Plant responses to plant growth promoting bacteria: Insights from proteomics

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ARTICLE INFO	ABSTRACT
	Plant growth-promoting bacteria (PGPB) modes of action are highly complex and the totality of mechanisms they are able to use for plant growth or stress amelioration remains unknown. Although there are well documented bacterial mechanisms (nitrogen fixation, phytohormones production, etc.), there are many plant responses to PGPB at the molecular level that are still clueless. Omics sciences offer large-scale and untargeted approaches to study them. Concretely, proteomics may unravel key events through the observation of protein expression dynamics in plants after PGPB inoculation. We summarized and discussed the existing literature about proteomic studies on plant response to PGPB, with special emphasis in crops. We also developed several meta-analyses to merge results of independent studies and detect potential key changes in plant proteome, through most common differentially expressed proteins. We found that effects of PGPB in plant growth were highly related to over-expression of ROS-reduction proteins, promotion of the photosynthetic machinery, transcription (especially histone-mediated), cell architecture, energy metabolism and nutrient uptake. On the other hand, PGPB inoculation of plants under different stresses generally induced the expression of ROS-related proteins, HSP for protein processing and proteasomes. We also observed an overlap between pathways, acting as general and shared responses to multiple biotic and abiotic stresses. Finally, we brought to the fore gaps of knowledge in the field for further research.

1. Introduction

Plant Growth Promoting Bacteria (PGPB) have widely shown to improve growth and stress management in plants (Bhat et al., 2022). These features have driven a gradual increase in the research towards the use of PGPB in agriculture, especially in the last five years (Fig. 1). Actually, according to Web of Science (WOS) database, 74% of publications related to PGPB have been published in the "Agriculture" research area (WOS, 2023). These data reflect the interest of the scientific community to understand PGPB modes of action, and to use this knowledge to achieve PGPB implementation as a biotool towards a sustainable agriculture, one of the challenges of the current society (Altieri, 2004; Vejan et al., 2016; Antoszewski et al., 2022). To date, it has been shown that PGPB include ectophytic, endophytic or epiphytic bacteria that ameliorate plant fitness by different mechanisms. Among the most extensively documented processes are the production of phytohormones (such as indole-3 acetic acid, cytokinins or gibberellins), the production of the enzyme ACC deaminase, and the supply of nutrients by

nitrogen fixation, phosphate and potassium solubilization, or production of siderophores. PGPB have also proven to play an important role in biocontrol of pathogens and pollutant detoxification (Gamalero and Glick, 2011; Goswami et al., 2016; Parray et al., 2016). However, there are still questions for further research, as PGPB are also known to affect the endogenous plant signaling pathways (for example, by modulation of hormones biosynthesis, transport and transduction, or plant antioxidant machinery) without providing any phytohormone (Zhang et al., 2007; Contesto et al., 2010; Kechid et al., 2013; Goswami et al., 2016). Additionally, PGPB are known to alter plant nutrition without direct nutrient supply, but via other processes like plant transporters upregulation (Saia et al., 2015; Kechid et al., 2022). These mechanisms are not as well documented, maybe because it is easier to characterize bacterial functions, rather than mechanistic plant responses. Moreover, since the "PGPB" term and concept were presented to the scientific community in 1978 (Kloeppler and Schroth, 1978), PGPB studies have been addressed by Microbiologists rather than Plant Physiologists. Given the complexity of PGPB modes of action and the whole range of plant responses to
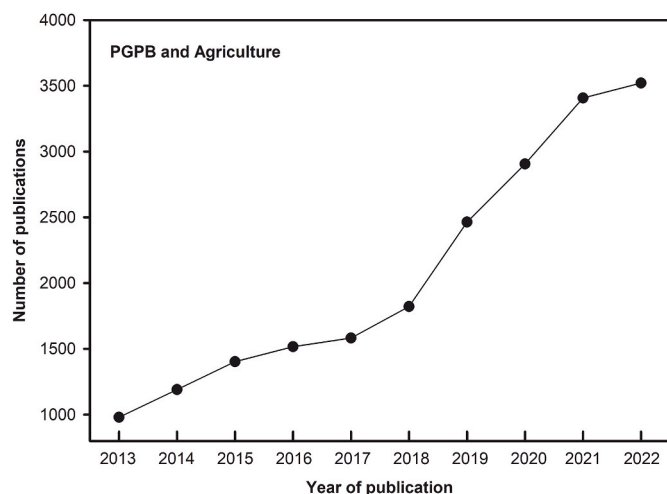

Fig. 1. Number of publications in Web of Science (WOS) database from the last 10 years, after a customized search with the topic "PGPB" or "PGPR" or "PGPE" or "plant growth promoting bacteria" or "plant growth promoting rhizobacteria" or "plant growth promoting endophyte" and "agriculture". Accessed on January 2023.

