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The influence of rootstock and biostimulants on the dynamics of antioxidant defense mechanisms under salt stress in potted Öküzgözü grapevines (*Vitis vinifera* L.)

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Abstract

Salt stress has become an increasingly serious threat to viticulture due to global climate change and a lack of irrigation resources. Salt accumulated in the soil causes ionic imbalance, osmotic stress and consequently oxidative stress in grapevines, negatively affecting the morphological, physiological and biochemical processes of the plant. The defense responses developed by the plant against these stress conditions may differ largely depending on the rootstock material used and the supporting external applications. In this context, in the study, two different levels of salt stress (Salt 1: 150 mM, Salt 2: 150 mM+150 mM) were applied on three different rootstocks (Ownroot, 1103P and 140Ru) of potted Öküzgözü (*Vitis vinifera* L.) and the effects of biostimulants (*Saccharomyces cerevisiae* and *Ascophyllum nodosum*) on the antioxidant system were investigated under salt stress conditions in 2023 vegetation period. The results showed that rootstocks developed different responses to salt stress and the severity of these responses varied depending on the type of treatment. Total phenolic compound level increased the most in high salt stress and biostimulants balanced this stress. Antioxidant activity, similar to total phenolic compounds and as expected, reached the maximum level at high salt stress and both parameters were highest on the 1103P rootstock. SOD level decreased with increasing salt stress and the highest SOD activity was measured in the control group 140Ru vines. CAT activity reached the highest level in 1103P at high salt stress. CAT and APX activities increased to higher levels with the second salt treatment than the first. The decrease in SOD enzyme more effectively manifested the use of biostimulants against stress, while CAT and APX activities showed an upward trend with the use of biostimulants, while CAT and APX activities showed an upward trend with the use of biostimulants.

Keywords: Antioxidant enzyme, *Saccharomyces cerevisiae*, *Ascophyllum nodosum*, *Vitis vinifera*, 140Ru, 1103P

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INTRODUCTION

The grapevine (*Vitis vinifera* L.), which has thousands of years of agricultural history, shows a high level of ecological adaptability. Although different grape varieties and rootstocks vary in their level of resistance to environmental stress conditions, their ability to adapt to various climatic changes makes this species of strategic importance for global agriculture (Deng et al., 2021; Zhou et al., 2022). Vineyards demonstrate their multifaceted economic importance not only through the production of table, dried and wine grapes, but also through their rich content of biological compounds that can be utilized in various sectors such as food, pharmaceuticals, cosmetics, fertilizers, energy production and functional materials (Baroi et al., 2022).

Climate change, especially temperature increase, is a major challenge for crop production worldwide due to reduced water resources and increased soil salinization (Nikolaou et al., 2021).

Under saline soil conditions, high salt concentrations lead to severe reductions in plant growth and yield. Salt stress triggers the accumulation of reactive oxygen species (ROS), causing damage to cellular structure and impairment of physiological functions, which significantly negatively affects vine yield and quality in viticulture (Meggio et al., 2014; Wei et al., 2023). It is estimated that about 20% of irrigated land worldwide is affected by salinity, which poses a significant threat to agriculture, especially grapevine cultivation (Huo, 2023).

Plants have evolved several defense mechanisms that confer tissue resilience to survive in saline environments (Parida and Das, 2005; Munns et al., 2006). These mechanisms include ion exclusion, vacuolar storage, osmotic compensation (e.g. proline accumulation) and enhancement of enzymatic and non-enzymatic antioxidant defenses (Demiral and Türkan, 2005; Cramer et al., 2007).

In plants, reactive oxygen species such as O_2^- and H_2O_2 are produced during normal metabolic processes (Lacuesta et al., 1997). However, ROS production increases under stress conditions and this balance is controlled by the antioxidant systems of the plant (Ashraf, 2009). It is known that plants with high antioxidant levels are more resistant to salt stress than those with low levels. Major enzymatic defense systems in plants include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR). The cooperation and balanced functioning of these enzymes, especially the interaction between APX and CAT, is critical in limiting the accumulation of toxic ROS (Özden et al., 2009). While CAT, together with SOD, constitutes the most effective defense mechanism (Scandalios, 1993), APX plays an important role in intracellular detoxification by inactivating H_2O_2 through ascorbate (Asada and Takahashi, 1987). Studies have revealed that there are inter-cultivar differences in the antioxidant defense responses of plants under saline conditions (Silveira et al., 2001).

Grapevine is traditionally a non-irrigated crop (Cifre et al. 2005), but in arid climates irrigation strategies are essential to maintain yield and fruit quality (Chaves et al., 2010). Salinity is therefore increased when poor quality irrigation water is used (e.g. borehole water containing significant amounts of salt) and/or when insufficient salt leaching occurs, for example when low irrigation rates are applied, which is typical during drought (Rengasamy, 2006).

In viticulture, soil salinity increases by accumulating in the root zone due to factors such as irrigation water with high salt content, water loss through evaporation and poor drainage (Várallyay, 1994; Phogat et al., 2020; Zhou-Tsang et al., 2021). The detrimental effects of salt stress on plants are mainly mediated by two mechanisms: osmotic stress and ion toxicity. An excess of Na^+ and Cl^- ions disrupts the osmotic balance between the root and soil, limiting water uptake (Abbasi et al., 2016; Raghda'a Ali Al-Khafajy et al., 2020); at the same time, excessive accumulation of these ions leads to ion toxicity by inhibiting the uptake of essential nutrients (Al-Abbassi et al., 2022)

Vines are grown on rootstocks that regulate the interactions between vines and the environment in terms of nutrient uptake, salinity tolerance and water stress tolerance, as well as phylloxera resistance. Rootstocks derived from wild *Vitis* species differ in their ability to exclude Cl^- and Na^+ ions, which determines their level of salinity tolerance. While *V. berlandieri* has a high exclusion capacity, this ability is reduced in rootstocks crossed with *V. vinifera*; therefore, hybrid rootstocks such as 41B show more limited tolerance to salt (Fisarakis et al., 2001).

Biostimulants are agronomic products that have become very important in agriculture because they are formulated with substances that help plants adapt to different environmental conditions and can stimulate physiological and biochemical processes (Wu et al., 2024). Biostimulants are materials that positively affect plant growth, nutrition, product quality and yield; which are applied to plants from leaves, soil or seeds in order to increase the resistance of plants against abiotic stress, which may contain organic or inorganic compounds, microorganisms, some of which also have soil structure regulating effects (Yılmaz and Şensoy, 2021).

The main group of plant biostimulants are humic acid and fulvic acid, protein hydrolysates and other N containing compounds, seaweed extracts and botanical preparations, chitosan and other biopolymers, inorganic compounds, beneficial fungi and bacteria (Du Jardin, 2015). Besides non-microbial biostimulants, microbial biostimulants have also recently been used in agriculture. Microbial inoculants mostly include plant growth-promoting rhizobacteria (PGPR) and endophytic fungi such as arbuscular mycorrhizal fungi and trichoderma and are used as biostimulants (De Pascale et al., 2017).

Seaweed extracts are a large group of macroscopic, multicellular seaweeds that can be brown, red and green. These substrates contain organic matter and fertilizer nutrients. They can improve yield and quality by increasing plant growth, photosynthetic activity and tolerance to biotic and abiotic stresses (Sharma et al., 2014; Bulgari et al., 2019). Seaweeds contain a variety of active minerals and organic compounds that contribute to the growth and development of plants, as well as various hormones (Battacharyya et al., 2015). Especially those from *Ascophyllum nodosum* and *Sargassum spp*. have been effective in conferring resistance to abiotic stresses in plants. These extracts reduce damage due to salt and temperature stresses by lowering leaf osmotic potential and support antioxidant metabolism and vitality (Anjos et al., 2020; El Boukhari et al., 2023).

