Plant and symbiont metabolic regulation and biostimulants application improve symbiotic performance and cold acclimation

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Abstract

Cold stress, including chilling and freezing temperatures, severely damages crop production and quality during the whole plant life from seed germination to the end of postharvest life. Cold stress can indirectly reduce plant yield and quality by suppressing symbiont growth and, thereby, symbiotic performance. In organic farming, application of bioactive compounds and/or symbiont microorganisms can be used as biostimulants to promote plant performance under normal and stressful conditions. Regulation of bioactive compounds and metabolites (by modifying gene expression, signalling and synthetic pathways) in plants and/or symbionts have the potential to promote plant and symbiont relationships and performance. So far, few studies have shown the effectiveness of regulating symbiont metabolites (for example, Sphingomonas faeni overexpressing 1-aminocyclopropane-1-carboxylate deaminase (ACCD) enzyme *activity that enhance cold tolerance), which can be referred to as microbiome breeding, on modulating plant and symbiont performance and stress responses. This review article incentivizes further studies to use microbiome breeding to not only promote symbiont and host tolerance, but also to promote symbiotic performance and, thereby, plant yield and quality, particularly when symbiosis is depressed by undesirable environmental conditions such as cold stress. The efficacy of using biostimulants and cold tolerant symbionts on improving plant metabolites, symbiotic performance, and cold acclimation are discussed in this review article.*

Keywords: biostimulants, chilling, cold stress, freezing, metabolite regulation, microbiome, symbiosis, tolerance to low temperatures

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Introduction

Optimizing crop performance, particularly where inhospitable environment constrains crop yield, is critical in order to increase agricultural production to meet the global food demand. Cold stress, including chilling and freezing temperatures, is one of the major abiotic stresses that severely disturbs plant yield and quality during whole plant life cycle from seed germination to the end of postharvest life. Upon exposure to low temperatures, plants use different strategies to increase freezing and chilling tolerance and mitigate cold stress damage, known as a whole as cold acclimation. After cold stress sensing, activation of signalling pathways lead to regulation of transcription factors activity and, consequently, changes in the expression of multitude of genes with the general aim of avoiding the deleterious effects of low temperatures and protecting cellular structures and functions by modifying plant metabolism, including anti-freezing components production, transport and allocation. Cold acclimation occurs by accumulating anti-freezing and osmolyte metabolites (e.g., sucrose, glucose, fructose, manose, glycine, raffinose, trehalose, galactinol and starch originated sugars like galactinol, phosphated and nucleotide sugars), proline, amino acids, organic acids (e.g., oxalic acid, citric, malic, and succinic, and gallicacids), polyamines (e.g., spermidine, putrescine), methionine, phenolic compounds, lignins, proteins (e.g., cold shock proteins classified as RNA chaperons, dehydrins, soluble proteins), probenazole-inducible protein, all of which can be mediated by vacuole acidification, in order to maintain inter- and intra-cellular transportation to escape from dehydration, denaturation, and collapse of macromolecules, to maintain water and nutrient uptake and, consequently, to facilitate water conductance, enzymatic and non-enzymatic antioxidant activities, energy use efficiency, and photosynthetic efficiency (Yamashiro et al. 1990; Zobel and Nighswander 1991; Naidu et al. 1991; Monroy et al. 1993; Guy et al. 1997; Rivero et al. 2001; Taji et al. 2002; Tanaka et al. 2006; Kwon et al. 2007; Iordachescu and Imai 2008; Cansev et al. 2008; Ruelland et al. 2009; Kim et al. 2009; Ferreres et al. 2011; Hanin et al. 2011; Sánchez-Bel et al. 2012; Fernandez et al. 2012; Schulze et al. 2012; Shi et al. 2014; Delorge et al. 2014; Ji et al. 2015; Yang et al. 2016; Xiaochuang et al. 2017; Yildiztugay et al. 2017). Managing plant-microbiome symbiosis, and deploying biostimulants and biotech approaches (for example, improving plant signalling and metabolic pathways) can be used as effective strategies to enhance plant tolerance to cold stress and promote plant cell homeostasis and, thereby, functions.