PGPB, scientists found the need for large-scale and untargeted approaches, which led to the use of "omic" sciences. Genomics and transcriptomics may result in overwhelming data and, sometimes, there is lack of correlation between the presence of a functional gene and the actual translation of that gene (Tartaglia et al., 2020). These concerns led to the valorization of proteomics as a valuable tool to unravel key

events in plants responses to PGPB, through the observation of protein expression dynamics (Jean-Beltran et al., 2017; Khatabi et al., 2019; Liu et al., 2019; Alberton et al., 2020). However, it is a relatively recent research field, and there is no bibliography compiling this knowledge or arising future prospects. Thus, this review summarizes and discusses the most outstanding findings in the existing literature from bibliographic databases (WOS, Scopus and PubMed) about proteomic studies on plant responses to PGPB. We focused on PGPB effects in plant growth and plant stress. These results led us to hypothesize that there may be key proteins that potentially may serve, after deep research, as biomarkers for plant responses to PGPB. Then, we also developed several meta-analyses to merge results of independent studies and detect potential key changes in plant proteome, through most common differentially expressed proteins (DEPs). Finally, we brought to the fore gaps of knowledge in the field for further research. We made special emphasis in crops and breeding, as research in PGPB - plant interaction is greatly oriented to agricultural purposes.

2. Proteomic changes involved in plant growth in response to PGPB inoculation

2.1. Poaceae family

Cereals are one of the most important crops in the world, with a production of 3 billion tons per year (FAO, 2021). They cover a large number of grasses of the Poaceae family such as maize, rice, wheat or sorghum. Concretely, maize (*Zea mays*) has an important impact in the economy of the world, with a production of 1.1 billion tons per year (FAO, 2021). Proteomic studies on maize have mainly studied the effect of two PGPB strains in roots, *Azospirillum brasilense*

Table 1

Research articles that study the effect of PGPB inoculation on plant development and growth. *References selected for further meta-analysis, location of the data within the publication.