Although not used as intensively as seaweeds, yeast-based biostimulants have proven to be effective against different plant diseases and have been commercialized as resistance inducers in the context of sustainable

agriculture (Reglinski et al., 1994; Tumpa and Khokon, 2020; Shahzadi et al., 2022). The mechanisms of yeasts as plant protection agents include production of volatile compounds, lethal toxins and lytic enzymes, competition for space and nutrients, mycoparasitism (Kowalska et al., 2022), and induction of plant immunity by triggering complex signaling cascades resulting in activation of complementary defense pathways and Induced Systemic Resistance (ISR) (Moon et al., 2015; Narusaka et al., 2015; Lee at al., 2017).

In our previous study (Karaman et al., 2024), we applied a single dose of 150 mM NaCl to Nero D'Avola cultivar on its own roots and observed the effects of yeast and seaweed In this study, we aimed to determine of the effects of *Ascophyllum nodosum* and *Saccharomyces cerevisiae* as biostimulants against low (150mM) and high salt stress (150 mM + 150 mM) and to compare the antioxidative responses in Öküzgözü cultivar on different roots (ownroot, 1103P, 140Ru).

MATERIALS AND METHODS

Plant Material

The plant material of the research was 2-year-old potted vines of Öküzgözü (*Vitis vinifera* L.) variety in the greenhouse of Ankara University, Faculty of Agriculture, Department of Horticulture. The vines consisted of groups of 16 vines each on their own roots, grafted on 140Ru rootstock (*Vitis berlandieri* × *Vitis rupestris*) and grafted on 1103P rootstock (*Vitis berlandieri* × *Vitis rupestris*). The pots had a volume of 15 liters and were filled with a medium consisting of peat, perlite, coccopite and sand (1:1:1:1, v/v).

Treatments

The Control group consisted of 4 vines on their own roots, grafted on 1103P and 140Ru. Only 200 mL of water was sprayed on the leaves of the Control group on the application dates. Salt+*Saccharomyces cerevisae* vines consisting of 12 vines were sprayed with 400 mg/200 mL *Saccharomyces cerevisiae* yeast (Zymaflore FX 10, Laffrot, France) and Salt+*Ascophyllum nodosum* vines consisting of 12 vines were sprayed with 0.4 mL /200 mL *Ascophyllum nodosum* moss (Searius, Gübretaş, Turkey) on 10.07.2023 (BBCH75). The application dose of biostimulants has been determined according to Karaman et al. (2024). On 17.07.2023, 150 mM of Salt 1 (Salt+*Saccharomyces cerevisae* 1, Salt+*Ascophyllum nodosum* 1) and on 24.07.2023, 150 mM of Salt 2 (Salt+Saccharomyces cerevisae 2, Salt+*Ascophyllum nodosum* 2) were applied to Salt group vines consisting of 12 vines and Salt+*Saccharomyces cerevisae* and Salt+*Ascophyllum nodosum* group vines.

Leaf sampling

Leaf samples were taken from the lower 4th node of each grapevine, 1 week after each salt application. The collected leaves were cleaned with distilled water to remove residues. The leaves were then frozen in liquid nitrogen and stored at -40°C until analysed.

Total phenolic compounds assay

Total phenolic compound levels (TPC) of leaf samples were measured according to Singletton and Rossi (1965). 500 mg of liquid nitrogen-frozen leaf samples were crushed in a homogenizer (Ultra-Turrax T25-Germany) by adding 5mL of methanol for 5 minutes. They were then kept in an ultrasonic bath (Jeiotech US-Korea) for 30 min, followed by centrifugation at 10000 rpm and 4°C for 10 min (Sigma 3K30-Germany). The supernatant was passed through 0.45 µm polyvinylidene difluoride filters (Millipores-USA). To determine the total phenolic compound level, 7.5 mL of distilled water was added to the tubes, followed by 100 µL of leaf extract. 500 µL of Folin Ciocalteu was added and kept for 3 minutes, 1 mL of 20% saturated sodium carbonate solution was added at the end of the time and the final volume was completed with 10 mL of pure water and kept in the dark for 1 hour. At the end of 1 hour, the absorbances at 765 nm were recorded with a Shimadzu UV 1208 model UV VIS spectrophotometer (Japan). The results were calculated as mg GAE/kg by calculating the absorbance values of the stock solutions prepared from gallic acid standards at concentrations of 500-5000 ppm and the equation obtained from this graph (R^2=0.998).

Antioxidant activity assay

The radical scavenging activities of grapevine leaf extracts were evaluated by DPPH assay (Brand-Williams et al., 1995). The antioxidant activities of the extracts were expressed as the effective concentration (EC_{50}), which is the concentration (mg/mL) of the extract required to reduce the absorbance of DPPH● solution by 50%.

Antioxidant enzyme assays

All antioxidant enzymatic measurements were performed at 0-4°C. Frozen leaf samples (0.5 g) were homogenized in a homogenizer (Ultra-Turrax T25-Germany) in 5 mL 100 mM sodium phosphate buffer (pH 7.5) containing 100 mM Na-phosphate, 0.5 mM EDTA-Na2 and 1 mM ascorbic acid. The homogenized samples were centrifuged at 8000 g for 30 minutes (Sigma 3K30-Germany). The supernatant was analyzed by spectrophotometer at 20°C for superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) enzyme assays (Şahin et al., 2024). Catalase activity was measured by the decrease in absorbance at 240 nm over 1 minute following the decomposition of H_2O_2 (Çakmak et al., 1993). Superoxide dismutase activity was measured using the nitroblue tetrazolium (NBT) method. The inhibition of the photochemical reduction of NBT was measured spectrophotometrically at 560 nm (Gong et al., 2005). Ascorbate peroxidase activity was determined by measuring

the decrease in ascorbate and the change in absorbance at 290 nm (Nakano & Asada, 1981). Enzyme activities were expressed as U/g.

Data analyses

The study was carried out according to the randomized block design with three replications. Statistical analyses of the data obtained were carried out using JMP 13.2.0 package software (SAS Institute Inc., Cary, NC) ; the significance of differences between treatments was evaluated at $p \leq 0.01$ significance level by subjecting all samples to the Tukey multiple comparison test. Principal component analysis (PCA) was performed to determine the interaction between all treatments and rootstocks and between parameters related to oxidative stress. All these analyses were performed using the relevant statistical software.