Plant-arbuscular mycorrhizal fungi (AMF) symbiosis optimize plant cell cycle processes by improving production of osmoregulators and antioxidants that optimize cellular functions under multiple stresses such as drought, salinity, and cold (Chen et al. 2014; Zhang, Zhang, and Huang 2014). It has been observed that in AMF-inoculated cucumber plants show significantly higher ATPase activities (H^+-ATPase, P-Ca^{2+}-ATPase, V-typeH^+-ATPase, and total ATPase activities), ATP concentration, plasma membrane protein content, and redox homeostasis by lowering NADPH oxidase activity that is responsible for H_2O_2 accumulation and, thereby, improving cold acclimation (Liu et al. 2014). Similar to advanced biotechnology approaches, the evergreen revolutionary techniques using symbiosis can improve plant growth, development, and tolerance to multiple stresses through various signalling and metabolic pathways and genetic modifications (Fu et al. 2017; Tiwari et al. 2017). However, such symbiotic relations can still be improved by breeding microbiome, host plants, and employing efficient biostimulants. Manipulation of signalling pathways and gene expression to modulate microbiome responses such as enzyme and hormone regulation would be a promising tool to improve symbiont development, activity, tolerance level and, thus, symbiosis. In addition to plant and microbiome breeding, understanding the interactions between multi-symbiotic components is necessary in order to improve symbiotic performance and the efficacy of biostimulants.

Many attempts have recently been made to develop diverse novel formula of biostimulants to promote crop performance in all aspects such as regulating gene expression, enzyme activity, secondary metabolite production, nutrients and hormones status, plant growth, and adaptation to biotic and abiotic stresses (Yakhin et al. 2016; Nardi et al. 2016; Berg et al. 2016). Hence, this review article discusses the efficacy of regulating plant and symbiont metabolic pathways and using biostimulants to promote symbiotic performance as well as plant and symbiont tolerance to cold stress.

Regulation of hormones action, gene expression and metabolism to modulate symbiosis and, thus, cold acclimation

Hormone homeostasis plays a key role in modulating plant and microbiome growth, development, and responses to environmental stimuli. Mediated by abscisic acid (ABA), hydrogen peroxide (H_2O_2), and nitric oxide (NO), *S*-adenosylmethionine synthetase (SAMS) enzyme catalyzes the conversion of methionine to *S*-adenosylmethionine (SAM), a precursor of polyamines and ethylene (Guo et al. 2014). Depending on the chilling conditions and plant species, SAM is converted into 1-aminocyclopropane-1-carboxylate (ACC) by ACC synthase and, then, to ethylene by ACC oxidase (Wang and Adams 1982; Kim et al. 2004; Zou et al. 2014). The 1-aminocyclopropane-1-carboxylate deaminase (ACCD) enzyme activity, which is widespread in diverse bacterial, fungal, and in some Stramenopile species (mostly in *Phytophthora*), enhances cold tolerance by breaking down ACC to *α*-ketobutyrate and ammonia, preventing ethylene formation by means of ACC oxidase and, therefore, ethylene responsive transcription factor activity, regulating the expression of cold stress-responsive genes, thereby exhibiting a dual function: decreasing ethylene biosynthesis and increasing cold tolerance (Nascimento et al. 2014; Singh et al. 2015; Subramanian et al. 2015). A recent study showed that inoculation of finger and foxtail millet seedlings with negative psychrotolerant bacteria (*Sphingomonas faeni*) overexpressing *acdS* (*ACC deaminase*) gene increased ACCD activity, and thereby cold tolerance (Srinivasan et al. 2017). It has been observed that endophytic bacterial ACCD activity may improve seed germination, plant growth, as well as biotic and abiotic stress tolerance by reducing ethylene biosynthesis and increasing indole-3-acetic acid (IAA) levels and root elongation and probably AMF-microbe-plant symbiotic relationships (Selvakumar et al. 2017). Given its role in inducing stress tolerance, understanding the effect of bacterial ACCD activity on symbiotic relationships and plant metabolism requires further investigations.

