horticulturae

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Exogenous Application of Gamma Aminobutyric Acid Improves the Morpho-Physiological and Biochemical Attributes in *Lavandula dentata* L. under Salinity Stress

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Abstract: Saline water has been proposed as a solution to partially supply plants with their water requirements due to a lack of fresh water for cultivation in arid and semi-arid sites. Gamma-aminobutyric acid (GABA) is a non-protein amino acid participating in numerous metabolic processes to mitigate the undesirable effects of salinity. A pot experiment was carried out during 2021 and 2022 at Sakha Horticulture Research Station to investigate the effect of foliar application of GABA at 20 and 40 mM on vegetative growth and biochemical changes in French lavender under increasing levels of sea water salinity irrigation treatments (0, 1000, 2000, and 3000 ppm). Results indicated that increasing salinity concentration noticeably decreased plant height, number of branches, herb fresh and dry weight, root length, root fresh and dry weights, photosynthetic pigments, relative water content, and essential oil percentage. On the other hand, accumulation of proline and antioxidant enzymes was increased under increasing salinity concentrations. We conclude that foliar application of GABA acid at 40 mM can alleviate the adverse effects of salinity on the abovementioned French lavender plant characteristics by improving vegetative growth and root characteristics, as well as diminishing chlorophyll degradation, maintaining high leaf relative water content, increasing proline accumulation and antioxidant activity.

Keywords: lavender; gamma-aminobutyric acid; antioxidant activity; essential oil; proline

Citation: Shala, A.Y.; Aboukamar, A.N.; Gururani, M.A. Exogenous Application of Gamma Aminobutyric Acid Improves the Morpho-Physiological and Biochemical Attributes in *Lavandula dentata* L. under Salinity Stress. *Horticulturae* **2024**, *10*, 410. https://doi.org/10.3390/horticulturae10040410

Academic Editors: Zhouli Liu and Yi Zhao

Received: 13 March 2024
Revised: 16 April 2024
Accepted: 16 April 2024
Published: 18 April 2024

1. Introduction

Water availability is a crucial factor that confines crop productivity in Egypt, as the environment is mainly arid and semiarid [1]. Thus, it is imperative in these areas to adopt alternative water sources, such as brackish, reclaimed, and drainage water, to combat water scarcity. Furthermore, the Egyptian water share of the Nile freshwater amount is fixed, and the Egyptian government tends to expand the cultivation of aromatic plants in new reclaimed desert regions that are located in arid zones and recognized by elevated salt levels. Additionally, fresh water will remain a scarce commodity, particularly with the anticipated impacts of global warming in addition to sea level rise that is becoming a serious issue in coastal areas. The availability of water will become a top priority and a great challenge for the Egyptian government in the foreseeable future.

Generally, the influences of salinity on plants are exhibited by a severe-to-moderate contraction in plant development and yield [2–6]. Plants can adapt to the adverse effects of salinity via both enzymatic and nonenzymatic antioxidant protective mechanisms to eliminate provoked ROS to protect plants against unfavorable influences of salinity. Antioxidant enzymes combining peroxidase, catalase, and superoxide dismutase are employed in enzymatic antioxidant defense systems [4,7–10]. Moreover, certain substances like proline,

soluble sugars, ascorbic acid, and phenolics are exploited by plant cells to counteract the negative impacts of salinity [4,8,11–13].

One of the most effective adaptation strategies as osmotic regulators is the exogenous application of plant growth compounds to enhance plant adaptation under adverse conditions. A nonprotein amino acid called gamma-aminobutyric acid (GABA) is among these stress-responsive compounds that can rapidly improve the resilience of plants to abiotic stress. The application of GABA alleviated drought stress by enhancing antioxidant activity, osmolytes accumulation, water absorption, chlorophyll, proline accumulation, and soluble sugar content, as well as water efficiency [14–17]. Moreover, GABA could boost saline-alkaline stress tolerance [18] via accumulating soluble sugars and boosting secondary antioxidant activity and lignification of roots. Additionally, it encourages plant adaptation to salinity stress through reinforcing the upregulation of antioxidant potential, photosynthesis, and proline content [7,19–21]. Also, a rising accumulation of endogenous GABA in plant tissue subjected to salt stress and other abiotic stresses was detected [7,15,19,20]. Considering these promising findings, GABA's protective role in revamping yields and quality of medicinal plants under a variety of environmental stresses must be taken into consideration.

French lavender (*Lavandula dentata* L.) is a flowering plant, belonging to the Lamiaceae family, native to the Mediterranean basin and is broadly cultivated around the world. Little shrubs with purple flower spikes begin to grow, highlighting their decorative potential, both as a garden and as a potted plant [22]. The French lavender essential oil is rich in oxygenated monoterpenes, which represent the major oil constituents of linalool, camphor, and borneol. Additionally, the oil has a wide spectrum of biological effects entailing antioxidants, antifungal, and insecticidal potencies [23,24].

Previous research unveiled that French lavender vegetative growth and plant chemical analysis were significantly affected by salinity stress [25]; hence, salinity stress could be a critical limiting factor influencing French lavender oil yield. Under sea water irrigation, however, neither lavender growth nor productivity nor biochemical characteristics have been examined with exogenous GABA application. We hypothesized that saline stress would inhibit the metabolism of lavender plants, but that exogenous GABA might alleviate its negative effects. The current study examined, for the first time, the protective effects of GABA on lavender plants' growth characteristics and biochemical changes under saline water irrigation.

2. Materials and Methods

2.1. Plant Growth and Experimental Conditions

At Sakha Horticulture Research Station (31°07′ N latitude, 30°05′ E longitude), Kafr El-Sheikh Governorate, North Nile Delta of Egypt, a pot experiment was executed during the two successive seasons of 2021 and 2022 to examine the effect of irrigation with the mixture of fresh water and natural sea water from the white sea (electrical conductivity EC of 35 dS m^{-1}), on elevated salinity levels.

Two-month-old rooted transplants with 2–3 true leaves were procured from El-Kanatar El-Khaireya Experimental Farm for Medicinal and Aromatic Plants, Horticulture Research Institute, Agricultural Research Center, Egypt. Then, they were transplanted into plastic pots (30 cm in diameter and 18 cm in height) containing 5 kg clayey soil and subjected to saline water treatments and foliar application of GABA. Physical and chemical soil properties of the used soil were determined according to Page et al. [26], and are displayed in Table 1. The experimental design was a complete randomized blocks design with four replications.

Table 1. Some physical and chemical soil properties of the experimental site as mean values of the two growth seasons.

