Managing plant-environment-symbiont interactions to promote plant performance under low temperature stress

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Abstract

Low temperature stresses, also referred to as cold temperature stresses, including chilling and freezing temperatures, are among the major abiotic stresses that severely reduces plant yield, quality, and marketability and pose a serious threat to plant production during whole plant life cycles. Plant-environment-symbiont interactions determine the symbiotic and crop performance and tolerance to biotic and abiotic stresses. To achieve the optimum outcome, it is essential to consider not only plant-symbiont relationships, but also symbiont adaptation and symbiont-symbiont interactions. Improving multi-symbiotic component systems and symbiont breeding together can be a useful strategy to improve symbiosis and, thus, crop production. In this review article, role of interactions between multi-symbiotic components and plant-environment-symbiont relationships and the related biotechnology approaches are discussed in order to find the most effective sustainable and environmentally friendly agricultural practices to improve crop performance and mitigate the adverse effects of low temperatures on plants.

Key words: arbuscular mycorrhizal fungi, rhizobacteria, chilling, freezing, microbiome, multisymbiotic relationships, symbiosis, cold stress

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Introduction

Low temperature stresses, including chilling and freezing temperatures, are among the major abiotic stresses that severely disturb agricultural system and ecosystem biodiversity worldwide, and lower plant quality, yield and, thus, economic value of the produce (Chen et al. 2014). Plant responses to low temperatures greatly vary in the plant kingdom. On sensing freezing or chilling, plants use adaptation mechanisms known as cold acclimation that activates signalling pathways, triggering genes at the transcriptional and post-transcriptional levels to modify plant biochemistry and metabolism, inducing changes in proteins, proline, soluble sugars, osmolytes, and membrane lipid composition and peroxidation. Cold acclimation processes induce antioxidant activity, stabilization of cellular components, enzymes, and other macromolecules to maintain their biological activities, prevention or diminution of freezing or chilling injury and dehydration, extending the freezing tolerance and survival under cold stress conditions (Kishitani et al. 1994; Warren 1998; Thomashow 1999; Kwon et al. 2007; Liu and Osborne 2008; Abdel Latef and Chaoxing 2011; Ouellet and Charron 2013; Strimbeck et al. 2015).

Co-evolution of plant-microbiome metaorganisms is determinant for plant growth, health, fitness, quality, productivity, diversity, and tolerance to biotic and abiotic stresses (Berg et al. 2016). Rhizospheric and phyllospheric (epiphytic), and endospheric (endophytic) microbiome consisted of bacteria, archaea, fungi (mycoflora), and protists are collectively referred to as plant growth promoting microbiota (Afifi 1984; Berg et al. 2016). Plant symbiotic relationship with symbionts such as arbuscular mycorrhizal fungi (AMF) benefits crop productivity and tolerance to different biotic and abiotic stress conditions, ecosystem biodiversity, soil health (i.e., structure, chemical composition, aggregation, degradation, organic matter decomposition, water and nutrient availability, reclamation, as well as enzymatic and microorganisms activity), and mitigates the adverse effects of climate change by, for example, improving nitrogen uptake by N₂-fixation, reducing input of synthetic

fertilizers and, thus, reducing N₂O emission (Medina and Azcón 2010; Abdel-Fattah and Asrar 2012; Berruti et al. 2015). Accordingly, this review article evaluates multi-symbiotic component interactions, and relationships between plants, environment conditions, and symbionts to provide the information for appropriate agricultural managements required for improving crop and symbiotic performance and, thus, tolerance to low temperature conditions.

Plant-fungal and plant-bacteria symbiosis and their roles in plant performance and stress tolerance

Mycorrhizae are fungi that colonize the host plant's root tissues, either intracellularly as arbuscular mycorrhizal fungi (AMF) or extracellularly as ectomycorrhizal fungi. Though the association mainly benefits both plant and fungal symbionts, in some specific species or circumstances the mycorrhizae may be considered parasitic (Johnson et al. 1997). AMF symbiosis is found in more than 80% of vascular plant species (Schüßler et al. 2001; Abdel Latef and Chaoxing 2011; Fan and Liu 2011). AMF species-specific differences even within the same genus may confer differential symbiotic responses (Varga and Kytöviita 2016). AMF belong to a monophyletic phylum, the Glomeromycota. AMF are obligate symbionts since they need to assimilate carbon from their host plants to complete their life cycle (Abdel Latef and Chaoxing 2011). In return, the fungus provides multiple benefits to the host plant such as improving water and nutrient uptake, water use efficiency (WUE), ion homeostasis and apoplastic and cell-to-cell water transport, photosynthetic pigments content, photosynthetic efficiency, stomatal conductance, gas exchange, osmoregulation, enzymatic and non-enzymatic antioxidant activities, lipid peroxidation, cell membrane stability and permeability, growth, metabolism associated with production of secondary metabolites and tolerance to biotic and abiotic stresses (Evelin et al. 2009; Zhu et al. 2010a; Abdel Latef and Chaoxing 2011; Beltrano and Ronco 2008; Abdel-Fattah and Asrar 2012; Birhane et al. 2012; Chen et al. 2013; Estrada et al. 2013; Quiroga et al. 2017). Agricultural management based on the plant-environment-symbiont relationships would allow farmers to harvest crops with higher quality and improved performance. Just as an example, applying regulated deficit irrigation (RDI) in vineyards improves both fruit quality and AMF colonization (Schreiner et al. 2007). This last process can improve plant cold tolerance directly by adjusting the plant water status and the concentrations of osmolytes and anti-freezing components and indirectly by improving plant-fungi symbiosis. Thus, agricultural management and symbiosis are both critical factors to improve crop performance and tolerance.