Plant species	PGPB	Tissue	Technology	Reference
Arabidopsis thaliana	*Herbaspirillum seropedicae*	Root Shoot	ESI-LC-MS/MS	Leandro et al. (2019)
Arabidopsis thaliana	*Kosakonia radicincitans* DSM 16656	Root	2-DE nanoLC-ESI-MS/MS	Witzel et al. (2017)
Arachis hypogaea ICGV-91114	*Bacillus sonorensis* RS4	Root	SDS-PAGE 2-DE MALDI-TOF	Ankati et al. (2018)
Citrullus lanatus	*Paenibacillus polymyxa* SQR-21	Root	LC-MS	Yaoyao et al. (2017)
Glycine max L.	*Bradyrhizobium japonicum*	Root hair	iTRAQ nanoRPLC-MS/MS (Phosphoproteome analysis)	Nguyen et al. (2012)
Medicago truncatula	*Sinorhizobium meliloti*	Root	2-DE NanoHPLC-Chip-MS/MS	Molesini et al. (2014)
Medicago truncatula	*Sinorhizobium meliloti*	Root nodule	SDS-PAGE Micro-LC/ESI/MS/MS LTQ/FT-Orbitrap	Oger et al. (2012)
Nicotiana tabacum "Xanthi" *Lactuca sativa* "Crispa"	*Bacillus* sp. JS	Shoot	2-DE MALDI-TOF	Kim et al. (2018)
Oryza sativa sp. Japonica cv.	*Herbaspirillum seropedicae* SmR1	Root	2-DE MALDI-TOF/TOF	Alberton et al. (2013)
Oryza sativa	*Azotobacter chroococcum* W5 and A41	Root	LC-MS/MS	Bandyopadhyay et al. (2022)
Oryza sativa L.	*Sinorhizobium meliloti* 1021	Root Leaf	2-DE MALDI-TOF/MS	Chi et al. (2010)
Oryza sativa L. MR219-9	*Stenotrophomonas maltophilia Bacillus* sp.	Leaf sheath	2-D PAGE MS	Naher et al. (2018)
Oryza sativa sp. Japonica cv.	*Herbaspirillum seropedicae* M1Sm300	Root	2-D PAGE MALDI-TOF/TOF	Valdameri et al. (2017)
Oryza sativa	*Bacillus cereus* NMSL88	Root Leaf	2-DE MS/MS	Wang et al. (2013)
Pisum sativum K-8274 (EIBSM) *Pisum sativum* K-3358 (Low-EIBSM)	*Rhizobium leguminosarum* bv. *Viciae Rhizobium irregularis*	Seed	SDS-PAGE Nano HPLC-ESI-Q-Orbitrap-MS	Mamontova et al. (2019)
Saccharum SP70-1143 (high inputs of N from BNF) *Saccharum* Chunee (low inputs of N from BNF)	*Gluconacetobacter diazotrophicus*	Root	ESI-Q-TOF	Lery et al. (2011)
Solanum lycopersicum	*Bacillus megaterium Enterobacter* sp. C7	Microsomal root	Nano LC-MS/MS	Ibort et al. (2018)
Sorghum bicolor	*Pseudomonas* sp. TLC 6-6.5-4 *Glomus aggregatum Glomus etunicatum Funnelliformis mosseae Rhizophagus irregularis*	Root	LC-MS/MS	Dhawi et al. (2017)
Sorghum bicolor	*Pseudomonas* sp. TLC 6-6.5-4	Root	LC-MS/MS	Dhawi, 2020
Triticum aestivum	*Bacillus subtilis*	Grain	EASY-nLC 1000	Yadav et al. (2022)
Zea mays cv. B73 *Solanum lycopersicum* cv. Boludo	*Azospirillum brasilense* Sp7	Leaf	2D-PAGE MALDI-TOF MALDI-TOF/TOF	Lade et al. (2018) *Table 1
Zea mays	*Azospirillum brasilense*	Root	2-DE MS	Cangahuala-Inocente et al. (2013) *Table 3
Zea mays	*Axospirillum brasilense* FP2	Root	2-DE MALDI-TOF	Faleiro et al. (2015) *Table 3
Zea mays cv. DKB240	*Herbaspirillum seropedicae* SmR1	Root	2-DE MALDI-TOF	Ferrari et al. (2014) *Table 2
Zea mays L. DKB 789	*Herbaspirillum seropedicae*	Root	Nano LTQ-Orbitrap	Nunes et al. (2021) *Table 1

(Cangahuala-Inocente et al., 2013; Faleiro et al., 2015; Lade et al., 2018) and *Herbaspirillum seropedicae* (Ferrari et al., 2014; Nunes et al., 2021) (Table 1). These works highlight the overexpression of ATPase-related proteins (BC-ARC domain protein and F-type H$^+$ transporting ATPase beta chain), which are known to be related to active protein extrusion, and may stimulate biochemical pathways related to nutrient uptake from the soil (Pii et al., 2019). Also, reactive oxygen and nitrogen species-scavenging enzymes were overexpressed after PGPB inoculation. They seem to have an important role in maintaining redox balance of the products of the Calvin-Benson cycle, as proteomics in maize leaf demonstrated an increase in photosynthesis pathway proteins and a reduction of photoinhibition-related proteins (Lade et al., 2018). Also, it has been observed an overexpression of proteins involved in cell dynamics, like tubulin and actin, for chromosome organization during cell division (Nunes et al., 2021). These results are in accordance with results obtained from gene expression in different maize genotypes inoculated with these two PGPB (Zeffa et al., 2019; Schultz et al., 2022). On the other hand, compared to maize, a wider variety of PGPB have been tested to study proteome changes derived from inoculation in rice (*Oryza sativa*) (Table 1). Among the results, it was noteworthy the overexpression of proteins in roots related to methionine recycling (methylthioribose kinase, acireductone dioxygenase 1 and S-adeno-sylmethionine synthetase), because it has been suggested that they are linked to the synthesis of siderophores and also would decrease ethylene synthesis (Alberton et al., 2013). Moreover, up-regulated proteins included cellular proteins such as xyloglucan endotransglycosylase, involved in cell wall formation during cell growth and division, proteins inducing tolerance to oxidative processes (peroxidases, kinases or glutathione S-transferases), or proteins facilitating higher acquisition of nutrients, among others (Chi et al., 2010; Wang et al., 2013; Valdameri et al., 2017; Naher et al., 2018; Bandyopadhyay et al., 2022). Other important crops in the Poaceae family have responded with an increase in plant yield and seed development to inoculation with different PGPB strains: wheat (*Triticum* sp.), sugarcane (*Saccharum* sp.) and sorghum (*Sorghum* sp.) (Table 1). An interesting result was obtained by Lery et al. (2011), who studied the effect of endophytic *Gluconacetobacter diazotrophicus* after 24h of inoculation in two sugarcane genotypes, SP70-1143 (high inputs of N from BNF) and Chunee (low inputs of N from BNF). The high BNF sugarcane genotype showed up-regulation of signaling cascades and enzymes such as ATP citrate lyase, involved in the regulation of lipids biosynthesis, which are important for the root colonization process. On the other hand, low BNF sugarcane genotype promoted protein degradation and protein chromatin remodeling, as defense systems that might limit *G. diazotrophicus* growth. In wheat, Yadav et al. (2022) highlighted the expression of proteins related to histone modulation pathways after PGPB inoculation, which has been also found in maize and will be deeper discussed in section 4.1. Finally, in sorghum, Dhawi et al. (2017, 2020) demonstrated that PGPB inoculation increased the expression of proteins related to carbohydrate synthesis, nutrient uptake and stress tolerance. See Table 1 for details.

