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# Unravelling the Role of Potassium and Calcium in Stomatal Regulation and Photochemical Efficiency of Olive (*Olea europaea* L.) under Salinity Stress

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**Abstract:** Climate change poses significant threats to the environment and agricultural productivity. To address these challenges, we aimed to enhance tolerance strategies to salinity stress by applying potassium and calcium to two-year-old potted olive plants grown under saline conditions. To better understand the mitigation of the detrimental effects of salinity stress, we elucidated the interaction between physiological and biochemical responses in olive plants. The results demonstrated that the application of calcium and potassium under salinity stress triggered an adaptive physiological response, notably enhancing photosynthetic efficiency, transpiration rate, and stomatal conductance. Under salinity conditions, the levels of neoxanthin and violaxanthin decreased, while their increase was strongly associated with higher potassium and calcium concentrations. Under stress conditions, the decreased photosynthetic efficiency increased sugar levels that may serve as part of the plant's adaptive strategy to cope with stress. Meanwhile, the positive interaction was depicted among the effective quantum yield of photosystem II (PSII), stomatal conductance, and the photosynthetic rate, underscoring the crucial role of potassium and calcium treatments in maintaining plant physiological and biochemical processes under salt stress.

**Keywords:** climate change; photosynthetic efficiency; olive tree; osmoprotectants; stress mitigation

## 1. Introduction

Climate change is predicted to influence biodiversity, food security, and water purity [1]. Temperature, precipitation, and wind are key climate factors affecting soil formation and subsequent development. Studies have shown that climate change increases salinization, which could affect soil characteristics [2], with over 7% of global land impacted by salinity [3]. Numerous studies have documented the negative effects of salinity on plant physiological and metabolic processes, depending on salt concentration, exposure duration, and plant cultivar [4,5]. In Mediterranean regions, water scarcity has led to the frequent use of saline water for irrigation in olive orchards, as olive trees exhibit moderate tolerance to salinity [6]. In Tunisia, sustainable agriculture is increasingly threatened by severe water shortages, which require careful management to maintain olive production, particularly in arid and semi-arid areas. Consequently, olive trees are often irrigated with brackish water, especially in coastal

and arid regions of the country [7]. It is well documented that the controlled application of saline water can enhance olive tree production within specific salinity thresholds [8]. However, the critical situation of climate change worsens water scarcity for irrigation, leading to an increase in saline lands [9].

Based on these challenges, plants exhibit several adaptive metabolic and physiological mechanisms as defense strategies to mitigate the harmful effects of salinity stress. The adaptation strategy was depicted through the tolerance to osmotic stress by an increase in leaf area, explained by $Na^+$ exclusion from roots and leaf blades, as well as tissue-specific tolerance to accumulated ions, particularly in response to elevated levels of sodium or, in certain species, chloride ($Cl^-$). These physiological adaptations contribute to coping under saline conditions [8]. Several research studies have demonstrated the importance of nutrients as a supplement to mitigate the effects of salt stress in various crops, including olive trees [10], as well as other crops [11]. Potassium (K) and calcium (Ca) supplementation play a crucial role in enhancing physiological functions and alleviating the detrimental effects of salinity, making them essential for improving olive productivity under salt-affected soils [4,7,10].

Potassium is vital for numerous physiological processes, including stomatal regulation, photosynthesis, translocation of photosynthates, enzyme activation, osmoregulation, stress resistance, and fruit quality improvement. Under saline conditions, olive trees often suffer from potassium deficiency, which negatively affects growth. Maintaining adequate potassium levels is therefore critical for plant survival under salt stress, as supplemental potassium helps regulate the $K^+/Na^+$ ratio as a key indicator of salt tolerance and improves the plant's ability to mitigate salinity conditions [3–10].

Similarly, calcium plays a vital role in plant physiology, with one of its most critical functions being the regulation of stomatal responses. As a key signaling molecule, calcium mediates the opening and closing of stomata in response to various abiotic stresses. In addition to this primary regulatory role, it also contributes structurally by reinforcing cell walls and supporting overall plant development. Its protective role against salinity has been well documented in olive and other crops, where it reduces sodium toxicity and supports nutrient balance under saline conditions [3,10–12].

Olive (*Olea europaea* L.) is an essential agricultural crop with significant economic and nutritional values, particularly in Mediterranean regions. However, environmental stressors, particularly salt stress, are exacerbated by climate change. Rising temperatures and changing precipitation patterns contribute to the salinization of soil and water resources, which can reduce agricultural yields and threaten food security. Previous studies have shown that salinity negatively affects olive tree growth, with significant reductions in internode length, smaller leaves with thickened mesophyll and cell walls, as well as a decline in blooming, leading to a lowering of fruit number [13]. In fact, the long-duration of salt stress exerts cumulative detrimental effects on olive plants, progressively impairing physiological functions and leading to visible foliar symptoms such as chlorosis, necrosis, and premature leaf abscission [14]. These disorders reflect the plant's ability to maintain ionic balance and membrane integrity under sustained saline conditions [10]. The dropping leaves' response to salinity stress was explained as the last defense mechanism against high salt concentrations, marked by a reduction in transpiration rate resulting in an accumulation of toxic ions in the leaves, like Na and Cl [15]. Overall, olive trees are moderately tolerant to salinity, with a marked difference in morphological and pomological traits among cultivars, influencing their adaptability and productivity [16].

Despite the identified strategies to mitigate the salinity stress on different crop productivity, the defence and mitigation mechanisms are not well understood, particularly in olive trees. To achieve this objective, we revealed the physiological and biochemical mechanisms in olive plants (cv. Arbequina I18) grown under saline conditions alleviated with two levels of K (10 and 40 mM $KNO_3$) and Ca (10 and 40 mM $CaCl_2$). Understanding alleviation mechanisms through studying biochemical and physiological interactions will develop sustainable agricultural practices to boost olive production in a challenging environment.