Improving cold stress tolerance through possible approaches of hormone and protein homeostasis

It is well known that plant hormone ethylene induces susceptibility to chilling stress (Sevillano et al. 2009). In transgenic cantaloupe melons, where the expression of ACC oxidase is inhibited and, therefore, autocatalytic production of ethylene is blocked, the fruits exhibit a remarkable resistance to chilling injury during refrigerated postharvest storage and posterior reconditioning compared with untransformed melons (Ben-Amor et al. 1999). As another strategy, organic and synthetic inhibitors of ethylene biosynthesis can be deployed to increase crop quality and tolerance levels. To name some of them, the recently identified ethylene inhibitor pyrazinamide, a clinical drug used to treat tuberculosis that converts to pyrazinecarboxylic acid in plant cells (Sun et al. 2017) or the well-known ethylene inhibitors like aminoethoxyvinylglycine (AVG) (Even-Chen et al. 1982), α-aminobutyric acid (AABA), γ-aminobutyric acid (GABA), β-aminobutyric acid (BABA), and their isomers (Wang et al. 2015), cobalt ions or aminooxy-acetic acid (AOA) (Podwyszyńska and Goszczyńska 1998; Pereira-Netto 2001), silver nitrate ($AgNO_3$) (Lemaire et al. 2013), silver thiosulphate (STS), nano-silver particles (NSPs), 8-hydroxyquinoline sulphate (8-HQS) (Jafarpour et al. 2015), NO (Zaharah and Singh 2011), and calcium chloride ($CaCl_2$) (Valero and Serrano 2010; Jafarpour et al. 2015) may have the potential to enhance crop yield, quality, longevity under low temperature stresses besides posing decontamination effects. Nitric oxide (NO) can inhibit N_2 fixation and trigger nodule senescence, while positively regulate nitrogen metabolism and maintain metabolic regulation and function and, thereby, energy status under different stress conditions by, for example, modulating proline accumulation under cold stress (Zhao et al. 2009; Hichri et al. 2015). However, more studies are required to demonstrate the efficacy of NO on improving symbiotic performance under low temperature stress conditions. The application of inhibitors of ethylene perception like1-methylcyclopropene (1-MCP) has a high potential to reduce chilling injury, improve fruit quality, and extend fruit shelf life by increasing antioxidant activities and, thus, reducing cell membrane degradation, lipid peroxidation and hydrogen peroxide production, and modulating redox status (Jin et al. 2011; Gapper et al. 2017). GABA, a four carbon non-protein amino acid that is widely distributed in plants, alleviates cold stress damages by promoting antioxidant activity and cell homeostasis, particularly hormone and redox homeostasis, and also regulates C:N balance (Mazzucotelli et al. 2006; Batushansky et al. 2015). Biostimulants like AABA and BABA alleviate chilling injury directly by improving antioxidant enzymatic activities and indirectly by improving metabolites such as phenolic contents (e.g., catechin, corilagin, epicatechin, and gallocatechin gallatein longan fruit) and at the same time increase the value of qualitative traits (Wang et al. 2015). Yet, there is a lack of knowledge about the influence of GABA, BABA, and AABA on symbiotic performance, particularly under cold stress conditions. Overall, manipulation of GABA, BABA, and AABA synthetic pathways might be effective in improving symbiotic performance under cold stress conditions and requires more investigations in the future.

The biostimulants influence on plants' physiological and morphological responses, particularly root and shoot architectural system, photosynthesis (Patrick et al. 2009), senescence (Podwyszyńska and Goszczyńska 1998; Valero and Serrano 2010; Jafarpour et al. 2015), symbiotic relationship, and hormones, particularly ethylene, cytokinin, jasmonic acid (JA), salicylic acid (SA), ABA (Den Herder et al. 2006; Khatabi and Schäfer 2012; Plett et al. 2014; Hu et al. 2017), and IAA (Qin et al. 2017) should be examined to assess their impact on industrial scales. With similar defense mechanisms, pre- and postharvest application of methyl jasmonate (MeJA) and methyl salicylate

(MeSA), salicylate, SA and SA-derived acetylsalicylic acid (ASA) have been effective in increasing fruit quality and tolerance to chilling and pathogens, which could be mediated by regulating of genes expression (e.g., associated with heat shock proteins), modifying membrane and cell wall composition (e.g., higher membrane unsaturated/saturated fatty acid ratio, inhibiting lignin accumulation and cell wall solubilization), improving energy use efficiency, and inducing high levels of antioxidant activity, ABA, polyamine, organic acids, vitamin C and phenolic contents (Wang and Buta 1994; Wang 1999; Ding et al. 2001; González-Aguilar et al. 2003; Fung et al. 2004; Jin et al. 2009a,b, 2013; Meng et al. 2009; Sayyari et al. 2009, 2011; Cao et al. 2010; Karaman et al. 2013). Similar to SA, oxalic acid prevents chilling injury by improving antioxidant properties (Ding et al. 2007). Hence, regulation of such hormones and the biostimulants that positively regulate these hormones might be effective in improving symbiotic performance under low temperature stresses.