RESULTS

Total phenolics

Phenolic compounds are important components of plant defense responses to environmental stresses and their synthesis levels are generally increased under stress conditions. In this study, the effects of two different salt stresses and two different biostimulants (*S. cerevisiae* and *A. nodosum*) on phenolic compound accumulation were evaluated on ownroot, 1103P and 140Ru rootstocks of Öküzgözü (*Vitis vinifera* L.) cultivar (Figure 1). In uninoculated grapevines, the phenolic compound level in the control group was measured as 4658 mg GAE/kg. Low dose salt treatment (Salt 1) increased this value by 61% to 7502 mg GAE/kg. High dose salt treatment (Salt 2) provided the highest increase in phenolic compound content and reached 12956 mg GAE/kg with an increase of 177% compared to the control group. This result indicates that salt stress activates phenolic metabolism more strongly in a dose-dependent manner. *S. cerevisiae* biostimulant applied together with Salt 1 increased the phenolic content to 6736 mg GAE/kg, which is lower than Salt 1 but 44% higher than the control group. For the same salt dose, *A. nodosum* application decreased the phenolic content to 4524 mg GAE/kg and remained below the control group. This suggests that *A. nodosum* had a negative or insufficient effect on phenolic compound production in this combination. On the other hand, *S. cerevisiae* biostimulant applied together with high dose salt (Salt 2) resulted in a very high level of phenolic accumulation with 13220 mg GAE/kg, which means an increase of approximately 184% compared to the control group. In the second treatment with *A. nodosum* (Salt + *A. nodosum* 2), the level of 12028 mg GAE/kg was reached, which means an increase of approximately 158% compared to the control group. In this context, it can be said that biostimulant applications strongly support phenolic metabolism, especially in high dose salt stress. Similar trends were observed in 1103P rootstock. While the control group was 5692 mg GAE/kg, Salt 1 treatment increased this value by 4.3% to 5936 mg GAE/kg. However, phenolic accumulation increased dramatically mainly at high dose salt stress; Salt 2 treatment increased by approximately 177% compared to the control group with 15744 mg GAE/kg. When biostimulant treatments were evaluated, a decrease to 5100 mg GAE/kg was observed in the combination of low dose salt and *S. cerevisiae*, which is about 10% below the control group. The application with *A. nodosum* gave a result close to the control level with 5782 mg GAE/kg. *S. cerevisiae* and *A. nodosum* applied together with high dose salt produced phenolic content of 6828 mg GAE/kg and 13544 mg GAE/kg, respectively. It was observed that *A. nodosum* was especially effective in the second application with high salt doses. In particular, A. nodosum was found to be highly effective in the second application with high doses of salt, increasing the phenolic compound content by 138%. In 140Ru rootstock, the control group was 4968 mg GAE/kg in terms of phenolic content. Salt 1 application provided a very low increase of 5058 mg GAE/kg, remaining below the control level. On the other hand, the Salt 2 application shows an increase of approximately 163% with 13076 mg GAE/kg. In biostimulant treatments, the combination of low dose salt and *S. cerevisiae* increased phenolic content to 5848 mg GAE/kg, 17.7% higher than the control group. *A. nodosum* provided a similar result (21% increase) with 6036 mg GAE/kg. *S. cerevisiae* applied with high doses of salt produced phenolic content of 11168 mg GAE/kg, while *A. nodosum* remained at a lower level with 9184 mg GAE/kg. These results indicate that *A. nodosum* was the most effective biostimulant against high salt stress in 140Ru rootstock, while both biostimulants showed limited effect at low doses. In general, salt stress increased phenolic compound content in all rootstocks. This increase was more pronounced at higher salt doses, confirming once again that phenolic metabolism is an important biochemical indicator of stress responses. The effect of biostimulant treatments differed depending on the dose and rootstock type. The most remarkable results were observed in *S. cerevisiae* and *A. nodosum* treatments in combination with high doses of salt on ownroot and 1103P rootstock. These findings suggest that biostimulants can enhance the phenolic response to salt stress, especially in appropriate combinations.

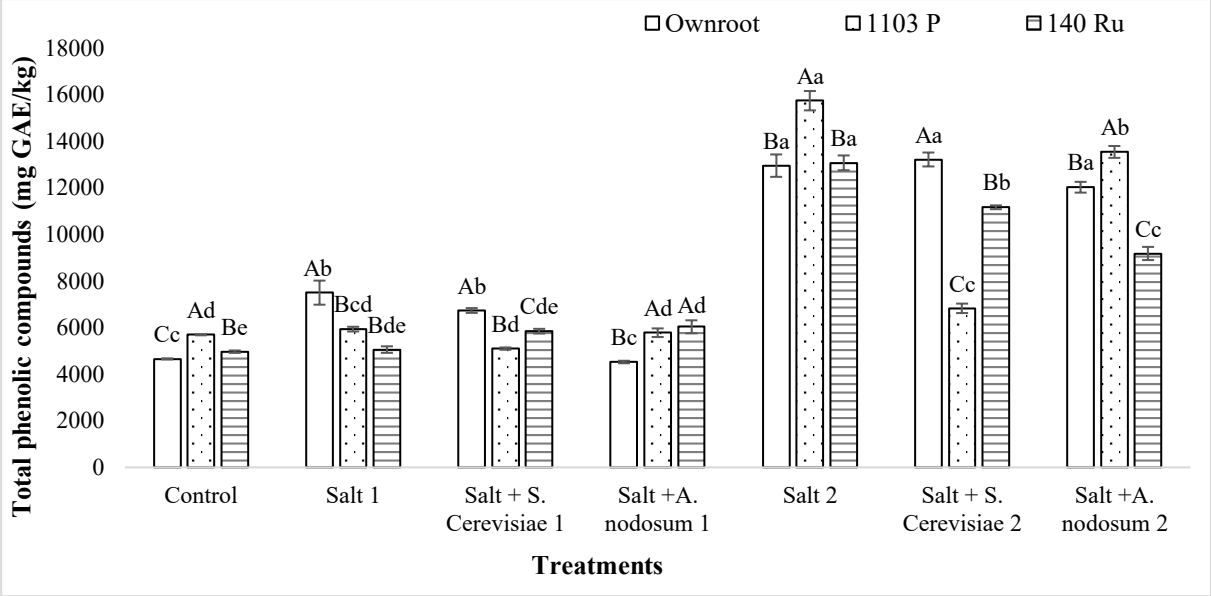

Figure 1. Total phenolic compound contents of leaves according to treatments. Each value represents the mean ± standard error of three replicates. Means indicated by different letters in the graph are significantly different ($p \leq 0.01$). Uppercase letters indicate difference between rootstocks and lowercase letters indicate difference between treatments. Vertical bars correspond to standard error.

EC_{50}

Since EC_{50} value is an inversely proportional measure reflecting antioxidant capacity, low EC_{50} values mean high antioxidant activity. As shown in Figure 2, while the EC_{50} value of the control group was 0.3310 mg/mL in ownroot grapevines, this value decreased by 24% to 0.2511 mg/mL with low dose salt application, and decreased by 65% to 0.1147 mg/mL with high salt application. This indicates that salt stress significantly increases antioxidant defense in a dose-dependent manner. In particular, the EC_{50} value of 0.0457 mg/mL obtained with Salt 2 + *S. cerevisiae* 2 treatment stood out as the lowest value among all groups and revealed that this biostimulant application most strongly promoted the antioxidant response against salt stress in ungrafted vines. In 1103P rootstock, the control group exhibited a basal level with an EC_{50} value of 0.3305 mg/mL. Salt treatments significantly reduced this value; 43% reduction was recorded with Salt 1 and 82% with Salt 2. However, the effect of biostimulant treatments was limited in this rootstock. Especially in Salt 2 + *S. cerevisiae* 2 treatment, the EC_{50} value increased to 0.4982 mg/mL, suggesting that antioxidant activity was suppressed. Similarly, in other biostimulant combinations, EC_{550} values close to or higher than the control group were obtained, indicating that the intrinsic defense capacity of 1103P rootstock is naturally active rather than supported by biostimulants. In 140Ru rootstock, the EC_{50} value of the control group was the highest at 0.3789 mg/mL, which represents the lowest basal antioxidant activity among the rootstocks. Salt treatments significantly decreased this value; in Salt 2 treatment, EC_{50} value decreased to 0.1424 mg/mL and antioxidant activity increased significantly. However, in biostimulant treatments, especially in Salt + *A. nodosum* 2 combination, EC_{50} increased to 0.3398 mg/mL, indicating that antioxidant activity was suppressed. In contrast, the combination of low doses of salt and *A. nodosum* (Salt 1 + *A. nodosum* 1) reduced the EC_{50} value to 0.2430 mg/mL increasing antioxidant capacity compared to the control group. In this context, it seems that biostimulant applications against high salt stress in 140Ru rootstock provided limited benefit and in some cases even weakened the defense response. Overall, the strongest antioxidant response was obtained with the second application of *S. cerevisiae* against high salt stress in ownroot vines. On the other hand, 1103P and 140Ru rootstocks could generate strong antioxidant responses even without biostimulant application, especially against high salt stress; however, biostimulant applications did not always provide the expected positive contribution in these rootstocks. These differences suggest that the physiological and biochemical defense capacities of rootstocks play a decisive role in biostimulant efficacy.