## 2. Materials and Methods

### *2.1. Plant Material and Experimental Design*

The experiment was carried out in a research greenhouse under controlled conditions to reveal the physiological and biochemical mechanisms of the olive plant according to our previous experiment set [10]. Two-year-old own-rooted olive trees were grown in 20 L plastic pots filled with a sand-perlite mixture (1:1). Following transplantation, plants were irrigated daily with 500 mL of a half-strength Hoagland nutrient solution [10]. Plants were acclimated for three months under these conditions. After the acclimation period, salinity treatments were initiated. Control plants were irrigated with the same nutrient solution containing 0.5 mM NaCl. Salinity stress was applied by supplementing the nutrient solution with NaCl at concentrations of 100 or 200 mM. Simultaneously, the supplementary $KNO_3$ and $CaCl_2$ at two doses of 10 and 40 mM were applied in conjunction with the saline solution for 23 months. Thus, nutrient treatments began at the same time as salinity treatments. Throughout the experimental period, plants were irrigated daily (except Sundays) with 500 mL of the appropriate treatment solution. Irrigation volumes were adjusted

according to substrate full capacity (FC), measured periodically via pot weight differences, maintaining substrate moisture at 80–90% FC without drainage. Irrigation doses varied seasonally: 0.5 L from October to February, 1 L from March to June, and 1.5 L from July to September. The physiological and biochemical analyses were performed at the end of the experiment. During the experimental period, the average minimum and maximum air temperatures were respectively 15 and 25 °C. The minimum air temperature of the coldest month (January) was 6.9 and 7.9 °C, respectively, and the maximum air temperature of the hottest month (August) was 32 and 32.3 °C during experimentation. The experiment was designed as a randomized complete block with ten replicates. Each block had two rows of five pots each (see Figure 1 for more details).

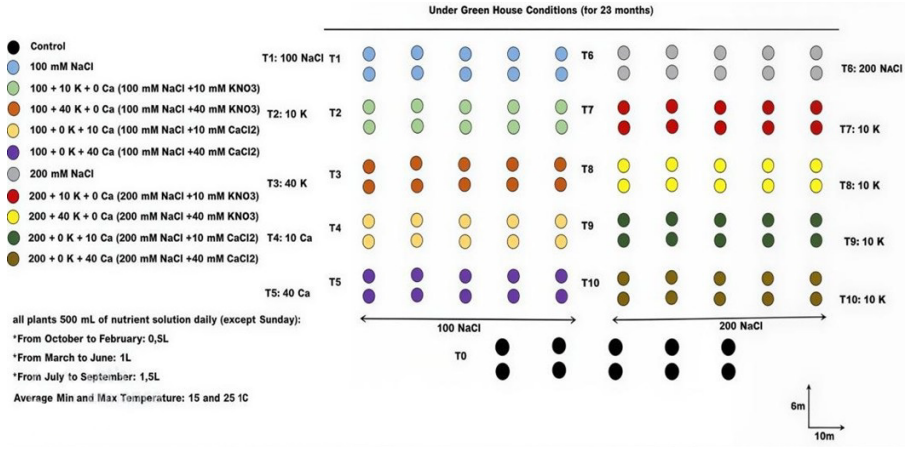


**Figure 1.** Experimental design.

### *2.2. Gas Exchange Measurements and Water Use Efficiency (WUE)*

At the end of the experiment, net photosynthetic rates (A), stomatal conductance (Gs), and transpiration rate (E) were recorded for each plant on three to five well-exposed and fully expanded leaves using a portable photosynthesis system (LI-COR Inc. 6200, Lincoln, NE, USA).

Water use efficiency (WUE) was measured as an A/E ratio. These measurements were taken on a sunny day from 8:00 to 10:00 a.m., at a saturating photon flux density (PPFD) of 1400 µmol·m$^{-2}$·s$^{-1}$, [$CO_2$] of 380 ppm, with an average temperature of 28 ± 2 °C and relative humidity ranging between 45 and 55%.

### *2.3. Modulated Chlorophyll Fluorescence Analyses*

Modulated Chl fluorescence measurements were made in attached leaves in the plastic greenhouse with a PAM2100 portable fluorometer (H. Walz, Effeltrich, Germany). The minimum fluorescence yield ($F_o$) was measured by switching on the modulated light at 0.6 kHz, with a photon flux density (PPFD) lower than 0.1 µmol·m$^{-2}$·s$^{-1}$ at the leaf surface. The maximum fluorescence yield ($F_m$) was measured at 20 kHz with a 1s saturating pulse of 6000 µmol photons·m$^{-2}$·s$^{-1}$ of white light. During light-adapted measurements, leaves were exposed to a constant actinic light intensity of approximately 1000 µmol·m$^{-2}$·s$^{-1}$, representative of high irradiance conditions for olive leaves. Under actinic illumination, the steady-state fluorescence ($F_s$) and the maximum fluorescence in the light-adapted state ($F_m'$) were recorded. The effective quantum yield of PSII photochemistry (ΦPSII) was calculated according to Genty et al. [17] as $(F_m' - F_s)/F_m'$. Non-photochemical quenching (NPQ), reflecting the thermal dissipation of excess excitation energy, was calculated according to Bilger and Björkman [18] as $(F_m - F_m')/F_m'$.

This experiment was recorded at the end of the experiment and is similar to the photosynthesis measurement, using the same fully expanded leaves.

### *2.4. Photosynthetic Pigment Composition*

Leaf disks were taken from the same area of the leaves in which gas exchange and modulated Chl fluorescence were measured [19]. Pigment extracts were thawed on ice, filtered through a 0.45 µm filter, and analysed by an isocratic HPLC method. Pigments were identified by comparison of their retention times and ultraviolet–visible (Waters UV–vis diode array detector) absorption spectra with those of pure standards. The mobile phase A (acetonitrile:methanol, 7:1 *v*:*v*) was pumped for 3.5 min, and then the mobile phase (acetonitrile:methanol:water:ethyl acetate, 7:0.96:0.04:8 by volume) was pumped for 4.5 min. Quantification was based on peak area measurements at 450 nm. Multipoint calibrations were performed for all pigments.

### *2.5. Soluble Sugar and Proline*

Proline contents were extracted from the fresh tissues of roots, stems, and leaves with 4 mM sulphosalicylic acid and centrifuged at 3000× *g* for 30 min. At the end of the experiment, the proline level was measured according to Bates et al. [20].

Soluble sugar was estimated according to the Robyt and White [21] method. The fresh olive leaves, stems, and roots were boiled for 30 min in 80% methanol at 70 °C. The obtained extract was combined with phenol in the range of 1:1 and mixed with 5 mL of concentrated sulphuric acid. After agitation and cooling, the absorbance was determined using a spectrophotometer at 640 nm. The soluble sugar concentration was determined using glucose solutions to develop a standard curve.