With similar functions, plant-bacteria symbiotic relationship can promote crop performance and tolerance to multiple biotic and abiotic stresses (Fernandez et al. 2012; González and Gonzalez-López 2013). Bacterial symbiosis improves plant tolerance to multiple biotic and abiotic stresses by modulating metabolism (e.g., 1-aminocyclopropane-1-carboxylate deaminase (ACCD) activity, tricalcium phosphate solubilization, proline, and osmoregulators, carbohydrates), genetic architecture (e.g., regulation of cold-responsive genes) and photosynthetic capacity and yield of plants (Theocharis et al. 2011; Shahzad et al. 2017; Tiwari et al. 2017). For instance, *Burkholderia phytofirmans* PsJN colonization imparted long-term chilling stress tolerance to grapevine by modulating host plant carbohydrate metabolism, photosynthesis, and growth under stress conditions (Fernandez et al. 2012).

Numerous studies have demonstrated the effectiveness of AMF on alleviating drought and salinity stresses (Evelin et al. 2009; Fan and Liu 2011; Abdel-Fattah and Asrar 2012; Zhang, Zhang, and Huang 2014; Bernardo et al. 2017; Quiroga et al. 2017; Selvakumar et al. 2017). However, not so much information is available regarding the influence of AMF on conferring tolerance to low temperatures (Charest et al. 1993; Zhu et al. 2010a,b; Zhu et al. 2016; Abdel Latef and Chaoxing 2011; Chen et al. 2013, 2014; Liu et al. 2014) and bacteria (Theocharis et al. 2011; Fernandez et al. 2012; Su et al. 2015; Subramanian et al. 2015, 2016; Srinivasan et al. 2017). More importantly, because of the adverse effects of low temperatures on symbiosis, improving plant and microbiome performance and tolerance to cold stress, which depends on plant-symbiont, symbiont-symbiont interactions, and symbiont activity threshold under cold climatic conditions, requires more investigations.

Symbiosis under low temperatures

Plant-arbuscular mycorrhizal fungi symbiosis under low temperatures

Low temperature constraints the penetration and spread of AMF (Gpey 1991). Some studies have shown that mycorrhizal fungi spore germination and hyphae colonization are almost completely inhibited at 10 °C (Gpey 1991; Wang et al. 2002; Sharma et al. 2013), although the growth of some fungal species may be severely inhibited, but not completely ceased at such low temperatures, for example at 10 °C for *Glomus intraradices* and at 5 °C for *Glomus caledonium* (Table 1) (Wang et al. 2002; Sharma et al. 2013). AMF capable of growing in cold soils may show contradictory results from beneficial to parasitic relationships

(Charest et al. 1993; Sharma et al. 2013). This could be due to inability of AMF to uptake and transfer nutrients to the host plant, while consuming plant carbon reservoir (Sharma et al. 2013). The optimum ambient temperature for developing many AMF would be between 20 to 30 °C with upper and lower activity thresholds of 34 and 16 °C, respectively, for most strains (Wang et al. 2002). Unlike endomycorrhizal arbuscular mycorrhizae (AM), ectomycorrhizae mycelium may remain active at 0 °C (Sharma et al. 2013). Interestingly, Zhou et al. (2012) study showed that the combined treatment of AMF (*Glomus versiforme*) along with 50 mg L⁻¹ foliar spray with the synthetic plant growth retardant paclobutrazol (PBZ) effectively reduced chilling injury of Teak (*Tectona grandis*) seedlings subjected to 6, 3, and 0 °C for 12 hours. The treatment improved chlorophyll (CHL) content, soluble proteins content, and antioxidant enzymes activities (Table 1) (Zhou et al. 2012). As another strategy to improve symbiotic relationship, the cold-stored mixed inoculum of spores and hyphae of *Glomus intraradices* and colonized roots of sorghum improved symbiont colonization, soil acid phosphatase activity, phosphorus and nitrogen uptake, CHL content and growth of hot pepper (Table 1) (Kim et al. 2002). Under cold dry climatic conditions, AMF colonization was greatly affected by temperature and rainfall and accordingly varied during the growth seasons (Allen 1983). AM extraradical hyphae have the potential to survive under freezing temperatures (Allen 1983; Kytöviita, 2005; Sharma et al. 2013). Due to the similarities between cold and drought adaptation mechanisms, extraradical AM mycelia are well adapted to tolerate prolonged periods of both cold and drought stresses in habitats with frequent prolonged dry spells such as sand dunes and deserts. AM and ectomycorrhizae mycelia tolerate short-term freezing at least up to -10 °C and prolonged freezing at -1 to -2 °C. Fungal spores have unique adaptation mechanisms that enable them to complete fungal life cycle, withstanding harsh conditions, particularly extreme temperatures. For instance, AM spores remain viable after exposure to -80 °C (Sharma et al. 2013). However, under freezing temperatures, it is hypothesized that the effectiveness and nature of symbiotic relationship may be strongly altered and even shifted from endomycorrhizal (i.e., AMF) to ectomycorrhizal fungi relationship (Sharma et al. 2013). Thus, the microbiome selection is critical to enhance symbiotic performance, multi-symbiotic interactions and consequently plant performance and tolerance to multiple stresses.