Having an overlap between plant defense mechanisms under stress condition, this review suggests that the examination of down-regulation of ethylene biosynthesis, overexpression of C_4 photosynthesis enzyme, co-expression of *ABA-Insensitive3* (*AB3*)/*Viviparious1* and *AtABI5* transcription factor that have been beneficial to improve crop performance under drought stress (Yu et al. 2017) might improve crop performance under cold stress conditions as well, particularly when deployed as multi-disciplinary approaches. Brassinosteroids (BRs) phytohormones have essential roles in regulating plant growth and development, and importantly root phenotypes such as maintenance of meristem size, root hair formation, lateral root initiation, gravitropic response, mycorrhiza formation, and nodulation in legume species (Wei and Li 2016). Brassinolide (the first isolated BR hormone) application has been effective in alleviating chilling stress damage of mango fruits stored at 5 $^{\circ}$C by modulating plasma membrane integrity and lipid fluidity, and expression of proteins, including remorin, abscisic stress ripening-like protein, type II SK2 dehydrin, and temperature-induced lipocalin (Li et al. 2012). Future studies can provide more information to demonstrate the efficacy of BRs in improving symbiotic performance under cold stress conditions. Since the influence of phytohormones on plant-microbiome symbiotic relations may vary depending on plant species, plant growth stages (e.g., prior to inoculation, SA may reduce nodule formation, number of nodules, dry mass, photosynthesis, and nitrogen fixation), phytohormones concentration, hormone crosstalk, microbiome strains and environmental conditions (González and Gonzalez-López 2013; Mabood and Smith 2007), the effectiveness of their manipulation should be verified to reach a sound conclusion.

Investigation on cell wall composition of different Miscanthus genotypes indicated that cellulose, lignin, (1→3), (1→4)-*β*-D-glucan, and phenylalanine ammonia-lyase were linked with cold acclimation as higher concentrations of these biomolecules were present in cold-tolerant genotypes (Domon et al. 2013). Hemicellulose, pectin, oligosaccharides, glycosidases, and arabinogalactan are also essential for modulating cold acclimation (Le Gall et al. 2015). Yet, more studies are required to demonstrate the impact of regulating cell wall composition on symbiotic performance under cold stress conditions. Accumulation of late embryogenesis abundant (LEA) proteins are well documented to be involved in plant development responses to diverse abiotic stresses such as cold, heat, drought, high salinity, ABA, and wounding (Espelund et al. 1992; Hundertmark and Hincha 2008; Battaglia and Covarrubias 2013; Gao et al. 2014). However, the influence of LEA proteins on symbiotic relations, particularly under cold stress conditions, remains to be investigated.

It is now well recognized that plant root system architecture is under the influence of crosstalk effects of nutrient and redox status with brassinosteroid-auxin-ethylene-ABA-gibberellic acid-cytokinin and plant metabolites (Giehl et al. 2014; Askari-Khorasgani and

Pessarakli 2018; Su et al. 2016; Khan et al. 2016), all of which can be modulated by applying biostimulants and symbiotic relationships. For example, rice seedling colonized with *Bacillus amyloliquefaciens* NBRI-SN13 (SN13) conferred tolerance to various biotic and abiotic stresses, including salt, drought, desiccation, heat, cold, and freezing by improving hormone and protein homeostasis, ROS detoxification, ACCD production, tricalcium phosphate solubilization, proline and other osmolytes production, and altering the expression patterns of stress responsive genes coding for dehydrins, glutathione *S*-transferase (GST), LEAs, non-apical meristem (NAM), glucosyltransferases, Rab-like GTPase activators, myotubularin (GRAM), and natural resistance-associated macrophage protein 6 (NRAMP6) (Tiwari et al. 2017). According to Yadav et al. (2017), *Bacillus amyloliquefaciens* is a cold tolerant bacteria and, thus, might be useful to enhance tolerance to cold stress, depending on microbe threshold level, environmental condition, and symbiotic relationship (Yadav et al. 2017). Evaluation of the effects of such symbionts on root system architecture, gene expression (e.g., cold-responsive genes), plant hormones, nutrient, and water status, as well as plant metabolites and symbiotic relations are required to provide deep insights into their influence on cold acclimation.