### *2.6. Statistical Analysis*

Data collected during the experiment were subjected to one-way analysis of variance (ANOVA) using the PC software package SPSS (version 20.0; SPSS Inc., Chicago, IL, USA). The mean values were compared using Duncan's multiple range test ($p < 0.05$).

## 3. Results

### *3.1. Gas, Exchange, and Water Use Efficiency*

Salinity stress influenced the physiological key mechanisms of olive plants, especially the photosynthesis rate, stomatal conductance, and transpiration, with an average reduction of 70%, 36.7%, and 44.5%, respectively, compared to the control. Thus, the water use efficiency was marked by an average decrease of 44.3% under both salinity doses (Figure 2). Overall, $KNO_3$ or $CaCl_2$ enhanced the physiological mechanisms of olive plants under saline treatments. It was noted that the best alleviation was induced by 40 mM $KNO_3$ and 10 mM $CaCl_2$, which was marked by an enhancement of photosynthetic rate and stomatal conductance by an average increase of 73.4% and 31%, respectively, under 200 mM NaCl. The same applied doses of potassium and calcium induced a medium effective impact for improving transpiration rates and Water Use Efficiency by a respective increase of 50.25 and 45.65% under 200 mM NaCl (Figure 2).

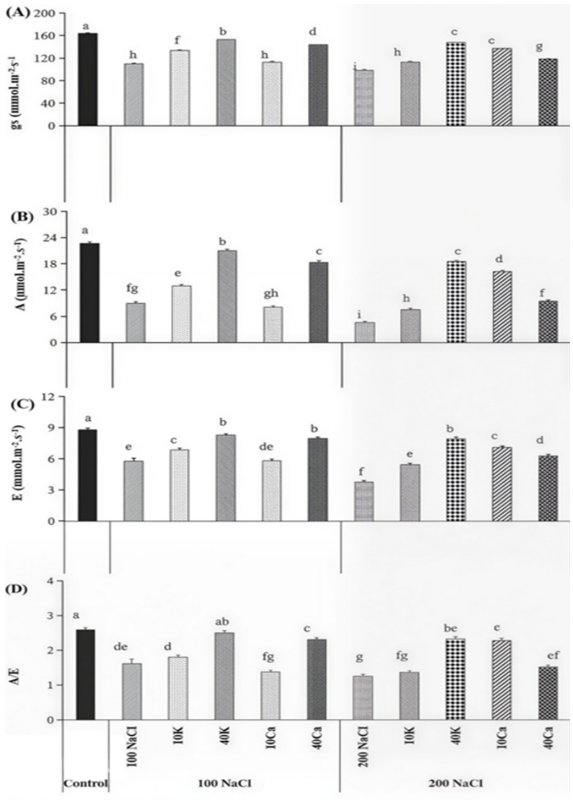


**Figure 2.** Stomatal conductance (gs) (**A**), photosynthetic rate (A) (**B**), transpiration (E) (**C**), water use efficiency (A/E) (**D**), in ArbequinaI18 olive plants under NaCl (100 and 200 mM), supplemented with potassium (10 and 40 mM $KNO_3$) and calcium (10 and 40 mM $CaCl_2$). The bars on each column show standard error. Values ($N = 5 \pm$ S.E.). Different letters in columns indicate significant differences among treatments at $p < 0.05$.

### *3.2. Impact on Chlorophyll Fluorescence*

The control of olive leaves had the maximal photochemical efficiency of PSII measured as Fv/Fm values of 0.8. Salinity stress significantly decreased this ratio with registered values of 0.76 and 0.73 at 100 and 200 mM NaCl, respectively (Figure 3A). The application of potassium and calcium alleviated the salinity stress, in which the Fv/Fm value was markedly approached to the control value through the application of 40 mM K under a salt concentration of 100 mM (Figure 3A). The effective quantum yield of PSII (ΦPSII) was influenced by salinity with a significant decrease of 44% and 62% at 100 mM and 200 mM NaCl, respectively (Figure 3B). This effect was related to a substantial reduction in the efficiency of excitation energy capture by open PSII reaction centers, which was depicted by an average decrease of 40.5% for Φexc and photochemical quenching (qP) under salinity doses. In contrast, plants cultivated in the presence of K and Ca showed a slight decrease in the amount used and captured within the electron transfer chain (Figure 3C,D) compared to the control. Contrary to all the mentioned fluorescence parameters, salinity stress significantly enhanced the non-photochemical quenching (NPQ) by an average increase of 67% under salt stress (Figure 3E).