Plant-bacteria and plant-yeast symbiosis under low temperatures

Depending on tolerance threshold to low temperatures, plant growth promoting bacteria (PGPB) and yeast can be distinguished in three groups: (i) extremophilic cold tolerant psychrotrophic (also, known as psychrotolerant) with activity threshold of 4-35 °C; (ii) cold loving psychrophilic bacteria (mostly, consisted of *Pseudomonas* genus) with activity threshold lower than 15 °C, which can grow at a minimum temperature of 0 °C, with rapid growth between 0.5-7 °C and no growth at 20 °C, and (iii) psychro-active bacteria that grow at or below -1 °C (Witter 1961; Morita 1975; Rayirath et al. 2009; Mishra et al. 2011; Junge et al. 2011; Subramanian et al. 2016).

Similar to AMF, the optimum ambient temperature for many rhizobia are 25-30 °C, with many of these bacteria unable to grow below 10 or at and above 37 °C. However, like arctic rhizobia that grow well at 10 °C, adapted strains are tolerant to heat or freezing temperatures (Graham 1992; Drouin et al. 2000; Alexandre and Oliveira 2013). Colonization of grapevine with plant growth promoting rhizobacterium (PGPR) *Burkholderia phytofirmans* PsJN (*BpPsJN*) strongly reduced the chilling-induced damage caused by 5 days of exposure to 4 °C, which could be attained by increasing ROS scavenging, carbohydrate metabolism, and photosynthetic capacity in parallel with the accumulation of more cryoprotective soluble sugars and starch (Table 2) (Theocharis et al. 2011; Fernandez et al. 2012). In *Arabidopsis thaliana*, *BpPsJN* root endophytic symbiosis prevented freezing-induced plasmalemma disruption after subjecting the plants to 3 days at -1 °C (Table 2) (Su et al. 2015).

In addition to improving photosynthetic capacity and, thus, yield and biomass production, these symbiosis influence carbohydrate metabolism (e.g., trehalose biosynthesis in *Pseudomonas fragi* P121 (Table 2), *Leucosporidium fellii* (Table 1), and *Mrakia frigida* (Table 3), trehalose and glycerol biosynthesis in *Saccharomyces cerevisiae*, and upregulation of malate dehydrogenase in *Rhizobium*), which play a crucial role in cold acclimation (Sardesai and Babu 2001; Panadero et al. 2006; Maggi et al. 2013; Mei et al. 2016). The production of unsaturated membrane lipids to maintain membrane fluidity, RNA chaperons to suppress the formation of undesired secondary RNA structures, the synthesis of antifreeze and cold shock proteins, as well as cold-active antioxidant enzymatic and non-enzymatic activities may also have a prominent role in microbiome cold acclimation (Maggi et al. 2013; Ghobakhlou et al. 2013). Since extensive studies indicate that indigenous strains have been resistant and effective in their environmental conditions (Berruti et al. 2015), the breeding

and selection strategies of these native strains might lead to more successful results. Improving microbiome responses to environmental stimuli can promote symbiotic relationship and, thus, crop performance. Among breeding strategies, regulation of protein homeostasis (e.g., by RNA-binding proteins, transcriptional and post-transcriptional regulation of small non-coding RNAs, RNA chaperons, heat and cold shock protein coding genes, proteases, and proteins involved in exopolysaccharide synthesis), regulation of carbohydrate metabolism (e.g., trehalose and glycerol as mentioned above), enzymes involved in energy generation and redox homeostasis (Fernandez et al. 2012; Maggi et al. 2013; Ghobakhlou et al. 2013; Poltronieri et al. 2014; Keto-Timonen et al. 2016; Zhang et al. 2016; Larrainzar and Wienkoop 2017; Paço et al. 2016; da-Silva et al. 2017; Janczarek et al. 2017; Michaux et al. 2017; Robledo et al. 2017; Yu et al. 2017), genes and enzymes involved in maintaining membrane fluidity, fatty acid composition, plastoquinone state (Maksimov et al. 2017), and nucleic acid metabolism (e.g., by ribonucleotides) (Larrainzar and Wienkoop 2017) are effective tools to confer bacteria resistance to extreme temperatures.