Soil Depth (cm)	Field Capacity (%)	Wilting Point (%)	Bulk Density (Mg m^{-3})	Total Porosity (%)	Sand (%)	Silt (%)	Clay (%)	Texture Class	pH
0–15	45.37	22.91	1.19	55.09	19.42	24.97	55.61	Clayey	7.92
	EC_e (dS m^{-1})	Inions concentration (meq L^{-1})				Cation concentration (meq L^{-1})			
		CO_3^-	HCO_3^-	Cl^-	SO_4^-	Ca^{++}	Mg^{++}	Na^+	K^+
0–15	2.74	---	2.52	14.94	12.28	5.02	6.84	17.22	0.66

2.2. Salinity Stress Treatments

The plants were irrigated with fresh water at 290 ppm (0.45 ds/m) from transplanting to 30 days; then, irrigation with saline water treatments was initiated when lavender plants had 4–5 fully grown leaves and continued until harvesting at the beginning of October for both growing seasons 2021 and 2022. The plants received their water requirements plus 20% as leaching requirements for all treatments during both growing seasons until harvest. The salinity levels 0, 1000 ppm (1.56 dS m^{-1}), 2000 ppm (3.12 dS m^{-1}), and 3000 ppm (4.69 dS m^{-1}) were achieved by adding the proper amount of sea water [EC 35,000 ppm (54.69 dS m^{-1})] to fresh water, which was adjusted via EC meter instrument.

The foliar spray of GABA on plants was performed two times in the morning; the first treatment was performed one month after the initiation of saline irrigation treatments, while the second foliar addition was carried out one month later. Different concentrations of GABA (20 and 40 mM) were prepared in 0.1% (*v*/*v*) Tween-20, while tap water was used as a control. The other agricultural practices were implemented according to the Egyptian Ministry of Agriculture and Land Reclamation recommendations.

2.3. Measurement of Growth Parameters

The plants were harvested at the full blooming stage at the beginning of October in both growing seasons; then, the following parameters were recorded: plant height (cm), root length, plant's fresh and dry weight, and root's fresh and dry weight.

2.4. Determination of Photosynthetic Pigments

Chlorophyll a, b and carotenoid contents in fresh lavender leaves were extracted by using 0.25 g with 80% acetone according to the method of Lichtenthaler and Buschmann [27]. Absorbances of leaf extract were estimated spectrophotometrically at 663 and 645 nm (for Chl. a and b) and 470 nm (for carotenoids). Finally, pigment concentrations were expressed as mg g^{-1} FW.

2.5. Relative Water Content

To determine the leaf relative water content (RWC), fully expanded young leaves were weighed immediately after harvesting, put in vials containing deionized water at room temperature for 24 h, blotted on dry filter paper to obtain the turgid weight, and finally dried in an oven at 70 °C for 48 h. To determine dry weight, RWC was calculated from the following equation: [fresh weight − dry weight/turgid weight − dry weight] × 100 [28].

2.6. Measurement of Proline Content

Centrifuging at 10,000× *g* for 10 min was executed after 0.5 g of fresh leaves was combined with 3% sulphosalicylic acid. A mixture of 2 mL of supernatant, glacial acetic acid, and ninhydrin reagent was prepared. For one hour, the reaction mixtures were maintained in a bath of boiling water. Next, the mixture was extracted using 4 mL of toluene after the reaction was stopped in an ice bath. Using spectrophotometry, the absorbance of the organic phase was detected at 520 nm. Proline was quantified in µmol g^{-1} and its concentration was estimated by a standard curve [29].

2.7. Essential Oil Extraction

Harvested lavender plants were air-dried, chopped, and subjected to hydrodistillation using Clevenger apparatus for 3 h, conforming to Pharmacopoeia [30]. Essential oil percentage was measured by the following formula: [Volume oil in graduated tube/sample dry weight] × 100, whereas essential oil yield (mL/plant) was calculated by using the dry weight of the plant aerial parts.

2.8. Antioxidant Enzyme Activities

To assess the antioxidant enzyme activities, 0.5 g of leaf tissue was homogenized in liquid nitrogen with 3 mL of extraction buffer that consisted of 1 mM ethylenediaminetetraacetic acid (EDTA), 1% (*w*/*v*) polyvinylpyrrolidone, 1 mM phenylmethylsulfonyl fluoride (PMSF), and 0.05% Triton X-100 in 50 mM potassium-phosphate buffer (pH = 7.0) via a prechilled mortar. After carrying out a four-layer cheesecloth filtering process, the homogenate was centrifuged at 12,000 rpm for 20 min at 4 °C. The total soluble enzyme activity assay was performed via a UV-160A spectrophotometer (160A, Shimadzu, Kyoto, Japan) on the supernatant, after it had been centrifuged again at 12,000 rpm for 20 min at 4 °C.

Catalase (CAT) activity was evaluated by the technique described by Aebi [31]. The reaction mixture was composed of 30 mmol L^{-1} H_2O_2 in a 50 mmol L^{-1} phosphate buffer (pH 7.0) and 0.1 mL enzyme extract in a total volume of 3 mL. By tracking the consumption of H_2O_2 at 240 nm, the activity of catalase was estimated.

Peroxidase activity (EC1.11.1.7) was ascertained in line with the method suggested by Hammerschmidt et al. [32] and expressed as units of peroxidase/mg protein.

Polyphenol oxidase activity (EC 1.10.3.1) was assessed concurring with the procedure claimed by Malik and Singh [33]. The reaction mixture comprised 3.0 mL of buffered catechol solution (0.01 M) newly prepared in 0.1 M phosphate buffer (pH 6.0). 100 mL of the crude enzyme extract was added to initiate the process. Absorbance alterations at 495 nm were noted at 30 s for 3 min. A rise in absorbance $min^{-1}g^{-1}$ fresh weight signified enzyme activity.

2.9. Statistical Analysis

All data were tested by analysis of variance (ANOVA) performed by the CoStat 6.45 software program. The comparison of means was evaluated via Duncan's multiple range test in agreement with Snedecor and Cochran [34].

3. Results and Discussion

3.1. Vegetative Growth Characteristics

Plant vegetative growth traits were negatively influenced under the highest concentration of saline water treatments as compared with the control (Table 2). In this regard, plant height and branch number were significantly cut down in plants exposed to saline irrigation water >2000 ppm, while no significant differences were noted among lower saline water application and control during both growing seasons. Additionally, herb fresh weight as well as herb dry weight gradually diminished with rising saline irrigation water concentration as paralleled to the unstressed plants.