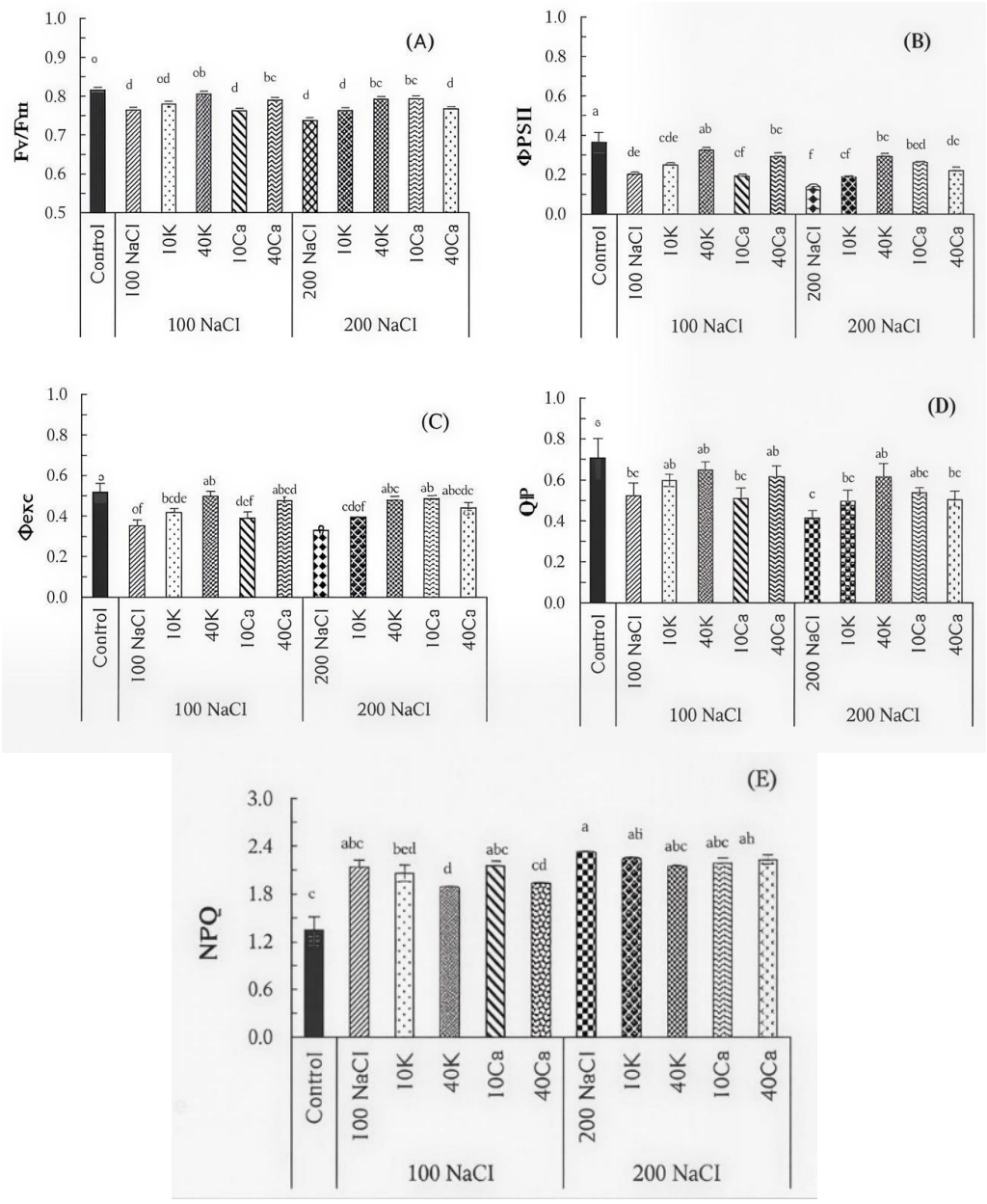


**Figure 3.** Maximum quantum efficiency of photosystem II (Fv/Fm) (**A**); effective quantum yield of PSII (ΦPSII) (**B**); excitation energy transfer efficiency (Φexc) (**C**); photochemical quenching (QP) (**D**); and non-photochemical quenching (NPQ) (**E**) of ArbequinaI18 cultivar under NaCl (100 and 200 mM) supplemented with potassium (10 and 40 mM $KNO_3$) and calcium (10 and 40 mM $CaCl_2$). The bars on each column show standard error. Values ($N = 5 \pm$ S.E.). Different letters in columns indicate significant differences among treatments at $p < 0.05$.

### *3.3. Soluble Sugar and Proline Accumulation*

A significant increase in proline and soluble sugar contents was recorded in the different parts of the olive tree (Figure 4). It was noted that olive leaves accumulate the highest level of soluble sugars compared with the other tissues under salinity stress and compared to the control (Figure 4A). This level was significantly accumulated in old leaves by 87.37 μmol·g$^{-1}$ at 200 mM NaCl rather than at 100 mM NaCl with a 59.65 μmol·g$^{-1}$ level. The lowest accumulation of soluble sugar was recorded in stems by values that did not exceed 10.28 μmol·g$^{-1}$ at 200 mM compared to the control (5.64 μmol·g$^{-1}$). However, this increase in the accumulation levels of soluble sugar was decreased through the potassium and calcium applications in all plant parts compared to plants grown under salt stress. The highest marked enhancement of soluble sugars was recorded in young and old leaves, an increase of 7.8% at the lowest dose of potassium (10 K) and calcium (10 Ca) under 100 mM NaCl (Figure 4A).

The proline content was markedly influenced, especially in old leaves, with an increase of 4.4 times under salt stress compared to the control. While the lowest level was recorded in stems with an accumulation of 0.67 μmol·g$^{-1}$, under salt stress, compared to the control (0.32 μmol·g$^{-1}$) (Figure 4B). Besides that, the applied potassium and calcium decreased the proline accumulation in all plant organs under salt stress. This decrease was markedly noted in young leaves and thin stems by an average reduction of 30.3% at 40 mM $KNO_3$ under salinity doses. In the medium roots, the decrease was markedly depicted at 40 mM $CaCl_2$ in plants grown at 100 mM NaCl, while at 10 mM $CaCl_2$, the proline level increased in all plant parts. At 200 mM NaCl, the proline content was significantly reduced in thin and medium roots by an average reduction of 38.6% at 10 mM $CaCl_2$ (Figure 4B).

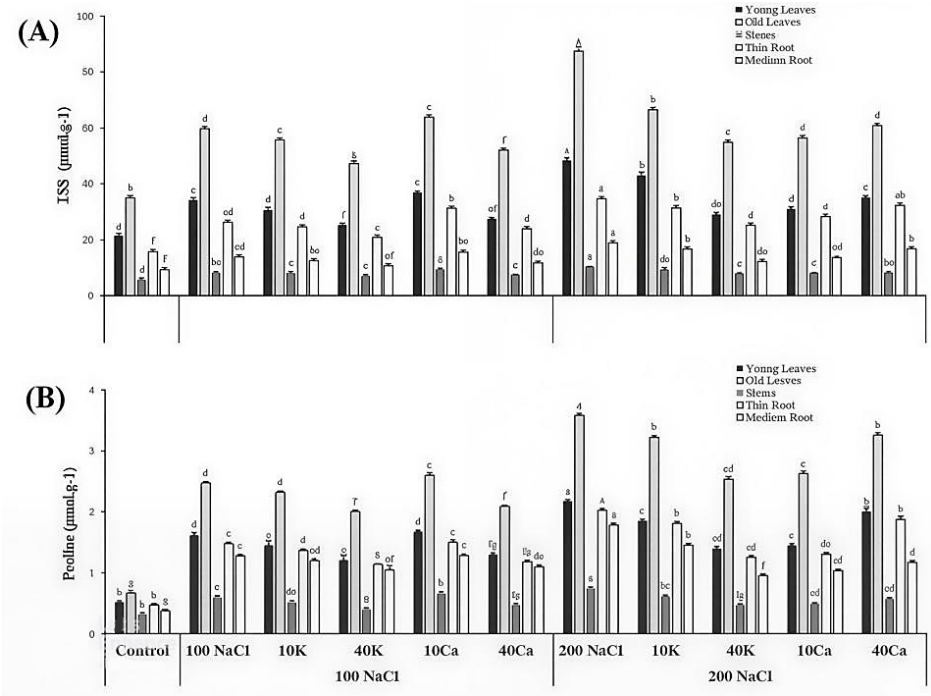


**Figure 4.** Total soluble sugar (TSS) (**A**), and proline contents (**B**) of Arbequina I18 cultivars under NaCl (100 and 200 mM), supplemented with potassium (10 and 40 mM $KNO_3$) and calcium (10 and 40 mM $CaCl_2$). The bars on each column show standard error. Values ($N = 5 \pm$ S.E.). Different letters in columns indicate significant differences among treatments at $p < 0.05$.