Although the functional mechanisms of these compounds may vary depending on plant species and bacteria strains, the symbiosomes surrounded by a specialized plant membrane peribacteroid membrane have a prominent role in symbiotic performance and tolerance to stresses (Larrainzar and Wienkoop 2017). In addition to conferring microbiome resistant to cold temperatures, regulation of gene expression, e.g. chaperons, proteases, enzymes involved in exopolysaccharides biosynthesis, and small non-coding RNAs can be used to promote symbiotic effectiveness, nodulation, and nitrogen fixation (Paço et al. 2016; da-Silva et al. 2017; Poltronieri et al. 2014; Robledo et al. 2017; Janczarek et al. 2017). In addition to microbiome breeding, because of the close symbionts interactions, such as fungal-bacterial genetic and metabolite (e.g., bacterial exopolysaccharides like lipopolysaccharide and chitinase secretion) interactions (Baltrus et al. 2017), the symbionts interactions should be taken into account to draw a sound conclusion about the influence of multi-symbionts on host plants.

Plant-microbe-fungi symbiotic relationships and diversity under low temperature

Bacteria usually establish their symbiotic relationship with fungal hyphae and/or spores, fruiting bodies, and even on mycorrhizal roots. These microbes work in soil primarily in three different ways, i.e. saprotrophy, pathogenicity, and symbiosis. Bacteria in soil move

towards or along fungal hyphae either by motility or chemotaxis (Hayat et al. 2017). In addition to the interrelationship between bacterial and fungal communities with respect to their structure, diversity, and activity (Tardy et al. 2014; Zhang et al. 2017), they are involved in regulating soil biochemistry (Zhang et al. 2017) and structure (Sessitsch et al. 2001; Gupta 2011; Sun et al. 2015), as well as in plant stress tolerance, content and composition of plant secondary metabolites, nutrient status, productivity and biodiversity (Van der Heijden et al. 1998, 2008, 2016; Hart and Klironomos 2003; Urcelay and Díaz 2003; Hu et al. 2017; Pistelli et al. 2017). Multi-component plant-fungal-bacterial symbiosis has shown higher potential for improving the above mentioned traits, particularly, under stress conditions. Besides, the microorganisms adaptation to stress conditions may be enhanced under the interaction of multiple symbiosis (Shtark et al. 2012, 2015; Van Der Heijden et al. 2016; Rahimzadeh and Pirzad 2017). Soil and also plant fungal and bacterial diversity either in leaves or roots positively mediate plant biodiversity, productivity, and phenotypic traits (Eisenhauer et al. 2017; Laforest-Lapointe et al. 2017).

Mediated by root exudates, plant diversity significantly affects fungal and bacterial biomass and fungal to bacterial biomass ratio. Root exudates influence soil biota diversity, biomass, and function (Eisenhauer et al. 2017) and, in return, synergistically soil biota promotes soil physico-chemical and structural properties and stability (Wright et al. 1999; Sessitsch et al. 2001; Gupta 2011; Sun et al. 2015; Zhang et al. 2017) as well as plant health, growth, productivity, and stress tolerance (Eisenhauer et al. 2017). Soil biochemistry and structure, microbial diversity, ecosystem biodiversity, and environmental alterations such as climate change affect microbial (Sessitsch et al. 2001; Zhang et al. 2017; Hayat et al. 2017; Eisenhauer et al. 2017) and fungal biomass, diversity, and activity (Sun et al. 2015; Zhang et al. 2017; Hu et al. 2017; Eisenhauer et al. 2017). Regarding environmental conditions, soil moisture and texture, clay content, pH, CO₂, nutrient concentration, particularly C, N and P, soil respiration, organic matter content and its decomposition, and soil temperature are the main influential factors in determining soil microorganisms' activity, strongly influencing mycorrhizal colonization, hyphae growth, bacterial to fungal ratio, and microbial composition and diversity (i.e., gram positive and negative), biomass and activity (Miltner et al. 2004; Lipson et al. 2005; Lekberg and Koide 2008; Gougoulas et al. 2014; Rinu and Pandey 2010; Classen et al. 2015; Berruti et al. 2015). Although the activity threshold levels of biota strains greatly depend on the species of biota and its host, for many strains soil acidity below pH 5.0, alkalinity above pH 8.5, clay content below 15%, extreme temperatures, extreme moisture

contents, and high nitrate content severely disturb biota population (Howieson and Ballard 2004).

