

Environmental interference of plant–microbe interactions

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Abstract

Environmental stresses can compromise the interactions of plants with beneficial microbes. In the present review, experimental results showing that stresses negatively affect the abundance and/or functionality of plant beneficial microbes are summarized. It is proposed that the environmental interference of these plant–microbe interactions is explained by the stress-mediated induction of plant signalling pathways associated with defence hormones and reactive oxygen species. These plant responses are recognized to regulate beneficial microbes within plants. The direct negative effect of stresses on microbes may also contribute to the environmental regulation of these plant mutualisms. It is also posited that, in stress situations, beneficial microbes harbour mechanisms that contribute to maintain the mutualistic associations. Beneficial microbes produce effector proteins and increase the antioxidant levels in plants that counteract the detrimental effects of plant stress responses on them. In addition, they deliver specific stress-protective mechanisms that assist to their plant hosts to mitigate the negative effects of stresses. Our study contributes to understanding how environmental stresses affect plant–microbe interactions and highlights why beneficial microbes can still deliver benefits to plants in stressful environments.

KEYWORDS

abiotic and biotic stresses, antioxidants, effectors, endophytes, mycorrhizae, phytohormones, reactive nitrogen species, reactive oxygen species

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1 | INTRODUCTION

Plants are constantly challenged by a broad range of biotic and abiotic environmental stressors. Biotic stressors include pathogens, herbivores and competitors, while abiotic stressors include drought, salinity, heat and nutrient scarcity (Suzuki et al., 2014). Environmental stressors typically affect the plant physiology and metabolism, which can reduce the growth and reproduction of plants (Branco et al., 2022). Furthermore, stressors often compromise the association of plants with beneficial microbes, which can also limit plant fitness (Kiers et al., 2010; Rudgers et al., 2020). Plant beneficial microbes confer to their hosts with mechanisms that efficiently mitigate the detrimental effects of stresses (Bastías et al., 2022). Foliar fungal endophytes of genus *Epichloë* endow to plants with specialized metabolites (mainly alkaloids) that increase the levels of resistance against herbivores (Schardl et al., 2004). They also stimulate certain plant responses that enhance the resistance/tolerance to pathogens, drought and other stresses (Card et al., 2021; Decunta et al., 2021). Similarly, root fungal endophytes trigger a wealth of molecular processes in the hosts, including calcium signalling and the production of osmolytes like proline or soluble sugars, that increase the plant tolerance to abiotic and biotic stresses (Giauque et al., 2019; Hereme et al., 2020; Lata et al., 2018; Vadassery & Oelmüller, 2009). Mycorrhizal fungi enhance the host acquisition of nutrients (such as phosphorus and nitrogen) and water that results in net benefits for plants specially growing in poor soils (Bennett & Groten, 2022). Furthermore, they stimulate host immune responses that increases the resistance levels of plants against pathogens and insect herbivores (Pieterse et al., 2014; Pozo et al., 2015).

Most of the research regarding stresses and plant–microbe interactions has been focused on investigating microbial stress-protective traits. However, stressors can compromise the associations of plants with beneficial microbes, and the mechanisms explaining this negative effect of stresses on plants have been scantily considered in the specialized literature. In this review, firstly, published results showing that environmental stresses compromised plant–microbe interactions were summarized. The study compilation was focused on distinct groups of beneficial microbes of plants: foliar endophytes, root endophytes and mycorrhizal fungi (mainly arbuscular mycorrhizae). Secondly, the potential mechanisms by which the stressors would interfere plant–microbe interactions were identified. It is proposed that beneficial microbes are affected by the plant responses triggered by the stresses (i.e., plant immunity and oxidative stress) and by the stress itself. Thirdly, putative mechanisms that beneficial microbes would use to counteract the plant stress responses and to alleviate the negative effects of stresses on plants and microbes were described. These microbial-derived mechanisms may contribute to maintain the mutualism between the plant and microbe and to enhance the performance of plants in stress situations.

2 | PLANT–MICROBE INTERACTIONS ARE COMPROMISED IN STRESS SITUATIONS

2.1 | Environmental interference of foliar endophytes

Environmental stress can compromise the associations between plants and beneficial foliar endophytes. Within foliar tissues, endophyte fungi can be locally or systemically distributed. They extend hyphae along intercellular spaces of plant hosts where they obtain nutrients and carbohydrates from the apoplast (Christensen et al., 2008; Christensen & Voisey, 2007). These endophytes are transmitted vertically via plant seed, horizontally via contagious spread of symbionts and some species simultaneously transmit both vertically and horizontally (Rodriguez et al., 2009). Vertically transmitted endophytes form mutualistic relationship with plants and generally reach high prevalence in plant populations. A remarkable example of this are endophytes of genus *Epichloë* that form persistent associations with grasses of subfamily Pooideae (Gundel et al., 2011; Schardl et al., 2004).