### *3.4. Photosynthetic Pigments*

The obtained results from this experiment showed that 100 and 200 mM NaCl salinity reduced photosynthesis pigments, including chlorophyll a (chla), chlorophyll b (chlb), total chlorophyll (chla + b), and total carotenoid (car) in comparison to the control (Table 1). Potassium and calcium-treated plants showed higher photosynthetic pigment contents compared to plants grown under saline stress. The highest levels were obtained at 40 mM $KNO_3$ and 40 mM $CaCl_2$ at 100 mM NaCl. Besides that, salinity stress decreased the neoxanthin (N) and violaxanthin (V) pigments, while an increase of anteraxanthin (A), lutein (L), β carotene (C), and zeaxanthin (Z) was observed only under 200 mM NaCl (Table 1). Potassium and calcium supplies improved these pigments, which are related to treatments. The total pool of xanthophyll cycle pigments (VAZ, sum of violaxanthin + antheraxanthin and zeaxanthin) increased under a high salinity dose. On the other hand, potassium and calcium induced a marked decrease under both salt treatments, but to different extents among treatments. In addition, the salinity increased

the lutein and chlorophyll ratio and carotene and chlorophyll ratio by 27.75 and 32.86%, respectively, at salinity doses. Salinity increased the (V + A+ Z)/Chl ratio by 15.45 and 28.46% at 100 mM and 200 mM NaCl, respectively, but it was decreased by potassium and calcium applications (Table 1).

**Table 1.** Total Chl (Chl a + b) (mg·g$^{-1}$·FW), Chl a/b, β-carotene (mmol·pigment·m$^{-2}$), lutein (mmol·pigment·m$^{-2}$), neoxanthin, and violaxanthin + antheraxanthin + zeaxanthin (VAZ) (mmol·pigment·m$^{-2}$). Lutein/Chl and V + A + Z/Chl (mol·pigment·mol$^{-1}$·Chl).

| Treatments | Total Chl | Chl a/b | β-Carotene | Lutein | Neoxanthin | VAZ | (A + Z)/ (V + A+ Z) | Lutein/Chl | V + A+ Z/Chl |
|---|---|---|---|---|---|---|---|---|---|
| Control | 655 ± 10 $^{bc}$ | 2.54 ± 0.67 $^{a}$ | 54 ± 90 $^{a}$ | 91 ± 17 $^{a}$ | 31 ± 50 $^{abc}$ | 63 ± 16 $^{a}$ | 0.17 ± 0.04 $^{cd}$ | 0.14 ± 0.01 $^{abc}$ | 0.09 ± 0.01 $^{ab}$ |
| 100 NaCl | 556 ± 44 $^{c}$ | 3.18 ± 0.39 $^{a}$ | 61 ± 19 $^{abc}$ | 98 ± 18 $^{a}$ | 26 ± 00 $^{abcd}$ | 60 ± 12 $^{a}$ | 0.28 ± 0.08 $^{abc}$ | 0.18 ± 0.01 $^{abc}$ | 0.11 ± 0.02 $^{ab}$ |
| 100NaCl–10 K | 588 ± 73 $^{c}$ | 2.87 ± 0.35 $^{a}$ | 61 ± 29 $^{abc}$ | 109 ± 33 $^{a}$ | 27 ± 90 $^{abcd}$ | 61 ± 21 $^{a}$ | 0.26 ± 0.09 $^{bcd}$ | 0.18 ± 0.04 $^{abc}$ | 0.10 ± 0.02 $^{ab}$ |
| 100NaCl–40 K | 652 ± 74 $^{bc}$ | 2.66 ± 0.82 $^{a}$ | 57 ± 50 $^{ab}$ | 93 ± 13 $^{a}$ | 29 ± 00 $^{abcd}$ | 60 ± 90 $^{a}$ | 0.24 ± 0.08 $^{bcd}$ | 0.14 ± 0.04 $^{abc}$ | 0.09 ± 0.02 $^{ab}$ |
| 100NaCl–10 Ca | 894 ± 23 $^{ab}$ | 3.05 ± 0.14 $^{a}$ | 73 ± 38 $^{ab}$ | 98 ± 34 $^{a}$ | 21 ± 30 $^{cd}$ | 47 ± 21 $^{a}$ | 0.11 ± 0.09 $^{d}$ | 0.12 ± 0.07 $^{bc}$ | 0.06 ± 0.03 $^{b}$ |
| 100NaCl–40 Ca | 627 ± 16 $^{c}$ | 2.74 ± 0.71 $^{a}$ | 49 ± 11 $^{ab}$ | 94 ± 50 $^{a}$ | 35 ± 13 $^{ab}$ | 60 ± 13 $^{a}$ | 0.26 ± 0.08 $^{bcd}$ | 0.15 ± 0.05 $^{abc}$ | 0.10 ± 0.01 $^{ab}$ |
| 200NaCl | 552 ± 98 $^{c}$ | 3.32 ± 0.62 $^{a}$ | 70 ± 11 $^{c}$ | 116 ± 23 $^{a}$ | 18 ± 90 $^{d}$ | 68 ± 15 $^{a}$ | 0.42 ± 0.07 $^{a}$ | 0.21 ± 0.07 $^{a}$ | 0.13 ± 0.04 $^{a}$ |
| 200NaCl–10 K | 620 ± 87 $^{c}$ | 3.10 ± 0.19 $^{a}$ | 67 ± 90 $^{bc}$ | 105 ± 50 $^{a}$ | 31 ± 30 $^{abc}$ | 79 ± 59 $^{a}$ | 0.25 ± 0.13 $^{bcd}$ | 0.17 ± 0.03 $^{abc}$ | 0.12 ± 0.07 $^{a}$ |
| 200NaCl–40 K | 961 ± 24 $^{a}$ | 3.05 ± 0.13 $^{a}$ | 47 ± 16 $^{abc}$ | 98 ± 70 $^{a}$ | 38 ± 80 $^{a}$ | 57 ± 10 $^{a}$ | 0.23 ± 0.04 $^{bcd}$ | 0.11 ± 0.03 $^{bc}$ | 0.06 ± 0.02 $^{b}$ |
| 200NaCl–10 Ca | 1031 ± 11 $^{a}$ | 3.08 ± 0.02 $^{a}$ | 57 ± 11 $^{abc}$ | 103 ± 60 $^{a}$ | 35 ± 40 $^{ab}$ | 60 ± 10 $^{a}$ | 0.25 ± 0.05 $^{bcd}$ | 0.10 ± 0.01 $^{c}$ | 0.06 ± 0.00 $^{b}$ |
| 200NaCl–40 Ca | 587 ± 10 $^{c}$ | 3.22 ± 0.07 $^{a}$ | 69 ± 17 $^{ab}$ | 105 ± 11 $^{a}$ | 23 ± 40 $^{bcd}$ | 68 ± 17 $^{a}$ | 0.36 ± 0.08 $^{ab}$ | 0.18 ± 0.04 $^{ab}$ | 0.11 ± 0.01 $^{ab}$ |