Plant growth cutback is a well-known response to salinity for diverse plant species. This impact has also been reported on other lavender species. In this concern, Szekely-Varga et al. [11] found a substantial curtailment in number of branches, stems, and leaves. The fresh weight of *Lavandula angustifolia* was pronounced in plants subjected to elevated salinity treatments (200 and 300 mM NaCl) with respect to nonstressed control. Also, thyme and lavender plants grown under 50 and 100 mM NaCl significantly reduced the growth as compared with nonsalinized control [2]. Additionally, Wang et al. [7] reported that plant height, leaf freshness, and dry weight of maize seedlings were curtailed under salinity stress (150 mM and 300 mM NaCl concentration). Furthermore, Moghith et al. [3] argued that elevating salinity levels lowered the vegetative growth of *Salvia hispanica* L. plants. In

a study conducted in Cyprus, the authors discovered that the plant height of *Lavandula angustifolia* Mill. crumbled in plants exposed to saline conditions >50 mM. Furthermore, all salinity concentrations (25, 50, and 100 mM) trimmed fresh biomass and biomass dry matter [4].

Table 2. The effect of saline irrigation water and GABA application on plant height, branch number, herb freshness, and herb dry weight of *Lavandula dentata* L. plants.

Treatments	Plant Height (cm)		No. of Branches		Herb Fresh Weight (g/Plant)		Herb Dry Weight (g/Plant)	
	1st Season	2nd Season	1st Season	2nd Season	1st Season	2nd Season	1st Season	2nd Season
Control (fresh water)	44.00 a	47.33 a	23.67 a	21.67 abc	68.09 cd	78.03 c	24.51 c	27.45 b
Sea water at 1000 ppm	42.33 ab	46.00 ab	21.33 ab	19.67 abc	64.30 d	70.63 d	24.57 c	27.38 b
Sea water at 2000 ppm	39.67 cd	44.00 bc	20.33 ab	18.33 c	57.13 e	61.24 f	20.78 d	22.61 c
Sea water at 3000 ppm	37.00 e	38.67 e	13.00 d	11.33 d	50.20 f	60.73 f	15.96 e	18.63 e
1000 ppm sea water + 20 mM GABA	43.00 a	47.00 a	24.00 a	22.00 ab	68.65 cd	77.94 c	26.27 bc	29.19 b
1000 ppm sea water + 40 mM GABA	42.67 ab	46.33 ab	22.00 ab	20.00 abc	71.27 c	80.32 c	26.15 bc	29.00 b
2000 ppm sea water + 20 mM GABA	40.33 bc	44.00 bc	21.33 ab	18.67 bc	83.59 b	91.43 b	29.34 ab	33.29 a
1000 ppm sea water + 40 mM GABA	42.33 ab	45.67 ab	24.33 a	22.67 a	90.50 a	96.02 a	31.37 a	34.20 a
3000 ppm sea water + 20 mM GABA	37.67 de	41.00 de	16.00 cd	13.67 d	51.91 ef	67.72 de	17.93 de	21.10 cd
3000 ppm sea water + 40 mM GABA	39.67 cd	42.00 cd	18.33 bc	14.00 d	55.83 ef	64.36 ef	16.10 e	19.14 de

Means followed by the same letter at each column are not significantly different at the 5% level according to Duncan's multiple range test.

Considering the effect of GABA on lavender growth, it was observed that the foliar spray of gamma-aminobutyric acid significantly advanced the abovementioned characteristics (Table 1) under saline conditions. This alleviated growth reduction caused by salinity was observed when it was combined with mixed fresh sea water at 1000 and 2000 ppm relative to GABA-untreated plants. Foliar spray with GABA at 20 and 40 mM on plants irrigated with mixed fresh water with concentration at 1000 ppm, as well as plants sprayed with 40 mM GABA and irrigated with mixed saline fresh water at 2000 ppm, noticeably boosted plant height and branches number without significant variations among treatments. Furthermore, applying GABA at 40 mM resulted in the highest values of fresh weight for plants irrigated with 2000 ppm, as well as the heaviest dry weight achieved from plants cotreated with GABA at 20 and 40 mM and irrigated with 2000 ppm without significant differences among them for both growing seasons.

Also, Wang et al. [7] stated that GABA application at 0.5 mM lifted all vegetative growth traits for maize seedlings grown under saline conditions (150 mM and 300 mM NaCl concentration). Similarly, Kalhor et al. [35] noticed that shoot fresh and dry weight of salt-exposed lettuce (40 mM and 80 mM NaCl) were expanded by exogenous supplementation with GABA at 25 µM. Likewise, Ullah et al. [36] reported that exogenous application of GABA at 2 mM inflated shoot length and shoot fresh weight, as well as shoot dry weight of chufa (*Cyperus esculentus*) under salinity stress (0, 100, and 200 mM NaCl and Na_2SO_4).

In our case, GABA exogenous application on plants under salinity produced vegetative growth enhancement especially at 1000 and 2000 ppm, respectively. Therefore, the effect of GABA was growth-enhancing at low-stress saline water levels but not at high-saline stress levels which was in accordance with the findings of Kaur and Zhawar [18]. Accordingly, Wang et al. [7] detected that endogenous GABA concentration was accumulated in moderately maize salt-stressed seedlings, while endogenous GABA accumulation was lessened in severely maize salt-stressed seedlings that were generated after exogenous GABA application.

3.2. Roots Characteristics

All root attributes were adversely affected by escalating salinity concentrations (Table 3). Additionally, applying GABA as a foliar spray ameliorated the negative effects of salinity on root characteristics, especially at low and medium salinity concentrations (1000 and

2000 ppm). The combination of GABA at both concentrations (20 and 40 mM) with plants irrigated with saline water (1000 and 2000 ppm) noticeably upgraded root length, as well as root fresh weight, without significant variations among these treatments and plants treated with nonsaline water (control). Otherwise, the highest dry weight value was obtained when salinity influences were amended via applying GABA at both concentrations (20 and 40 mM) with plants exposed to saline water at 1000 ppm without significant variations in between for both seasons and plants subjected to saline water at 2000 ppm without significant variation in between for the first season only. The curtailment of root aspects observed in our study was in harmony with the formerly published outcomes by Chrysargyris et al. [4] on *Lavandula angustifolia* Mill. who claimed that root fresh weight and root length declined at 50 and 100 mM NaCl, respectively. Also, Moghith et al. [3] ascertained that escalating salinity levels trimmed root growth characteristics of the *Salvia hispanica* L. plant. Furthermore, Szekely-Varga et al. [11] disclosed that a substantial cutback in root fresh weight of *Lavandula angustifolia* was pronounced in plants subjected to elevated salinity treatments (200 and 300 mM NaCl) with respect to nonstressed controls. Salinity stress (100 and 200 mM NaCl and Na_2SO_4) negatively impacted root length and root fresh and root dry weight of *Cyperus esculentus* plants [36].

Table 3. Effect of saline irrigation water and GABA application on root length, root fresh weight, and root dry weight of *Lavandula dentata* L. plants during both growing seasons.