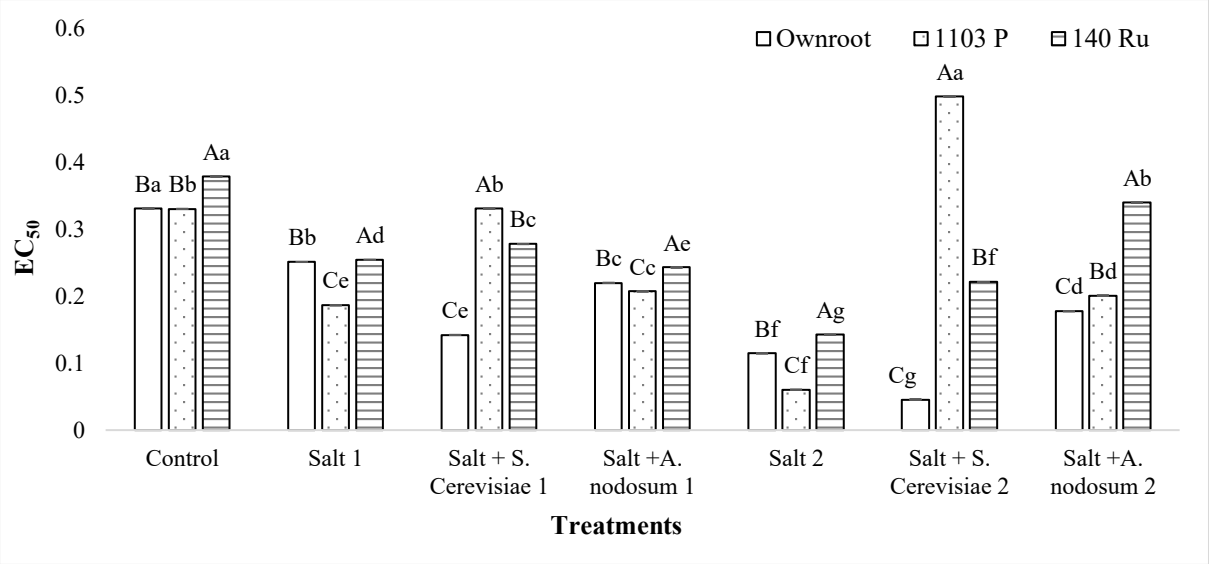

Figure 2. EC_{50} levels of leaves according to treatments. Each value represents the mean ± standard error of three replicates. Means indicated by different letters in the graph are significantly different ($p \leq 0.01$). Uppercase letters indicate difference between rootstocks and lowercase letters indicate difference between treatments. Vertical bars correspond to standard error.

Superoxide dismutase (SOD)

The SOD enzyme is involved in the detoxification of reactive oxygen species under oxidative stress conditions and reflects the defense capacity of the plant under stress. Therefore, increasing the stress level usually leads to an increase in SOD activity, whereas reducing the stress through biostimulants may lead to a decrease in enzyme levels. As can be seen from Figure 3, SOD activity in ungrafted grapevines, which was 482.778 U/g in the control group, remained almost constant (481.444 U/g) at the low level of salt stress (Salt 1), suggesting that the low salt level did not create an additional oxidative stress load in the ungrafted plant. However, the enzyme level decreased to 68.474 U/g in Salt 2 treatment, indicating that plant defense was suppressed under very high stress conditions. The increase in SOD activity to 86.889 and 97.000 U/g with the second applications of *S. cerevisiae* and *A. nodosum*, respectively, indicates that biostimulants can partially support the enzymatic response of the plant under high stress conditions. On the other hand, at low salt level, SOD activity decreased to 361.167 U/g with *S. cerevisiae* 1st application and 192.778 U/g with *A. nodosum*, indicating that these biostimulants reduce the enzyme production requirement of the plant by reducing the stress level. In 1103P rootstock, while SOD activity in the control group was 360.167 U/g, this value decreased by 42% to 207.714 U/g with low salt application. However, the activity increased to 480.444 U/g with *S. cerevisiae* application, indicating that this biostimulant is effectively combating oxidative stress by triggering the enzymatic defense system. In high salt stress, SOD level decreased to 118.061 U/g; this value increased to 187.571 U/g with *S. cerevisiae*, again supporting the protective effect of this microorganism. In *A. nodosum* treatment, the activity was close to the control level with 363.167 U/g under low salt; however, the lowest value of 67.140 U/g was observed at high salt dose. This indicates that *A. nodosum* was ineffective enough in the 1103P rootstock under high stress conditions. In 140Ru rootstock, the SOD activity in the control group had the highest basal value of 582.333 U/g, indicating that the natural defense system of this rootstock is more active compared to other rootstocks. At the low salt stress level, this value decreased by 45% to 320.407 U/g, indicating that stress suppresses the defense system. Biostimulant treatments, especially with *S. cerevisiae*, increased SOD activity again up to 482.778 U/g, indicating that this treatment balanced the defense system by reducing the stress level. Under high salt conditions (Salt 2), SOD level decreased to 130.333 U/g; however, *S. cerevisiae* (107.778 U/g) and *A. nodosum* (117.727 U/g) treatments were able to compensate this decrease to a limited extent. It is understood that the effects of both biostimulants were limited under high dose salt stress, but *S. cerevisiae* was more effective in maintaining enzymatic balance, especially under low stress conditions. In general, it was observed that high salt stress suppressed SOD enzyme activity in all rootstocks, but *S. cerevisiae* application contributed to the fight against oxidative stress by reducing this suppression especially at low stress levels. While the most dramatic enzyme decreases were observed in ungrafted plants, 140Ru rootstock stood out with its stronger basal defense capacity, while 1103P responded more positively to *S. cerevisiae* treatment. These findings suggest that rootstock selection and biostimulant applications are critical for managing of plant defense systems under salt stress conditions.

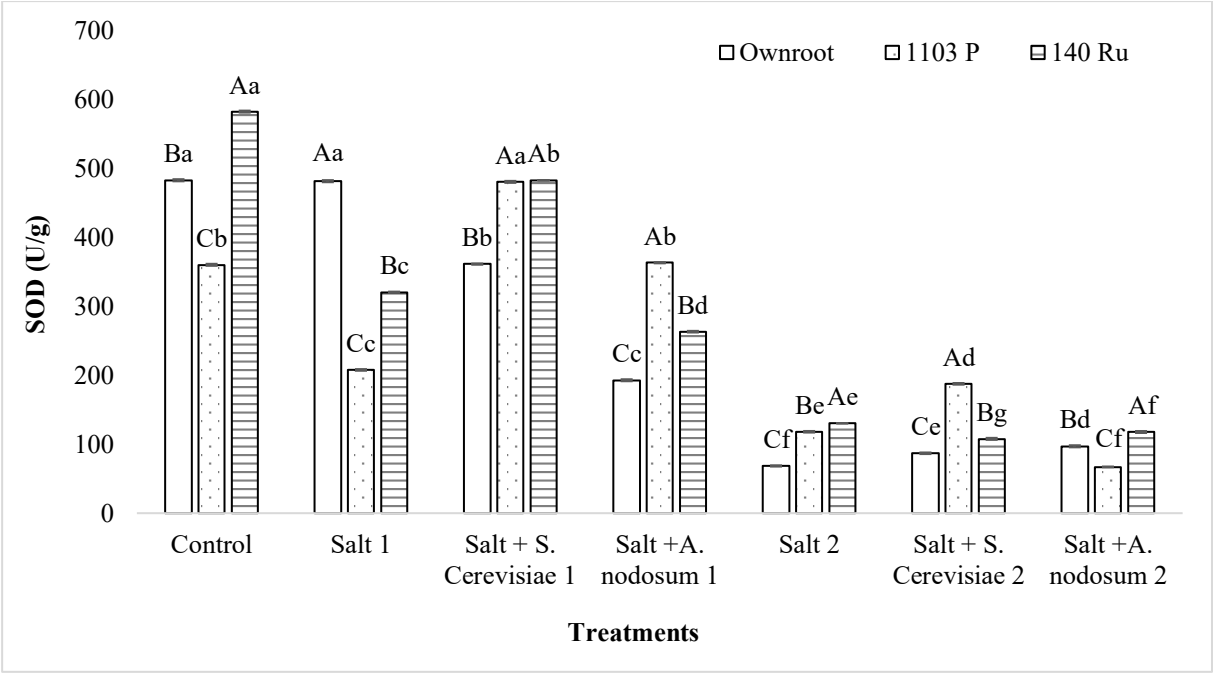

Figure 3. Superoxide dismutase (SOD) levels of leaves according to treatments. Each value represents the mean ± standard error of three replicates. Means indicated by different letters in the graph are significantly different ($p \leq 0.01$). Uppercase letters indicate difference between rootstocks and lowercase letters indicate difference between treatments. Vertical bars correspond to standard error.