Values ($N$ = 5 ± S.E.). Means followed by different letters (a, b, c, d) within the same column are significantly different ($p$ < 0.05).

### *3.5. Physiological and Biochemical Interactions*

Overall, this study highlights the importance of the positive interaction between the effective quantum yield of PSII (ΦPSII), stomatal conductance (Gs), and photosynthetic rate (A), to adapt plants for maintaining their physiological and biochemical processes (Figure 5). This positive correlation between photosynthetic rate and Gs can indicate how effectively plants can regulate their stomatal openings to optimize carbon dioxide uptake and water conservation under salinity stress (Figure 5a,b). This study has shown that higher Gs correlate with increased ΦPSII, as stomatal opening ensures a continuous supply of $CO_2$ for photosynthesis. A clear negative correlation was found between photosynthetic rate and osmoprotectant molecules such as proline and sugar (Figure 5c–f). Understanding this relationship led researchers to develop strategies to improve plant tolerance to salinity stress and enhance crop productivity.

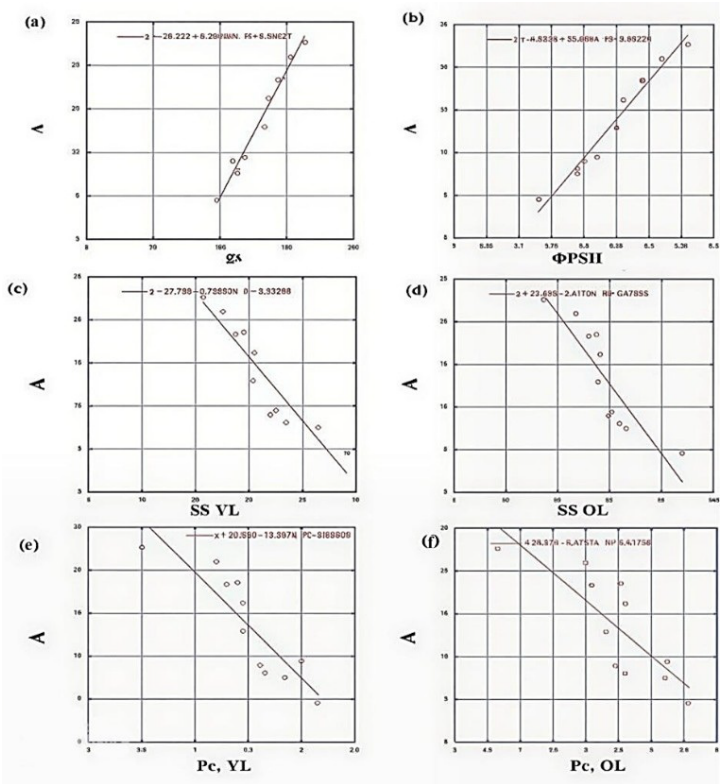


**Figure 5.** Interactions with photosynthetic rate (A), stomatal conductance (gs), and osmoprotectant (SS: soluble sugar; Pr: proline); OL: Old leaves; YL: Young leaves; (**a**): A/gs; (**b**): A/ ΦPSII; (**c**): A/SS YL; (**d**): A/SS OL; (**e**): A/Pr YL; (**f**): A/Pr OL.

## 4. Discussion

Salinity stress adversely affects plant productivity by reducing growth and yield, primarily through decreased carbon fixation caused by stomatal closure, restricted photosynthesis, impaired osmotic adjustment, and nutritional imbalances [10] (Figure 6). Similar detrimental effects of salinity on plant physiological processes have been widely reported in olive trees [4,7,10,22]. The reduction in photosynthesis under salt stress may be attributed to both stomatal and non-stomatal limitations. Salinity exerts direct effects on chlorophyll content and photosynthetic efficiency by altering the activity and expression of enzymes involved in chlorophyll biosynthesis and photosynthesis, while indirect effects occur through specific regulatory pathways, including those associated with antioxidant enzyme systems [7–10]. These physiological responses are consistent with our previous findings [10], where prolonged exposure to saline solutions for 23 months resulted in a significant reduction in shoot dry weight relative to root biomass**,** indicating a higher sensitivity of aerial tissues to salinity stress**.** Overall, these results suggest that although olive trees exhibit a general tolerance to long-term saline conditions, pronounced physiological impairments are clearly induced.

