non-covered plants (lower by 40%, Figure 4c). However, the concentrations of ZR in the heads increased significantly with drought stress in all mulching treatments, while not being affected by mulching under either control or stress conditions (Figure 4d). The concentrations of iP in the leaves increased with water stress in all treatments, except for RH. Importantly, MS-covered plants presented the highest concentrations of this hormone under both control and water-stress conditions (Figure 4e). In the heads, iP concentrations also increased with drought but no significant differences were observed in the hydromulching treatments compared to BS (Figure 4f).

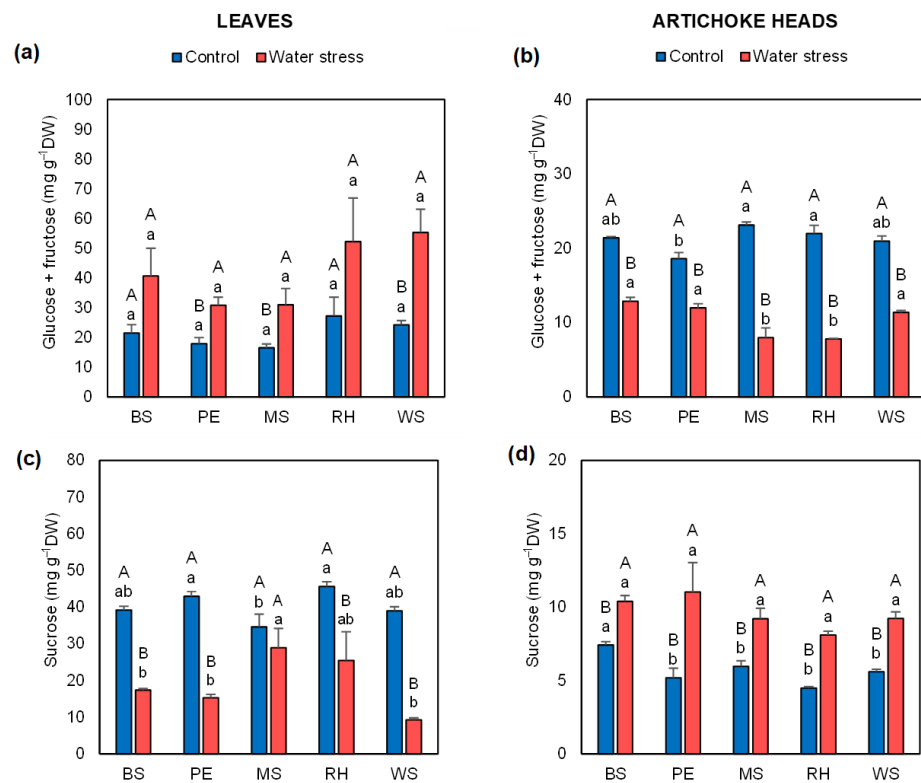


Figure 2. Hexose (glucose + fructose) concentrations in (a) leaves and (b) heads, and sucrose concentrations in (c) leaves and (d) heads of artichoke plants of the commercial Symphony variety non-mulched or subjected to different mulching treatments and cultivated under control (well-watered) and water-stress (70% ETc) conditions. Bars show the means of five plants \pm standard error. Different capital letters indicate significant differences due to the water-stress treatment, while different small letters show significant differences among mulching treatments according to Tukey's test ($p \leq 0.05$). Abbreviations used: bare soil (BS), polyethylene mulch (PE), mushroom-substrate-based hydromulch (MS), rice-hull-based hydromulch (RH), and wheat-straw-based hydromulch (WS).