Stresses can interfere with symbioses between plants and foliar endophytes by altering the magnitude of the benefits provided by symbionts (e.g., herbivory protection and plant growth promotion) (Bastías et al., 2021; Schardl et al., 2004). Elevated ozone levels reduced the *Epichloë* endophyte-derived resistance to insects in *Lolium multiflorum* plants (Ueno et al., 2016). More severe was the effect of UV-B radiation on *Epichloë*-derived benefits. Elevated UV-B levels completely suppressed the endophyte-based herbivore resistance in *Festuca pratensis* plants. Even worse was the effect of UV-A radiation on the endophyte-based herbivore resistance. Elevated UV-A levels made the endophyte-symbiotic plants more susceptible to insect herbivores than their nonsymbiotic counterparts (McLeod et al., 2001). Similarly to the UV-B radiation, low temperature also suppressed the endophyte-based resistance to insects in symbiotic *L. multiflorum* plants (Hennessy et al., 2016). Under drought stress, *Festuca arundinacea* plants associated with endophytes were more susceptible to insect herbivores than their nonsymbiotic counterparts in situations of water restriction (the opposite occurred under high water availability) (Bultman & Bell, 2003). Drought also suppressed the disease protection conferred by endophytes against phytopathogens in *Lolium perenne* plants (i.e., *Bipolaris sorokiniana*) (Li et al., 2020). Stress can also affect plant growth stimulation conferred by endophytes to their hosts (Bastías et al., 2021). For example, drought suppressed the endophyte-mediated growth promotion in *L. perenne* and *Festuca sinensis* plants (Marks & Clay, 2007; Xu et al., 2021). Furthermore, the endophyte-based resistance to insects was reduced by the presence of mycorrhizal fungi that presumably competed for resources in *L. perenne* plants (Vicari et al., 2002). Interestingly, the detrimental effect of stresses on the endophyte-derived benefits can be transmitted intergenerationally. Daughter symbiotic plants of *L. multiflorum* produced from mothers that were exposed to ozone exhibited lower levels of resistance to insects compared to mother

plants that were not exposed to the stress (Bubica Bustos et al., 2020).

The stress-mediated compromise of *Epichloë*-derived benefits may be explained by the reduction in concentrations of endophyte-derived antiherbivore alkaloids and alteration in fungal mycelial biomass within plant tissues. Elevated carbon dioxide levels reduced the concentrations of endophytic alkaloids in *F. arundinacea* plants (Brosi et al., 2011; Ryan, Rasmussen et al., 2014). Similarly, decreased contents of endophyte-derived alkaloid were exhibited by endophyte-symbiotic *L. perenne* plants simultaneously associated with mycorrhizal fungi. In this experiment, the mycorrhizal treatment also reduced the mycelial biomass of *Epichloë* endophytes within plant tissues (Liu et al., 2011). Certain experimental results suggest that stresses inhibit the performance of endophyte-symbiotic plants. Under drought conditions, endophyte-symbiotic *L. perenne* plants accumulated less biomass and produced less seeds than nonsymbiotic plants (Cheplick et al., 2000; Hesse et al., 2003). Similarly, plants of the same species associated with endophytes exhibited lower biomass than nonsymbiotic plants during the recovery period post drought (Cheplick, 2004). Furthermore, lower regrowth rate following a treatment of simulated folivory was documented in certain genotypes of *L. perenne* plants associated with endophytes compared to their nonsymbiotic counterparts (Cheplick, 1998).

2.2 | Environmental interference of root endophytes

As with the foliar endophytes, environmental stresses can interfere with symbioses between plants and beneficial root endophytes. Most root endophyte fungi grow in the apoplast of epidermal and cortex cells, without entering the central cylinder of their host plants' root. They form loose hyphal networks that invaginate the plasma membranes of the plant cells. In contrast to mycorrhizal fungi, most root endophyte fungi, like for instance *Serendipita indica*, do not induce the formation of differentiated plant or fungal structures, when penetrating and colonizing the cells of their host plants (Weiß et al., 2016). At present, there is only very little known about the mechanisms by which plants and microbes steer their interactions under ever-changing environmental conditions. However, there is mounting evidence that plants have to tightly control their root microbiota to maintain their fitness (Wolinska et al., 2021). A striking example of this are the major changes observed in root-associated fungal communities in *Triticum aestivum* plants under drought stress (Salamon et al., 2020). Another study from the same group pointed into the same direction, highlighting that drought stress indirectly affected the plant–fungal interactions in roots of *T. aestivum* (subspecies *vulgare* and *spelta*), while still promoting plant growth and several physiological parameters, including photosynthetic activity, electron transport rate and water use efficiency (Ratajczak et al., 2020).

Multiple studies have demonstrated that environmental stresses contribute to control the colonization of roots by endophytes. For example, soils with high levels of both copper (Cu) and lead (Pb)

