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MINOR REVIEW

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Where biotic and abiotic stress responses converge: Common patterns in response to salinity and *Plum pox virus* infection in pea and peach plants

Jose A. Hernández[1] | Pedro Diaz-Vivancos[1] | José Ramón Acosta-Motos[1,2] | Gregorio Barba-Espín[1]

[1]Group of Fruit Tree Biotechnology, Department of Plant Breeding, CEBAS-CSIC, Murcia, Spain

[2]Cátedra Emprendimiento en el Ámbito Agroalimentario, Universidad Católica, San Antonio de Murcia, Campus de los Jerónimos, Guadalupe, Spain

Correspondence
Dr. Jose A. Hernández, CEBAS-CSIC, P.O. Box 164, Murcia 30100, Spain.
Email: jahernan@cebas.csic.es

Abstract

Herbaceous and woody plants display specific mechanisms allowing them to adapt and survive to a broad variety of environmental stresses. Nevertheless, all plant species share certain basic physiological and biochemical mechanisms. Under both abiotic and biotic challenges, the extent to which reactive oxygen species (ROS) accumulate relies on the antioxidative system, which is in charge to maintain cellular homeostasis and prevent ROS damage. Moreover, a tight control of ROS production is crucial so that they perform their signalling function. Thus, antioxidative metabolism and redox biology are key players in the physiological response to stress. However, little attention has been paid to the overlapping mechanisms and convergent pathways of antioxidant metabolism between abiotic and biotic stress responses. In the present review, the responses of an herbaceous plant (*Pisum sativum* L.) and a woody plant (*Prunus persica* L.) against two forms of stress—salinity and infection by *Plum pox virus*—were compared, placing emphasis on common response patterns. This information may serve to devise agronomic approaches conferring stress tolerance to many economically relevant crops.

KEYWORDS
antioxidative metabolism, oxidative stress, pea, peach, photosynthesis, plant physiology, *plum pox virus*, reactive oxygen species, salt stress

1 | INTRODUCTION

Throughout its evolution, plants have evolved specific mechanisms allowing them to adapt and survive to a broad variety of environmental challenges (Diaz, 2018; Fürst-Jansen, De Vries, De Vries, 2020). The exposure to abiotic (salinity, water scarcity, high light intensity, extreme temperatures) or biotic (virus, bacterial and fungal infections) stresses induces a disturbance of plant metabolism, which ultimately may affect plant productivity. Following the perception of a stress, multiple cell signalling pathways are activated, which include activation of ion channels, kinase cascades, over-production of reactive oxygen species (ROS), activation of the antioxidant defences and phytohormones regulation, which is reflected in a gene expression reprogramming triggering stress responses (Fraire-Velázquez, Rodríguez-Guerra, & Sánchez-Calderón, 2011; Laloi, Apel, & Danon, 2004; Spoel & Dong, 2008).

Under a stress situation, the extent to which ROS accumulate relies on the antioxidant metabolism, which enables plant to maintain cellular homeostasis and avoid the deleterious effect of ROS overaccumulation. In this context, redox biology and antioxidant network are identified as pivotal elements in the physiological response to stress (Foyer & Noctor, 2005, 2011). However, little attention has been paid to the overlapping mechanisms and convergent pathways of antioxidant metabolism between abiotic and biotic stress responses.

This minor review aims to dissect the responses of an herbaceous plant (*Pisum sativum* L.) and a woody plant (*Prunus persica* L.) to two

All the authors contributed equally to this work.

forms of stress: salinity and infection by *Plum pox virus* (PPV), as representatives of abiotic and biotic stimuli, respectively. Firstly, the response of each plant species to the two forms of stress is independently dissected. Finally, placing the emphasis on the role of antioxidant metabolism, common patterns are highlighted in both forms of stress, which may contribute to a better understanding of cross-tolerance phenomena and a focus change in plant stress research.

2 | PLANT RESPONSES TO SALINITY

Soil salinisation is a major constraint on agricultural productivity, affecting over 800 million hectares of farmlands on a world scale. Moreover, the current scenario is expected to be aggravated due to both climate change and secondary salinisation—i.e., that due to human activity. In plants, salt stress primarily causes an ion-independent growth inhibition, followed by ion toxicity due to an over-accumulation of Cl^- and Na^+ in the cytosol. This generates a nutrient imbalance, which affects numerous physiological processes and ultimately causes premature senescence and cell death (Acosta-Motos et al., 2017; Isayenkov & Maathuis, 2019). Importantly, salt stress is associated with an oxidative stress, due to a cell over-accumulation of ROS. In this context, antioxidant mechanisms—comprising ROS-scavenging enzymes and non-enzymatic antioxidants—are crucial to deal with salt stress, and salt resistance mechanisms underlying antioxidant responses appear now to be conserved among plant families (Hernández, Campillo, Jiménez, Alarcón, & Sevilla, 1999; Mittler et al., 2011; Molassiotis & Fotopoulos, 2011; Soares, Carvalho, Azevedo, & Fidalgo, 2019).

Overall, plant responses to salt stress are evaluated in terms of productivity, water relations and ion balance. It is widely documented that the majority of plants are salt-tolerant during germination, while seedlings are sensitive to salt stress. On the other hand, adult plants become more tolerant with age (Pirasteh-Anosheh, Saed-Moucheshi, Pakniyat, & Pessarakli, 2016). However, plants species differ remarkably in their tolerance to salt stress and particularly, most crop species are salt-sensitive (Munns, Passioura, Colmer, & Byrt, 2020). Therefore, it is of crucial importance to focus on the overlapping plant responses to salt stress, as a valuable tool in future breeding programs and in the application of molecular approaches such as genome editing techniques. In this section, the response to salt stress in *P. sativum*, a representative herbaceous plant, and in *P. persica* is dissected. It is important to note that there is much more information in the literature about the response to salinity in pea than in peach plants.

2.1 | Salinity and pea plants

2.1.1 | The importance of genotype

There are significant differences in the response of pea genotypes to salt stress, from which a distinction between salt-sensitive and salt-tolerant genotypes can be assumed (Shahid et al., 2012). The capacity of certain pea genotypes to tolerate moderate salt levels relies ultimately on genetic factors. In a study with three pea populations derived from crosses between tolerant (ATC1836, Parafield and Yarrum) and a sensitive (Kaspa) genotypes, a probable multigenic control of salt stress response was suggested (Leonforte, Forster, Redden, Nicolas, & Salisbury, 2013). In the broader screening conducted to date on pea, the response of 780 accessions to salinity of up to 16 dS m^{-1} (equivalent to 200 mM NaCl) was compared, resulting in remarkable differences (Leonforte et al., 2013). Nevertheless, gradual responses to NaCl concentration can be found in both tolerant and sensitive cultivars. For example, shoot dry weight of pea cv. Lincoln, considered a sensitive cultivar, was not affected by 50 mM NaCl, but it decreased to 50% when exposed to 70 mM (Hernández, Ferrer, Jiménez, Barceló, & Sevilla, 2001); on the other hand, the growth of the tolerant cv. Puget remained unchanged when grown in NaCl concentrations up to 90 mM (Hernández et al., 1999).

As salinity increases, pea water consumption decreases. In general, concentrations higher than 70 mM NaCl decrease pea leaf water potential (ψ_l) and leaf osmotic potential (ψ_s). Salt stress is also accompanied by extensive lipid peroxidation, derived from the reduction of the photosynthetic rate and the consequent over-production of ROS (Hernández, Jiménez, Mullineaux, & Sevilla, 2000; Hernández, Olmos, Corpas, Sevilla, & del Río, 1995; Imlay, 2003; Munns et al., 2020). The levels of both stress indicators (ROS content and lipid peroxidation), which are associated to membrane instability, were found to be higher in sensitive genotypes than in tolerant ones (Shahid, Balal, et al., 2012). As a result of salt stress, plant growth, leaf area and chlorophyll content decreased (Hernández et al., 1999; Shahid et al., 2012), accompanied by visual symptoms that include marginal necrosis and/or progressive yellowing of older leaves, while seeds may fail to germinate or seedlings die after emergence (Hernández et al., 1999; Shahid, Balal, et al., 2012).

Upon salt stress, the ratio ascorbate/dehydroascorbate (ASC/DHA) decreases progressively with the intensity of the stress. In this context, the pool of symplastic ASC dropped up to 52% in leaves of pea cv. Lincoln, whereas the corresponding decrease in a tolerant variety (cv. Puget) was 20% (Hernández, Ferrer et al., 2001). In this sense, the different degree of NaCl-tolerance of pea genotypes has been attributed to the functioning of the antioxidant defences, displaying tolerant cultivars higher antioxidant capacity by enhanced activity of ascorbate-glutathione (ASC-GSH) recycling enzymes (Hernández, Ferrer et al., 2001). Moreover, a strong interaction between symplastic and apoplastic compartments is suggested in the control of apoplastic ascorbate. Nevertheless, the antioxidant machinery is not sufficient to cope with salt stress and avoid the deleterious effects of high salinity. This observation is more patent in sensitive cultivars, where growth inhibition was correlated with increased apoplastic H_2O_2 and $O_2^{\cdot-}$ contents, carbonylated protein levels and lipid peroxidation. In turn, the apoplastic oxidative stress generated seems to be associated with highly localised necrotic lesions in the leaf minor veins (Hernández, Ferrer, et al., 2001).