The bioassociative effect of rhizospheric cold-tolerant *Pseudomonas* spp. strain NARs1 with effective root nodulating symbiotic N₂ fixer *Rhizobium leguminosarum*-PR1 effectively promoted iron acquisition, nutrient (N and P) uptake, CHL content, and growth of co-inoculated lentil (*Lens culinaris* L.) (Tables 1, 2, and 4) (Mishra 2011). The synergistic, antagonistic, parasitic, mutualistic, neutral, amensalistic, commensalistic, and competitive relationships of double or triple AMF-*Rhizobium*-PGPR on specific plants under different environmental conditions may vary depending on symbiont combinations, abundance, diversity, functional mechanism, host species, and environmental conditions (Zaidi and Khan 2005; Mishra 2011; Berruti et al. 2015; Duperron 2017). In addition to the activities and the tolerance levels to environmental stimuli, it has been hypothesized that different microorganisms such as diverse AMF strains differentially improve antioxidant activities and cold tolerance (Chen et al. 2014). Thus, symbiont diversity and combinations are essential to improve stress tolerance because they are able to modulate different adaptation mechanisms through functional heterogeneity as well as threshold activities, thereby when one strain stops working, the other one may have higher capacity of symbiosis.

Moreover, the synergistic effects between diverse symbionts may increase the potential of conferring stress tolerance and improving crop performance. However, because of differences in reported results of multi-component symbiotic systems, probably due to plant-symbiont and symbiont-symbiont relations, symbionts combinations, diversity and abundance, as well as environmental conditions, the efficiency of mixtures needs to be tested (Zaidi and Khan 2005; Mishra 2011; Berruti et al. 2015). *Bradyrhizobium* sp. (vigna) and phosphate solubilizing microorganisms (PSM) *Pseudomonas striata* or *Penicillium variable* enhanced nodulation, N and P uptake and, thus, yield in green gram [*Vigna radiata* (L.) Wilczek] plants in a sandy clay loam soil, while their symbiotic relationship was negatively affected by the addition of *Glomus fasciculatum* AM fungus (Table 4) (Zaidi and Khan 2005). Similarly, in green gram (*Vigna radiata* L.), boron (soil or foliar applied borax solution) had a positive impact on nutrient uptake such as P and K and, thus, yield in a boron-deficient calcareous soil; however, N uptake was negatively affected (Padbhushan and Kumar 2015). Among different N sources, including glycine, ammonium, and nitrate, glycine-treated rice crops maintained high levels of N uptake, soluble proteins, soluble sugars, proline, antioxidant activities, CHL content, photochemical efficiency, biomass production, energy use efficiency, and root/shoot ratio, strengthening cold acclimation (Xiaochuang et al. 2017).

Using another microorganisms combination, *Azospirillum* spp. and *Pseudomonas striata*, and *Rhizobium* spp. co-inoculation successfully increased the nodules number, plant dry weight and height, and yield in pigeon pea (Table 4) (Mishra 2011).

In addition to improving cold acclimation and biomass production in bacterized wheat plants, *Pseudomonas* sp. has also been effective in improving total CHL, anthocyanin, proline, total phenolics, and starch content and reducing the Na^+/K^+ ratio, and electrolyte leakage, yield and tolerance to multiple stresses (Tables 2 and 4) (Mishra et al. 2012). While increasing anthocyanin, proline, and phenolic contents and reducing electrolyte leakage promote ROS detoxification and, thus, cold acclimation, increasing CHL content and carbohydrate metabolism would be efficient to enhance photosynthesis and crop yield. The possibility of antipathetic symbiosis might be due to microorganisms' competition as a result of nutrients scarcity or unavailability (mainly, C, N, P), the symbiont type and combination, the soil environment, and plant genotype (e.g., hormonal status, physiology and defense characteristics) (Mishra 2011). Thus, understanding symbiont-symbiont and plant-symbiont interactions is necessary in order to improve symbiotic performance under cold temperature stresses.

Conclusions

In sum, this review remarks that understanding the relationships between symbiotic components (combinations, diversity, tolerance, ratios, abundance, genetic, metabolic and symbiont interactions, threshold activities, adaptation and functional mechanisms), soil characteristics and environmental changes (soil biochemistry and structure, CO_2 , moisture, nutrient and clay content, pH, temperature, and ecosystem biodiversity) are required to make accurate agricultural management decisions. In addition to managing plant, environment, and multi-symbiotic relationships, symbiotic performance and cold acclimation can be improved by using cold tolerant symbionts and regulating plant and symbiont metabolic pathways.

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Table 1. Effects of plant-fungi symbiosis on plant tolerance to cold stress