negatively affected the colonization of *S. indica* fungi on roots of *Ocimum basilicum* plants, while individual treatments with either Cu or Pb showed no negative impact on the colonization (Sabra et al., 2018). Noteworthy in this context is the additional finding that the simultaneous infection of *O. basilicum* roots with *S. indica* and the arbuscular mycorrhizal fungus *Rhizophagus irregularis* reduced the colonization of plant roots by *S. indica* when grown in presence of Pb alone. Furthermore interesting is the observation that the co-colonization of roots with both fungi could significantly stimulate the mycorrhization with *R. irregularis* under Cu and combined Cu and Pb stress, although it remains to be remarked that the abundance of mycorrhizae was generally low under heavy metal stress. Furthermore, a recent study provided comprehensive evidence that a number of climate change-related abiotic stresses, including drought and mechanical stress (through an increased compactness of the soil), had a negative effect on the root colonization of *S. indica* on *Zea mays* plants (Hosseini et al., 2018). The study also highlighted that, plants inoculated with this root endophyte fungus still performed better when exposed to combined drought and mechanical stress, even though the fungal load was diminished. This would imply that host plants may possess mechanisms to maintain a necessary level of symbiosis to gain the benefits under stress, without putting their own survival into jeopardy. In the context of soil compactness, a recent study reported that compacted soils reduced the free diffusion of plant-produced ethylene which, in turn, accumulated in the rhizosphere and the root tissue, where it restricted root growth (Pandey et al., 2021). Another work on the root colonization of *Arabidopsis* plants with *S. indica* demonstrated that ethylene signalling and ethylene-targeted transcription factors were essential to establish the plant–fungal interaction (Camehl et al., 2010). Overall, there is currently very limited insights into climate change-mediated abiotic stresses in the rhizosphere (Fonseca de Lima et al., 2021), and much more work is needed to obtain a deeper understanding of the intricacies of plant–fungal interactions under these conditions.

Multiple experimental results suggest that distinct root endophytes enhance the tolerance of plants to salt stress (e.g., *S. indica*, *Fusarium culmorum*, *Talaromyces minioluteus*, *Penicillium murcianum* fungi) (González-Teuber et al., 2022; Pérez-Alonso et al., 2020; Rodríguez et al., 2008). However, there are few studies that empirically evaluate whether salt stress exerts negative effects on the symbiosis between plants and fungal root endophytes. One of these studies documented a significant reduction in the colonization rate of *Oryza sativa* roots by *S. indica* when symbiotic plants were subjected to salt stress (Jogawat et al., 2016).

Depending on the given host plant–root endophyte combination and the specific environmental stress applied, the beneficial effect of the symbiont can be considerably reduced. To give just a few examples, severe drought stress significantly reduced the *S. indica*-mediated root growth promotion on *Z. mays* plants (Zhang et al., 2018), while high salt conditions minimized the root growth promoting effect of *Aspergillus aculeatus* endophytes on *Cynodon dactylon* plants (Xie et al., 2017). However, there is only scarce information on scenarios in which the interaction of beneficial root

endophytes with their host plants converts into a burden for the plant, drastically hampering its fitness. In this context, it has been reported that several endophytes possess a considerable phenotypic plasticity, which allows them to switch between endophytic and necrotrophic lifestyles (Delaye et al., 2013). This could possibly be taken as an additional indication for the intimate control of the symbiotic relationship of the interacting organisms.

2.3 | Environmental interference of mycorrhizal fungi

Similar to foliar and root endophytes, most studies regarding stresses and plant-mycorrhizal associations have described the stress-protective traits that these fungi confer to their hosts (Balestrini et al., 2018; Porcel et al., 2012; Rivero et al., 2018). However, multiple evidence suggest that abiotic and biotic stresses compromise these plant-microbe interactions.

Drought can reduce the colonization of arbuscular mycorrhizal fungi (although mycorrhizal plants generally perform better than their nonsymbiotic counterparts) (Augé, 2001; Balestrini et al., 2018; Chitarra et al., 2016). This reduction in mycorrhizal root colonization is explained in part by the negative effect of the stress on the development of the fungus in soil and rhizosphere. For instance, drought (and other stresses as well) inhibited the spore germination and elongation of germinative hyphae of mycorrhizal fungi in soil (Lenoir et al., 2016). The stress-mediated alteration in the plant metabolisms and/or development (e.g., by reducing root size) also contributes to the detrimental effect of drought on the mycorrhizal root colonization (Lenoir et al., 2016; Millar & Bennett, 2016). For example, drought reduced the ability of mycorrhizal fungi to promote the expression of plant genes involved in the transport of nutrients between the plant and fungus in *Solanum lycopersicum* (e.g., transporters of phosphate, ammonium, peptides, amino acids) (Balestrini et al., 2019). The decreased expression of these plant genes may be explained by a reduced abundance of mycorrhizal arbuscules in plant roots (Chitarra et al., 2016).

Soil nutrients, such as phosphorus and nitrogen, are known to be involved in the regulation of plant-mycorrhizal symbioses. The addition of phosphorus and nitrogen in soil decreased the diversity (and abundance) of mycorrhizal fungal species in plants (Ma et al., 2021). This reduced diversity of fungi has been explained by a shortage in the allocation of carbon-based compounds towards mycorrhizae because plant hosts apparently rely less on the fungus to obtain nutrients from the soil (Branco et al., 2022). At physiological level, high nutrient contents in soil down-regulated the expression of plant genes that facilitate the mycorrhizal root colonization (e.g., phosphate transporters) and promote the development of arbuscules in roots (i.e., half-size ATP-binding cassette transporters) (Breuillin et al., 2010; Wang et al., 2017). Furthermore, high phosphorus levels repressed the expression of plant genes involved in the biosynthesis of strigolactones that stimulate the growth and branching of mycorrhizal hyphae. Low strigolactone levels in plants normally

decrease the germination of mycorrhizal fungi (López-Ráez, 2016; Wang et al., 2017). The pH is another soil aspect that control plant-mycorrhizal symbioses. Soils with acidic pH reduced the abundance of mycorrhizal fungal arbuscules (and impeded their development) in roots of *S. lycopersicum* plants. The disrupted transfer of lipids between the plant and fungus seemed to explain the negative effect of this stress on the symbiosis (Feng et al., 2020; Liu et al., 2020).