On the other hand, the over-production of H_2O_2 and $O_2^{\cdot-}$ radicals under salt stress is predominantly due to mitochondrion and chloroplast metabolisms. At the ultrastructural level, enhanced ROS content in the chloroplast is associated with a disorganisation of the

thylakoidal structure and a reduction in starch accumulation (Hernández et al., 1995). Again, tolerant genotypes have been reported to behave differently to sensitive ones, as activities of superoxide dismutase (SOD) isoenzymes (mitochondrial Mn-SOD and chloroplastic CuZn-SOD) were higher in tolerant (cv. Puget, cv. Granada) than in sensitive (cv. Lincoln, cv. Challis) cultivars in response to 70 mM NaCl (Hernández, Ferrer, et al., 2001; Hernández et al., 1995; Hernández, Corpas, Gómez, del Río, & Sevilla, 1993). Accordingly, salt-tolerant callus of pea showed the induction of two CuZn-SOD in comparison with sensitive cells (Olmos, Hernández, Sevilla, & Hellín, 1994). Furthermore, in a more recent study, screening nine pea cvs. differing in their salinity response-enhanced, CAT activity was proposed as a marker of salt resistance in both sensitive and tolerant cultivars (Noreen & Ashraf, 2009).

2.1.2 | Understanding the different phases in the response to salt stress

In the events that occur in the plant following exposure to salt stress, primary and secondary responses can be distinguished. One of the prompt and significant responses to salt stress is a massive K^+ efflux found in both leaves and roots, which reduces the intracellular K^+ pool and may last for several hours (Wu, Zhang, Giraldo, & Shabala, 2018). In agreement with this, an amelioration of K^+ efflux correlated with enhanced salt tolerance (Carden, Walker, Flowers, & Miller, 2003; Chen et al., 2007). In this sense, in pea mesophyll cells, polyamines were effective in preventing NaCl-induced K^+ efflux by blocking non-selective cation channels; this was explained by a probable role of polyamines in the cytosol as modulators of the activity of plasma membrane ion channels, therefore facilitating plant adaptation to salinity (Chen et al., 2007).

Leaf necrotic lesions have been easily monitored during the first hours of salt stress exposure. This was shown in pea cv. Lincoln treated with 90 mM NaCl, in which lesions were associated to enhanced accumulation of ROS in the apoplastic space. Over time, the lesions became brown and of a size visible to the naked eye (Hernández, Ferrer, et al., 2001).

To maintain water balance during salt stress, leaf stoma may be closed to decrease transpiration. Therefore, modified stomatal physiology and morphology are considered an immediate defensive mechanism against salinity. This may result in a reduction of CO_2 acquisition and photosynthesis (Miyashita, Tanakamaru, Maitani, & Kimura, 2005; Zouaoui et al., 2019), which directly affects plant growth. This, in turn, would provoke a drop in the $NADP^+$ available to accept electrons from photosystems I and II, acting thereby O_2 as alternative acceptor with the consequent formation of ROS (Foyer & Shigeoka, 2011). In this sense, a correlation between lipid peroxidation extent and stomatal closure was observed in pea leaves (Hernández & Almansa, 2002). Moreover, when short-term salt stress (70 mM for 48 hr) was applied, an early peak of lipid peroxidation was observed at 8 hr of treatment, which subsequently declined until 48 hr of treatment (Hernández & Almansa, 2002). In the same study, a progressive drop of the osmotic potential of up to 30%, coupled to a linear increase of Na^+, were registered in the first 48 hr of stress. Similarly, it has been reported an increase of lipid peroxidation and protein oxidation in mitochondria of pea leaves under short-term salinity conditions (Martí et al., 2011).

Concerning the antioxidant enzymes, during the first 8 hr of stress, no changes in ascorbate peroxidase (APX), SOD, or glutathione reductase (GR) were observed. Subsequently, an increase of above 50% of SOD activity was registered at 48 hr of stress, whereas GR activity decreased by 71% at 24 hr, and APX remained unchanged (Hernández & Almansa, 2002).

On the other hand, long-term salt stress (15 days) enhanced ASC-GSH cycle activities in a salt-tolerant cultivar, whereas these activities remained unchanged and cytosolic CuZn-SOD decreased remarkably in a sensitive cultivar (Hernández et al., 2000), suggesting a prominent role of symplastic antioxidants in the response to salt stress. Moreover, the enhanced dehydroascorbate reductase (DHAR) activity in both cultivars indicated that ascorbate is regenerated via glutathione under stress conditions in the long term. At the transcriptional level, the expression of Mn-SOD, chloroplastic CuZn-SOD, glutathione peroxidase (GPX), GR and APX was remarkably increased in a salt-tolerant cv. but not in a sensitive one (Hernández et al., 2000). In mitochondria of pea leaves, thioredoxin activity increased under long-term salinity, providing protection to this organelle during the oxidative stress generated (Martí et al., 2011). Overall, these data suggest a more relevant role of antioxidant system in the long term compared to its role in the short term during salt stress.

In a recent work, the importance of cytochrome c oxidase (COX) and alternative oxidase (AOX) pathways for the photosynthetic performance has been reported in pea plants grown under NaCl stress conditions. In this sense, the use of specific inhibitors (Antimycin A and salicylhydroxamic acid for COX and AOX, respectively) led to enhanced ROS accumulation while aggravating the decrease in CO_2 assimilation rates, affecting the photosynthesis process (Analin, Mohanan, Bakka, & Challabathula, 2020).

2.1.3 | Alternative strategies to confer salt tolerance to pea plants

Alternative approaches to cope with salt stress include the use of phytoprotectants such as plant growth promoting rhizobacteria, mycorrhizal fungi and osmoprotectants. Phytoprotectants mode of action converge into the regulation of nutrient and water balance, photosynthesis efficiency and the stimulation of antioxidant defence machinery, which leads to the amelioration of salt-induced oxidative stress (Acosta-Motos et al., 2020). The growth of pea cv. Alderman exposed to 70 or 130 mM NaCl increased by 25 and 54%, respectively, upon the soil inoculation with the 1-aminocyclopropane-1-carboxylate (ACC)-deaminase containing rhizobacterium *Variovorax paradoxus* 5C-2 (Wang, Dodd, Belimov, & Jiang, 2016). Moreover, ACC-deaminase would act diminishing stress-induced ethylene production, taking into account that ethylene inhibits plant growth through diverse mechanisms (Ali, Charles, & Glick, 2014). In other work,

Planomicrobium sp. strain MSSA-10, isolated from pea rhizosphere, improved growth of pea plants under salt stress, which was associated with decreased ROS content and enhanced antioxidative enzyme activities and nutrient mobilisation (Shahid et al., 2018).

The use of plant osmoprotectants has expanded in the last years due to the introduction of osmoprotectant genes into crop plants via genetic engineering (Acosta-Motos et al., 2020; Zulfiqar, Akram, & Ashraf, 2020). In the pea salt-sensitive cv. Ran 1, an increase in proline was coupled to enhanced photorespiration and glycolate oxidase activity, while photosynthesis was significantly inhibited in response to 50 mM NaCl (Fedina, Tsonev, & Guleva, 1994). Moreover, the expression of Δ1-pyrroline-5-carboxylate reductase (*proC*) gene, which catalyses the last step in proline biosynthesis, was found to be osmoregulated in pea (Williamson & Slocum, 1992). It has been also reported that the addition of osmoprotectant compounds (KH_2PO_4 and thiamine) in the rooting medium alleviated the effect of salt stress in pea plants in terms of growth, stomatal conductance and chlorophyll content (Balliu, Sallaku, & Nasto, 2016).

Salinity negatively affects seed germination and early seedling growth due to the occurrence of osmotic stress, ion-specific phytotoxicity and oxidative stress (Acosta-Motos et al., 2017). Therein, seed priming appears as a suitable strategy leading to uniform germination rate and, at the same time, conferring a certain degree of salt tolerance to adult plants. In this regard, seed priming within organic salt solutions (osmopriming) or water (hydropriming) were reported as efficient and economic alternatives (Matias, Torres, Leal, Leite, & Carvalho, 2018; Singh et al., 2015). Moreover, the pre-treatment of pea seeds with licorice root extracts or with GA_3 alleviated the negative effects of salt stress in the seedlings (Ahmad et al., 2020; Desoky, ElSayed, Merwad, & Rady, 2019). In both cases, the increased salt tolerance was related with the induction of the antioxidant system, increases in chlorophyll, proline and soluble sugars levels, and improved ion homeostasis and gas exchange parameters (Ahmad et al., 2020; Desoky et al., 2019).

Other authors pointed out that exposure of pea seedlings to 10 mM NaCl for a week resulted in an acclimation response of adult plants when exposed to 80 mM NaCl, preventing K^+ leakage and Na^+ accumulation mainly in primary roots, coupled to increased xylem K^+/Na^+ given by Na^+ sequestration in mesophyll cells (Pandolfi, Mancuso, & Shabala, 2012). As K^+ is a compatible solute for plants, whereas Na^+ ions are toxic, an osmotic effect of salt stress rather than a specific ionic effect of Na^+ was suggested (Lechno, Zamski, & Tel-Or, 1997). In agreement with a probable role of low NaCl concentration as a priming treatment, it has been reported an enhancement of the net photosynthetic rate of pea when exposed to low NaCl content, but an inhibitory effect at 80 mM NaCl (Hamada & El-Enany, 1994).

2.2 | Salinity and peach plants

It is widely accepted that peach plants (*Prunus persica*, (L.) Batsch) are susceptible to NaCl levels higher than 1.7 dS m^{-1}, equivalent to 20 mM NaCl, although information concerning the effect of NaCl stress on peach plants is very limited. The research about the effect of salinity on the growth and antioxidant metabolism in fruit trees of *Prunus* genus is also very scarce, having been conducted mostly under in vitro conditions. The response of peach GF305 to irrigation with 34 mM NaCl during 8 weeks was studied (Bernal-Vicente, Cantabella, Hernández, & Diaz-Vivancos, 2018; Bernal-Vicente, Petri, Hernández, & Diaz-Vivancos, 2020). The authors observed no effect of NaCl treatment on plant growth, although a slight decrease in the fresh weight of leaves and roots was observed. Salt stress produced a decrease in chlorophyll a content, but not in chlorophyll b content. In addition, salinity also affected some chlorophyll fluorescence parameters, as reflected by the increase in the photochemical quenching (qP) and the quantum yield of photosystem II (Φ PSII) parameters, as well as in the decrease of non-photochemical quenching yield Y(NPQ) (Bernal-Vicente et al., 2018). All these data confirmed that salinity alters the photosynthetic machinery in peach plants.