Treatments	Root Length (cm)		Root Fresh Weight (g/Plant)		Root Dry Weight (g/Plant)	
	1st Season	2nd Season	1st Season	2nd Season	1st Season	2nd Season
Control (fresh water)	12.33 a	14.00 ab	4.04 ab	5.87 ab	1.30 b	1.72 c
Sea water at 1000 ppm	10.67 bc	13.50 abc	3.30 b	5.10 b	1.30 b	1.90 bc
Sea water at 2000 ppm	10.33 bc	12.00 c	2.37 c	4.08 c	1.01 c	1.54 d
Sea water at 3000 ppm	8.33 d	10.00 d	1.90 c	2.55 d	0.71 d	0.90 f
1000 ppm sea water + 20 mM GABA	11.5 ab	13.33 abc	4.09 a	6.23 a	1.57 a	2.27 a
1000 ppm sea water + 40 mM GABA	11.67 ab	13.5 abc	4.20 a	6.17 a	1.61 a	2.23 a
2000 ppm sea water + 20 mM GABA	12.17 a	14.00 ab	3.90 ab	5.44 ab	1.49 a	2.01 b
2000 ppm sea water + 40 mM GABA	12.5 a	15.00 a	3.82 ab	5.23 ab	1.45 ab	1.94 bc
3000 ppm sea water + 20 mM GABA	10.00 c	12.50 bc	2.32 c	3.13 cd	1.02 c	1.22 e
3000 ppm sea water + 40 mM GABA	9.50 cd	12.67 bc	2.12 c	2.97 d	0.97 c	1.21 e

Means followed by the same letter at each column are not significantly different at the 5% level according to Duncan's multiple range test.

In the present study, many growth parameters were evaluated in lavender salt-stressed plants, involving the reduction of herb, fresh and dry weight of roots, and leaves' relative water content which is probably the major reliable features to identify growth inhibition.

Plants often respond quickly to salinity stress via inhibiting growth which causes osmotic stress in plants and, as a first result, lessens cell expansion as well as cell turgor [37]. However, growth inhibition under stress is eventually linked to the reallocation of plant resources, which are normally utilized for growth and primary metabolism (i.e., biomass accumulation) towards the stimulation of defense mechanisms [37].

Some investigations have highlighted the valuable impacts of GABA on plants subjected to saline conditions as well as unstressed conditions. In this concern, Sheteiwy et al. [19] marked that shoot length and fresh and dry weight of rice seedlings crumbled under salinity conditions. In contrast to unstressed seedlings, the abovementioned physiological parameters were augmented when seeds were primed with 0.5 mM GABA. Likewise, in chufa (*Cyperus esculentus*), Ullah et al. [36] uncovered that exogenous supplementation of GABA at 2 mM enlarged root length and root fresh weight, as well as root dry weight under salinity stress (0, 100, and 200 mM NaCl and Na_2SO_4). On lettuce plants, Kalhor et al. [35] outlined that root fresh and dry weight were cut down under NaCl concentrations (40 and 80 mM),

but GABA application (25 µM) alleviated the negative influences of salinity on fresh and dry weight. Additionally, Yousef and Nasef [38] declared that the exogenous spray of GABA (1 mM and 2 mM) significantly refined the vegetative growth and yield of garlic genotypes under unstressed conditions which were attributed to rising chlorophyll content, endogenous total phenols, and elements content. Moreover, Feizi et al. [21] divulged that GABA application at 10 mM upgraded root length and root fresh weight of saffron plants under salinity level (15 dS m^{-1}). Also, Ramzan et al. [39] recognized that GABA application noticeably amended length as well as fresh and dry biomass of shoots and roots of *Capsicum annuum* L. under salinity stress.

3.3. Photosynthetic Pigments

Proliferating mixed fresh saline water from 0 to 3000 ppm led to a gradual decline in Chl. A, Chl. B, and total carotenoid content in *Lavandula dentata* L. leaves under saline water conditions (Figure 1; Table S1). The lowest values in this respect were noted from plants that received the highest concentration of saline water (3000 ppm). On the other hand, foliar spraying of GABA significantly promoted the accumulation of photosynthetic pigments under salinity conditions; hence, the highest content of Chl. a and Chl. b was marked when GABA was exogenously applied at both concentrations (20 and 40 mM) with plants exposed to saline water at 2000 ppm and control without significant differences in between during both growing seasons (Figure 1a–d).

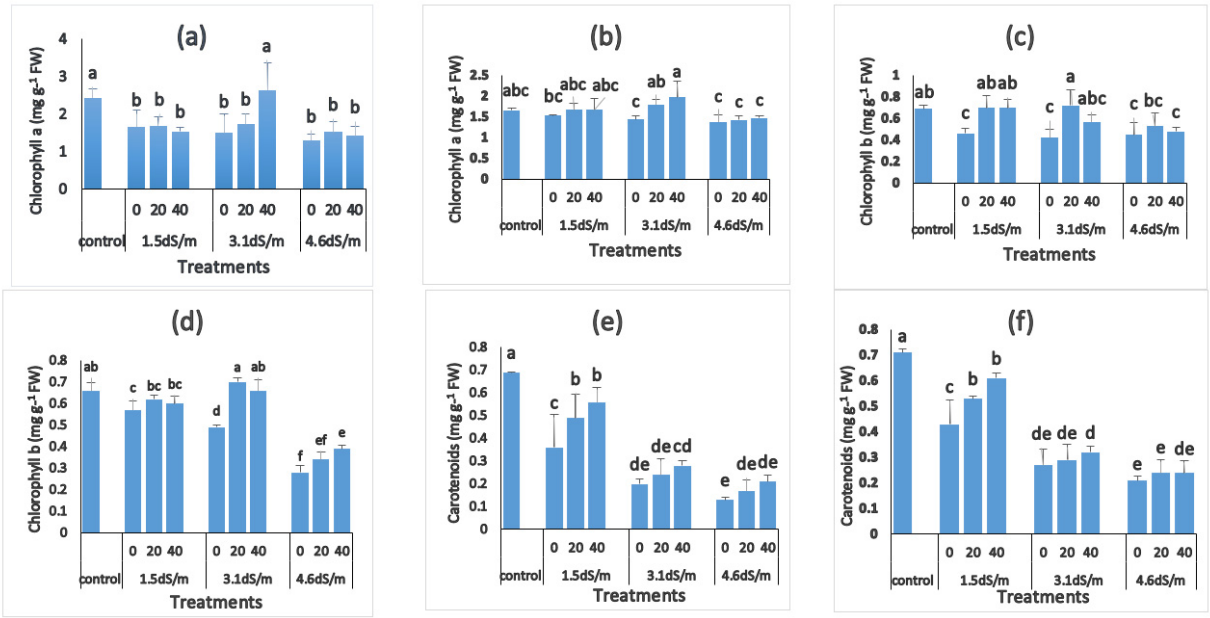

Figure 1. Effect of saline irrigation water and GABA application on chlorophyll a: (**a**) first season; (**b**) second season, on chlorophyll b; (**c**) first season; (**d**) second season; and carotenoid content of (**e**) first season and (**f**) second season, of *Lavandula dentata* L. plants (0, 20, 40 (GABA) gamma-aminobutyric acid) and (1.5, 3.1, 4.6 ds/m saline water treatments). Means ± SEs, $n = 3$; different letters indicate significant differences ($p \leq 0.05$) between the treatments after performing Duncan multiple range test.