2.2. Fabaceae family

Legumes are an important source of protein in human and animal food, and the second most valuable food source after cereals (Maphosa and Jideani, 2017). *Medicago truncatula* shows a well-known symbiotic association with N-fixing bacteria, like *Sinorhizobium meliloti*, through the formation of root nodules (Rose, 2008). Molesini et al. (2014) showed that an early stage of *S. meliloti* infection caused a notable induction of proteins involved in the utilization of photosynthates, C-consuming processes and redox enzymes. Oger et al. (2012) also found induced redox enzymes in the early stage of infection, while amino-acid and carbohydrate metabolism were the major changes one month after infection. Additionally, they found that sulfenylation may be a major post-translational regulatory mechanism during the development and functioning of the symbiotic interaction. This finding highlights the role

of some ROS, such as H_2O_2, as signaling molecules in the establishment and functioning of the nitrogen-fixing legume–*Rhizobium* symbiosis, and may partly explain the altered expression of redox enzymes observed at early stages of infection by several authors. On the other hand, Nguyen et al. (2012) focused on the role of root hair in the symbiosis and studied in soybean (*Glycine max*), because of its larger root size, phosphoproteome differences among root hairs and stripped roots during colonization of *Bradyrhizobium japonicum*. They found increased expression in root hairs of phosphoproteins involved in trafficking, RNA processing, translation and signal transduction, compared to stripped roots. These results suggested unique features of root hair, including a complex network of kinase-substrate and phosphatase-substrate interactions in response to rhizobial inoculation. In pea (*Pisum sativum*), a comparative study with two genotypes with high and low efficiency of interaction with beneficial soil microorganisms (EIBSM) revealed that the high-EIBSM line responded to inoculation by up-regulation of proteins involved in cellular respiration, protein biosynthesis, and down-regulation of late-embryogenesis abundant (LEA) proteins, which led to prolongation of seed filling. In contrast, the low-EIBSM line demonstrated lower levels of proteins related to cell metabolism. See Table 1 for details.

2.3. Other crops and model plants

In Solanaceae family, Kim et al. (2018) hypothesized that *Bacillus* sp. volatiles induced de novo expression of proteins in plants. Certainly, they found that *Bacillus* sp. volatiles acted as elicitors that induced chlorophyll synthesis in shoots of tobacco (*Nicotiana tabacum*) and lettuce (*Lactuca sativa*). For their part, Ibort et al. (2018) found that PGPB inoculation affected tomato (*Solanum lycopersicum*) proteomic profile in a bacterial strain- and plant genotype-dependent manner. For example, it was observed that ethylene perception was essential for correct recognition of *Bacillus megaterium* and growth promotion, while for *Enterobacter* sp. C7 it was independent. Proteome changes associated with plant growth improvement after PGPB inoculation have also been observed in watermelon (Yaoyao et al., 2017) and groundnut (Ankati et al., 2018). In the model plant *Arabidopsis thaliana*, Witzel et al. (2017) suggested that the plant proteasome, which is a known target for plant pathogenic bacteria, was also involved in the establishment of beneficial interactions with *Kosakonia radicincitans*. In the same line, Leandro et al. (2019) demonstrated that *A. thaliana* roots, which were successfully colonized by *Herbaspirillum seropedicae*, showed a remarkable up-regulation of phenylpropanoid biosynthesis-related proteins. The phenylpropanoid pathway is the basis for the production of several compounds that can act on plants both as signaling agents for the establishment of the plant-bacterial association and as inhibitors of bacterial growth, so it may play a major role in the colonization of plant roots by PGPB. Also, these authors demonstrated that, even though *H. seropedicae* was absent from *A. thaliana* shoots one month after inoculation, there was an accumulation of photosynthesis-related proteins in the leaves. See Table 1 for details.