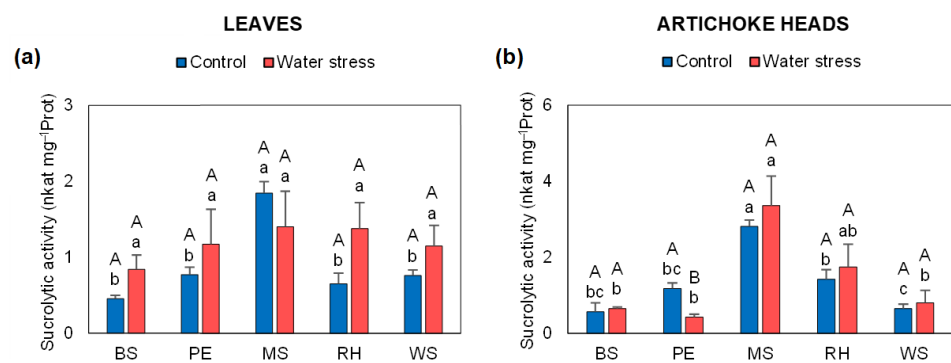


Figure 3. Sucrolytic activity in (a) leaves and (b) heads of artichoke plants of the commercial Symphony variety non-mulched or subjected to different mulching treatments and cultivated under control (well-watered) and water-stress (70% ETc) conditions. Bars show the means of five plants \pm standard error. Different capital letters indicate significant differences due to the water-stress treatment, while different small letters show significant differences among mulching treatments according to Tukey's test ($p \leq 0.05$). Abbreviations used: bare soil (BS), polyethylene mulch (PE), mushroom-substrate-based hydromulch (MS), rice-hull-based hydromulch (RH), and wheat-straw-based hydromulch (WS).