NaCl also affected the mineral nutrition in leaves and roots from peach GF305. In this sense, a significant decline in K^+, Ca^{2+} and Na^+ occurred in leaves, whereas a significant accumulation of Cl^- and Na^+ was observed in roots, which could be considered as a mechanism of adaptation to salinity in order to avoid excess accumulation of Na^+ and Cl^- in leaves (Bernal-Vicente et al., 2018).

More recently, the effect of salinity on the antioxidant defences and on the level of the stress-related hormones salicylic acid (SA), abscisic acid (ABA) and jasmonic acid (JA) in peach GF305 was studied (Bernal-Vicente et al., 2020). In that regards, the authors reported that NaCl stress produced a decline in the H_2O_2-scavenging enzymes APX and CAT (Bernal-Vicente et al., 2020), as well as an increase in the DHAR and a decrease in the reduced GSH levels (unpublished results). Salinity strongly enhanced the level of the stress-related hormone SA in peach leaves, as well as the ABA and JA contents (Bernal-Vicente et al., 2020).

2.2.1 | Strategies to improve salt tolerance in peach

The use of an appropriate rootstock can improve the response of peach plants to salt stress. In that regards, the effect of 80 and 120 mM NaCl on three different rootstocks normally used for peaches (Mr.S.2/5, G.F.655/2, G.F.677), as well as in peach seedlings, were analysed (Massai, Gucci, & Tattini, 1998). The authors observed that rootstocks G.F.655/2 and Mr.S.2/5 improved the CO_2 assimilation rate, whereas the use of G.F.677 and G.F.655/2 rootstocks produced less Na^+ accumulation in leaves than the use of the other rootstocks when treated with 120 mM NaCl. In another study, eight different NaCl concentrations, from 0 to 4,000 ppm, were used to evaluate the salt tolerance of plantlets from in vitro Hassawi peach rootstocks, in terms of plantlet survival, number and length of the shoots, number of fresh leaflets, number and length of the roots, elongation of plantlets and percentage of acclimatised plants. As a conclusion, the use of bitter almond as rootstock was found optimal for

Hassawi peach grafting, as it displayed the highest values in each of the parameters indicated above, even in the treatment with the highest salt concentration (4,000 ppm) (Shehata & Alturki, 2020).

Other strategies are based on irrigation combinations. Boland, Mitchell, and Jerie (1993) analysed the effect of four salinity levels (0.1, 0.25, 0.5 and 1.0 dS m^{-1}) combined with the application of regulated deficit irrigation. As a result, a strong negative correlation between the severity of the salt treatment and the growth and size of fruits was found. Both phytotoxic ions (Na^+ and Cl^-) increased their levels in fruits and in the wood depending on the severity of the saline treatment (Boland et al., 1993). Likewise, the presence of phytotoxic ions in the soil led to a reduced tree water use due to the difficulties of the root system to absorb water. The highest level of salinity negatively affected photosynthesis, due to an enhanced stomata closure. Consequently, the authors recommended to apply periodic fractions of leaching to avoid an excessive accumulation of salts in the soil that could negatively affect the subsequent growth and development of the tree (Boland et al., 1993).

In a recent work, using biochemical and metabolomics strategies, cyanogenic glycosides (CNglcs) turnover was suggested to be implicated, at least in part, in SA biosynthesis in peach plants under control and stress conditions. Herein, mandelonitrile (MD) would act as the intermediary molecule between the suggested new SA biosynthetic pathway and CNglcs turnover, regulating the biosynthesis of both CNglcs (prunasin and amygdalin) and SA (Diaz-Vivancos, Bernal-Vicente, Cantabella, Petri, & Hernández, 2017). In micropropagated peach shoots, although MD treatment did not increase SA content under abiotic stress conditions, a small amount of MD was found to be metabolised to SA. With this evidence it was concluded that under salt stress condition, this new SA biosynthetic pathway would contribute much less, at least under in vitro conditions, to the total amount of SA than the phenylalanine ammonia-lyase pathway (Diaz-Vivancos et al., 2017).

In another work, MD and phenylalanine (MD precursor) were applied to GF305 peach seedlings to investigate the role of the new SA biosynthetic pathway previously described (Diaz-Vivancos et al., 2017) on plant performance under salt stress (2 g L^{-1} NaCl) (Bernal-Vicente et al., 2018). Under these conditions, MD treatment induced certain photosynthesis protection, as suggested by the maintenance of chlorophyll content and the increase on non-photochemical quenching parameters compare to control plants (Bernal-Vicente et al., 2018). This suggests an effective way to protect photosynthetic machinery, as it has been observed in other plant species (Acosta-Motos et al., 2017). Moreover, the increase in non-photochemical quenching parameters has been suggested as a mechanism to dissipate excess energy in a safe way under salt stress conditions (Acosta-Motos et al., 2015; Cantabella et al., 2017; Ikbal et al., 2014).

Regarding the nutritional status, the application of MD under salt stress conditions triggered the accumulation of phytotoxic ions in peach roots (Bernal-Vicente et al., 2018), which was considered a salt-adaptation mechanism, as previously studied in other plant species tolerant to salinity (Acosta-Motos et al., 2015, 2016). Similar results were observed in different plant species like mung bean, camomile and Arabidopsis, in which SA application mitigated the toxic effects of salts by decreasing Na^+ and increasing K^+ levels in roots (Ghassemi-Golezani & Lotfi, 2015; Jayakannan, Bose, Babourina, Rengel, & Shabala, 2015; Kováčik, Klejdus, Hedbavny, & Bačkor, 2009). Therefore, it is concluded that SA application or the MD-induced SA provides protection to some plants species against salt stress.

In a recent work, Bernal-Vicente et al. (2020) studied the levels of MD and the stress-related hormones ABA and JA in salt-treated peach GF305 seedlings, in order to provide more information about this proposed SA biosynthetic pathway. In the absence of NaCl stress, SA and ABA levels remained unchanged by MD-treatments, but a significant decline in JA was produced, whereas under salinity conditions, no important changes in these stress-related hormones were observed (Bernal-Vicente et al., 2020). These results suggested that the contribution of this pathway to the SA pool does not seem to be very important under salt stress, and therefore, it cannot be ruled out that MD, and hence CNglc, may affect other signalling pathways, leading to the observed differences in the response to salinity. Taken together, more assays are necessary to elucidate the physiological importance of the new SA biosynthetic pathway from MD in response to salt stress (Bernal-Vicente et al., 2020). ABA is a key phytohormone in the response to abiotic stress due to its important role in stomatal closure. In addition, JA could act as a regulator of ABA biosynthesis (de Ollas & Dodd, 2016). In this sense, an increased SA/JA ratio in control seedlings was found in response to salinity, whereas in MD treatment the SA/JA ratio slightly diminished, suggesting that NaCl stress showed no major effect on the development of MD-treated seedlings (Bernal-Vicente et al., 2020). Therefore, an increase in the SA/JA ratio was proposed as a marker of saline stress in other plant species (Acosta-Motos et al., 2016).

Concerning the antioxidative metabolism analysis, in the absence of NaCl MD-treated plants displayed a lower APX, POX and CAT activities, whereas in NaCl-treated plants, the addition of MD significantly enhanced APX and SOD activities by ca. 75% in relation to the NaCl-treated plants grown in absence of MD (Bernal-Vicente et al., 2020). Some authors have described that the coordinated up-regulation of the antioxidant enzyme activities could be one of the mechanisms involved in the salt tolerance response (Acosta-Motos et al., 2017; Hernández, Ferrer, et al., 2001; López-Gómez et al., 2007).

3 | PLANT RESPONSES TO BIOTIC STRESS: THE CASE OF PPV INFECTION

PPV, the causal agent of sharka disease, is one of the most studied plant viruses. This widespread disease affecting many stone fruits including *Prunus* species produces severe economic losses (Clemente-Moreno, Hernández, & Diaz-Vivancos, 2015). Transcriptomic, proteomic, metabolomic and morphological changes, as well as physiological and biochemical alterations, are induced by viral infections. Among them, alterations in the photosynthetic machinery leading to ROS accumulation have been described in many plant–virus interactions. These alterations are usually related to the appearance of the typical

PPV disease symptoms, that is, chlorotic and necrotic spots in leaves, suggesting that chloroplast are the target organelles to plant viruses (Clemente-Moreno et al., 2015).

Both biotic and abiotic stresses produce ultrastructural alterations in plants, being the chloroplast one of the most affected organelles. PPV infection affected mainly chloroplasts from cells associated with the vascular system (Díaz-Vivancos et al., 2008). In both pea and peach, a disorganised granal structure as well as lower starch content were observed in chloroplasts of PPV-infected plants (Clemente-Moreno et al., 2015; Díaz-Vivancos et al., 2008).

3.1 | PPV infection and pea plants

Sharka disease has had a significant agronomic impact during the last 40 years, leading to important economic losses, affecting mostly the *Prunus* genus (Cambra, Capote, Myrta, & Llácer, 2006). However, PPV not only infects stone fruit trees of *Prunus*, but also herbaceous plants such as *Nicotiana clevelandii*, *N. benthamiana*, *N. glutinosa*, *Arabidopsis*, *Chenopodium foetidum* and certain pea cvs. (e.g., cv. Alaska), although other pea cultivars are not susceptible to PPV (Babu, Griffiths, Huang, & Wang, 2008; Clemente-Moreno, Díaz-Vivancos, Barba-Espín, & Hernández, 2010; Díaz-Vivancos et al., 2008; Visedo, Fernández-Piqueras, & García, 1991; Yi, Yu, & Choi, 1999).