Catalase (CAT)

Catalase (CAT) enzyme is an essential antioxidant defense component that prevents the harmful effects of oxidative stress by degrading reactive oxygen species (ROS) into water and oxygen in plant cells. Especially under environmental stress conditions, an increase in catalase activity is an indication that the plant responds to oxidative stress (Gill and Tuteja, 2010). Salt stress leads to oxidative damage by increasing ROS production in plants and therefore the enzyme catalase plays a central role in defense systems under stress (Mittler, 2002). According to the data obtained, low salt stress treatment (Salt 1) did not cause any change in vines on their own roots compared to the control group, and the enzyme level remained constant (Figure 4). However, catalase activity increased by 266.7% in *S. cerevisiae* treatment. Similarly, *A. nodosum* treatment showed a more limited but positive effect with an increase of 13.3%. The most remarkable finding was observed in high salt stress (Salt 2) and *S. cerevisiae* 2 treatments. High dose salt stress resulted in a 393.3% increase in catalase activity. However, the *S. cerevisiae* 2 treatment exceeded even this value, showing the most dramatic increase with a 660% increase. Finally, the *A. nodosum* 2 treatment produced an increase of 120%. On 1103P rootstock, Salt 1 treatment increased catalase activity by 150% compared to the control. This increase suggests that the plant showed a moderate stress response. On the other hand, a 50% decrease was observed in *S. Cerevisiae* treatment. This indicates that yeast treatment alone may not have promoted an adequate defense response to salt stress. In the *A. nodosum* treatment, the catalase level remained constant. Another remarkable finding was observed in the high salt treatment (Salt 2), which resulted in an extremely high increase of 1056.3% in catalase activity. This increase indicates that high levels of salt stress significantly increase the amount of reactive oxygen species (ROS) in the cell and therefore catalase enzymes are intensively activated. However, *S. cerevisiae* 2 treatment also significantly increased by 106.3%. *A. nodosum* 2 treatment produced a smaller increase (12.5%). In 140 Ru rootstock, a significant 72.7% decrease in catalase activity was observed with Salt 1 treatment compared to the control group. This decrease suggests that the antioxidative defense response of 140 Ru rootstock may be weak at low salt concentrations. Similarly, a 27.3% decrease was observed in *A. nodosum* treatment. However, this situation was reversed in *S. Cerevisiae* treatment and a slight increase of 3% was realized compared to the control group. This increase indicates that yeast application may have triggered the antioxidant defense to some extent. Catalase activity increased by 96.9% with Salt 2 treatment. This increase indicates that high salt concentration creates a stronger oxidative stress and the catalase enzyme level increased significantly in response. *S. Cerevisiae* 2 treatment also strengthened the defense mechanism with an increase of 42.4%. The highest catalase activity was observed in *A. nodosum* 2 treatment and this group showed an increase of 151.5% compared to the control group. This result suggests that seaweed application especially seaweed application promotes an effective antioxidative response against high salt stress.

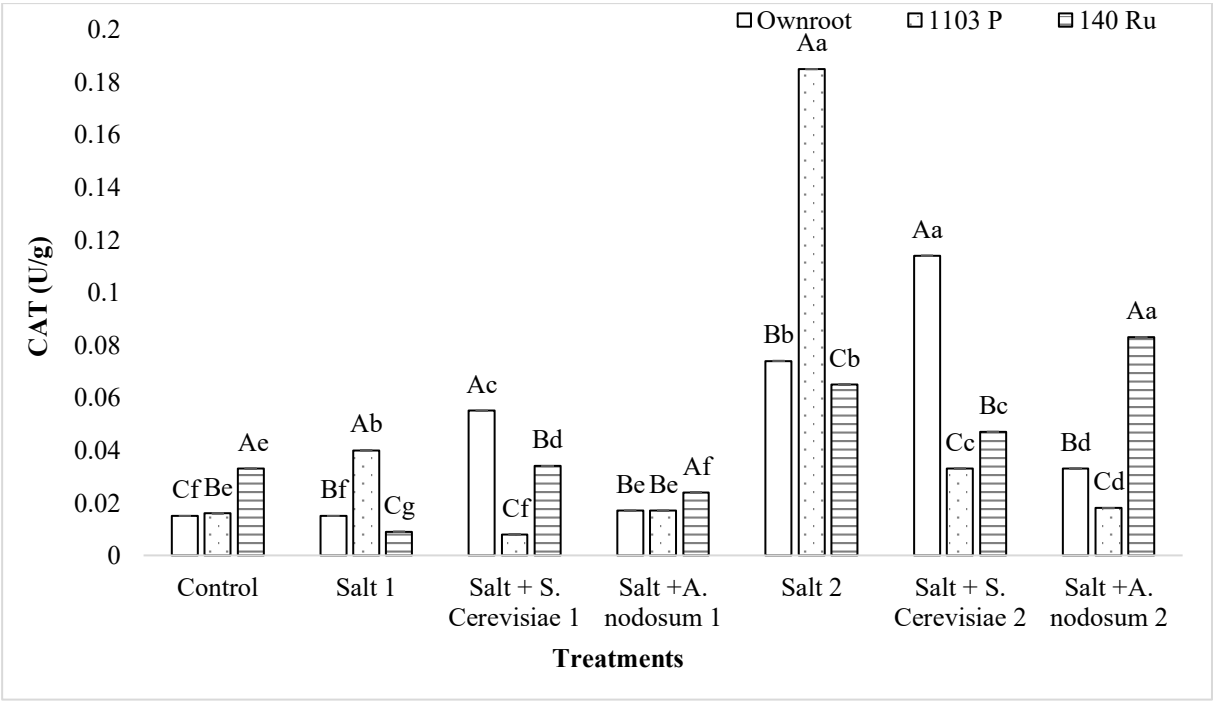

Figure 4. Catalase (CAT) levels of leaves according to treatments. Each value represents the mean ± standard error of three replicates. Means indicated by different letters in the graph are significantly different ($p \leq 0.01$). Uppercase letters indicate difference between rootstocks and lowercase letters indicate difference between treatments. Vertical bars correspond to standard error.