Additionally, total carotenoid content was reduced in response to booming concentrations of saline water as observed. The elevated contraction occurred at high salinities (3000 ppm) in both seasons. On the other hand, the highest carotenoid content resulted from plants irrigated with fresh water (control) (Figure 1e,f; Table S1). An earlier published report exhibited that photosynthetic pigment decline was recognized as a useful biochemical stress in plants subjected to salinity conditions. Regarding this, Szekely-Varga et al. [11] unveiled that high salinity treatments (100 and 200 mM NaCl) lowered Chl. a and Chl. B,

as well as total carotenoid contents as paralleled with control in *L. angustifolia*. Likewise, Chrysargyris et al. [4] revealed that Chl. a and Chl. b contents were considerably decreased in *Lavandula angustifolia* plants exposed to salinity stress with >50 mM NaCl. Additionally, the promotion effect of GABA on the photosynthetic pigment accumulation has been previously reported by Yousef and Nasef [38]. They discovered that foliar supplementation of GABA at 1 mM and 2 mM significantly heightened total chlorophyll content in garlic genotypes under unstressed conditions and was associated with the enhancement in plant growth as well as garlic yield. Recently, Ullah et al. [36] documented that chlorophyll a and b concentrations were diminished on chufa plants subjected to salinity stress (100 and 200 mM NaCl and Na_2SO_4), while these pigments were progressed via exogenous application of GABA at 2 mM. The enhancement role of GABA for growth and photosynthetic pigments in lavender plants may be attributed to the fact that the exogenous application of GABA diminished chlorophyll degradation and developed photosynthetic capacity, as well as growth under salinity conditions [35,36].

3.4. Relative Water Content

When the salinity level was aggravated, the relative water content steadily fell (Figure 2a,b; Table S2), which led to a decline in growth rate and a discernible impact on the growth of lavender. The control group had the highest relative water content. On the other hand, foliar application of GABA intensified the relative water content of *Lavandula dentata* L. leaves under medium 2000 ppm diluted sea water followed by low diluted sea water level. Therefore, the greatest relative water content was noted for control and plants that received GABA at 20 and 40 mM under 2000 ppm diluted sea water. This lessened the adverse effects of salinity on leaves' water content without significant differences in between during both growing seasons. A decrease in relative water content under saline conditions is in harmony with the previous results on *Nigella sativa* [40] and *Cassia italica* [41] that significantly declined the growth of these plants. In addition, the GABA-treated plants not only maintained high leaf relative water content, but also ameliorated the negative impacts induced by salinity than non-GABA-treated plants in salt-stressed *Cassia italica*, maize, and rice seedlings. This may be because GABA helps to restore hydration status in addition to protecting cell and organelle membranes from oxidative damage [7,19,41].

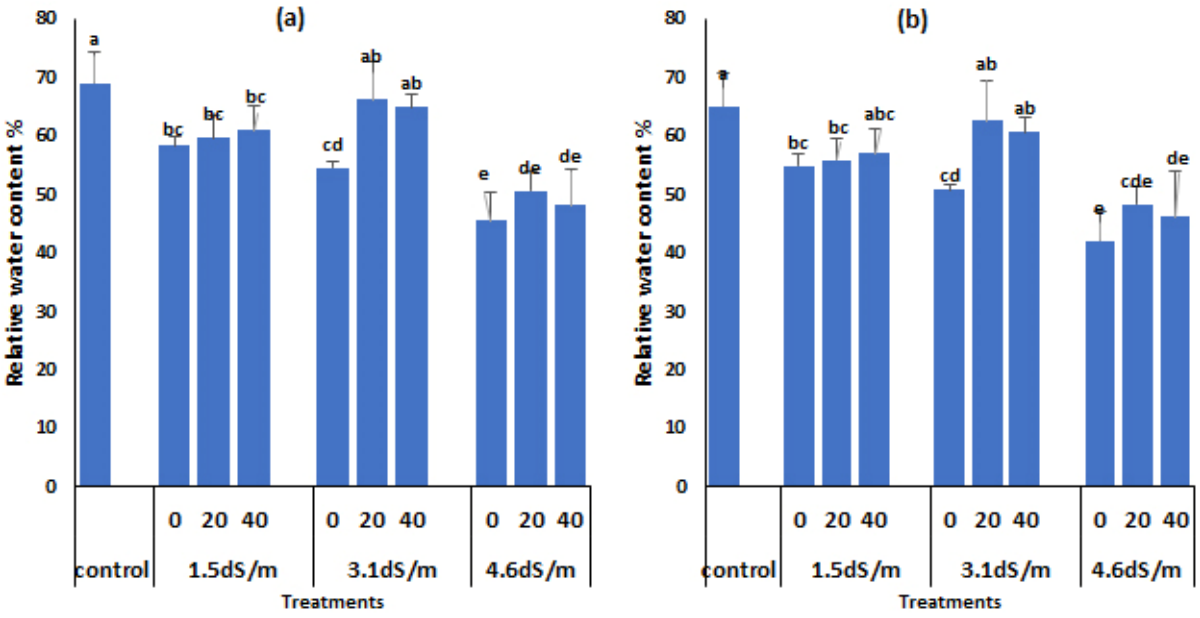

Figure 2. Effect of saline irrigation water and GABA application on relative water content of *Lavandula dentata* L. plants (**a**) first season, (**b**) second season, (0, 20, 40 gamma-aminobutyric acid) and (1.5, 3.1, 4.6 ds/m saline water treatments). Means ± SEs, $n = 3$; different letters indicate significant differences ($p \leq 0.05$) between the treatments after performing Duncan multiple range test.

3.5. Changes in Proline Accumulation

Proliferating the diluted sea water concentration from 1000 to 3000 ppm gradually inflated proline concentrations (Figure 3a,b; Table S2). Plants subjected to the high saline irrigation water treatment (3000 ppm) and treated with GABA at 20 and 40 mM noticeably expanded proline concentration, followed by plants exposed to diluted sea water at 3000 ppm. The GABA-treated plants at 40 mM combined with 2000 ppm saline irrigation water without significant differences were remarked among treatments; conversely, the control plants reported the least proline concentration in the fresh leaves of *Lavandula dentata* L. The significant increment in leaf proline concentrations in our findings is high enough to have an appropriate osmotic impact in the protective role against elevated salinity.