The symptoms produced by PPV in pea cv. Alaska include chlorotic spots in systemic leaves at 13–15 days post-inoculation (dpi). In addition, necrotic spots also appear in the oldest leaves (Clemente-Moreno et al., 2010, 2015; Díaz-Vivancos et al., 2008). PPV infection, as salinity, affected plant growth in pea plants. In cv. Alaska, at 15 dpi, PPV produced a decrease in the biomass of the aerial part of the plant, measured as fresh weight (Clemente-Moreno et al., 2010).

At short-term (3 dpi) no apparent symptoms were observed, but changes in the antioxidant metabolism at the subcellular level, as well as in the protein expression, took place (Díaz-Vivancos et al., 2008). In that sense, PPV decreased APX activity in the soluble fraction and in chloroplasts, whereas POX activity was enhanced in soluble fraction but declined in chloroplasts. As results of the decrease of these two H_2O_2-scavenger enzymes in chloroplasts, an accumulation of H_2O_2 was observed in this organelle at short-term. Such chloroplastic H_2O_2 accumulation could be considered as an early reaction to PPV-infection in pea plants (Díaz-Vivancos et al., 2008).

At long-term, PPV produced an oxidative stress manifested in a H_2O_2 over-accumulation in chloroplasts and in soluble fractions, and also in an increase in lipid peroxidation, protein oxidation and electrolyte leakage in leaves (Clemente-Moreno et al., 2010; Díaz-Vivancos et al., 2008). This response was parallel to an imbalance of the antioxidant enzymes in both compartments. In this sense, increases in APX and POX activities but decreases in CAT and glutathione S-transferase (GST) were observed in soluble fractions, whereas in chloroplasts, a decline in APX, GR, SOD and glutathione peroxidase (GPX) was recorded (Clemente-Moreno et al., 2010; Díaz-Vivancos et al., 2008). At long-term, H_2O_2 accumulated in the soluble fraction and in chloroplasts, in spite of the increased levels of the H_2O_2-scavenging enzymes in the soluble fraction. In contrast, in the soluble fraction, PPV infection decreased CAT activity. This response could contribute to the accumulation of H_2O_2 in the mentioned compartment. Catalase is a peroxisomal enzyme and, in this sense, a decline in this activity correlates with H_2O_2 accumulation in peroxisomes, from which H_2O_2 may diffuse through the peroxisomal membrane into the cytosol (Del Río et al., 1998).

PPV infection also has an effect on the non-enzymatic antioxidant glutathione. In this sense, PPV infection induced an accumulation of the oxidised glutathione form (GSSG), while no effect in the reduced form (GSH) was observed, and accordingly, a drop in the redox state of glutathione was induced by PPV infection (Clemente-Moreno et al., 2010).

The increase in chloroplastic H_2O_2 in both phases of the PPV infection can partially be explained by the reduced expression of proteins related to photosynthesis, including rubisco, oxygen-evolving enhancer protein and photosystem II stability factor (Díaz-Vivancos et al., 2008). In that regards, the decrease in rubisco can lead to a deceleration of the Calvin cycle, and therefore a minor generation of $NADP^+$, the final electron acceptor at photosystem I (PSI), hence favouring the reduction of O_2 to $O_2^{\cdot-}$, which would eventually give rise to H_2O_2 by action of SOD activity (Asada, 1999).

The aforementioned results highlight that chloroplasts are the main target organelle of PPV infection. Chlorophyll fluorescence has emerged as a useful tool to study the effect of plant pathogens, including virus, on the photosynthetic machinery. By using chlorophyll fluorescence imaging many works have linked virus-induced photosynthesis alterations with other host physiology disturbances. In this sense, PPV infection alters chloroplast metabolism and modifies chlorophyll fluorescence parameters such as non-photochemical quenching (NPQ), photochemical quenching (qP) and the quantum yield of photosystem II (Φ PSII) (Díaz-Vivancos et al., 2008; Hernández, Rubio, Olmos, Ros-Barceló, & Martínez-Gómez, 2004).

At long term, PPV produced a decline in NPQ in symptomatic leaves (Díaz-Vivancos et al., 2008). In contrast, Clemente-Moreno et al. (2015) found a slight increase in NPQ and its coefficient (qN), along with a decrease in qP and Φ PSII in symptomatic pea leaves, whereas asymptomatic leaves showed the opposite response. In susceptible pea plants, the alteration in these photosynthetic parameters was correlated with a reduction in the amount of rubisco and several polypeptides associated with PSII (Díaz-Vivancos et al., 2008). A decrease in NPQ could reflect a diminished capacity for the safe dissipation of excess light energy, resulting in an enhanced production of harmful species, such as $^1O_2$, which would lead to worsened functioning and/or deterioration of the photosynthetic apparatus in the long term (Fryer, Oxborough, Mullineaux, & Baker, 2002).

3.2 | PPV infection and peach plants

Although PPV infection has been largely studied in many herbaceous plants, not many works can be found in the literature about the response of woody plants to PPV infection. A pioneering work in this

field studied the levels of antioxidant enzymes in crude extracts of two PPV-infected apricot (*P. armeniaca*) cultivars differing in their susceptibility to PPV (Hernández, Talavera, Martínez-Gómez, Dicenta, Sevilla, 2001). In the resistant cv. (Goldrich), PPV infection produced an increase in SOD and DHAR as well as a decrease in CAT activities (Hernández, Talavera, et al., 2001). On the other hand, in the susceptible cv. (Real Fino), an increase in APX, MDHAR and DHAR as well as a decrease in CAT, SOD and GR took place by PPV infection. Taking into account that SOD and APX, H_2O_2-generating and -scavenging enzymes respectively, behaved differently, the authors proposed that a transient and controlled increase until sub-lethal levels of H_2O_2 could be responsible for the different response to PPV of the apricot cultivars studied (Hernández, Talavera, et al., 2001). In this sense, it has been widely described that transient elevations in ROS levels led to both abiotic and biotic stress tolerance (Gechev, Van Breusegem, Stone, Denev, & Laloi, 2006).

Later, the effect of PPV infection on the antioxidative metabolism was studied at subcellular level in the apricot cvs Stark Early Orange (SEO; PPV-resistant) and Real Fino, as well as in the PPV-susceptible peach (*P. domestica*) cv. GF305 (Diaz-Vivancos et al., 2006; Hernandez et al., 2006; Hernández et al., 2004). These works confirmed that PPV infection produced an oxidative stress only in susceptible plants (apricot Real Fino and peach GF305), as indicated by the increase in different oxidative stress parameters. In addition, these susceptible plants showed an accumulation of H_2O_2 that correlated with a decrease of the enzymatic antioxidant capacity, mainly in chloroplasts (Diaz-Vivancos et al., 2006; Hernandez et al., 2006; Hernández et al., 2004). Opposite to those susceptible cultivars, the resistant apricot SEO displayed minor H_2O_2 production due to the increase in some antioxidant enzymes in the apoplastic space and in the soluble fraction (Hernandez et al., 2006; Hernández et al., 2004).

Focusing in the response of peach GF305, the levels of antioxidant enzymes were determined at the subcellular level, including the soluble fraction, chloroplasts and the apoplastic space. In the apoplast, an increase in APX and POX activities was recorded, which seemed to be insufficient to deal with the PPV-induced oxidative stress, as suggested by the strong increase observed in the apoplastic H_2O_2 content (Diaz-Vivancos et al., 2006). On the other hand, in the soluble fraction, the increase in these H_2O_2-scavenging activities was accompanied by a decrease in SOD activity (Diaz-Vivancos et al., 2006; Hernández et al., 2004). In chloroplasts, an increase in APX activity as well as a decrease in SOD, MDHAR and GR activities were recorded (Hernández et al., 2004). Similarly, in the pea cv. Alaska, PPV infection produced a decrease in the chloroplastic levels of some antioxidative enzymes that led to a H_2O_2 accumulation in chloroplasts (Díaz-Vivancos et al., 2008).

In peach, PPV infection altered chloroplast metabolism and modified chlorophyll fluorescence parameters such as NPQ, qP and the efficiency of excitation energy capture by PSII (F_v'/f_m') (Bernal-Vicente et al., 2018; Hernández et al., 2004). These alterations were correlated to enhanced ROS production and reduced scavenging capacity in PPV susceptible plants, leading to symptom development. In fact, it has been long established that symptom development is usually accompanied by chlorophyll fluorescence changes (Rolfe & Scholes, 2010). For example, soybean mosaic virus infection induced a decrease in Φ PSII in the areas where ROS accumulation was observed (Aldea, Frank, & DeLucia, 2006). Moreover, in *Abutilon* mosaic virus-infected leaves, a decrease in NPQ was only observed when yellow-mosaic areas emerged (Lohaus, Heldt, & Osmond, 2000).

3.3 | Biochemical-based approaches to cope with PPV infection

Stress acclimation can be achieved by direct application of ROS or redox-associated metabolites leading to a transient increase in ROS content and/or to an enhanced antioxidant capacity. In order to induce PPV tolerance, a functional analogue of salicylic acid (benzothiadiazole, BTH) and an artificial cysteine precursor leading to total GSH accumulation (L-2-oxo-4-thiazolidine-carboxylic acid, OTC) were assayed, because these compounds were described to induce protection against different types of viruses (Gullner, Tobias, Fodor, & Komives, 1999; Zechmann, Zellnig, Urbanek-Krajnc, & Müller, 2007).