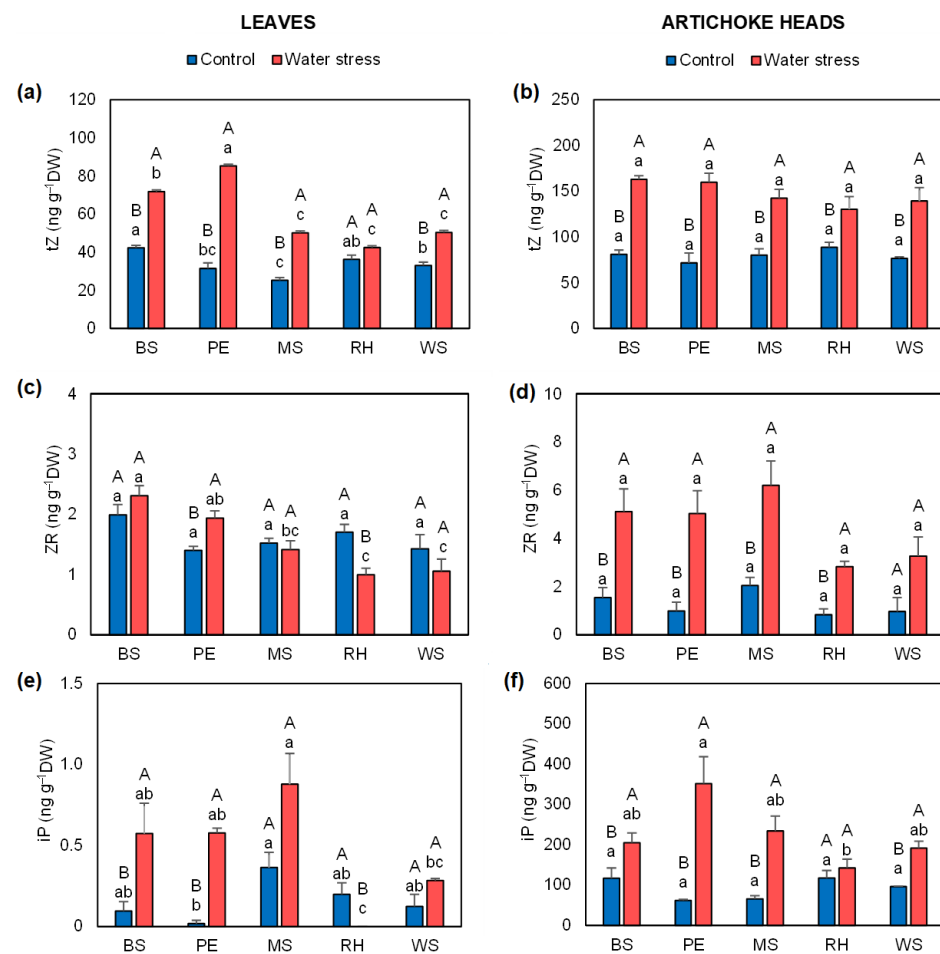


Figure 4. (a,b) Trans-zeatin (tZ), (c,d) zeatin riboside (ZR), and (e,f) isopentenyladenine (iP) in leaves and heads of artichoke plants of the commercial Symphony variety non-mulched or subjected to different mulching treatments and cultivated under control (well-watered) and water-stress (70% ETc) conditions. Bars show the means of five plants \pm standard error. Different capital letters indicate significant differences due to the water-stress treatment, while different small letters show significant differences among mulching treatments according to Tukey's test ($p \leq 0.05$). Abbreviations used: bare soil (BS), polyethylene mulch (PE), mushroom-substrate-based hydromulch (MS), rice-hull-based hydromulch (RH), and wheat-straw-based hydromulch (WS).

Concerning GAs, only GA4 was detected in leaves and heads. Its concentrations in the leaves increased significantly with drought, while no effect of the mulching treatment was observed under either control or stress conditions (Figure 5a). In contrast, in the heads, GA4 concentrations were depleted with water stress, and a tendency to increase in the hydromulched plants was observed under non-stressed conditions (Figure 5b). The concentrations of the active auxin, IAA, were extremely low in the leaves of artichoke plants, and only non-covered plants and especially MS-covered plants under stress showed apparent values (Figure 5c). However, in the heads, IAA concentrations were higher, but the mulching treatment did not affect its concentrations under either control or water stress (Figure 5d). The classical abiotic stress-related hormone, ABA, significantly increased in the leaves of water-stressed plants (Figure 5e). While no differences among mulching treatments were observed in leaf ABA under control conditions, MS-covered plants presented the highest ABA concentrations under stress. In the heads, ABA also increased with drought (Figure 5f). Interestingly, although the hydromulching treatment did not affect ABA concentrations under control conditions, the three hydromulching treatments significantly reduced ABA concentrations in the artichoke heads under water stress (Figure 5f). The ethylene precursor ACC presented erratic leaf concentrations, being only detected in MS- and non-covered

concentrations under control conditions and in RH-covered plants under the two water regimes studied (Figure 5g). Importantly, in the heads, ACC concentrations were higher in all mulching treatments compared to BS under control conditions, while water stress provoked a significant reduction in ACC in the heads of covered plants but a significant increment in the non-covered plants (Figure 5h). Indeed, ACC concentrations in the heads of mulched plants under water stress were significantly lower than those of non-covered plants (lower by 75%). The concentrations of JA in the leaves decreased significantly with drought in all mulching treatments, except for WS (Figure 5i). Interestingly, MS-covered plants presented the highest and lowest leaf JA concentrations under control and water stress, respectively. In the heads, JA concentrations also decreased with drought, and hydromulched plants presented significantly higher JA levels than non-covered plants (by 20%) under stress conditions (Figure 5j). Regarding SA, its concentrations in the leaves increased with water stress, especially in PE- and non-covered plants (Figure 5k). In fact, hydromulched plants registered significantly lower leaf SA concentrations than non-covered plants under drought conditions, with MS-plants showing the lowest concentrations (75% lower than BS). In the artichoke heads, drought provoked a significant reduction in SA, but the mulching treatment did not affect its concentration under either control or water-stress conditions (Figure 5l).

To have a general view of the changes in the hormonal balance in both leaf (source) and artichoke head (sink) tissues associated with (hydro)mulching and water stress, a cluster heat plot showing log changes compared to BS was performed (Figure S1). In the leaves, the CKs, tZ and ZR, and SA presented a marked downregulation in all mulching treatments, especially under water stress. Regarding artichoke heads, a notable depletion of ACC occurred under water stress in all mulching treatments. Besides this, ABA, IAA, and tZ decreased with drought in the three hydromulching treatments in comparison to the non-covered plants (Figure S1).

3.8. Principal Component Analysis

First, we performed a score-PCA that represents the dispersion around two principal components (PCs) by plotting the scores of the transformed coordinates of four biological replicates for each mulching treatment under well-watered and drought-stress conditions (Figure 6a). The score-PCA clearly separated plants grown under control conditions from plants subjected to water stress (Figure 6a). Importantly, the four biological replicates of each mulching and BS treatment were grouped separately, with the BS plants showing the highest separation, particularly under stress conditions.