Ascorbate peroxidase (APX)

While the increase in APX activity under stress conditions indicates that the plant tries to limit oxidative damage; biostimulant applications may play a regulatory role in enzymatic activity by reducing this stress level (Mittler, 2002; Gill & Tuteja, 2010). In this study, when APX enzyme activity was evaluated in ownroot, 1103P and 140Ru rootstocks, 0.197, 2.125 and 0.214 U/g protein values were determined in the control groups, respectively (Figure 5). In ownroot plants, low dose salt treatment (Salt 1) increased APX activity by about 18% to 0.232 U/g. This increase indicates that the plant senses oxidative stress and initiates enzymatic defense. High dose salt stress (Salt 2) increased APX level by about 878% to 1.928 U/g, indicating that the plant showed maximum enzymatic response to severe stress. The second applications with *S. cerevisiae* and *A. nodosum* biostimulants reduced this high activity to 0.875 and 0.911 U/g, respectively, thereby significantly improving the stress level by approximately 54–52%. These results suggest that both biostimulants were effective in regulating APX activity in ungrafted plants, but *A. nodosum* showed a higher effect. The high APX activity (2.125 U/g) in 1103P rootstock in the control group indicates that the basal defense capacity of this rootstock is quite strong. However, this value decreased by 79% to 0.446 U/g in low salt stress and decreased by 83% to 0.357 U/g in high salt stress. These decreases indicate that 1103P has difficulty in maintaining APX activity in the face of salt stress. Biostimulant treatments reversed this situation: Salt 2 + *S. cerevisiae* 2 treatment increased the activity to 0.911 U/g and *A. nodosum* 2 to 0.768 U/g. These rates correspond to 155% and 115% increases in enzyme level, respectively. Therefore, *S. cerevisiae* treatment stands out as the biostimulant that best supports the APX activity of this rootstock. In 140Ru rootstock, the control group showed an APX activity of 0.214 U/g. With Salt 1 treatment, this value decreased by 24% to 0.161 U/g, but increased to 1.357 U/g under high salt stress, i.e. an increase of approximately 535%. This increase indicates that 140Ru also gives an active defense response under stress. The second treatment of *S. cerevisiae* further alleviated the stress effect by increasing this value to 1.536 U/g. This represents an increase of approximately 618% compared to the control group. Similarly, the application of *A. nodosum* made a significant contribution, reaching a value of 0.893 U/g. However, the response of this rootstock to biostimulants was stronger in favor of *A. nodosum*. In conclusion, APX enzyme formed an important defense response against salt stress in all rootstocks and the highest activity increases were observed especially in high dose salt treatments. Biostimulant applications alleviated the stress by regulating this excessive enzymatic defense and tended to normalize APX levels. Especially in ungrafted plants and 1103P rootstock, *A. nodosum* and 140Ru rootstock, *S. cerevisiae* were the most successful biostimulants.

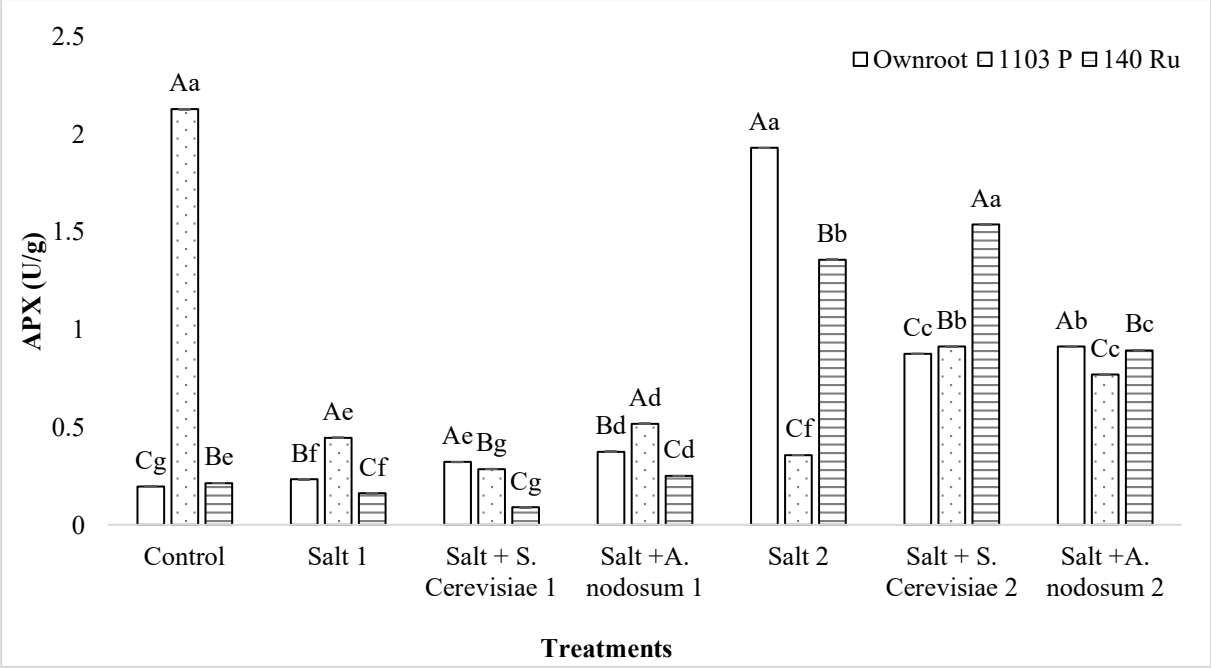

Figure 5. Ascorbate peroxidase (APX) levels of leaves according to treatments. Each value represents the mean ± standard error of three replicates. Means indicated by different letters in the graph are significantly different ($p \leq 0.01$). Uppercase letters indicate difference between rootstocks and lowercase letters indicate difference between treatments. Vertical bars correspond to standard error.

PCA analysis of all treatments and rootstocks

Principal Component Analysis (PCA) was performed to evaluate the antioxidant defense responses of 21 different treatments induced by different rootstocks (Ownroot, 1103P and 140Ru), two levels of salt stress (Salt 1 and Salt 2) and biostimulant treatments (*Saccharomyces cerevisiae* and *Ascophyllum nodosum*) were presented in Figure 6. According to the PCA results, 60.7% of the total variance was explained by the first component (PC1) and 20.6% by the second component (PC2); these two components together represented 81.3% of the variance, reflecting the majority of the variables in the analysis. When vectorial loadings were evaluated, total phenolic compound content (TPC) and catalase (CAT) activity had a positive effect on PC1, while EC_{50} and superoxide dismutase (SOD) showed negative loadings. APX (ascorbate peroxidase) positively contributed mostly on the PC2 axis. Among the treatments in the lower right quadrant of the graph, 14, especially the groups in which 1103P rootstock was applied under high salt conditions, stood out with high total phenolic content and catalase activity. This indicates that 1103P rootstock developed a more effective defense response against salt stress. Especially treatment 14 (Salt 2/1103P) and treatment 16 (Salt 2/Ownroot/*S. cerevisiae*) were the groups with the highest antioxidant capacity. The treatments in which APX activity was dominant were located in the upper right part of the graph and it was observed that treatments 18 (Salt 2/140Ru/S. *cerevisiae*), 20 (Salt 2/1103P/*A. nodosum*) and 21 (Salt 2/140Ru/*A. nodosum*) exhibited high ascorbate peroxidase activity. This reveals that an effective defense response developed in these groups, especially against H_2O_2 detoxification. In contrast, treatments 1, 3, 6, 8 and 9, located on the left side of the PCA plot and close to the EC_{50} and SOD vectors, were characterized by lower antioxidant capacity and higher oxidative stress indicators. Treatments located around the center (e.g. 5, 10, 11, 12), on the other hand, exhibited more balanced and average responses in terms of both antioxidant capacity and enzymatic defense. In conclusion, this analysis revealed that antioxidant defense systems differed depending on the applied rootstock and stress conditions. In particular, *S. cerevisiae* and *A. nodosum* biostimulants applied under high salt conditions increased the capacity of plants to cope with oxidative stress by stimulating total phenolic compound synthesis and enzymatic defense systems. The PCA graph clearly revealed these differences with its multidimensional structure and was evaluated as an effective tool in understanding the dynamics of antioxidant defense systems.