PPV-infected pea plants treated with OTC or BTH displayed a reduction in the percentage of leaves showing symptoms and enhanced the growth of PPV-infected peach plantlets under in vitro conditions. However, none of the treatments reduced the virus content (Clemente-Moreno et al., 2010). In peach seedlings, under greenhouse conditions, both BTH and OTC conferred a partial protection against PPV infection, providing OTC a better response than BTH. In addition, OTC stimulated the growth of peach seedlings and provided protection to the photosynthetic machinery, as suggested by the increased levels of proteins related to photosynthesis, carbohydrate and amino acid metabolisms and photorespiration (Clemente-Moreno, Díaz-Vivancos, Rubio, Fernández-García, & Hernández, 2013). Moreover, in PPV-infected peach seedlings, OTC treatment ameliorated the reduction of starch content and preserved the thylakoids structure. On the other hand, BTH treatment did not protect thylakoidal structure but similarly to OTC it avoided a major drop in starch content (Clemente-Moreno et al., 2013).

It has been proposed that the effect of OTC and BTH in plant protection against pathogens is related to their effects on the antioxidative metabolism, especially on glutathione. In fact, in non-infected plants, OTC treatment increased total glutathione content in both pea and peach plants (Clemente-Moreno et al., 2010, 2013). In addition, the levels of antioxidants enzymes were altered in PPV infected pea and peach plants treated with either BTH or OTC (Clemente-Moreno et al., 2010, 2013; Clemente-Moreno, Díaz-Vivancos, Piqueras, & Hernández, 2012). Moreover, BTH and OTC reduced GSSG levels in asymptomatic leaves of pea plants (Clemente-Moreno et al., 2010) and in symptomatic leaves of peach seedlings (Clemente-Moreno et al., 2013). Accordingly, a higher glutathione redox state was observed, which could be related to the partial protection against PPV conferred by these compounds. This protection was also recorded in peach seedlings using chlorophyll fluorescence techniques. In PPV-infected peach

seedlings treated with BTH or OTC, no changes in chlorophyll fluorescence parameters were observed. In contrast, in the absence of treatments, PPV induced a decrease in the electron transport efficiency, as indicated by reduced F_v/F_m, Φ PSII and qP (Clemente-Moreno et al., 2013) levels.

More recently, it has been described that MD also provided a partial protection against PPV infection that was correlated with increased SA levels (Diaz-Vivancos et al., 2017). Moreover, MD treatment increased the levels of other stress related hormones (ABA and JA) and modulated the antioxidative metabolism in PPV-infected peach seedlings (Bernal-Vicente et al., 2020).

4 | ESTABLISHING COMMON PATTERNS IN THE RESPONSE TO STRESS: A COMPENDIUM

Herbaceous and woody plants have distinct growth and development habits. Nevertheless, all plant species share certain basic physiological and biochemical mechanisms. Among the points of convergence of abiotic and biotic stress responses in plants, ROS and hence the antioxidative metabolism have been described as common key players in the abiotic and biotic stress signalling networks. Different molecular analysis and approaches have revealed that the ROS scavenging

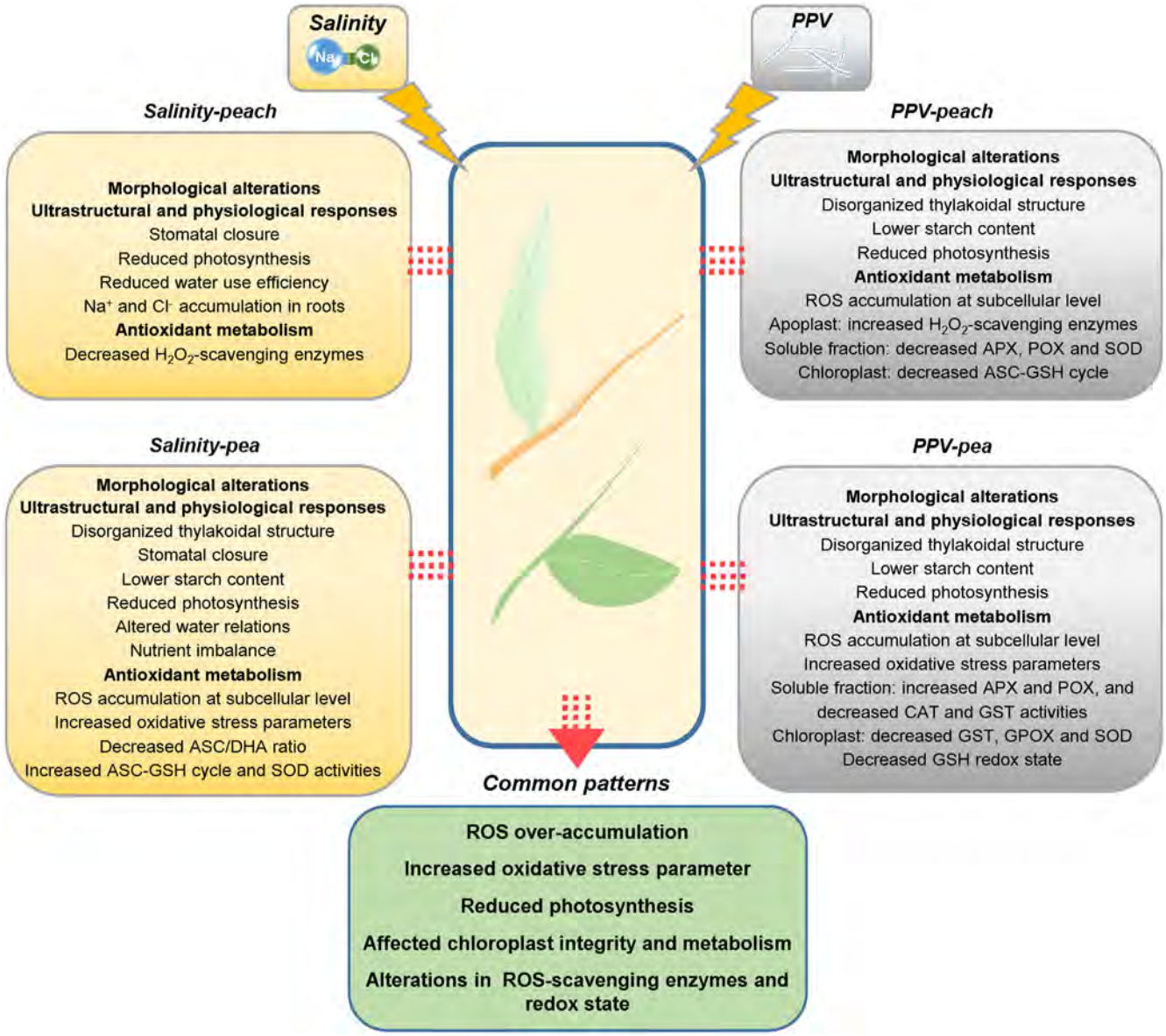

FIGURE 1 Overview of factors involved in the response to salt stress and PPV infection in pea and peach plants. In soluble fractions, an oxidative stress was observed, including H_2O_2 and O_2^- accumulation, in spite of increased ROS-scavenging enzymes. In chloroplasts, PPV-infection and salt stress affected negatively photosynthesis, which was reflected in an oxidative stress in the organelle, accompanied by decreases in activity of H_2O_2-scavenging enzymes and a disorganisation of thylakoidal structure. APX, ascorbate peroxidase; ASC, ascorbate; CAT, catalase; DHA, dehydroascorbate; GPOX, glutathioneperoxidase; GSH, reduced glutathione; GSSG, oxidised glutathione; GST, glutathione-S-transferase; ROS, reactive oxygen species; SOD, superoxide dismutase

mechanisms are involved in both biotic and abiotic stress responses (Clemente-Moreno et al., 2015; Fujita et al., 2006). However, the mechanisms implied in the over-generation of ROS are somewhat different (Apel & Hirt, 2004). In general, ROS over-generation under abiotic stress is related with the damage induced by such stress (Hernández et al., 1993; Hernández, Ferrer, et al., 2001; Ikbal et al., 2014), although the role of ROS as signalling molecules at low concentrations has also been reported (Miller, Suzuki, Ciftci-Yilmaz, & Mittler, 2010; Mittler et al., 2011; Suzuki, Koussevitzky, Mittler, & Miller, 2012). In this sense, ROS generated at short term under biotic stress may serve as signalling molecules to induce defence mechanisms to cope with the stress situation, including programmed cell death and stomatal movements. However, at both short and long-term, ROS over-generation was related with the appearance of symptoms and damage caused by the pathogen in question (Clemente-Moreno et al., 2010, 2015; Díaz-Vivancos et al., 2008; Hernandez et al., 2016).

Both salinity and PPV infection affected plant growth and induced an imbalance in the antioxidative defences in pea and peach plants, including ROS accumulation and the increase in some oxidative stress parameters, which is ultimately related to symptoms development (Figure 1). In addition, in both stresses, chloroplasts seemed to be the most affected cell organelle, being reduced photosynthesis a common effect. In fact, chloroplast integrity and performance is compromised as indicated by changes in chlorophyll and starch contents, in chlorophyll fluorescence parameters and ultrastructural alterations (Figure 1). At nutritional level, salt stress provoked an over-accumulation of Na^+ and Cl^- in both species, coupled to the leakage of K^+. Predominantly, peach plants accumulated Na^+ and Cl^- in roots, which was considered a mechanism of adaptation to salinity in order to avoid their excess accumulation in leaves (Figure 1).

In the last years, high-throughput separation and identification techniques have allowed researchers to expand understanding on plant cellular responses to stress in a more complex way, as well as to identify markers for crop breeding purposes (Kosová et al., 2015; Rubio et al., 2015). By means of RNA-seq conducted on PPV-infected peach leaves, a high expression of mRNA target genes associated with pathogen resistance (such as chitinases, cytokinin glucosyl transferases, jasmonic acid and Lys-M proteins), carbohydrate and lipid metabolism, and negative regulation of catalytic activity was found. Interestingly, a major proportion of those differentially expressed genes were found at the early asymptomatic phase of infection (Rubio et al., 2015). In pea, a proteomic study in roots of salt-stressed plants showed the over-expression of pathogenesis-related 10 proteins, and antioxidant enzymes such as SOD, among others (Kav, Srivastava, Goonewardene, & Blade, 2005). In the future, combination of omics approaches together with traditional strategies such as grafting (Soares et al., 2019) should be critical to elucidate precisely the intricate response to stress in both pea and peach plants.