A loading-PCA was then constructed to identify important parameters associated with the variability factors used in this study, mulching and drought stress, in relation to the growth and physiological responses of artichoke plants (Figure 6b,c). The loading-PCA uses an orthogonal transformation to convert the evaluated physiological parameters with high autocorrelation into a set of values of linearly uncorrelated variables, the PCs. Under optimal watering conditions, the mulching treatment grouped the growth-related parameters with WUEi and chlorophyll content, and with important hormonal (JA in leaf, and GA4 and ACC in artichoke head) and metabolic (sucrolytic activity in leaf and artichoke head) parameters (Figure 6b). In an opposite cluster associated other gas exchange (stomatal conductance and transpiration rate), hormonal (tZ, ZR, GA4, and SA in leaf, and iP, ABA, and JA in artichoke head), and sucrose metabolism (sucrose in leaf) parameters (Figure 6b). Importantly, the mulching treatment under drought stress grouped the growth-related parameters with WUEi and photosynthetic rate, and with hormonal (JA in artichoke head) and metabolic (sucrolytic activity in leaf and artichoke head) parameters (Figure 6c). In contrast, most hormonal (tZ, iP, ZR, and ABA in leaf, and tZ, ZR, iP, IAA, ABA, SA, and ACC in artichoke head) and sucrose metabolism (sucrose in artichoke head) parameters associated in an opposite cluster to the growth parameters (Figure 6c).