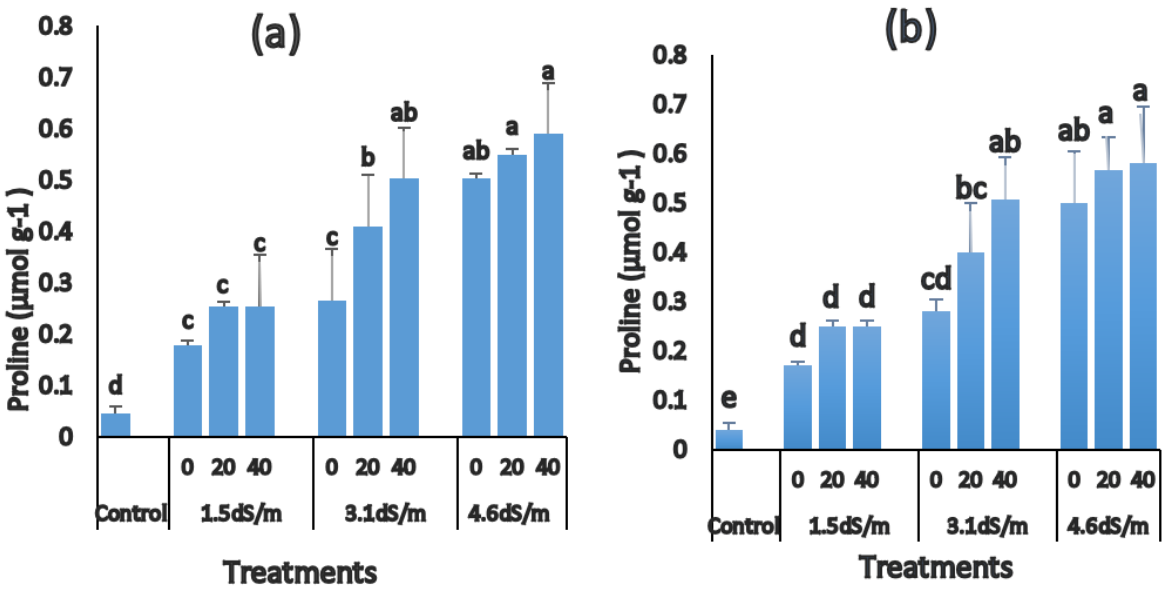

Figure 3. Effect of saline irrigation water and GABA application on proline of *Lavandula dentata* L. plants (**a**) first season, (**b**) second season, (0, 20, 40 (GABA) gamma-aminobutyric acid) and (1.5, 3.1, 4.6 ds/m saline water treatments). Means ± SEs, $n = 3$; different letters indicate significant differences ($p \leq 0.05$) between the treatments after performing Duncan multiple range test.

Our results were in accordance with the formerly reported outcomes in which proline concentration was significantly enhanced in the fresh leaves of *Lavandula angustifolia* L. and *Salvia hispanica* L. plants exposed to high salt treatments and high saline irrigation water concentration (4.96 dS m^{-1}) [3,4,11].

GABA application significantly progressed proline accumulation in irrigated plants with fresh mixed water at 2000 and 3000 ppm as compared with that of control, which was in agreement with Wang et al. [7], who argued that GABA application at 0.5 mM markedly promoted proline content by 1.2-fold of salt-stressed maize seedlings relative to untreated plants. Lately, Ullah et al. [36] unearthed that proline crumbled in the chufa seedlings with escalating salinity stress (100 and 200 mM NaCl and Na_2SO_4); on the contrary, GABA supplementation (2 mM) inflated proline concentrations. Additionally, Ramzan et al. [39] documented that proline decreased in NaCl-stressed *Capsicum annuum* L. seedlings while proliferating in exogenously GABA-applied plants.

On the other hand, Sheteiwy et al. [19] unveiled that proline content significantly developed in rice seedlings subjected to salinity as compared with the unstressed seedlings. Furthermore, proline concentration significantly decreased by priming seeds with 0.5 mM GABA relative to unprimed seeds. Also, proline level was heightened under salt stress in lettuce plants Kalhor et al. [35], but GABA application (at 25 µM) lessened proline content in both saline conditions (40 and 80 mM of NaCl), which may be attributed to the fact that GABA function can partially bypass proline participation in ROS scavenging activities and

generate a decrease in proline biosynthesis. Moreover, their results proposed GABA as a plant-boosting antioxidant component, which was able to diminish oxidative damage through enzymatic and nonenzymatic metabolism being activated under salt stress.

The accumulation of stress-protective proline induced by GABA application in plants subjected to salinity stress has been demonstrated. This proved to be efficient in relieving stress as stress-relieving solute due to the role of GABA in inhibiting proline degradation, as well as its participation indirectly in the citric acid cycle under NaCl stress, which will improve the capacity of plants to withstand adverse conditions [7,20].

3.6. Changes in Essential Oil Yield

Lavender essential oil percentage as well as essential oil yield of hydrodistilled aerial parts declined in plants grown under elevated saline irrigation water compared with plants cultivated in nonsaline conditions and low saline irrigation water (Figure 4a–d; Table S2). Interestingly, the highest essential oil percentage and oil yield resulted from plants exposed to medium saline irrigated plants with 2000 ppm and sprayed with GABA at both concentrations without significant differences among them. Therefore, the foliar application of GABA significantly weakened the reduced oil percentage and oil yield noted in medium saline irrigated plants (Table S2).