Overall, the present review points common response mechanisms of plants to biotic and abiotic stresses, which may serve to devise agronomical approaches to confer stress tolerance to many economically relevant crops.

ORCID

Jose A. Hernández https://orcid.org/0000-0001-7211-5147

REFERENCES

Acosta-Motos, J. R., Diaz-Vivancos, P., Álvarez, S., Fernández-García, N., Sanchez-Blanco, M. J., & Hernández, J. A. (2015). Physiological and biochemical mechanisms of the ornamental *Eugenia myrtifolia* L. plants for coping with NaCl stress and recovery. *Planta*, *242*(4), 829–846. https://doi.org/10.1007/s00425-015-2315-3

Acosta-Motos, J. R., Ortuño, M. F., Bernal-Vicente, A., Diaz-Vivancos, P., Sanchez-Blanco, M. J., & Hernandez, J. A. (2017). Plant responses to salt stress: Adaptive mechanisms. *Agronomy*, *7*(1), 18. https://doi.org/10.3390/agronomy7010018

Acosta-Motos, J. R., Ortuño, M. F., Álvarez, S., López-Climent, M. F., Gómez-Cadenas, A., & Sánchez-Blanco, M. J. (2016). Changes in growth, physiological parameters and the hormonal status of *Myrtus communis* L. plants irrigated with water with different chemical compositions. *Journal of Plant Physiology*, *191*(Suppl C), 12–21. https://doi.org/10.1016/j.jplph.2015.11.010

Acosta-Motos, J. R., Penella, C., Hernández, J. A., Díaz-Vivancos, P., Sánchez-Blanco, M. J., Navarro, J. M., … Barba-Espín, G. (2020). Towards a sustainable agriculture: Strategies involving phytoprotectants against salt stress. *Agronomy*, *10*(2), 194. https://doi.org/10.3390/agronomy10020194

Ahmad, F., Kamal, A., Singh, A., Ashfaque, F., Alamri, S., Siddiqui, M. H., & Khan, M. I. R. (2020). Seed priming with gibberellic acid induces high salinity tolerance in *Pisum sativum* through antioxidant system, secondary metabolites and upregulation of antiporter genes. *Plant Biology*. https://doi.org/10.1111/plb.13187

Aldea, M., Frank, T. D., & DeLucia, E. H. (2006). A method for quantitative analysis of spatially variable physiological processes across leaf surfaces. *Photosynthesis Research*, *90*, 161–172. https://doi.org/10.1007/s11120-006-9119-z

Ali, S., Charles, T. C., & Glick, B. R. (2014). Amelioration of high salinity stress damage by plant growth-promoting bacterial endophytes that contain ACC deaminase. *Plant Physiology and Biochemistry*, *80*, 160–167. https://doi.org/10.1016/j.plaphy.2014.04.003

Analin, B., Mohanan, A., Bakka, K., & Challabathula, D. (2020). Cytochrome oxidase and alternative oxidase pathways of mitochondrial electron transport chain are important for the photosynthetic performance of pea plants under salinity stress conditions. *Plant Physiology and Biochemistry*, *154*, 248–259. https://doi.org/10.1016/j.plaphy.2020.05.022

Apel, K., & Hirt, H. (2004). Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. *Annual Review of Plant Biology*, *55*, 373–399. https://doi.org/10.1146/annurev.arplant.55.031903.141701

Asada, K. (1999). The water-water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. *Annual Review of Plant Physiology and Plant Molecular Biology*, *50*, 601–639. https://doi.org/10.1146/annurev.arplant.50.1.601

Babu, M., Griffiths, J. S., Huang, T. S., & Wang, A. (2008). Altered gene expression changes in Arabidopsis leaf tissues and protoplasts in response to *Plum pox virus* infection. *BMC Genomics*, *9*, 325. https://doi.org/10.1186/1471-2164-9-325

Balliu, A., Sallaku, G., & Nasto, T. (2016). The effects of some osmoprotectant compounds on growth parameters of pea plants (*Pisum sativum*) under saline conditions. *Acta Horticulturae*, *1142*, 377–382. https://doi.org/10.17660/ActaHortic.2016.1142.57

Bernal-Vicente, A., Cantabella, D., Hernández, J. A., & Diaz-Vivancos, P. (2018). The effect of mandelonitrile, a recently described salicylic acid precursor, on peach plant response against abiotic and biotic stresses. *Plant Biology*, *20*(6), 986–994. https://doi.org/10.1111/plb.12894

Bernal-Vicente, A., Petri, C., Hernández, J. A., & Diaz-Vivancos, P. (2020). Biochemical study of the effect of stress conditions on the

mandelonitrile-associated salicylic acid biosynthesis in peach. *Plant Biology*, *22*(2), 277–286. https://doi.org/10.1111/plb.13066

Boland, A. M., Mitchell, P. D., & Jerie, P. H. (1993). Effect of saline water combined with restricted irrigation on peach tree growth and water use. *Australian Journal of Agricultural Research*, *44*(4), 799–816. https://doi.org/10.1071/AR9930799

Cambra, M., Capote, N., Myrta, A., & Llácer, G. (2006). Plum pox virus and the estimated costs associated with sharka disease. *EPPO Bulletin*, *36* (2), 202–204. https://doi.org/10.1111/j.1365-2338.2006.01027.x

Cantabella, D., Piqueras, A., Acosta-Motos, J. R., Bernal-Vicente, A., Hernández, J. A., & Díaz-Vivancos, P. (2017). Salt-tolerance mechanisms induced in *Stevia rebaudiana* Bertoni: Effects on mineral nutrition, antioxidative metabolism and steviol glycoside content. *Plant Physiology and Biochemistry*, *115*, 484–496. https://doi.org/10.1016/j.plaphy.2017.04.023

Carden, D. E., Walker, D. J., Flowers, T. J., & Miller, A. J. (2003). Single-cell measurements of the contributions of cytosolic Na^+ and K^+ to salt tolerance. *Plant Physiology*, *131*(2), 676–683. https://doi.org/10.1104/pp.011445

Chen, Z., Zhou, M., Newman, I. A., Mendham, N. J., Zhang, G., & Shabala, S. (2007). Potassium and sodium relations in salinised barley tissues as a basis of differential salt tolerance. *Functional Plant Biology*, *34*(2), 150–162. https://doi.org/10.1071/FP06237

Clemente-Moreno, M. J., Díaz-Vivancos, P., Barba-Espín, G., & Hernández, J. A. (2010). Benzothiadiazole and L-2-oxothiazolidine-4-carboxylic acid reduce the severity of Sharka symptoms in pea leaves: Effect on antioxidative metabolism at the subcellular level. *Plant Biology*, *12*(1), 88–97. https://doi.org/10.1111/j.1438-8677.2009.00204.x

Clemente-Moreno, M. J., Díaz-Vivancos, P., Piqueras, A., & Hernández, J. A. (2012). Plant growth stimulation in *Prunus* species plantlets by BTH or OTC treatments under in vitro conditions. *Journal of Plant Physiology*, *169*(11), 1074–1083. https://doi.org/10.1016/j.jplph.2012.03.012

Clemente-Moreno, M. J., Díaz-Vivancos, P., Rubio, M., Fernández-García, N., & Hernández, J. A. (2013). Chloroplast protection in *plum pox virus*-infected peach plants by L-2-oxo-4-thiazolidine-carboxylic acid treatments: Effect in the proteome. *Plant, Cell and Environment*, *36*(3), 640–654. https://doi.org/10.1111/pce.12003

Clemente-Moreno, M. J., Hernández, J. A., & Diaz-Vivancos, P. (2015). Sharka: How do plants respond to plum pox virus infection? *Journal of Experimental Botany*, *66*(1), 25–35. https://doi.org/10.1093/jxb/eru428

de Ollas, C., & Dodd, I. C. (2016). Physiological impacts of ABA–JA interactions under water-limitation. *Plant Molecular Biology*, *91*, 641–650. https://doi.org/10.1007/s11103-016-0503-6

Del Río, L. A., Pastori, G. M., Palma, J. M., Sandalio, L. M., Sevilla, F., Corpas, F. J., … Hernández, J. A. (1998). The activated oxygen role of peroxisomes in senescence. *Plant Physiology*, *116*(4), 1195–1120. https://doi.org/10.1104/pp.116.4.1195

Desoky, E. S. M., ElSayed, A. I., Merwad, A. R. M. A., & Rady, M. M. (2019). Stimulating antioxidant defenses, antioxidant gene expression, and salt tolerance in *Pisum sativum* seedling by pretreatment using licorice root extract (LRE) as an organic biostimulant. *Plant Physiology and Biochemistry*, *142*, 292–302. https://doi.org/10.1016/j.plaphy.2019.07.020

Diaz-Vivancos, P., Bernal-Vicente, A., Cantabella, D., Petri, C., & Hernández, J. A. (2017). Metabolomics and biochemical approaches link salicylic acid biosynthesis to cyanogenesis in peach plants. *Plant and Cell Physiology*, *58*(12), 2057–2066. https://doi.org/10.1093/pcp/pcx135

Díaz-Vivancos, P., Clemente-Moreno, M. J., Rubio, M., Olmos, E., García, J. A., Martínez-Gómez, P., & Hernández, J. A. (2008). Alteration in the chloroplastic metabolism leads to ROS accumulation in pea plants in response to plum pox virus. *Journal of Experimental Botany*, *59*(8), 2147–2160. https://doi.org/10.1093/jxb/ern082.