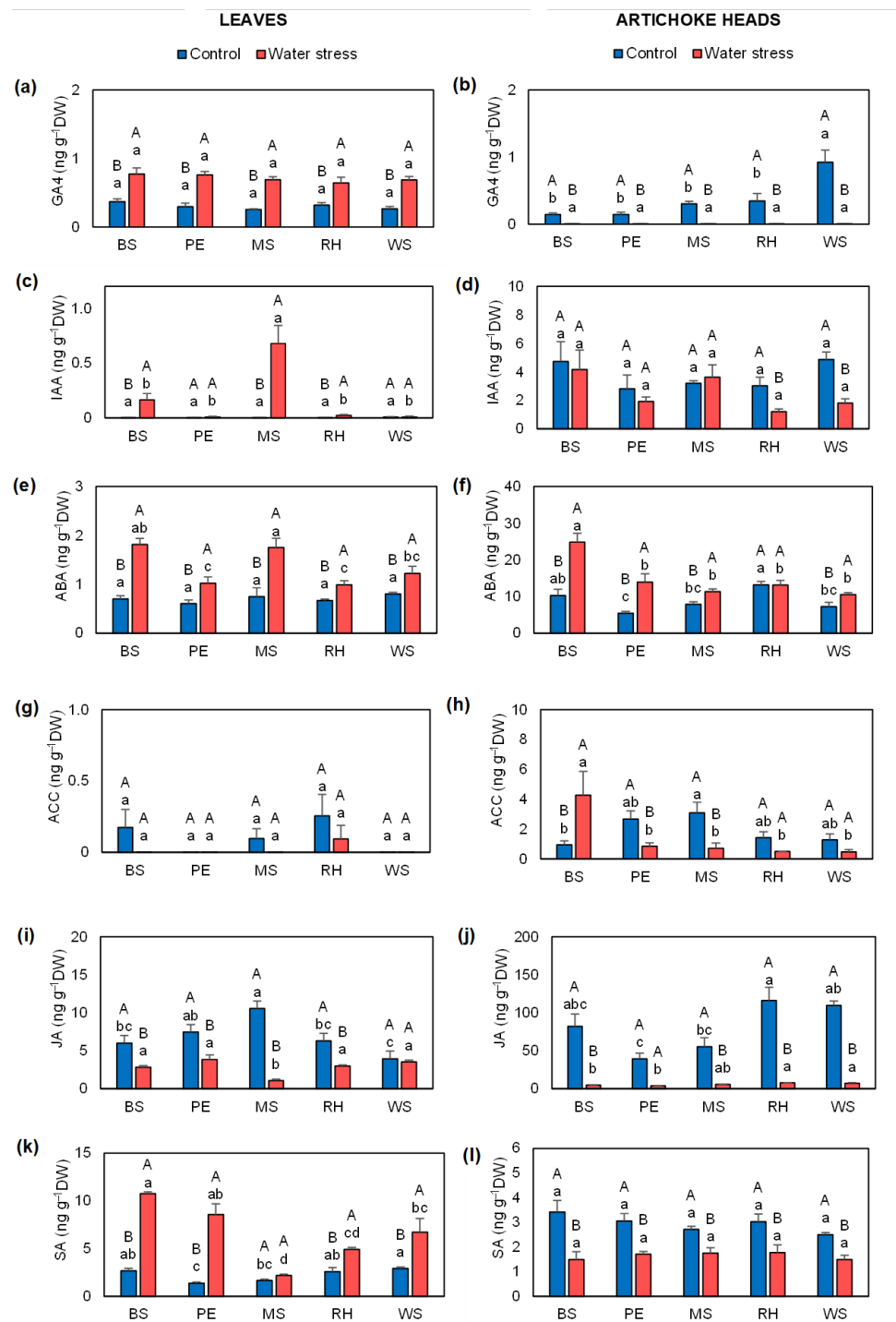


Figure 5. (a,b) Gibberellin A4 (GA4), (c,d) indoleacetic acid (IAA), (e,f) abscisic acid (ABA), (g,h) 1-aminocyclopropane-1-carboxylic acid (ACC), (i,j) jasmonic acid (JA) and (k,l) salicylic acid (SA) in leaves and heads of artichoke plants of the commercial Symphony variety non-mulched or subjected to different mulching treatments and cultivated under control (well-watered) and water-stress (70% ETc) conditions. Bars show the means of five plants \pm standard error. Different capital letters indicate significant differences due to the water-stress treatment, while different small letters show significant differences among mulching treatments according to Tukey's test ($p \leq 0.05$). Abbreviations used: bare soil (BS), polyethylene mulch (PE), mushroom-substrate-based hydromulch (MS), rice-hull-based hydromulch (RH), and wheat-straw-based hydromulch (WS).