Insect herbivory compromises the abundance and diversity of arbuscular mycorrhizal species in plants (Frew, 2022; Shi et al., 2022). The presence of the phloem-feeding aphid *Acyrtosiphon pisum* decreased the colonization of mycorrhizal fungi in *Vicia faba* plants (Babikova et al., 2014). Similarly, a treatment of simulated folivory reduced the abundance of mycorrhizal arbuscules in *Medicago sativa* plants. In this experiment, the reduction in arbuscule abundance was associated with limited availability of photosynthates in plant tissues (Saravesi et al., 2014).

3 | PLANT BENEFICIAL MICROBES ARE AFFECTED BY ENVIRONMENTAL STRESSES: MECHANISTIC PERSPECTIVES

Plants respond to environmental stresses by inducing signalling cascades that are governed by phytohormones, reactive oxygen species (ROS) and other signalling molecules (Figure 1). The signalling cascades converge in the activation and/or repression of master regulators that control the expression of phytohormone- and ROS-responsive transcription factors (Devireddy et al., 2021; Zhang et al., 2022). These transcription factors regulate the expression of plant genes encoding for proteins involved in the adjustment of plant phenotypes to stresses (Kranner et al., 2010; Pozo et al., 2015). Although phytohormone, ROS and other signalling pathways are critical for plants to adequate their phenotypes to the environmental context, the induction of some of these signalling pathways can compromise the presence and/or functionality of beneficial microbes (Foo et al., 2013; Xu et al., 2018) (Figure 1).

3.1 | Defence-related phytohormones interfere plant-microbe interactions

In addition to their major roles in plant stress responses, defence-related phytohormones salicylic acid, jasmonic acid and ethylene are master regulators of the interaction of plants with beneficial symbionts (Pieterse et al., 2014). These hormones are activated following the plant perception of multiple abiotic/biotic stresses and also beneficial microbes (Broekaert et al., 2006; Khan et al., 2015; Per et al., 2018; Pieterse et al., 2014). The perception is carried out by specific receptors located in plant cell membranes such as receptor-like kinases and histidine kinases that recognize specific signals in the stressors (e.g., microbe-associated molecular patterns) (Osakabe et al., 2013). During the recognition, plants increase calcium (Ca^{2+}) contents in cells, accumulate ROS in the apoplast, and phosphorylate