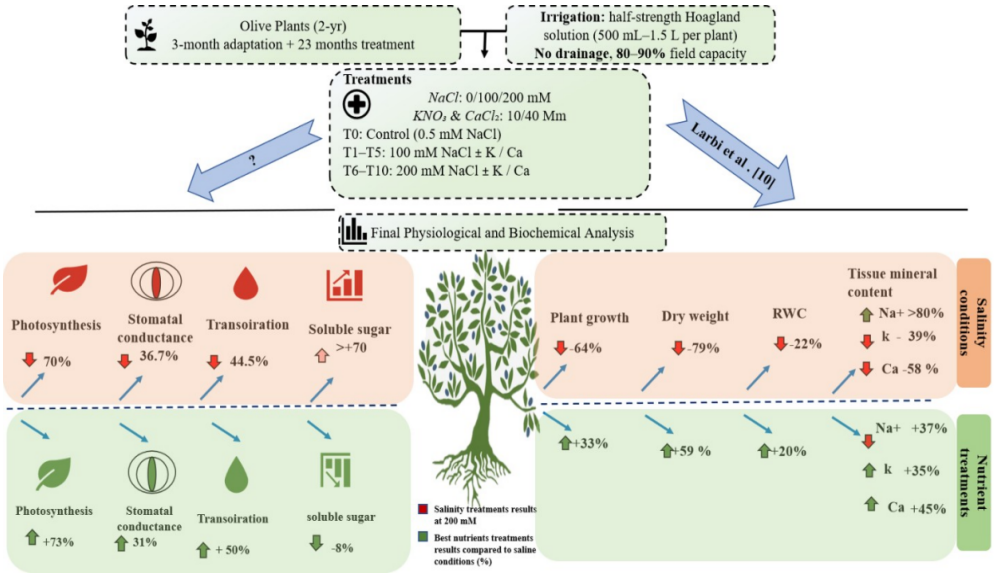


**Figure 6.** Effects of potassium and calcium on the biochemical and physiological responses of ArbequinaI18 cultivar under NaCl (200 mM).

According to our previous results [10], the application of potassium (as $KNO_3$) and Calcium (as $CaCl_2$) is considered an effective strategy to alleviate the negative effects of salinity in olive plants, by improving growth parameters and maintaining membrane stability. Ion content analysis in roots, stems, and leaves demonstrated that supplementary potassium or calcium mitigated the salinity stress by limiting sodium translocation from roots to shoots and enhancing sodium exclusion at the root level. Additionally, the present study aimed to investigate the role of physiological and biochemical interactions in salt stress mitigation in olive plants. Our results are consistent with those reported by Chartzoulakis et al. [23], who demonstrated that the potassium at 100 mM increased photosynthesis activity in olive leaves. Similarly, Cha-um et al. [24] showed that the low level of potassium maintained the stabilization of photosynthetic pigments in rice, leading to improved growth under 200 mM NaCl stress. From a physiological perspective, potassium plays a central role in the osmotic regulation of guard cells, thereby controlling stomatal movement and facilitating $CO_2$ diffusion into the leaf, which ultimately enhances photosynthetic carbon assimilation [23]. In agreement with this mechanism, Jafari et al. [25] showed that calcium supplementation markedly increased the photosynthetic rate in sorghum exposed to 80 mM NaCl, with values rising from 17.5 to 27.4 μmol $CO_2$ $m^{-2} \cdot s^{-1}$, highlighting the role of calcium in alleviating salt stress. In addition, potassium is widely recognized as an essential macronutrient for plant growth and for maintaining ionic and nutritional balance, particularly under salinity stress conditions, where it helps counteract sodium toxicity and preserve metabolic functions [26]. Consistent with the observed decline in photosynthetic rate, stomatal conductance was also significantly reduced under salinity stress compared to control conditions, as previously reported in olive and other crops [7,23,27]. This reduction in stomatal conductance represents a common adaptive response to salinity, aimed at limiting transpirational water loss, although it may concurrently restrict $CO_2$ uptake and photosynthetic performance.

The combination of salinity with the addition of both calcium and potassium supplements to the plants increased stomatal conductance. These findings support our initial hypothesis that extra calcium may ameliorate the effect of salinity on stomatal conductance. Similar responses have been reported in several crops, including rice [28], guava [29], cucumber [30], and endive [31].

It was noted that the reduction in transpiration under salinity stress was closely associated with decreased stomatal conductance. This response reflects a typical stomatal limitation induced by salt stress to reduce water loss. However, supplementary foliar nutrient application partially counteracted this effect and significantly increased the transpiration rate compared to salinity treatment alone. The strongest alleviation was observed with the combined application of 40 mM $KNO_3$ and 40 mM $CaCl_2$ under 100 mM NaCl, indicating an optimal interaction between potassium and calcium in mitigating salinity-induced constraints on gas exchange. Consistent with previous findings, olive trees exposed to salinity stress undergo pronounced physiological alterations, including a marked reduction in the photosynthetic assimilation rate (A), stomatal conductance (gs), and transpiration (E) [32–34]. Our results confirm these trends and further demonstrate that targeted nutrient supplementation can effectively alleviate salinity-induced physiological limitations. Therefore, water use efficiency (WUE) was significantly impacted by salinity stress but showed moderate improvement with the application of 40 mM $KNO_3$ and 10 mM $CaCl_2$. Trabelsi et al. [35], who reported a reduction of WUE in both young and old olive leaves of plants grown under salinity stress, highlighted this effect. Some studies have shown that K plays an important role in growth and water use efficiency in olives [36] and could be useful in ameliorating the biotic stress effect in olive plants [37].

Some studies have shown that salt stress inhibits PSII photochemistry [38]. In the present study, the decline of ΦPSII under salinity conditions might cause excess light energy, which would increase the excitation pressure on PSII, raising the probability of reactive oxygen species (ROS) generation and photo-inhibition of PSII [39]. Such conditions enhance the risk of oxidative damage to the photosynthetic apparatus. The increase in non-photochemical quenching (NPQ) may indicate a reduced demand for the products of electron transport, which are typically utilized for assimilation, leading to the dissipation of excess light energy [40]. This increase in NPQ reflects a protective photoprotective mechanism that allows plants to safely dissipate surplus excitation energy under stress conditions. Potassium and calcium application enhanced the operating yield of PSII and chlorophyll, with the maximum impact observed at 40 mM $KNO_3$ and 40 mM $CaCl_2$ in plants exposed to salt stress. Chlorophyll concentration can be considered ~~used~~ as a sensitive indicator of the cellular metabolic state; therefore, its decrease indicates toxicity in tissues due to the accumulation of ions. The repair of higher chlorophyll levels following potassium and calcium supplementation suggests a mitigation of ion toxicity and preservation of chloroplast integrity. This result agreed with Kaya et al. [41], who found that the chlorophyll concentration was reduced in strawberry plants under 35 mM NaCl compared to the control, while the potassium at 3 mM ($K_2SO_4$) increased the chlorophyll concentration. Besides that, the photosynthetic pigment was influenced by salinity stress and was alleviated by potassium and calcium, which is in agreement with the obtained results of Melgar et al. [22].