Diaz-Vivancos, P., Rubio, M., Mesonero, V., Periago, P. M., Barceló, A. R., Martínez-Gómez, P., & Hernández, J. A. (2006). The apoplastic antioxidant system in Prunus: Response to long-term plum pox virus infection. *Journal of Experimental Botany*, *57*(14), 3813–3824. https://doi.org/10.1093/jxb/erl138

Diaz, I. (2018). Plant defense genes against biotic stresses. *International Journal of Molecular Sciences*, *19*(8), 2446. https://doi.org/10.3390/ijms19082446

Fedina, I. S., Tsonev, T. D., & Guleva, E. I. (1994). ABA as a modulator of the response of *Pisum sativum* to salt stress. *Journal of Plant Physiology*, *143*(2), 245–249. https://doi.org/10.1016/S0176-1617(11)81695-0

Foyer, C. H., & Noctor, G. (2005). Oxidant and antioxidant signalling in plants: A re-evaluation of the concept of oxidative stress in a physiological context. *Plant, Cell & Environment*, *28*(8), 1056–1071. https://doi.org/10.1111/j.1365-3040.2005.01327.x

Foyer, C. H., & Noctor, G. (2011). Ascorbate and glutathione: The heart of the redox hub. *Plant Physiology*, *155*(1), 2–18. https://doi.org/10.1104/pp.110.167569155/1/2

Foyer, C. H., & Shigeoka, S. (2011). Understanding oxidative stress and antioxidant functions to enhance photosynthesis. *Plant Physiology*, *155*(1), 93–100. https://doi.org/10.1104/pp.110.166181

Fraire-Velázquez, S., Rodríguez-Guerra, R., & Sánchez-Calderón, L. (2011). Abiotic and biotic stress response crosstalk in plants. In A. Shanker and B. Venkateswarlu (Eds.) *Abiotic stress response in plants—Physiological, biochemical and genetic perspectives*. London, UK: IntechOpen.

Fryer, M. J., Oxborough, K., Mullineaux, P. M., & Baker, N. R. (2002). Imaging of photo-oxidative stress responses in leaves. *Journal of Experimental Botany*, *53*(372), 1249–1254. https://doi.org/10.1093/jxb/53.372.1249

Fujita, M., Fujita, Y., Noutoshi, Y., Takahashi, F., Narusaka, Y., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2006). Crosstalk between abiotic and biotic stress responses: A current view from the points of convergence in the stress signaling networks. *Current Opinion in Plant Biology*, *9*(4), 436–442. https://doi.org/10.1016/j.pbi.2006.05.014

Fürst-Jansen, J. M. R., De Vries, S., & De Vries, J. (2020). Evo-physio: On stress responses and the earliest land plants. *Journal of Experimental Botany*, *71*(11), 3254–3269. https://doi.org/10.1093/jxb/eraa007.

Gechev, T. S., Van Breusegem, F., Stone, J. M., Denev, I., & Laloi, C. (2006). Reactive oxygen species as signals that modulate plant stress responses and programmed cell death. *BioEssays*, *28*, 1091–1101. https://doi.org/10.1002/bies.20493

Ghassemi-Golezani, K., & Lotfi, R. (2015). The impact of salicylic acid and silicon on chlorophyll a fluorescence in mung bean under salt stress. *Russian Journal of Plant Physiology*, *62*, 611–616. https://doi.org/10.1134/S1021443715040081

Gullner, C., Tóbiás, I., Fodor, J., & Kömives, U. (1999). Elevation of glutathione level and activation of glutathione-related enzymes affect virus infection in tobacco. *Free Radical Research*, *31*, S155–S161.

Hamada, A. M., & El-Enany, A. E. (1994). Effect of NaCl salinity on growth, pigment and mineral element contents, and gas exchange of broad bean and pea plants. *Biologia Plantarum*, *36*, 75–81. https://doi.org/10.1007/BF02921273

Hernández, J. A., & Almansa, M. S. (2002). Short-term effects of salt stress on antioxidant systems and leaf water relations of pea leaves. *Physiologia Plantarum*, *115*(2), 251–257. https://doi.org/10.1034/j.1399-3054.2002.1150211.x

Hernández, J. A., Corpas, F. J., Gómez, M., del Río, L. A., & Sevilla, F. (1993). Salt-induced oxidative stress mediated by activated oxygen species in pea leaf mitochondria. *Physiologia Plantarum*, *89*, 103–110. https://doi.org/10.1111/j.1399-3054.1993.tb01792.x

Hernández, J. A., Campillo, A., Jiménez, A., Alarcón, J. J., & Sevilla, F. (1999). Response of antioxidant systems and leaf water relations to NaCl stress in pea plants. *New Phytologist*, *141*, 241–251. https://doi.org/10.1046/j.1469-8137.1999.00341.x

Hernandez, J. A., Diaz-Vivancos, P., Rubio, M., Olmos, E., Ros-Barcelo, A., & Martinez-Gomez, P. (2006). Long-term plum pox virus infection produces an oxidative stress in a susceptible apricot, *Prunus*

armeniaca, cultivar but not in a resistant cultivar. *Physiologia Plantarum*, *126*(1), 140–152. https://doi.org/10.1111/j.1399-3054.2005.00581.x

Hernández, J. A., Ferrer, M. A., Jiménez, A., Barceló, A. R., & Sevilla, F. (2001). Antioxidant systems and O_2.-H_2O_2 production in the apoplast of pea leaves. Its relation with salt-induced necrotic lesions in minor veins. *Plant Physiology*, *127*(3), 817–831. http://www.ncbi.nlm.nih.gov/pubmed/11706165

Hernández, J. A., Gullner, G., Clemente-Moreno, M. J., Künstler, A., Juhász, C., Diaz-Vivancos, P., & Király, L. (2016). Oxidative stress and antioxidative responses in plant-virus interactions. *Physiological and Molecular Plant Pathology*, *94*, 134–148. https://doi.org/10.1016/j.pmpp.2015.09.001

Hernández, J. A., Jiménez, A., Mullineaux, P., & Sevilla, F. (2000). Tolerance of pea (*Pisum sativum* L.) to long-term salt stress is associated with induction of antioxidant defences. *Plant, Cell and Environment*, *23*, 853–862. https://doi.org/10.1046/j.1365-3040.2000.00602.x

Hernández, J. A., Olmos, E., Corpas, F. J., Sevilla, F., & del Río, L. A. (1995). Salt-induced oxidative stress in chloroplasts of pea plants. *Plant Science*, *105*(2), 151–167. https://doi.org/10.1016/0168-9452(94)04047-8

Hernández, J. A., Rubio, M., Olmos, E., Ros-Barceló, A., & Martínez-Gómez, P. (2004). Oxidative stress induced by long-term plum pox virus infection in peach (*Prunus persica*). *Physiologia Plantarum*, *122*(4), 486–495. https://doi.org/10.1111/j.1399-3054.2004.00431.x

Hernández, J. A., Talavera, J. M., Martínez-Gómez, P., Dicenta, F., & Sevilla, F. (2001). Response of antioxidative enzymes to plum pox virus in two apricot cultivars. *Physiologia Plantarum*, *111*(3), 313–321.

Ikbal, F. E., Hernández, J. A., Barba-Espín, G., Koussa, T., Aziz, A., Faize, M., & Diaz-Vivancos, P. (2014). Enhanced salt-induced antioxidative responses involve a contribution of polyamine biosynthesis in grapevine plants. *Journal of Plant Physiology*, *171*(10), 779–788. https://doi.org/10.1016/j.jplph.2014.02.006

Imlay, J. A. (2003). Pathways of oxidative damage. *Annual Review of Microbiology*, *57*, 395–418. https://doi.org/10.1146/annurev.micro.57.030502.090938

Isayenkov, S. V., & Maathuis, F. J. M. (2019). Plant salinity stress: Many unanswered questions remain. *Frontiers in Plant Science*, *10*, 80. https://doi.org/10.3389/fpls.2019.00080

Jayakannan, M., Bose, J., Babourina, O., Rengel, Z., & Shabala, S. (2015). Salicylic acid in plant salinity stress signalling and tolerance. *Plant Growth Regulator*, *76*(1), 25–40. https://doi.org/10.1007/s10725-015-0028-z

Kav, N. N. V., Srivastava, S., Goonewardene, L., & Blade, S. F. (2005). Proteome-level changes in the roots of *Pisum sativum* in response to salinity. *Annals of Applied Biology*, *145*(2), 217–230. https://doi.org/10.1111/j.1744-7348.2004.tb00378.x

Kosová, K., Vítámvás, P., Urban, M. O., Klíma, M., Roy, A., & Prášil, I. T. (2015). Biological networks underlying abiotic stress tolerance in temperate crops-a proteomic perspective. *International Journal of Molecular Sciences*, *16*(9), 20913–20942. https://doi.org/10.3390/ijms160920913

Kováčik, J., Klejdus, B., Hedbavny, J., & Bačkor, M. (2009). Salicylic acid alleviates NaCl-induced changes in the metabolism of *Matricaria chamomilla* plants. *Ecotoxicology*, *18*(5), 544–554. https://doi.org/10.1007/s10646-009-0312-7

Laloi, C., Apel, K., & Danon, A. (2004). Reactive oxygen signalling: The latest news. *Current Opinion in Plant Biology*, *7*(3), 323–328. https://doi.org/10.1016/j.pbi.2004.03.005

Lechno, S., Zamski, E., & Tel-Or, E. (1997). Salt stress-induced responses in cucumber plants. *Journal of Plant Physiology*, *150*(1–2), 206–211. https://doi.org/10.1016/S0176-1617(97)80204-0

Leonforte, A., Forster, J. W., Redden, R. J., Nicolas, M. E., & Salisbury, P. A. (2013). Sources of high tolerance to salinity in pea (*Pisum sativum* L.). *Euphytica*, *189*, 203–216. https://doi.org/10.1007/s10681-012-0771-4

Lohaus, C., Heldt, H. W., & Osmond, C. B. (2000). Infection with phloem limited abutilon mosaic virus causes localized carbohydrate accumulation in leaves of *Abutilon striatum*: Relationships to symptom development and effects on chlorophyll fluorescence quenching during photosynthetic induction. *Plant Biology*, *2*, 161–167. https://doi.org/10.1055/s-2000-9461