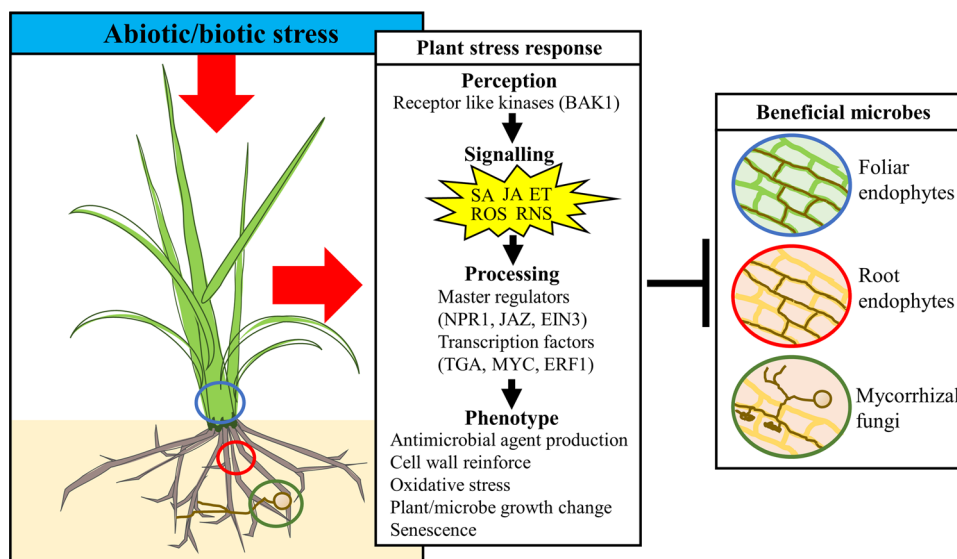


FIGURE 1 Beneficial microbes are affected by plant stress responses. Plants are challenged by distinct abiotic and/or biotic stresses. They perceive stresses by cell membrane receptors including receptor like kinases (e.g., BAK1). Activated receptors coordinate multiple responses in plant cells, such as calcium (Ca^{2+}) fluxes and phosphorylation of proteins, that stimulate the biosynthesis of signalling molecules including hormones salicylic acid (SA), jasmonic acid (JA) and ethylene (ET), reactive oxygen species (ROS) and reactive nitrogen species (RNS) (Poza et al., 2015). Hormones and ROS orchestrate signalling cascades that modulate master regulators (e.g., NPR1, JAZ, EIN3) of the expression of key stress-responsible transcription factors (e.g., TGA, MYC, ERF1). The activation of these transcription factors, during the processing of the stress signalling, leads to massive transcriptome changes that modulate the phenotype of plants in response to the stress. We propose that plant SA-, JA-, ET- and ROS-associated stress responses can negatively affect beneficial microbes (e.g., foliar endophytes, root endophytes, mycorrhizal fungi). This is because these responses typically are associated with production of antimicrobial proteins (e.g., glucanases, chitinases), changes in growth of microbes within plant tissues, reinforcement of plant cell walls, oxidative stress and senescence of plant tissues (i.e., programmed cell death). The list of molecules is focused on defence-related hormonal and ROS signalling pathways and is not exhaustive (roles of these molecules are explained in the main text). Arrows indicate positive regulation and truncated lines inhibition or negative regulation. Red connectors denote direct effects of stresses on plants. BAK1, BOTRYTIS-INDUCED KINASE1; EIN3, ET-INSENSITIVE 3; ERF1, ET RESPONSE FACTOR 1; JAZ, JASMONATE ZIM DOMAIN; MYC, MYC-type basic helix-loop-helix transcription factor; NPR1, NONEXPRESSOR OF PR GENES 1; TGA, TGACG sequence-specific binding.

distinct mitogen-associated protein kinases. These early responses terminate by inducing proteins that regulate the production and accumulation of salicylic acid, jasmonic acid and/or ethylene hormones (Saijo et al., 2018). The accumulation of defence-related phytohormones also occur in distant tissues as result of proteins that systemically distribute defence signals (e.g., pipecolic acid, methyl salicylate) (Pieterse et al., 2014). High salicylic acid levels in cells induce activities of NONEXPRESSOR OF PR GENES 1 proteins that in turn induce TGACG sequence-specific binding transcription factors. These transcription factors regulate the expression of salicylic acid-responsive genes (Li et al., 2019). In case of jasmonic acid, the accumulation of this hormone in cells triggers the conjugation with amino acids that produces the active form, the jasmonoyl-isoleucine. This conjugated hormone induces the ubiquitination of JASMONATE ZIM DOMAIN (JAZ) proteins by the coronatine insensitive 1 containing the *skp1-cullin 1-f-box* ubiquitin ligase complex. Ubiquitinated JAZ are degraded via 26-S proteasomes. JAZ proteins are repressors of transcription factors that induce the expression of jasmonic acid-responsive genes (e.g., MYC-type basic helix-loop-helix transcription factor). Therefore, the degradation of JAZ proteins by proteasomes promotes the

expression of jasmonic acid-related response genes (Ballaré, 2014; Li et al., 2019). The accumulation of ethylene in cells stimulates its binding with specific intracellular receptors (e.g., ethylene-receptor 1/2), and this binding prevents the proteasome-mediated degradation of ETHYLENE-INSENSITIVE (EIN) 2/3 and EIN3-LIKE 1 proteins. These depressed proteins activate several transcription factors that regulate the expression of the gene ETHYLENE-RESPONSE FACTOR (ERF) 1 (and other genes) encoding for a protein that activates ethylene-responsive genes (Broekaert et al., 2006). The ERF1 transcription factor is also activated by jasmonic acid (Lorenzo et al., 2003).

Multiple lines of evidence show that the activities of defence-related hormone signalling pathways (i.e., salicylic acid, jasmonic acid and ethylene) negatively affect plant beneficial microbes. For example, endophyte-symbiotic *L. multiflorum* and *F. arundinacea* plants treated with salicylic acid or methyl jasmonate (an activator of jasmonic acid-related defence responses) reduced the concentration of fungal-derived alkaloids and promoted susceptibility of symbiotic plants against insect herbivores (Bastías et al., 2018a, 2018b; Simons et al., 2008). Similarly, the endophyte-mediated growth promotion in *Achnatherum sibiricum* plants was erased when

symbiotic plants were exposed to methyl jasmonate (Qin et al., 2019). Furthermore, the colonization of roots by arbuscular mycorrhizal fungi is affected by plant defence hormones (Foo et al., 2013). Plants of *Nicotiana tabacum* with enhanced salicylic acid levels showed reduced mycorrhization (Herrera Medina et al., 2003). Reduced colonizations of arbuscular mycorrhizal fungi were also documented in ethylene-exposed *Pisum sativum* plants and ethylene-overproducing *S. lycopersicum* plants (Geil et al., 2001; Torres de Los Santos et al., 2011; Zsögön et al., 2008). Similar outcomes have been documented in root endophytes. The over-expression of the plant ERF1 transcription factor reduced the root colonization and also eliminated the benefits of the endophyte *S. indica* in *A. thaliana* plants (Camehl et al., 2010). Further experimental results suggested that the activation of jasmonic acid and ethylene plant signalling pathways reduced the root colonization of *S. indica* endophytes in *A. thaliana* and *Dimocarpus longan* plants (Cheng et al., 2022; Khatabi et al., 2012).

Beneficial fungal microbes may be regulated by the action of certain proteins of response to defence-related hormonal signalling pathways. These proteins include β -1,3-glucanases, chitinases and pathogenesis-related enzymes that degrade fungal cell walls via hydrolysis of structural components (e.g., glucans) and callose synthase enzymes that block the spread of the fungal mycelia in plants tissues via the reinforcement of plant cell walls (Dupont et al., 2015; Kou et al., 2021; Redkar et al., 2022). Furthermore, defence-related hormones could control the abundance of beneficial microbes in plant tissues by activating senescence responses (= programmed cell death) in infection sites (Bernacki et al., 2021; Brodersen et al., 2005).