Fungi	Activity threshold	Host plant	Function	References
<i>Glomus mosseae</i>	Active at 5 °C.	<i>Elymus nutans</i> Griseb	Enhanced tolerance to 5 °C; improved CHL content, photosynthetic capacity, antioxidative activity, soluble sugar and glutathione accumulation.	(Chu 2016)
<i>Glomus claroideum</i> ; <i>Claroideoglomus claroideum</i>	Need to be tested.	No report was found.	It is suggested that they may confer tolerance to cold stress.	(Cartmill et al. 2007; Beltrano and Ronco, 2008; Millar and Bennett 2016)
<i>Glomus geosporum</i>	Need to be tested.	No report was found.	It is suggested that it may confer tolerance to cold stress.	(Evelin et al. 2009)
<i>Glomus viscosum</i>	Need to be tested.	No report was found.	It is suggested that it may confer tolerance to cold stress.	(Campanelli et al. 2013)
<i>Glomus etunicatum</i> , <i>G. tortuosum</i> , <i>Acaulospora scrobiculata</i> , <i>G. intraradices</i>	Colonization rate at 25 °C in maize: <i>Glomus etunicatum</i> > <i>G. tortuosum</i> > <i>Acaulospora scrobiculata</i> > <i>G. intraradices</i> Colonization rate at 15°C: <i>G. intraradices</i> > <i>A. scrobiculata</i> > <i>G.</i>	Maize	They may confer tolerance to cold stress, depending on plant species and environmental conditions and thus more studies are required; they enhance plant antioxidant activity; <i>Glomus etunicatum</i> enhanced maize tolerance to 5 °C; improved stomatal conductance, water status, WUE, CHL content, and photosynthetic capacity	(Wang et al. 2002; Evelin and Kapoor 2014; Chen et al. 2014; Zhu et al. 2010a; Sharma et al. 2013)

	<i>tortuosum</i> and <i>G. etunicatum</i>			
	Threshold activity for <i>Glomus intraradices</i> is 10 °C and 5 °C for <i>Glomus caledonium</i>			
<i>G. albidum</i>	Need to be tested.	No report was found.	It is suggested that it may confer tolerance to cold stress.	(Cartmill et al. 2007)
<i>G. diaphanum</i>	Need to be tested.	No report was found.	It is suggested that it may confer tolerance to cold stress.	(Cartmill et al. 2007)
Antarctic strain of <i>Geomyces pannorum</i>	<i>G. pannorum</i> is a cold tolerant strain; however, its activity threshold need to be tested.	Its symbiotic relationship, performance and effectiveness need to be tested.	<i>G. pannorum</i> has high capacity for antioxidant activity and phenolics biosynthesis under cold condition and thus might improve plant tolerance to cold stress	(Maggi et al. 2013)
<i>Cladosporium cladosporioides</i> and Antarctic strain of <i>Cadophora fastigiata</i>	These strains are cold tolerant; however, their threshold activity need to be tested.	Their symbiotic relationship, performance and effectiveness need to be tested.	Have high levels of unsaturated fatty acids/saturated fatty acids at 8 °C. It is suggested that they may confer tolerance to cold stress.	(Maggi et al. 2013)
<i>Funneliformis mosseae</i>	Sensitive to temperature lower than 15 °C.		Non effective.	(Gavito and Azcón-Aguilar 2012)
PBZ (80 ppm);	Effective at 5 °C.	Green bean (<i>Phaseolus vulgaris</i> L.)	Enhanced tolerance to 5 °C; enhanced antioxidant activity.	(Alizadeh Frutan et al. 2016)

PBZ + <i>Piriformospora indica</i> fungi				
PBZ (50 ppm) and <i>Glomus versiforme</i> fungi	PBZ, <i>G. versiforme</i> and their combination was effective at 0 °C for 12 h; the combination was more effective than either AMF or PBZ treatment.	Teak (<i>Tectona grandis</i>)	Enhanced tolerance to 0 °C for 12 h; improved the CHL content, soluble protein content, and antioxidant enzyme activities; PBZ and AMF could induce cytokinin biosynthesis and thus hamper CHL degradation under cold stress.	(Zhou et al. 2012)
<i>Acaulospora scrobiculata</i> and <i>Rhizophagus intraradices</i>	Need to be tested.	No report was found.	It is suggested that they may confer tolerance to cold stress.	(Shi et al. 2016)
<i>Cold adapted endophytic fungi Penicillium, Aspergillus, Cephalosporium, Sirococcus</i>	Adapted to the cold environment of Baima Snow Mountain, Southwest China; however, their activity threshold needs to be tested.	More studies are required.	It is suggested that they may confer tolerance to cold stress.	(Li et al. 2012)

Ascomycetous fungi genera including <i>Embellisia</i> , <i>Phoma</i> , <i>Geomyces</i> , <i>Tetracladium</i> and <i>Thelebolus</i>	All genera can grow at -1 °C	More studies are required.	It is suggested that they may confer tolerance to cold stress.	(Margesin et al. 2005 ; Thomas-Hall et al. 2010 ; Maggi et al. 2013 ; Tsuji 2016)
Basidiomycetous fungi including <i>Cryptococcus</i> , <i>Dioszegia</i> , and <i>Leucosporidium fellii</i>				