López-Gómez, E., San Juan, M. A., Diaz-Vivancos, P., Mataix Beneyto, J., García-Legaz, M. F., & Hernández, J. A. (2007). Effect of rootstocks grafting and boron on the antioxidant systems and salinity tolerance of loquat plants (*Eriobotrya japonica* Lindl.). *Environmental and Experimental Botany*, *60*(2), 151–158. https://doi.org/10.1016/j.envexpbot.2006.10.007

Martí, M. C., Florez-Sarasa, I., Camejo, D., Ribas-Carbó, M., Lázaro, J. J., Sevilla, F., & Jiménez, A. (2011). Response of mitochondrial thioredoxin PsTrxo1, antioxidant enzymes, and respiration to salinity in pea (*Pisum sativum* L.) leaves. *Journal of Experimental Botany*, *62*(11), 3863–3874. https://doi.org/10.1093/jxb/err076

Massai, R., Gucci, R., & Tattini, M. (1998). Salinity tolerance in four different rootstocks for peach. *Acta Horticulturae*, *465*, 363–370. https://doi.org/10.17660/actahortic.1998.465.45

Matias, J. R., Torres, S. B., Leal, C. C. P., Leite, M. d. S., & Carvalho, S. M. C. (2018). Hydropriming as inducer of salinity tolerance in sunflower seeds. *Revista Brasileira de Engenharia Agricola e Ambiental*, *22*(4), 255–260. https://doi.org/10.1590/1807-1929/agriambi.v22n4p255-260

Miller, G., Suzuki, N., Ciftci-Yilmaz, S., & Mittler, R. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant Cell and Environment*, *33*(4), 453–467. https://doi.org/10.1111/j.1365-3040.2009.02041.x

Mittler, R., Vanderauwera, S., Suzuki, N., Miller, G., Tognetti, V. B., Vandepoele, K., … Van Breusegem, F. (2011). ROS signaling: The new wave? *Trends in Plant Science*, *16*(6), 300–309. https://doi.org/10.1016/j.tplants.2011.03.007

Miyashita, K., Tanakamaru, S., Maitani, T., & Kimura, K. (2005). Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. *Environmental and Experimental Botany*, *56*, 24–34. https://doi.org/10.1016/j.envexpbot.2004.03.015

Molassiotis, A., & Fotopoulos, V. (2011). Oxidative and nitrosative signaling in plants: Two branches in the same tree? *Plant Signaling and Behavior*, *6*(2), 210–214. https://doi.org/10.4161/psb.6.2.14878

Munns, R., Passioura, J. B., Colmer, T. D., & Byrt, C. S. (2020). Osmotic adjustment and energy limitations to plant growth in saline soil. *New Phytologist*, *225*(3), 1091–1096. https://doi.org/10.1111/nph.15862

Noreen, Z., & Ashraf, M. (2009). Assessment of variation in antioxidative defense system in salt-treated pea (*Pisum sativum*) cultivars and its putative use as salinity tolerance markers. *Journal of Plant Physiology*, *166*(16), 1764–1774. https://doi.org/10.1016/j.jplph.2009.05.005

Olmos, E., Hernández, J. A., Sevilla, F., & Hellín, E. (1994). Induction of several antioxidant enzymes in the selection of a salt-tolerant cell line of *Pisum sativum*. *Journal of Plant Physiology*, *144*, 594–598. https://doi.org/10.1016/S0176-1617(11)82142-5

Pandolfi, C., Mancuso, S., & Shabala, S. (2012). Physiology of acclimation to salinity stress in pea (*Pisum sativum*). *Environmental and Experimental Botany*, *84*, 44–51. https://doi.org/10.1016/j.envexpbot.2012.04.015

Pirasteh-Anosheh, H., Saed-Moucheshi, A., Pakniyat, H., & Pessarakli, M. (2016). Stomatal responses to drought stress. In: P. Ahmad (Ed.), *Water stress and crop plants: A sustainable approach* (Vol 1, First Edition, pp. 24–40). Hoboken, NJ: John Wiley & Sons, Ltd.

Rolfe, S. A., & Scholes, J. D. (2010). Chlorophyll fluorescence imaging of plant-pathogen interactions. *Protoplasma*, *247*(3–4), 163–175. https://doi.org/10.1007/s00709-010-0203-z

Rubio, M., Rodríguez-Moreno, L., Ballester, A. R., de Moura, M. C., Bonghi, C., Candresse, T., & Martínez-Gómez, P. (2015). Analysis of gene expression changes in peach leaves in response to *Plum pox virus* infection using RNA-Seq. *Molecular Plant Pathology*, *16*(2), 164–176. https://doi.org/10.1111/mpp.12169

Shahid, M. A., Balal, R. M., Pervez, M. A., Abbas, T., Ashfaq, M., Ghazanfar, U., … Mattson, N. S. (2012). Differential response of pea

(*Pisum sativum* L.) genotypes to salt stress in relation to the growth, physiological attributes antioxidant activity and organic solutes. *Australian Journal of Crop Science*, *6*(5), 828–838.

Shahid, M. A., Pervez, M. A., Balal, R. M., Abbas, T., Ayyub, C. M., Mattson, N. S., … Iqbal, Z. (2012). Screening of pea (*Pisum sativum* L.) genotypes for salt tolerance based on early growth stage attributes and leaf inorganic osmolytes. *Australian Journal of Crop Science*, *6*(9), 1324–1331.

Shahid, M., Akram, M. S., Khan, M. A., Zubair, M., Shah, S. M., Ismail, M., … Tariq, M. (2018). A phytobeneficial strain *Planomicrobium* sp. MSSA-10 triggered oxidative stress responsive mechanisms and regulated the growth of pea plants under induced saline environment. *Journal of Applied Microbiology*, *124*, 1566–1579. https://doi.org/10.1111/jam.13732

Shehata, W. F., & Alturki, S. M. (2020). Utilizing biotechnology tools for silecting salt tolerant rootstock of peach Hassawi. *Iraqi Journal of Agricultural Sciences*, *51*, 148–156. https://doi.org/10.36103/IJAS.V51ISPECIAL.892

Singh, S., Sengar, R. S., Kulshreshtha, N., Datta, D., Tomar, R. S., Rao, V. P., … Ojha, A. (2015). Assessment of multiple tolerance indices for salinity stress in bread wheat (*Triticum aestivum* L.). *Journal of Agricultural Science*, *7*(3), 49–56. https://doi.org/10.5539/jas.v7n3p49

Soares, C., Carvalho, M. E. A., Azevedo, R. A., & Fidalgo, F. (2019). Plants facing oxidative challenges—A little help from the antioxidant networks. *Environmental and Experimental Botany*, *161*, 4–25. https://doi.org/10.1016/j.envexpbot.2018.12.00

Spoel, S. H., & Dong, X. (2008). Making sense of hormone crosstalk during plant immune responses. *Cell Host and Microbe*, *3*(6), 348–351. https://doi.org/10.1016/j.chom.2008.05.009

Suzuki, N., Koussevitzky, S., Mittler, R., & Miller, G. (2012). ROS and redox signalling in the response of plants to abiotic stress. *Plant, Cell and Environment*, *35*(2), 259–270. https://doi.org/10.1111/j.1365-3040.2011.02336.x

Visedo, G., Fernández-Piqueras, J., & García, J. A. (1991). Peroxidase isozyme analysis of factors involved in development of symptoms in *Nicotiana clevelandii* infected by plum pox virus. *Physiologia Plantarum*, *83*, 165–169. https://doi.org/10.1034/j.1399-3054.1991.830125.x

Wang, Q., Dodd, I. C., Belimov, A. A., & Jiang, F. (2016). Rhizosphere bacteria containing 1-aminocyclopropane-1-carboxylate deaminase increase growth and photosynthesis of pea plants under salt stress by limiting Na^+ accumulation. *Functional Plant Biology*, *43*(2), 161–172. https://doi.org/10.1071/FP15200

Williamson, C. L., & Slocum, R. D. (1992). Molecular cloning and evidence for osmoregulation of the Δ^1-pyrroline-5-carboxylate reductase (*pro*C) gene in pea (*Pisum sativum* L.). *Plant Physiology*, *100*(3), 1464–1470. https://doi.org/10.1104/pp.100.3.1464

Wu, H., Zhang, X., Giraldo, J. P., & Shabala, S. (2018). It is not all about sodium: Revealing tissue specificity and signalling roles of potassium in plant responses to salt stress. *Plant and Soil*, *43*, 1–17. https://doi.org/10.1007/s11104-018-3770-y

Yi, S. Y., Yu, S. H., & Choi, D. (1999). Molecular cloning of a catalase cDNA from *Nicotiana glutinosa* L. and its repression by tobacco mosaic virus infection. *Molecules and Cells*, *9*(3), 320–325.

Zechmann, B., Zellnig, G., Urbanek-Krajnc, A., & Müller, M. (2007). Artificial elevation of glutathione affects symptom development in ZYMV-infected *Cucurbita pepo* L. plants. *Archives of Virology*, *152*(4), 747–762. https://doi.org/10.1007/s00705-006-0880-2

Zouaoui, R., Ammari, Y., Abassi, M., Ben Ahmed, H., Smaoui, A., & Hilali, K. (2019). Physiological and biochemical responses of *Rhus tripartita* (Ucria) Grande under water stress. *Pakistan Journal of Botany*, *51*(4), 1215–1221. https://doi.org/10.30848/PJB2019-4(22

Zulfiqar, F., Akram, N. A., & Ashraf, M. (2020). Osmoprotection in plants under abiotic stresses: New insights into a classical phenomenon. *Planta*, *251*, 3. https://doi.org/10.1007/s00425-019-03293-1

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