3.2 | ROS interfere plant–microbe interactions

ROS, and other free radicals, also regulate the interaction of plants with beneficial symbionts (Calcagno et al., 2012; Tanaka et al., 2006; Wawra et al., 2016). ROS are normally produced in chloroplasts, peroxisomes and mitochondria organelles as by-products of the metabolism (Miller et al., 2010). These molecules are formed by transferring electrons with high-energy to molecular oxygen and include hydrogen peroxide, singlet oxygen and superoxide radical. At high levels, ROS cause oxidative damage to DNA, lipids and proteins that can lead to cell death (Raja et al., 2017). ROS contents in cells rapidly augment in presence of stressors (Huang et al., 2019). This abrupt increment in ROS levels is due, in part, to the action of the enzyme nicotinamide adenine dinucleotide phosphate (NADPH) oxidase. NADPH oxidases belong to the respiratory burst oxidase homolog (RBOH) family in plants, and RBOH-derived ROS can act as signalling molecules (Miller et al., 2010). RBOH enzymes are located in plasma membranes and transfer electrons from cytosolic NADPH or nicotinamide adenine dinucleotide to apoplastic molecular oxygens which leads to the generation of superoxide radicals that can be converted to hydrogen peroxide by the superoxide dismutase enzyme (Sukuzi et al., 2012). RBOHs possess several regions of

regulation including phosphorylation sites, Ca^{2+} -binding EF-hand sites and phosphatidic acid-binding sites (Kadota et al., 2015). RBOHs are normally induced by phosphorylation upon the perception of stressors. For instance, the enzyme RBOHD is phosphorylated by the receptor-like kinase receptor BOTRYTIS-INDUCED KINASE 1 in presence of pathogens. This RBOHD phosphorylation causes a ROS-mediated induction of defences in *A. thaliana* (Kadota et al., 2015).

The plant production of ROS in response to stress may compromise beneficial microbes. ROS can cause oxidate damage in microbial cells, potentially leading to cell death (Kadota et al., 2015). In *Z. mays*, the accumulation of ROS in the cytoplasm of plant cells containing mycorrhizal fungi apparently promoted the degradation of fungal arbuscules (Fester & Hause, 2005). Furthermore, ROS alter the development of fungal hyphae within plant tissues which reduces the fitness of their hosts (Kayano et al., 2018). Symbiotic *L. perenne* plants with reduced ROS levels showed stunted (and sometime lethal) phenotypes due to an unrestricted growth of *Epichloë* endophytes within plant tissues. This plant phenotype was associated with endophytes that exhibited mutations in the *NoxA* gene which encodes for a ROS-producer NADPH oxidase (Tanaka et al., 2006). Moreover, stunted phenotypes have also been documented in *L. perenne* plants associated with endophytes with mutations in genes that regulate the activity of fungal NADPH oxidases (Kayano et al., 2018). Finally, ROS-mediated responses also strengthen plant cell walls (via cross-linking of glycoproteins and callose deposition) that could potentially restrict the mycelial dissemination of beneficial fungi within plant tissues (Kadota et al., 2015).

It is worth mentioning that environmental stresses can affect plant–microbe interactions by mechanisms not related to plant stress responses. For instance, environmental stresses directly inhibit the development of beneficial microbes in soil and reduce the plant production of strigolactones (e.g., Lenoir et al., 2016; López-Ráez, 2016; Ryan, Rasmussen et al., 2014). This direct effect of stresses is particularly relevant in those plant–microbe interactions that the microbe has to colonize the plant (Branco et al., 2022; Lenoir et al., 2016; Nivedita et al., 2021).

4 | BENEFICIAL MICROBES HARBOUR MECHANISMS OF PROTECTION AGAINST ENVIRONMENTAL STRESSES

Several experimental results show that, even when stresses compromise the performance of plant beneficial microbes, these organisms still deliver benefits to their plant hosts. For instance, while nitrogen limitation in soil reduced the concentration of endophyte-derived antiherbivore alkaloids in *F. arundinacea*, symbiotic plants still were more resistant to aphids than their non-symbiotic counterparts (Ryan, Rasmussen et al., 2014; Ryan, Shukla et al., 2014). Beneficial microbes harbour mechanisms that counteract plant stress responses and protect hosts from stresses (Figure 2). These mechanisms may contribute to maintain the mutualistic associations in stress situations.