Role of biostimulants and biotechnology in improving crop performance and tolerance to cold stress

Improving cold tolerance by application of biostimulants requires deep understanding of the relationship of plants and biostimulants under stress conditions. In this regard, not only plant tolerance to cold stress, but also biostimulants function in such tolerance and their symbiotic relationships should be taken into consideration. In addition to using cold-tolerant symbionts and biostimulants as green agriculture, biotechnology practices can be used to improve biostimulants efficacy, symbiont and host tolerance and, therefore, symbiosis effectiveness under cold stress conditions.

Acting as both biofertilizer and biostimulant, extracts of the brown seaweed *Ascophyllum nodosum* enhance plant growth (e.g., increase root and shoot growth and branching) and tolerance to biotic and abiotic stresses (e.g., diseases, drought, salinity, and freezing). *A. nodosum* extract enhanced *Arabidopsis* tolerance to freezing temperature of -7.5 °C in vitro and -5.5 °C in vivo assays. Treated plants maintained membrane integrity, presented 30-40% reduced tissue damage, and 70% less chlorophyll (CHL) damage during freezing recovery, all of which is correlated with increased expression of cold-responsive genes *responsive to dehydration 29A* (*RD29A*), *cold responsive 15A* (*COR15A*), and *C-repeat binding factor 3* (*CCAAT motif-binding factor subunit C* or *CBF3*) and suppression of *AtCHL1* and *AtCHL2* mediated by bioactive components (Rayirath et al. 2009). The application of 3.5 L h^{-1} *A. nodosum* extract effectively improved phenolic and flavonoid contents of cabbage (*Brassica oleraceae*). The commercial seaweed product of AlgaeGreen™ was more effective than XT brand (Table 1) (Lola-Luz et al. 2013). In spinach leaves, *A. nodosum* extract increased the total phenolics and flavonoids contents, total antioxidant activity, and Fe^{2+} chelating ability (Table 1) (Fan et al. 2011). *A. nodosum* extract, nano-size calcium fertilizer and their combination effectively improved grapevines yield and quality attributes (i.e., zinc acquisition and CHL content) under alkaline soil condition (Sabir et al. 2014). Because calcium, particularly oscillations in cytosolic free calcium concentrations, is an essential subcellular messenger in osmotic, salt, and cold stress signalling (Table 1) (Knight et al. 1996; Kiegle et al. 2000), its combined application with *A. nodosum* extract might have a positive impact on improving cold acclimation.

As described by Aremu et al. (2016), commercial biostimulant Kelpak® derived from brown seaweed *Ecklonia maxima* (Osbeck) Papenfuss (*Phaeophyceae*) enhanced endogenous cytokinin level and bioactive compounds (mainly phenolics, flavonoids *p*-coumaric acid, and eucomic acid) of hydroponically grown *Eucomis autumnalis* (Aremu et al. 2016). Commercial oak extract was effective to promote grapevine qualitative traits and phenolic content which can consequently improve the antioxidant capacity and, thus, cold tolerance. Grapevines treated with oak extract had higher polyphenols such as gallic acid, hydroxycynnamoyltartaric acid, acylated anthocyanins, flavanols and stilbenes, and produced less alcoholic and acid wines with higher color intensity, lower shade and, therefore, a more stable color (Pardo-García, 2014). In tomato, biostimulant EXPANDO®, containing different bioactive compounds such as mineral elements (potassium, phosphorus, and molybdenum), amino acids, vitamins, and phytohormone-like substances improved soluble proteins, photosynthetic pigments, total phenolic compounds, yield, and antioxidant activities (Contartese et al. 2016). Therefore, EXPANDO® might be effective to improve cold acclimation, which needs to be tested. Chitosan is an environmentally friendly biodegradable organic compound, containing cationic polysaccharides mainly derived from waste materials from seafood processing, effective for improving crop growth, quality, and tolerance to biotic and abiotic stresses. It has been so far effective for crops such as peanut, carrot, wheat, rice, and maize. Maize seeds priming with chitosan solution increased the speed of seed germination, and increased root and shoot growth, and antioxidant enzyme activities of seedlings under low temperatures (Guan et al. 2009).