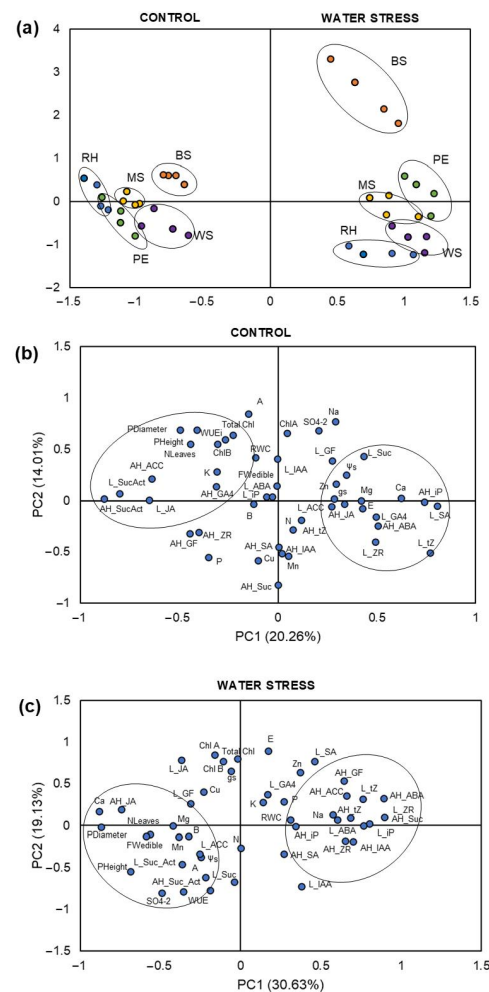


Figure 6. (a) Bi-plot representing the score values and (b,c) two axes of a principal component (PC1, PC2) analysis showing the loadings of various growth-related, ionic, sucrose metabolism, and hormonal variables (denoted by abbreviations) of artichoke plants of the commercial Symphony variety non-mulched or subjected to different mulching treatments and cultivated under control (well-watered) and water-stress (70% ETc) conditions. Circles enclose those variables/scores which cluster together in score-PCA and loading-PCA. Abbreviations used: boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), phosphorus (P), chloride (Cl^-), sulfate (SO_4^{2-}), plant height (PHeight), plant diameter (PDiameter), number of leaves (NLeaves), edible part fresh weight (FWedible), chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophylls (Total Chl), net CO_2 fixation rate (A), stomatal conductance (gs), transpiration rate (E), intrinsic water-use efficiency (WUEi), osmotic potential (Ψ_s), relative water content (RWC), leaf glucose and fructose (L_GF), leaf sucrose (L_Suc), artichoke head glucose and fructose (AH_GF), artichoke head sucrose (AH_Suc), leaf sucrolytic activity (L_SucAct), artichoke head sucrolytic activity (AH_SucAct), leaf abscisic acid (L_ABA), leaf 1-aminocyclopropane-1-carboxylic acid (L_ACC), leaf indole acetic acid (L_IAA), leaf salicylic acid (L_SA), leaf jasmonic acid (L_JA), leaf gibberellin A4 (L_GA4), leaf trans-zeatin (L_tZ), leaf zeatin riboside (L_ZR), leaf isopentenyladenine (L_iP), artichoke head abscisic acid (AH_ABA), artichoke head 1-aminocyclopropane-1-carboxylic acid (AH_ACC), artichoke head indole acetic acid (AH_IAA), artichoke head salicylic acid (AH_SA), artichoke head jasmonic acid (AH_JA), artichoke head gibberellin A4 (AH_GA4), artichoke head trans-zeatin (AH_tZ), artichoke head zeatin riboside (AH_ZR), artichoke head isopentenyladenine (AH_iP), bare soil (BS), polyethylene mulch (PE), mushroom-substrate-based hydromulch (MS), rice-hull-based hydromulch (RH), and wheat-straw-based hydromulch (WS).

4. Discussion

Abiotic stresses, such as drought and salinity, modify source–sink relations which influence plant growth and consequently crop productivity [16]. In our study, artichoke growth reduction by drought conditions (Table 1) might be due to the inability to maintain the assimilate supply required to support productivity and stress-adaptation processes [27]. Leaf gas-exchange regulation seems to be directly connected with sink activity, biomass allocation, and water availability as these all influence assimilate transport [31,32]. Importantly, (hydro)mulched plants were able to maintain significantly higher growth and productivity than non-covered plants under water limitation (Table 1), which was related to their higher photosynthetic rate (Figure 1a), WUEi (Figure 1d), and sucrolytic activity in both leaves and artichoke heads (Figure 3), as indicated by their association in the same cluster in the loading-PCA (Figure 6b). Indeed, Chen et al. [33] demonstrated that a rise in sucrolytic activity was correlated with stomatal aperture regulation, which contributed to drought tolerance. Considering that hydromulching provoked a reduction in stomatal conductance (Figure 1b) and transpiration rate (Figure 1c), especially in MS-covered plants, stomatal aperture regulation can reduce water loss while maintaining enough carbon uptake to sustain biomass and yield under drought conditions [34]. The use of mulching also affected the leaf mineral composition, particularly in MS-mulched plants, which presented the highest concentrations of K and SO_4^{2-} under water depletion (Table 3). In leaves, K allows an efficient osmotic adjustment within the cells, which is a key process in retaining water. Efficient stomatal closure prevents excessive water loss, which is conducted by K release from guard cells [35]. This suggests that the growth increase observed in the hydromulched plants might be also partially explained by improved ion homeostasis. Therefore, an optimal relation between stomatal conductance, ion homeostasis, photoassimilation, and carbon transport may be the reason why reduced transpiration rates did not affect CO_2 net assimilation, thus resulting in an increase in WUEi and an improvement in yield stability under water-stress conditions [35–37].