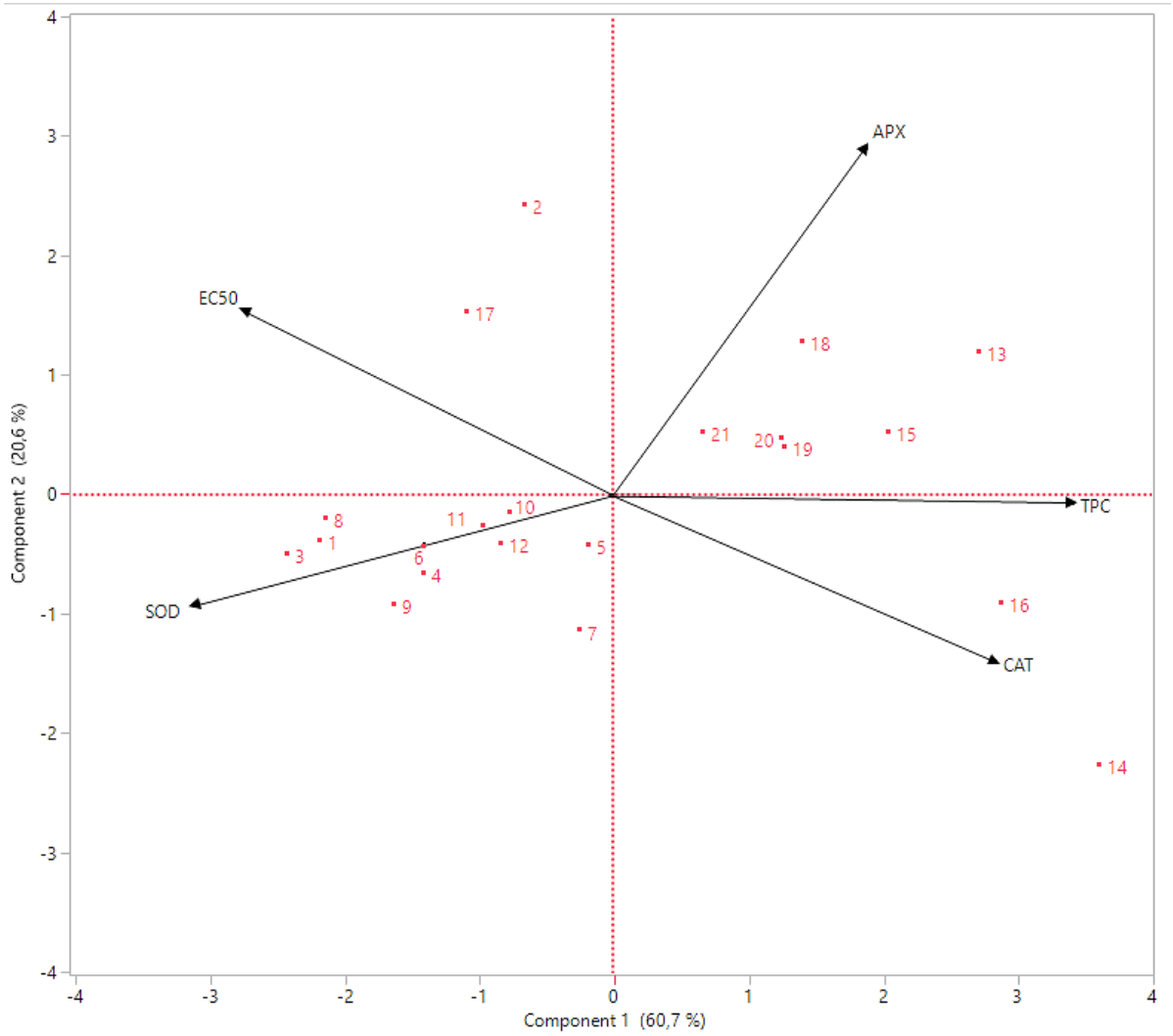

Figure 6. PCA biplot of all treatments and rootstocks.
1: Control/Ownroot, 2: Control/1103P, 3:Control /140Ru, 4: Salt 1/Ownroot, 5: Salt 1/1103P, 6: Salt 1/140Ru, 7: Salt 1/ Ownroot/*S. Cerevisae*, 8: Salt 1/ 1103P/*S. Cerevisae*, 9: Salt 1/ 140Ru/*S. Cerevisae*, 10: Salt 1/ Ownroot/ *A. Nodosum*, 11: Salt 1/ 1103P/ *A. Nodosum*, 12: Salt 1/ 140Ru/ *A. Nodosum*, 13: Salt 2/Ownroot, 14: Salt 2/1103P, 15: Salt 2/ 140Ru, 16: Salt 2/ Ownroot/*S. Cerevisae*, 17: Salt 2/ 1103P/*S. Cerevisae*, 18: Salt 2/ 1140Ru/*S. Cerevisae*, 19: Salt 2/ Ownroot/ *A. Nodosum*, 20: Salt 2/ 1103P/ *A. Nodosum*, 21: Salt 2/ 140Ru/ *A. Nodosum*.

DISCUSSION

It has been well documented in previous studies that when plants are exposed to adverse environmental conditions such as extreme temperature, heavy metals, drought, water availability, air pollutants, nutrient deficiency or salt stress, the production of ROS such as $^1O_2$, O_2^-, H_2O_2 and OH● increases (Gill and Tuteja, 2010; Choudhury et al., 2017; Wang et al., 2024). To protect themselves against these toxic oxygen intermediates, plant cells and organelles such as chloroplasts, mitochondria and peroxisomes employ antioxidant defense systems. SOD is a potent metalloenzyme common in all aerobic organisms and forms the first line of defense against oxidative stress in plants by inactivating reactive oxygen species (ROS), which increase due to environmental stresses (Gill and Tuteja, 2010). Catalase (CAT) is a high turnover rate antioxidant enzyme with a tetrameric structure that plays a critical role in the elimination of oxidative stress in plants by converting hydrogen peroxide (H_2O_2), especially formed in peroxisomes, into water and oxygen with high efficiency (Polidoros and Scandalio, 1999). APX is known to detoxify H_2O_2 into water and oxygen during stress. APX plays an important role in the salinity tolerance of plants since it has higher activity in salt tolerant species (Sudha and Ravishankar, 2002). In this study, as the dose of salt stress increased, the levels of enzymes other than SOD increased as expected. Under normal conditions, an increase in SOD activity is expected in plants exposed to salt stress because SOD forms the first line of defense by converting superoxide radical into hydrogen peroxide and oxygen. However, in some studies, similar to our results, SOD activity remained unexpectedly low or did not increase under high salt

conditions. Hernández et al. (1994) showed that high salt stress suppressed the activity of different SOD isozymes to different degrees in *Vigna unguiculata*. They emphasized that mitochondrial Mn-SOD was particularly sensitive to salt stress and that in leaves, mitochondrial Mn-SOD activity was significantly reduced (up to 35% and 60%, respectively) at 35 mM and 100 mM NaCl concentrations. The researchers have reported that SOD enzyme will break down superoxide to produce H_2O_2 and H_2O_2 will be cleared by APX/CAT. It has been suggested that when high levels of H_2O_2 are formed, this molecule may act as a signal, triggering feedback mechanisms that prevent SOD from working further, and H_2O_2 formed as a result of SOD activity may decrease the expression of SOD genes (Qu et al., 2010). The rootstock used in grafted vines can determine the distribution of salt within the plant and the severity of stress. Salt-resistant rootstocks can reduce the stress level in the leaves of the grafted cultivar by retaining Na^+ ions in the roots or transmitting them in a more controlled manner. For example, under salt stress, the amount of Na and Cl accumulated in the leaves of vines grafted on some rootstocks is lower than on others. If the rootstock partially blocked the salt and allowed less of it to pass to the leaves, superoxide production in the leaf tissue may also have been relatively low. In this case, APX and CAT may still increase (to scavenge H_2O_2, albeit to a lesser extent), but there may not have been a significant increase in SOD activity because superoxide levels were not very high. In addition, rootstock-induced hormonal/signaling effects may also alter antioxidant enzyme profiles; some rootstocks may have transmitted signals that promote other enzymes instead of SOD (Şahin, 2009). In the results of the study, SOD was the most abundant antioxidant enzyme in accordance with previous studies (Aazami et al., 2023; Gajjar et al., 2023). Similar to this study, Desoky et al. (2019) found lower levels of antioxidant enzymes in biostimulant-treated groups against salt stress compared to untreated groups.