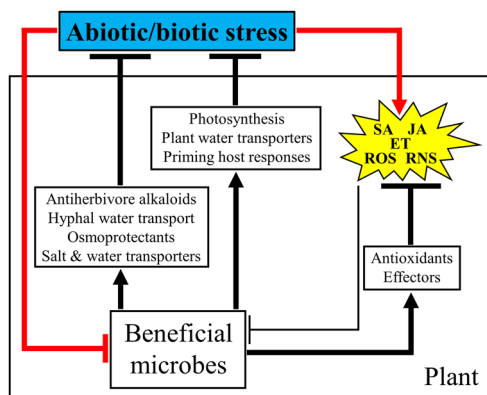


FIGURE 2 Beneficial microbes counteract plant stress responses and protect hosts from stresses. Abiotic and biotic stresses induce stress responses in plants that are governed by signalling molecules including salicylic acid (SA), jasmonic acid (JA), ethylene (ET), reactive oxygen species (ROS) and reactive nitrogen species (RNS) (Poza et al., 2015). Plant beneficial symbionts are affected directly by abiotic/biotic stresses or indirectly by plant stress responses (i.e., SA-, JA-, ET-, ROS- and RNS-associated responses). These symbionts protect themselves from plant stress responses by the production of antioxidants that reduce ROS- and RNS-derived oxidative damage and fungal effectors that efficiently repress defensive hormone- and ROS-associated host responses. Additionally, plant beneficial symbionts protect from stresses by producing stress-protective mechanisms (e.g., antiherbivore alkaloids, osmoprotectant molecules) and/or inducing plant tolerance/resistance mechanisms against stresses (e.g., photosynthesis, priming of plant immune responses). The symbionts' mechanisms that counteract plant stress responses or protect plants from stresses are described in the main text. Arrows indicate positive regulation and truncated lines inhibition or negative regulation. Red connectors denote direct effects of stresses on plants and beneficial microbes. The plant regulation of beneficial microbes is represented with a thinner truncated line since plant stress responses may be attenuated by the microbial production of effectors and increase in antioxidant levels in plants. [Color figure can be viewed at wileyonlinelibrary.com]

Plant beneficial microbes counteract plant stress responses by secreting effector proteins that reduce or prevent the induction of defence-related hormonal signalling pathways (Hassing et al., 2019). Plant JA-related defence responses were repressed by *Laccaria bicolor* mycorrhizal fungi that produced the effector mycorrhizal induced small secreted protein (MISSP) 7. The defence suppression occurred since the fungal MISSP7 stabilized and prevented the degradation of plant JAZ proteins that are repressors of jasmonic acid-responsive genes (Plett et al., 2014). Similarly, plant ethylene-related defence responses were inhibited by the arbuscular mycorrhizal fungus *R. irregularis* that produced the effector secreted protein (SP) 7. In this case, the inhibition of the plant defence was since the SP7 interfered with the plant transcription factor ERF19 (Kloppholz et al., 2011). Plant immune responses were also repressed by the fungus *R. irregularis* that produced the effector nuclear localized effector 1 that prevented the mono-ubiquitination of the plant histone 2B. Mono-ubiquitinated histone 2B proteins regulate

salicylic acid and jasmonic acid/ethylene plant signalling pathways (Wang et al., 2021). Additionally, crinkler (CRN) 1 is another effector produced by *R. irregularis* that control plant immune responses. While the specific mechanism of action of CRN1 is unknown, a reduced expression of this fungal effector decreased the size and abundance of mycorrhizal arbuscules in roots of *Medicago truncatula* plants (Voß et al., 2018).

Plant beneficial microbes also secrete effectors that counteract ROS-associated plant stress responses. The root endophyte *S. indica* inhibited ROS-derived plant immune responses by producing the effector fungal glucan-binding 1 that altered the cell wall composition of the fungus. This remodelled cell wall would bypass the plant recognition of the fungus, avoiding the plant production of ROS and the associated immune response (Wawra et al., 2016). Furthermore, beneficial microbes stimulate the formation of antioxidants in plants that efficiently neutralize ROS (Balestrini et al., 2018; Hamilton et al., 2012; Li et al., 2021; Noctor & Foyer, 1998). Antioxidants with major roles in plants include catalase, flavonoids, peroxidases, proline and superoxide dismutase (Noctor et al., 2018). For instance, the presence of *Epichloë* endophytes promoted the growth of *Elymus dahuricus* plants under drought which was associated with increased antioxidant contents and reduced oxidative damage in plants (Zhang & Nan, 2007). Similarly, endophytes of the same genus in *L. perenne* plants challenged by distinct phytopathogens increased antioxidant concentrations (i.e., peroxidases, proline and superoxide dismutase) and decreased the levels of oxidative damage in plants (Ma et al., 2015). The symbiosis of *Colobanthus quitensis* with the beneficial root endophyte fungi *Penicillium brevicompactum* and *P. chrysogenum* triggered the formation flavonoid antioxidants, including quercetin, which increased the protection of host plants against highly damaging UV-B radiation (Barrera et al., 2020). The increased drought tolerance in mycorrhizal-symbiotic *S. lycopersicum* plants was associated with enhanced concentrations of proline antioxidants and reduced accumulation of hydrogen peroxide compounds (Chitarra et al., 2016). In the same plant species, the presence of mycorrhizal fungi alleviated the negative effects of combined drought and heat stresses by increasing the activities of antioxidant enzymes that reduced the peroxidation of lipids and accumulation of hydrogen peroxide in plant tissues (Duc et al., 2018).