Radiolabeled sucrose assays showed that osmotic stresses produced a drastic decrease in the tomato fruit's capacity to attract photoassimilates owing to a reduction in sink activity [27,38], thus promoting both sucrose and hexose accumulation in the leaves [39–41]. In our study, artichoke plants showed a differential carbon partitioning between source leaves and sink heads during the exposure to water stress, especially in hydromulched plants, which can be explained by the regulation of sucrolytic activities. In the leaves, the increased sucrolytic activity of hydromulched plants during the water stress (Figure 3a) resulted in higher sucrose hydrolysis into hexoses (Figure 2a) to activate stress-defense responses that maintain growth and productivity [42,43]. In the artichoke heads, despite sucrose hydrolysis being kept activated under drought in hydromulched plants (Figure 3b), hexose concentrations decreased (Figure 2b), suggesting an increase in their metabolic use for sink growth and, eventually, storage [44,45].

The regulation of sucrolytic activity under stress might be mediated by changes in hormonal balance [23,27]. In fact, the crosstalk of invertases with plant hormones has been demonstrated to affect plant growth and crop yield under abiotic stress by controlling sink activity [14,46]. It has been stated that the increase in sucrose partitioning from source leaves to the fruits in salinized transgenic tomato plants was due to an increase in the expression of a cell-wall invertase gene and its activity along with the downregulation of the CK tZ and the ethylene precursor ACC [27]. It is well known that plant growth is modulated during abiotic stress by the sink strength and CKs might control rate-limiting steps that determine photoassimilate availability (reviewed in [16]). Indeed, invertase activity has been demonstrated to be co-induced by CKs, thus delaying leaf senescence and inducing dehydration avoidance via an effect on source–sink relations [26,47]. Surprisingly, in our study, tZ and ZR decreased in the leaves of hydromulched plants (Figure 4a,c and Figure S1) and were grouped in a cluster opposite to that of leaf sucrolytic activity (Figure 6c). This may suggest that hydromulched plants were less affected by the drought stress while the leaf senescence of non-covered plants was buffered by increased CK con-

centrations. It is also plausible that there was a negative regulation of carbon partitioning by CKs during the water stress. In fact, recent works on CK homeostasis presented CKs as having both positive and negative regulatory functions in drought-stress plant adaptation [48]. Different studies have demonstrated the negative regulatory function of CKs in water-stress responses, such as in CK-deficient plants, which showed a higher ability for survival and tolerance under water-deficit conditions [49,50]. Although CK crosstalk with other stress-related phytohormones as ACC and ABA is well known [51–53], our study reveals that the most important hormonal changes provoked by hydromulching during drought stress corresponded to an SA decrease in the leaves and ACC and ABA reduction in the artichoke heads (Figures 5 and S1), while clustering inversely to sucrolytic activities in the loading PCA (Figure 6c). Importantly, the negative regulation of sucrose metabolism by ethylene (i.e., ACC) in source leaves and sink tomato fruits in response to water and salinity stresses has been previously demonstrated [26,27]. Moreover, silencing an invertase inhibitor delayed ABA-induced leaf senescence and increased seed weight and fruit hexose contents in tomato [54]. Notably, SA has been shown to play a key role in the translocation and storage of photoassimilates in response to abiotic stresses [55]. Indeed, increased sink strength by foliar application of SA was found in grain crops, such as wheat [56] and maize [57] plants subjected to salinity, which is considered an osmotic stress. Besides this, the carbohydrate metabolism in both source and sink tissues was regulated by SA-activating plant defense responses against environmental stresses through increasing sucrolytic activity in *Chenopodium rubrum* [58] and maize [59] plants.

5. Conclusions

We have investigated the effect of different sustainable mulching formulations on the growth and productivity responses of artichoke plants subjected to water deficit. As hypothesized, those responses were associated with improved photosynthesis and water-use efficiency and controlled by the hormonal regulation of source–sink relationships. In this regard, the crosstalk of growth-promoting hormones (CKs) with the stress-related hormones ACC, ABA, and SA has been shown to regulate sucrolytic activities in both source leaves and artichoke heads under drought stress [16,60,61]. The results of this study provide new insights into the physiological mechanisms implicated in the growth improvement of hydromulched artichoke plants under drought, with the identified hormonal factors as good candidates for breeding programs focused on the regulation of photoassimilate partitioning.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy12071713/s1>, Figure S1: Heat map of hormonal factors affected by mulching and water stress.

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