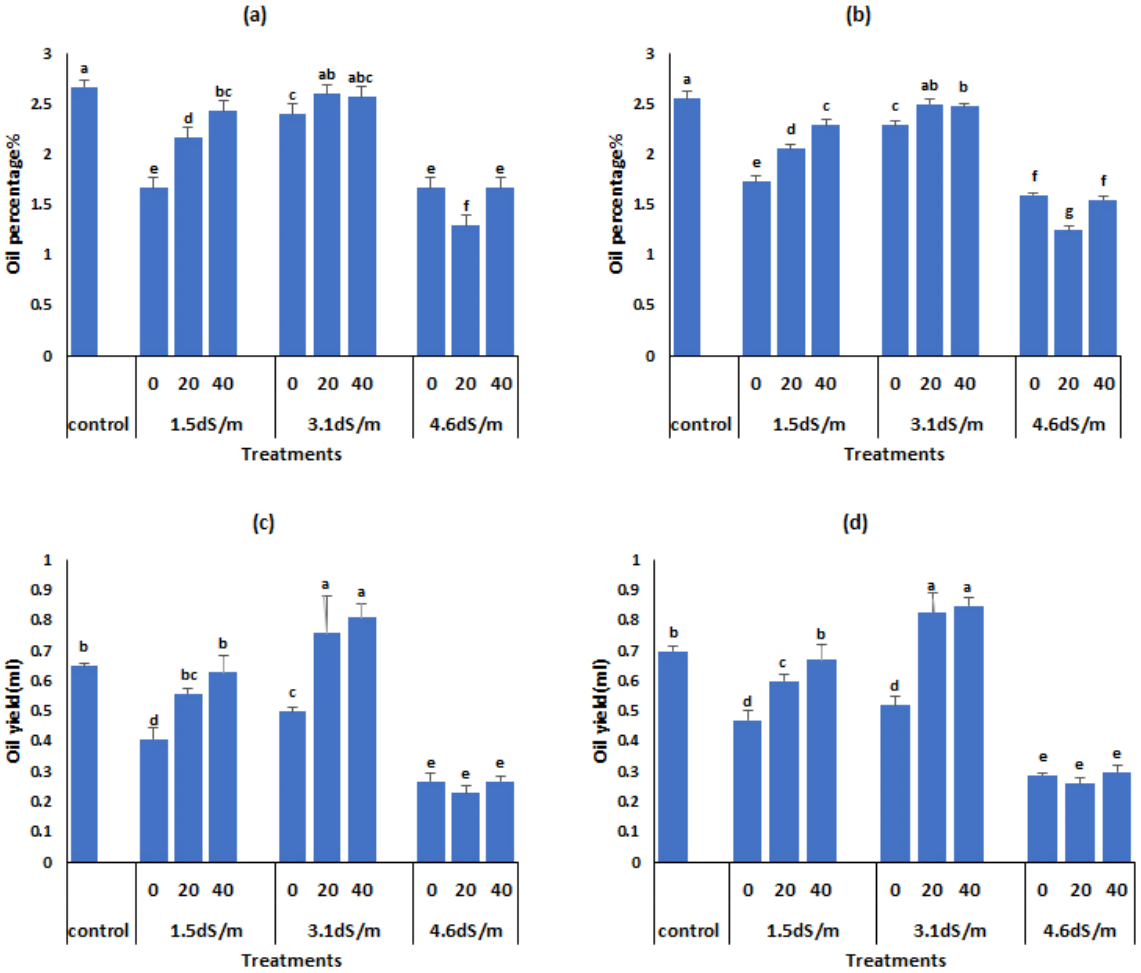

Figure 4. Effect of saline irrigation water and GABA application on oil percentage% (**a**) first season, (**b**) second season, and on oil yield (**c**) first season, (**d**) second season of *Lavandula dentata* L. plants (0, 20, 40 (GABA) gamma-aminobutyric acid) and (1.5, 3.1, 4.6 ds/m saline water treatments). Means ± SEs, $n = 3$; different letters indicate significant differences ($p \leq 0.05$) between the treatments after performing Duncan multiple range test.

The extracted essential oil percentage in nonsaline irrigated plants is 2.67 and 2.56% for both seasons, respectively, which is higher than that obtained by Barkaoui et al. [23]. They uncovered that the essential oil percentage of hydrodistilled aerial parts in Morocco was 1.06%. The variation in essential oil yield depended on diverse factors, namely, species, environmental factors, geographical origin, harvest time, and drying method.

The abovementioned outcomes are in harmony with the previous results of Cordovilla et al. [2] who declared that elevated salinity (100 mM) advanced essential oil production of thyme that might be ascribed to the accumulation of secondary metabolites, as a self-defense component versus stress conditions. Also, Chrysargyris et al. [4] mentioned that high salinity (100 mM) trimmed oil yield of *Lavandula angustifolia* as compared with control and low saline levels (25–50 mM).

The stimulation of French lavender essential oil percentage in response to medium saline conditions may be ascribed to an increment in glandular hair number and their densities, as well as the role of secondary metabolites involving essential oil as a self-defense component versus stress conditions [2]. The rise in oil content noticed in plants under salt stress may be attributed to the cutback of the primary metabolites as a result of salinity impacts which, in turn, releases intermediary compounds that facilitate the synthesis of secondary metabolites.

Additionally, the changes in essential oil yield may also be due to herb dry weight variations in plants exposed to irrigation with saline water. Furthermore, the role of GABA application on essential oil yield may be due to photosynthetic pigment enhancement, which produced more metabolites being available to be transformed into essential oil.

3.7. Changes in Antioxidant Activity

Antioxidant enzyme activities (peroxidase, catalase, and polyphenol) were significantly surged in moderately salt-stressed (1000 and 2000 ppm) and declined in severely salt-stressed (3000 ppm) plants as compared with control (Figure 5a–f; Table S3). Additionally, the application of external GABA to plants markedly boosted the efficacy of selected enzymes in plants exposed to salinity conditions. In plants exposed to a combination of 2000 ppm saline water and 20 or 40 mM GABA, there was a noticeable amplification in the activities of antioxidant enzymes, such as polyphenol, peroxidase, and catalase. Our findings of augmented antioxidant enzymes potential under saline conditions concur with those of Alqarawi et al. [41] for *Cassia italica*, Wang et al. [7] for *Zea mays* L., Chrysargyris et al. [4] for *Lavandula angustifolia*, Sheteiwy et al. [19] for *Oryza sativa* L., Szekely-varga et al. [42] for *Lavandula angustifolia*, and Ullah et al. [36] for *Cyperus esculentus*.

Salinity induces the formation of reactive oxygen species which can be eliminated via antioxidant enzyme activity (peroxidase, catalase, and polyphenol) and play a crucial role in protecting plants from cellular damage resulting from oxidative stress. In our results, GABA-treated plants displayed elevated antioxidant activity and hence mitigated the detrimental impacts of salinity which is repeatedly described in previous studies. For instance, in *Cassia italica* Alqarawi et al. [41], reported that antioxidant enzyme activities (catalase, ascorbate peroxidase, peroxidase, and polyphenol oxidase) were remarkably intensified in plants subjected to 250 mM NaCl + 50 mM GABA. As claimed by Wang et al. [7], in maize plants, all enzyme activities were significantly boosted in GABA-treated plants under salinity stress conditions. It has been demonstrated that the application of GABA to lettuce plants provoked an advancement in their ability to withstand salt stress. This advancement is attributed to the increased activities of catalase and ascorbate peroxidase enzymes. Thus, this finding is significant, as it suggests that GABA plays a vital role in regulating the redox state of the plants and preventing the excessive accumulation of ROS [35]. Additionally, Sheteiwy et al. [19] showed that priming rice seeds with 0.5 mM GABA upgraded the efficacy of catalase, polyphenol oxidase, and ascorbic peroxidase enzymes as compared to the unprimed rice seeds. Also, the authors assumed that the application of 0.5 mM GABA could regulate the antioxidant enzymes efficacy, which played a profound role in scavenging H_2O_2 and helping to minimize excessive ROS levels in the stressed plants.