The present study showed that the increase in proline content was related to NaCl concentrations. This accumulation reflects a typical osmotic adjustment response of olive trees to increasing salinity stress. Proline could protect the photosynthetic activity of salt-stressed olive trees by regulating hydration and osmotic adjustment, thus promoting growth even under stressful conditions [42–44]. Ben Ahmed et al. [45] noted similar results in olive cv. Chemlali. Furthermore, Poury et al. [46] emphasized that proline accumulation constitutes a key tolerance mechanism developed by plants in response to environmental stresses. Overall, the supplied $KNO_3$ and $CaCl_2$ decreased proline content, with the most pronounced effect observed at 40 mM under 100 mM NaCl, Calcium application effectively alleviated the adverse effects of salinity on proline content, indicating improved stress tolerance and ionic balance [47]. According to Wang et al. [26], the application of potassium significantly reduced the uptake of $Na^+$ and enhanced $K^+$ levels in plants under salinity conditions, thereby improving osmotic regulation and reducing the requirement for excessive proline accumulation. Potassium maintains ionic and osmotic balance in plant cells and reduces the need for proline accumulation as an osmoprotectant. In addition, potassium can enhance the activity of enzymes involved in proline metabolism, promoting the efficient utilization of proline in plants under salt-stress conditions. Proline accumulation in plants was reviewed by [48,49], highlighting the involvement of the key biosynthetic enzyme $\Delta^1$-pyrroline-5-carboxylate synthetase (P5CS) in stress-induced proline upregulation. Potassium-mediated regulation of stress-signaling pathways, including calcium-dependent signaling, may further contribute to the activation of stress-responsive genes and improved salinity tolerance. This increase reflects an adaptive metabolic response that contributes to osmotic adjustment, prevention of tissue dehydration, and protection of cellular structures against oxidative damage under saline conditions [44]. In the present study, the combined application of potassium and calcium under salt stress resulted in a reduction of soluble sugar content in olive tissues, suggesting an alleviation of stress intensity. Farooq et al. [50]

demonstrated that potassium supplementation under salt stress significantly increased soluble sugar content in olive leaves, indicating that potassium can modulate carbohydrate metabolism depending on stress severity and nutritional balance. Zhao et al. [51] highlighted that calcium supplementation increased sugar accumulation by stabilizing cell membranes and promoting the activity of transport proteins involved in sugar movement within the plant. In addition, calcium acts as a secondary messenger, regulating the expression of genes associated with sugar metabolism and stress signaling pathways, thereby contributing to improved stress tolerance.

The recorded positive correlation indicates that higher stomatal conductance (gs) is associated with increased ΦPSII, suggesting a coordinated regulation between gas exchange and photochemical efficiency. Enhanced the stomatal conductance (gs) facilitates $CO_2$ diffusion into the leaf, which can reduce photorespiration and minimize the generation of reactive oxygen species (ROS), thereby protecting PSII and sustaining ΦPSII [52]. While Stomatal conductance is proportional to $CO_2$ concentration and air humidity [53], salinity stress may lead to decreased stomatal conductance as well as chlorophyll content, which negatively affects the photosynthetic efficiency of olive trees [54]. However, potassium and calcium supplementation enhance the interaction between stomatal conductance (gs) and ΦPSII [55]. The detrimental effects of salt on photosynthesis, stomatal conductance, and transpiration rate may be considerably mitigated by adding K and Ca to irrigation solutions [56]. This suggests that the effect of potassium and calcium alleviates salt stress in olive plants and can maintain a higher photosynthetic rate under salinity stress, possibly due to their ability to regulate stomatal conductance more effectively. However, the clear negative correlation between photosynthetic rate and osmoprotectant molecules could be explained by the stomatal closure, reduction of $CO_2$ uptake, or damage to the photosystem II (PSII) [57]. Stress conditions can limit photosynthetic efficiency, causing a rise in sugar levels, which could be part of a plant's stress adaptation strategy, where accumulated sugars help mitigate damage by serving as osmolytes, stabilizing cellular structures, or acting as signals that trigger protective pathways [58]. Overall, the potassium and calcium significantly enhanced the osmoprotectant molecule levels in olive tissues, which are related to salinity tolerance. Moreover, they protect physiological processes against harmful inorganic compounds [59]. In addition, soluble sugar and proline are considered efficient means of preserving the potential of a passive osmotic process in the cytoplasm and in maintaining ribosomes and protein stability against the harmful impacts of $Na^+$ ions.

## 5. Conclusions

Salt stress negatively influences olive trees by affecting physiological and biochemical efficiency. The high salinity levels influence the osmotic stress, resulting in reduced stomatal conductance and impaired gas exchange, ultimately affecting the tree's ability to photosynthesize. Thus, highlighting the effective strategies to enhance salt tolerance in olive trees is critical for maintaining their productivity in increasingly saline conditions. The obtained results confirmed mainly the impact of potassium and calcium supplies in reducing the detrimental effects of salinity in olive trees.

## Author Contributions

A.L. (Ajmi Larbi) and H.B.: conceptualization; A.L. (Ajmi Larbi) and H.B.: methodology; R.L., A.E.K. and F.M.: software; A.L. (Afef Ladhari), H.B. and R.L.: validation; A.L. (Afef Ladhari), R.L., F.M. and A.K.: formal analysis; A.L. (Afef Ladhari), A.E.K. and H.B.: investigation; H.B. and A.L. (Afef Ladhari): data curation; A.L. (Ajmi Larbi), A.E.K. and H.B.: writing—original draft preparation; A.L. (Afef Ladhari), H.B., A.L. (Ajmi Larbi) and A.E.K.: writing—review and editing; A.L. (Ajmi Larbi): supervision; H.B.: project administration; A.K.: funding acquisition. All authors have read and agreed to the published version of the manuscript

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Not applicable.

## Informed Consent Statement

Not applicable.

## Data Availability Statement

All data generated or analyzed during this study are included in this published article.

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## Conflicts of Interest

The authors declare no conflict of interest. Given the role as Editor-in-Chief, Fermín Morales had no involvement in the peer review of this paper and had no access to information regarding its peer-review process. Full responsibility for the editorial process of this paper was delegated to another editor of the journal.

## Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

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