Beneficial microbes confer to plant hosts multiple mechanisms of protection against stresses. We briefly summarized some of these mechanisms since there are several comprehensive reviews regarding this topic (e.g., Branco et al., 2022; Pérez-Alonso et al., 2020; Scharld et al., 2004). Foliar *Epichloë* endophytes confer bioactive alkaloids to plant hosts that increase the plant resistance to herbivores (Bastias et al., 2017). These endophytes also produce mannitol, a sugar alcohol with osmotic and antioxidant effects, that would increase the plant tolerance to drought (Nagabhyru et al., 2013; Rasmussen et al., 2008). Arbuscular mycorrhizal fungi increase the plant tolerance to drought by the direct transport of water from soil to plant root via a hyphal extracytoplasmic pathway (Kakouridis et al., 2022). Root endophytes enhance the plant tolerance to salinity by the action of

several fungal salt transporter proteins (e.g., ENA ATPases) that efficiently reduce the accumulation of sodium within root cells. Additionally, the up-regulation of the fungal high osmolarity glycerol gene, encoding a mitogen-activated protein kinase involved in osmoregulation, increased the salt stress tolerance in *O. sativa* plants (Jogawat et al., 2016; Nivedita et al., 2021). Beneficial microbes also mitigate the negative effects of stresses by promoting stress-protective responses in their plant hosts. For example, foliar *Epichloë* endophytes induced plant salicylic acid and jasmonic acid signalling pathways that were correlated with enhanced resistance of host plants to *Blumeria graminis* and *Curvularia lunata* phytopathogens (Kou et al., 2021; Shi et al., 2020). The fungal root endophyte *Thermomyces lanuginosus* was reported to improve the heat stress tolerance of *Cucumis sativus* plants by affecting photosynthetic parameters, water use efficiency and inducing antioxidant activities (Ali et al., 2018). In addition to the direct transport of water from soil, under drought situations, arbuscular mycorrhizal fungi increased the expression of plant (and fungal) genes encoding for aquaporins in roots of *S. lycopersicum* plants. The enhanced expression of aquaporin genes improved the hydraulic conductivity and cytoplasm-to-cytoplasm water flow in symbiotic plants (Chitarra et al., 2016; Quiroga et al., 2019). Furthermore, mycorrhizal fungi can stimulate a 'prime state' of plant responses to stresses (Pozo et al., 2015). In this state, plant responses are faster, stronger and/or more sustained upon the stress (Martinez-Medina et al., 2016). For example, a priming of jasmonic acid-related responses induced by the mycorrhizal fungus *Funneliformis mosseae* increased the level of resistance of *S. lycopersicum* plants against *Helicoverpa arimigera* caterpillars (Song et al., 2013). Similarly, the mycorrhizal-based primed accumulation of antiherbivore compounds in the same plant species increased the resistance of plants against *Spodoptera frugiperda* caterpillars (Rivero et al., 2021). Under salinity stress, *S. lycopersicum* plants showed a primed accumulation of salt-protective compounds including plant catechins and B6 vitamins in presence of mycorrhizal fungi (Rivero et al., 2018).

5 | CONCLUSION AND FUTURE PERSPECTIVES

In the present review, several experimental results showing that environmental stresses compromised plant-microbe interactions were highlighted. It was proposed that this environmental interference of plant-microbe interactions is explained by the stress-mediated induction of salicylic acid, jasmonic acid, ethylene, ROS and other signalling pathways (Figure 1). These plant signalling pathways are recognized to regulate beneficial microbes (e.g., Klopffholz et al., 2011; Plett et al., 2014; Wawra et al., 2016). The direct effects of stresses on microbes may also explain the environmental interference of plant-microbe associations (Figure 2). Further experiments manipulating plant stress responses will be critical for determining the relative importance of direct and plant-mediated effects of stressors in compromising plant-microbe

interactions. For instance, mutant plants for hormone (i.e., salicylic acid, jasmonic acid, ethylene) and/or ROS production are useful tools for altering the relationship between direct and plant-mediated effects of stressors on beneficial microbes (e.g., Jayakannan et al., 2015; Nadarajah, 2020). Beneficial microbes harbour mechanisms that counteract plant stress responses. They produced effector proteins that reduced or prevented the induction of plant hormonal and ROS signalling pathways (Hassing et al., 2019; Wawra et al., 2016). In addition, they increased the antioxidant levels in plants that reduced the oxidative damage caused by ROS bursts in stress situations (Hamilton et al., 2012). Beneficial microbes also confer to their hosts effective stress-protective mechanisms (Figure 2). Both microbial counter-defences to plant stress responses and microbial-derived stress-protective mechanisms might contribute to maintain the mutualisms. Further research manipulating beneficial microbes will be essential to determine the contribution of the distinct microbial-derived mechanisms of mutualism protection in stress situations. For example, mutant *Epichloë* endophytes with disrupted alkaloid production would increase the relative importance of the microbial mechanisms of counter-defences over the stress-protective ones in relation to the mutualism maintenance (e.g., Miller et al., 2022). Furthermore, considering that plant responses to stresses depend on the complexity of the environment (Song et al., 2022; Suzuki et al., 2014), it would be valuable in further investigations to determine whether the microbial mechanisms of stress protection can still maintain the mutualisms in contrasting stress scenarios (e.g., chronic vs. sporadic, severe vs. mild). Our work contributes to understand how environmental stresses affect plant-microbe interactions and highlights why beneficial microbes still deliver benefits to plants under stressful environments.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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