Table 2. Effects of plant-bacteria symbiosis on plant tolerance to cold stress

Bacteria	Activity threshold	Host plant	Function	Reference
<i>Burkholderia phytofirmans</i>	Remain effective at -1 °C.	Grapevine	Enhanced tolerance to 4 °C.	(Fernandez et al. 2012 ; Theocharis et al. 2011 ; Su et al. 2015)
Psychrotolerant bacterium <i>Pseudomonas fragi</i> P121	Active at 4-25 °C.	No report was found.	It is suggested that it may confer tolerance to cold stress; It produces trehalose to cope with cold stress.	(Mei et al. 2016)
<i>Pseudomonas migulae</i> S10724; <i>P. palleroniana</i> N26; psychrotrophic diazotrophs <i>Dyadobacter psychrophilus</i> B2; <i>Pseudomonas jessenii</i> MP1	Need to be tested.	More studies are required.	It is suggested that they may confer tolerance to cold stress.	(Suyal et al. 2017)
Psychrotrophic cold-acclimated <i>Rhizobium</i> ATR1	Needs to be tested.	More studies are required.	It is suggested that it may confer tolerance to cold stress.	(Sardesai and Babu 2001)
Psychrotolerant <i>Pseudomonads</i> from north-western Indian Himalayas	Active at 4-35 °C.	Wheat	Enhanced tolerance to 4 °C.	(Mishra et al. 2011)

<i>Pseudoalteromonas</i> , <i>Psychrobacter</i> , <i>Halomonas</i> , <i>Pseudomonas</i> , <i>Hyphomonas</i> , <i>Sphingomonas</i> , <i>Arthrobacter</i> , <i>Planococcus</i> , and <i>Halobacillus</i>	Active at 4-15 °C; tolerant to 0 °C.	More studies are required to determine their symbiotic relationships and effectiveness	It is suggested that they may confer tolerance to cold stress.	(Bowman et al. 1997)
<i>Paenibacillus darwinianus</i> , <i>Colwellia psychrerythraea</i> , <i>Planococcus halocryophilus</i> , <i>Pseudoalteromonas haloplanktis</i> , <i>Psychromonas ingrahamii</i> , psychrophilic archaeon <i>Methanococcoides burtonii</i> , and bacterium <i>Desulfotalea psychrophila</i>	Need to be tested.	Their activity, effectiveness, and symbiotic relationship need to be tested under low temperatures.	They might be effective in improving cold acclimation.	(Dsouza et al. 2014)
<i>Microbacterium</i> sp. (e.g., <i>M. smegmatis</i> , <i>M. sp.</i> SK0812),	Need to be tested.	Its activity, effectiveness, and symbiotic relationship need to be tested under low temperatures.	It might be effective in improving cold acclimation.	(Shires and Steyn 2001; Kang et al. 2009)
<i>Arthrobacter</i> , <i>Flavimonas</i> , <i>Flavobacterium</i> , <i>Massilia</i> , <i>Pedobacter</i> and <i>Pseudomonas</i>	Active at 5 °C	Tomato	Improved germination, growth, and tolerance to chilling stress of 15 °C by reducing membrane damage and inducing antioxidant activity	(Subramanian et al. 2016)

<p>K-solubilizing psychrotolerant <i>Methylobacterium phyllosphaerae</i> strain IARI-HHS2-67; <i>Halobacterium lacusprofundi</i>, <i>Sphingobacterium antarcticus</i>, <i>Octadecabacter arcticus</i>, <i>Hymenobacter roseosalivarius</i>, <i>Cellulophaga algicola</i>, <i>Flavobacterium frigidarium</i>, <i>Oleispira antarctica</i>, <i>Flavobacterium psychrolimnae</i>, <i>Psychromonas ingrahamii</i>, <i>Exiguobacterium soli</i>, <i>Pseudomonas extremaustralis</i>, <i>Cryobacterium roopkundense</i>, <i>Sphingomonas glacialis</i>, <i>Pedobacter arcticus</i>, <i>Sphingobacterium psychroaquaticum</i>, <i>Lacinutrix jangbogonensis</i>, <i>Massilia eurypsychrophila</i>, <i>Glaciimonas frigoris</i>, and <i>Psychrobacter pocilloporae</i>, <i>Arthrobacter nicotianae</i>, <i>Arthrobacter methylotrophus</i>, <i>Brevundimonas terrae</i>, <i>Paenibacillus tylopili</i> and <i>Pseudomonas cedrina</i>, <i>Pseudomonas rhodesiae</i>, <i>Alishewanella</i> sp., <i>Aurantimonas altamirensis</i>, <i>Bacillus baekryungensis</i>, <i>Bacillus marisflavi</i>, <i>Desemzia incerta</i>, <i>Paenibacillus xylanexedens</i>, <i>Pontibacillus</i> sp., <i>Providencia</i> sp., <i>P. frederiksbergensis</i>, <i>Sinobaca beijingensis</i>, <i>Vibrio metschnikovii</i>, <i>Bacillus psychrosaccharolyticus</i>, <i>Bacillus amyloliquefaciens</i>, <i>Bacillus altitudinis</i>, <i>Bacillus Muralis</i>, <i>Paenibacillus tylopili</i>,</p>	<p>Active at 5 °C; <i>Pseudomonas</i> and <i>Exiguobacterium</i> are more cold tolerant genera. However, more studies are required to demonstrate their symbiotic relationship and effectiveness at low temperatures.</p>	<p>It is suggested that they may confer tolerance to cold stress.</p>	<p>(Verma et al. 2015; Yadav et al. 2017)</p>
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<i>Paenibacillus pabuli</i> , <i>Paenibacillus terrae</i> and <i>Paenibacillus lautus</i>				
<i>Sphingomonas faeni</i>	Active at 5 °C.	Finger and foxtail millet. More host plants need to be tested.	It is has a potential to improve plant cold acclimation and to reduce pathogenic diseases.	(Mageswari et al. 2015 ; Wachowska et al. 2013 ; Srinivasan et al. 2017)
Arctic adapted <i>Mesorhizobium</i> sp.	Active at 0-30 °C. Tolerant to extreme temperatures, salt, and pH stresses.	Symbiont of <i>Astragalus</i> . More host plants need to be tested.	Improving legume symbiosis, growth and cold acclimation under low temperature.	(Prévost et al. 2003 ; Laranjo and Oliveira 2011 ; Mishra et al. 2012 ; Ghobakhlou et al. 2013)
<i>Sinorhizobium meliloti</i>	Tolerant to 4 °C.	Symbiont of Alfalfa. More host plants need to be tested.	Improving growth and cold acclimation under low temperature.	(Mishra et al. 2012)
<i>Rhizobium leguminosarum</i> and <i>R. gallicum</i> .	Tolerant to 4 °C. <i>R. leguminosarum</i> bv. viciae showed a very good growth at 5 °C.	Symbionts of <i>Lathyrus</i> , <i>Trifolium repens</i> , <i>Pisum sativum</i> , <i>Phaseolus vulgaris</i> .	Improving nitrogen fixation, growth and cold acclimation under low temperatures.	(Laguerre et al. 1997 ; Drouin et al. 2000 ; Mishra et al. 2012)
<i>Pantoea dispersa</i>	Grow at 4-42 °C, with maximum growth at 30 °C.	Wheat	Improves phosphate solubilization, indole-3-acetic acid (IAA) production,	(Selvakumar et al. 2008)