Total phenolic compounds and antioxidant activity in grapevine (*Vitis vinifera* L.) leaves may show significant changes due to environmental stresses and agricultural treatments. Recent studies have focused on the effects of salt stress, different rootstocks and biostimulant treatments on phenolic accumulation and antioxidant defense mechanisms in plants. Plants are exposed to various abiotic stresses throughout their life cycle. Their interactions with changing environmental conditions have been an important driving force behind the emergence of certain natural products (Lattanzio, 2013). When a plant is exposed to abiotic stress, a number of genes are turned on or off, resulting in increased levels of various metabolites and proteins, some of which may be responsible for providing a certain degree of defense against these stresses (Ahmad et al., 2008; Jaleel et al., 2009). The accumulation of phenolics in plant tissues is considered an adaptive response of plants to adverse environmental conditions, thereby enhancing evolutionary fitness (Naikoo et al., 2019). A large proportion of arable land is facing abiotic stresses (drought, salinity, cold, heat, heavy metal toxicity, UV radiation, etc.), which are expected to increase due to climate change (Sharma et al., 2019). Salt stress can significantly affect secondary metabolite production in plants. Many studies show that salinity increases phenolic and flavonoid compound levels in plants by activating the phenylpropanoid pathway (Zargoosh et al., 2019,). The ionic and osmotic stress that occurs when the plant transports the salt taken by the roots to organs such as leaves can trigger the synthesis of phenolic compounds for defense. Indeed, it has been reported that leaf flavonoid and phenol content increases under increasing salt stress conditions. This is due to the fact that phenolic compounds are part of the non-enzymatic antioxidant defense in plants; phenolics together with molecules such as proline and ascorbic acid are mechanisms that neutralize reactive oxygen species (ROS) (Gajjar et al., 2023). In this study on salt stress, with increasing salinity, leaf total phenolic compound concentration increased in stressed plants, thus this increase was concentration dependent and the highest total phenol concentration was observed in vines treated with 150+150 mM NaCl. Salt-induced oxidative stress may induce a kind of protective response by promoting the accumulation of phenolic substances in plant cells. For example, increased production of phenolic compounds (especially stilbenes and flavonoids) has been observed in salt-treated grapevine cell cultures, leading to an increase in total antioxidant capacity (Almagro et al., 2022). In this study, salt treatment was reported to increase phenylalanine ammonia lyase (PAL) enzyme activity, resulting in more phenolics synthesized. Similarly, in another study, total phenolic content in leaves of Merlot and Cabernet Franc cultivars treated with salt for 60 days increased by 59-70% compared to control plants (Nikolaou et al., 2021). This finding indicates that salt stress strongly induces phenolic accumulation in grapevines. In parallel with the increase in phenolic matter, the DPPH radical scavenging capacity of leaf extracts also increases. The literature shows a generally positive correlation between total phenolic content measured by Folin-Ciocalteu and DPPH antioxidant activity, similar to our results (Pérez, et al, 2023). Biostimulant-treated vines showed lower levels of total phenolic compounds than vines under salt stress alone, suggesting that this may act as an adaptation mechanism to overcome salinity-induced oxidative stress (Jamalian et al., 2013; Karimi and Ershadi, 2015). The importance of flavonoids stems from their role in non-enzymatic defense systems (Apel and Hirt, 2004). Similarly, previous studies reported that total phenolic compound content increased after salt stress as in this research (Karaman et al., 2024; Mohammadkhani and Abbaspour, 2018; Karimi et al., 2022).

The rootstock iIn grafted plants such as grapevines, used can significantly influence the physiological and biochemical responses of the variety. To understand why different rootstocks give different results in grapevines under salt stress, the salt tolerance mechanisms provided by the rootstocks and traits such as vigor should be considered (Klimek et al., 2022).

In our results, although the total phenolic compound content increased in the biostimulant groups as the stress dose increased, the EC_{50} value was the highest in the second salt treatment, but not as high as expected in the high salt + biostimulant groups. Although total phenolics and anthocyanins were lower in some cultivars with 1103P rootstock, antioxidant capacity was reported to be high in previous studies (Bouza et al., 2024). This may be related to the composition and type of phenolic compounds, i.e. different rootstocks affect not only the amount of phenolics but also the type of phenolics (e.g. flavonols vs. tannins with stronger antioxidant effect) that accumulate.

The mechanism by which yeast-derived biostimulants increase phenolic compounds is explained by stimulating the phenylpropanoid pathway as an immune response in the plant. In viticulture, in a study focusing on the effect of foliar applied yeast derivatives on grape quality components, it was found that total phenolic content increased significantly in theTempranillo grape variety (Portu et al., 2016). Similarly, Monteiro et al. (2023) showed that *Ascophyllum nodosum* treatment significantly increased phenolic compound contents in *Touriga Franca* grape variety under drought stress conditions by applying different concentrations before vintage.

As a result, under salt stress, the conversion of superoxide radicals to H_2O_2 in leaf tissues was initially achieved by an increase in SOD activity; however, due to the degradative effect of elevated NaCl concentrations on metal cofactors, SOD activity was downregulated and the detoxification of H_2O_2 accumulation was undertaken by CAT and APX enzymes. Rootstock differences in tolerance were found to determine the severity of this defense response: 1103P rootstock exhibited a balanced ROS management, while ion exclusion was accelerated and CAT and APX levels were more sharply elevated by 140Ru rootstock; ungrafted Öküzgözü was subjected to the most intense oxidative stress as a result of high ion accumulation. Biostimulant treatments were shown to enhance CAT-APX expression through *Saccharomyces cerevisiae* extract with a "priming" effect. In contrast, *Ascophyllum nodosum* extract supported the entire SOD-CAT-APX defense network by providing osmotic buffering and modulating ROS signaling. Thus, it was concluded that the increase in CAT and APX activities observed in parallel with the increase in phenolic defense and the relative decrease in SOD is a reflection of negative feedback mechanisms due to high NaCl dose and measurement timing in accordance with the literature.

CONCLUSION

This study aimed to reveal the decisive role of rootstock selection and biostimulant applications in managing antioxidative defense mechanisms in *Vitis vinifera* grapevines under salt stress. The severity and direction of the biochemical responses developed by different rootstocks to salt stress varied significantly depending on their genotypic tolerance levels. Significant increases in total phenolic compound content and catalase activity were observed under high salt stress, whereas a general suppression of superoxide dismutase activity occurred. In particular, rootstock 1103P activated phenolic metabolism more strongly and maintained enzymatic defense more effectively under high salt conditions, indicating its greater capacity to maintain ion homeostasis and manage oxidative stress. Biostimulant treatments modulated plant defense against salt stress in different ways and these effects varied depending on the treatment dose and the type of rootstock used. In ungrafted vines, *S. cerevisiae* application was the most effective biostimulant because it in increased the antioxidant activity. In 1103P and 140Ru rootstocks, the effect of biostimulants was limited, and in some cases, it was observed that intrinsic defense mechanisms could work effectively without biostimulant support. In general, biostimulant applications have the potential to increase phenolic compound production and antioxidative enzyme activities of plants against salt stress, but the success of this effect is closely related to the severity of stress and the rootstock used. In this context, selecting appropriate rootstock-biostimulant combinations is strategically important in developing sustainable viticultural practices against salt stress. Further research is needed in this area to demonstrate the performance and contributions of different rootstocks and biostimulant applications under salt stress conditions.

Compliance with Ethical Standards

Peer-review

Externally peer-reviewed.

Declaration of Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Author contribution

The contribution of the authors to the present study is equal. All the authors read and approved the final manuscript. All the authors verify that the Text and Table are original and that they have not been published before.

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