Hence, it boosts a defense mechanism against oxidative stress via upregulation of phenylalanine ammonia lyase, polyphenol oxidase, and shikimate dehydrogenase activity in rice seedlings exposed to salinity. In saffron plants, the foliar application of GABA substantially fortified salt resistance by triggering antioxidant defense mechanisms [21]. Also, it was stated that GABA supplementation at 50 mmol/L alleviated the damage symptoms of *Morus multicaulis* seedlings under salt stress and lowered oxidative damage, as well as antioxidant activity [43].

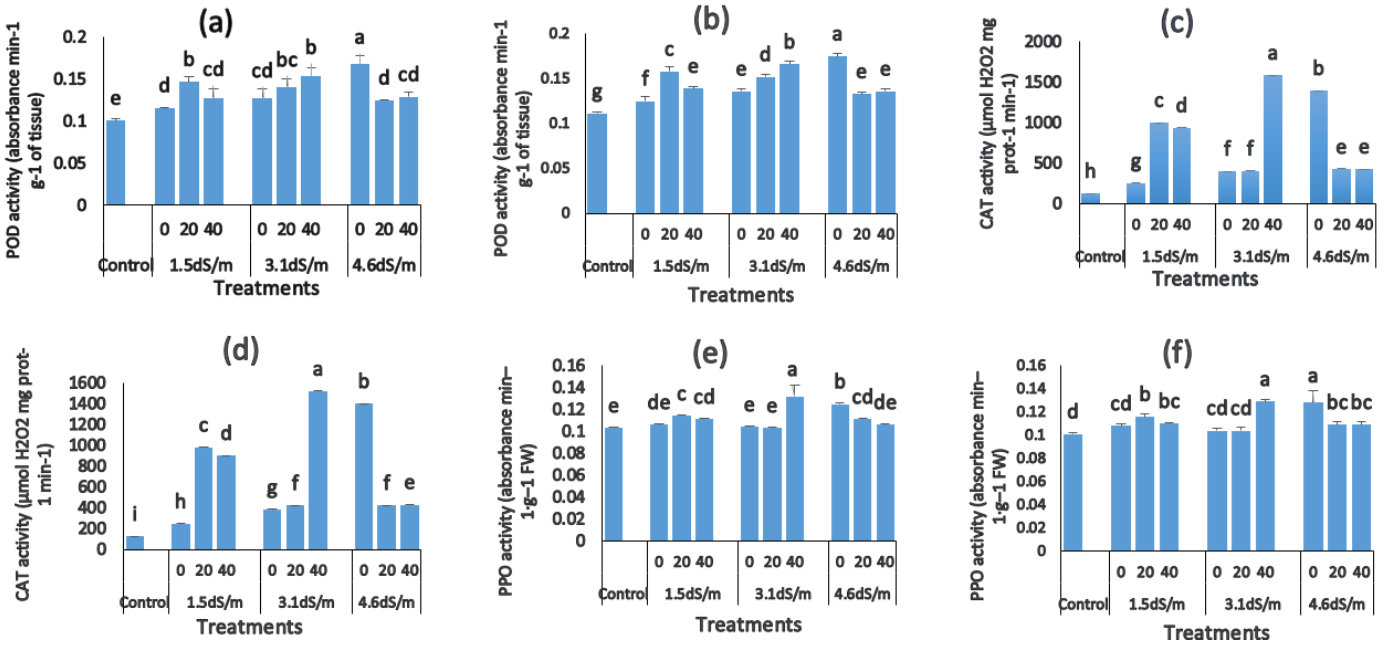

Figure 5. Effect of saline irrigation water and GABA application on peroxidase (POD) activity (**a**) first season, (**b**) second season, catalase (CAT) activity (**c**) first season, (**d**) second season, and (0, 20, 40 gamma-aminobutyric acid) and polyphenol (PPO) activity (**e**) first season, (**f**) second season (1.5, 3.1, 4.6 ds/m saline water treatments) of *Lavandula dentata* L. plants. Means ± SEs, $n = 3$; different letters indicate significant differences ($p \leq 0.05$) between the treatments after performing Duncan multiple range test.

Lately, Ullah et al. [36] proclaimed that the GABA application (2 mM) to the chufa seedlings magnified peroxidase activity exposed to salinity levels (100 and 200 mM NaCl and Na_2SO_4). On the other hand, GABA supplementation did not foster catalase activity under salinity conditions. Furthermore, Ramzan et al. [39] divulged that GABA application promoted salt tolerance of *C. annuum* L. by reinforcing peroxidase and catalase enzyme activities.

4. Conclusions

Our results showed that GABA supplementation positively adjusted various physiological and biochemical mechanisms which could alleviate the detrimental impacts of salinity on growth and biomass. It could magnify vegetative root growth characters, photosynthetic pigment content, relative water content, proline concentration, and antioxidant enzyme activity. Based on our outcomes, GABA is an effective growth regulator that alters growth as well as biochemical responses of lavender plants. We thus suggest that the exogenous application of GABA can help the production of lavender plants in salinity-affected soils in arid and semiarid regions through alleviation of the undesirable impacts of saline irrigation water, which is only available from ground water sources. Thus, we suggest that GABA application at 40 mM could be a viable strategy to alleviate the adverse effects of salinity when French lavender plants are irrigated with saline water at 2000 ppm. Potential

studies should delve deeper into the molecular processes underlying GABA's protective benefits in medicinal plants.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae10040410/s1, Table S1. The effect of saline irrigation water and GABA application on chlorophyll (a and b) mg/g F.W and carotenoid content mg/g F.W of *Lavandula dentata* L. leaves during both growing seasons. Table S2. The effect of saline irrigation water and GABA application on relative water content, proline, essential oil percentage, and oil yield of *Lavandula dentata* L. plants. Table S3. The effect of saline irrigation water and GABA application to peroxidase, catalase, and polyphenol activity of *Lavandula dentata* L. plants.

Author Contributions: A.Y.S. and A.N.A. conceived the study, designed, and performed the experiments, and wrote the manuscript. M.A.G. contributed to data analysis, compilation and writing of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding. The APC was funded by UAEU-AUA grant [12R172] received by MAG.

Data Availability Statement: The original contributions presented in the study are included in the article and Supplementary Materials, further inquiries can be directed to the corresponding authors.

Acknowledgments: Authors gratefully acknowledge the El-Kanatar El-Khaireya Experimental Farm for Medicinal and Aromatic Plants, Horticulture Research Institute, Agricultural Research Center, Egypt for providing French lavender transplants.

Conflicts of Interest: The authors declare no competing interests.

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