			siderophore and hydrocyanic acid production and thus plant growth and tolerance to biotic and abiotic stresses.	
<i>Pseudochrobactrum kiredjianaie</i> A4	<i>P. kiredjianaie</i> A4 is a cold-adapted strain from cave that tolerate prolong low light, temperature and nutrient, but high humidity and salinity conditions.	Wheat	Improving root and shoot growth, fungal disease resistance, antioxidant enzyme activity, plant growth promotion compounds like IAA, salicylic acid (SA), and siderophore under microgravity.	(Fu et al. 2017 ; Qin et al. 2017)
<i>Bacillus amyloliquefaciens</i>	<i>B. amyloliquefaciens</i> is a cold adapted strain; however, its threshold activity need to be tested.	Rice	Improves crop performance and tolerance to multiple abiotic stresses.	(Shahzad et al. 2017 ; Tiwari et al. 2017 ; Yadav et al. 2017)

Table 3. Effects of plant-yeast symbiosis on plant tolerance to cold stress

Yeast	Activity threshold	Host plant	Function	Reference
<i>Candida tropicalis</i>	Need to be tested.	Its activity, effectiveness, and symbiotic relationship need to be tested under low temperatures.	It might be effective in improving cold acclimation.	(Kang et al. 2009)
Cold-active basidiomycetous psychrophilic yeast <i>Mrakia frigida</i> , <i>Mrakia robertii</i> sp. nov., <i>Mrakia blollopis</i> sp. nov. and <i>Mrakiella niccombsi</i> sp. nov. and <i>Rhodotorula</i>	All genera can grow at -1 °C	More studies are required.	It is suggested that they may confer tolerance to cold stress.	(Margesin et al. 2005 ; Thomas-Hall et al. 2010 ; Tsuji, 2016)

Table 4. Effects of plant-bacteria-fungi symbiosis on plant tolerance to cold stress

Bacteria-fungi	Activity threshold	Host plant	Function	Reference
Bacteria <i>Pseudomonas striata</i> <i>Bradyrhizobium</i> ; <i>Azospirillum</i> spp.; <i>Pseudomonas striata</i> ; Fungi <i>Penicillium variable</i>	Need to be tested.	Their activity, effectiveness, and symbiotic relationship need to be tested under low temperatures in different host plants.	They have been effective in improving antioxidant activities, biosynthesis of photosynthetic pigments, nutrient uptake, and biomass production and thus might be useful for cold acclimation.	(Mishra 2011; Mishra et al. 2012)
<i>Pseudomonas</i> spp. NARs1 fungi + <i>Rhizobium leguminosarum</i> -PR1 (Tables 1, 2, and 4)	Need to be tested.	Lentil (<i>Lens culinaris</i> L.). Their activity, effectiveness, and symbiotic relationship need to be tested under low temperatures in different host plants.	Effectively promoted iron acquisition, nutrient uptake (P and N), CHL content, and growth of co-inoculated lentil. It is suggested that they may confer tolerance to cold stress.	(Mishra 2011)