Biostimulants such as lipophilic components (rich in fatty acids such as butyric acid, palmitic acid, oleic acid, linoleic acid the sterol fucosterol), hydrolyzed amino acids, melatonin, glycine betaine (Rayirath et al. 2009), cold-adapted microorganisms such as growth promoting rhizobacterium (PGPR) *Pantoea dispersa* (Selvakumar et al. 2008), PGPR *Burkholderia phytofirmans* (Theocharis et al. 2011; Fernandez et al. 2012), and Antarctic basidiomycetous yeast *Mrakia blollopis* (Tsuji 2016) have so far been effective in promoting tolerance to low temperatures. The information on the influence of melatonin and glycine betaine on symbiosis under cold stress conditions is still lacking. After finding the most effective combination of biostimulants and multi-component symbiotic system, identifying the genes responsible for optimum synergistic capacity and cold acclimation of both host plants and symbionts would help to develop cold resistant cultivars with high efficacy in improving symbiotic performance and plant/crop yield and quality under cold stress conditions.

Recently, OMICS study of pschrophiles such asmarine Antarctica bacteria *Pseudoalteromonas haloplanktis* TAC125 that survive at −20 °C has gained attention. Understanding their cold adaption provide insight into improving plants cold acclimation (De Maayer et al. 2014). However, the potential of their application as biostimulant needs to be tested.

Outlooks and concluding remarks

This review article highlights the importance of regulating signalling and metabolic pathways in both plant and symbionts to improve symbiotic performance and, thereby, plant yield and quality. Analysis of symbiont-symbiont and symbiont-host genetic (e.g., RNA sequencing, regulation of cold-responsive genes and chaperons), metabolic (e.g., symbiont secretions, ACCD activity, carbohydrate metabolism, proteins, peptides, peptide transporters, dehydrins, membrane unsaturated/saturated fatty acid ratio), and hormonal changes are essential in order to optimize crop and symbiont tolerance and, thus, symbiotic performance and tolerance to cold stress. Single and joint application of biostimulants and tolerant symbionts can be used as eco-friendly strategies to promote phytometabolites' synthesis, root structure, symbiotic relationships and, thereby, plant yield and quality.

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Table 1. Effects of other biostimulants on plant tolerance to cold stress

Biostimulants	**Activity threshold**	**Host plant**	**Function**	**Reference**
Extract of the brown seaweed *Ascophyllum nodosum; A. nodosum* + Zn/Mn and nano-size calcium fertilizer; the commercial seaweed product of AlgaeGreen^{TM}	*A. nodosum* enhanced *Arabidopsis* tolerance to freezing temperature of -7.5 °C in vitro and -5.5 °C in vivo assays; it is suggested that the combined application of nano-size calcium fertilizer plus seaweed extract might be more useful	*Arabidopsis*, cabbage (*Brassica oleraceae*), grapevine	Seaweed extracts enhanced tolerance to cold stress; improved membrane stability and biosynthesis of CHL and bioactive compounds such as phenolic and flavonoid contents, as well as yield and qualitative traits and might be more effective when it is combined with nano-size calcium fertilizer or Mn/Zn; the combined application of seaweed extracts with other plant symbionts is suggested	(Rayirath et al. 2009; Fan et al. 2011; Lola-Luz et al. 2013; Sabir et al. 2014; Bradáčová et al. 2016)
Nodule-specific cysteine-rich peptides by the inverted repeat lacking clade and Dalbergoid legumes,	Need to be tested.	Soybean	Control host adapted endosymbiotic (intercellular) bacterial population. Improve bacteroid differentiation	(Barrière et al. 2017)

BclA/BacA peptide transporters, and DD-carboxypeptidase enzyme encoded by *DD-CPase1* gene	and thus symbiotic performance.