3. Proteomic changes in plants under stress and PGPB inoculation

3.1. Biotic stress

Biotic stress on plants such as caused by fungi, nematodes, insects, virus and bacteria are an important cause of crop devastation (Strange and Scott, 2005; Sergeant and Renaut, 2010). The use of chemicals can cause health problems in humans as well as environmental pollution (Wang et al., 2020). Thus, strategies of biocontrol using PGPB are gaining considerable attention and demand. Despite the studies carried out (Table 2), clear pathways for plant responses to pathogens have not been established. It seems to depend on plant species, plant tissue, pathogen and PGPB species. For example, inoculation of PGPB into

Table 2
Research articles that study the effect of PGPB inoculation in plants under biotic stress. *References selected for further meta-analysis, location of the data within the publication.

Pathogen and exposure time	Plant species	PGPB	Tissue	Technology	Reference
Aphanomyces euteiches (Oomycete) (6h and 24h)	*Medicago truncatula*	*Glomus intraradices Sinorhizobium meliloti*	Root	2-DE DIGE MALDI-TOF	Schenkluhn et al. (2010)
Botrytis cinerea (Fungus) (7d)	*Arabidopsis thaliana*	*Paenibacillus polymyxa* E681	Root Shoot	2-DE ALDI-TOF/TOF	Kwon et al. (2016)
Didymella pinodes (Fungus) (10w)	*Pisum sativum*	*Rhizobium leguminosarum* bv. *viceae* (*Rlv*)	Seed	Nano ESI LC-MS/MS	Sistani et al. (2017) *Table S5
Fusarium oxysporum f. sp. *cucumerinum* (Fungus) (9d)	*Cucumis sativus* L. cv. Jinchun No. 2	*Paenibacillus polymyxa* NSY50	Root	2-DE MALDI-TOF/TOF	Du et al. (2016) *Table 2
Heterodera glycines (Nematode) (3, 7, 14, 21, 28 d)	*Glycine max* cv. Liaodou 15	*Sinorhizobium fredii*	Root	iTRAQ HPLC	Wang et al. (2020)
Phytophthora capsici (Oomycete) (72h and 96h)	*Piper nigrum* L.	*Trichoderma harzianum*	Leaf	LTQ Orbitrap MS	Umadevi and Anandaraj (2019) *Table S3
Potato virus X KJ631111 Maize dwarf mosaic virus AM110558 (2, 9, 16, 21 d)	*Solanum lycopersicum* L. cv. Boludo *Zea mays*	*Azospirillum brasilense* Sp7	Leaf	2D-PAGE MALDI-TOF/TOF	Lade et al. (2019) *Table 1
Meloidogyne incognita (Nematode) (30d)	*Morinda citrifolia*	*Bacillus subtilis*	Root	2-DE MALDITOF-MS/MS	Govindasamy et al. (2016) *Table 3
Xanthomonas translucens (Bacteria) (50d)	*Triticum aestivum*	AMF *Funneliformis mosseae Azospirillum brasilense Paraburkholderia graminis*	Root Leaf	LC-MS/MS	Vannini et al. (2021) *Table S3

maize exposed to maize dwarf mosaic virus increased photosynthesis and chloroplast functions through upregulation of NADP-dependent malic enzyme expression, which has been associated with early response to prevent viral infection in uninfected cells (Lade et al., 2019). On the opposite, PGPB inoculated tomato exposed to potato virus X showed an inhibition of PSII activity and lower photosynthesis rate (Lade et al., 2019). Moreover, Vannini et al. (2021) concluded that wheat proteome response to pathogen *Xanthomonas translucens* strongly depended on the inoculum composition (single vs. multiple microbes, arbuscular mycorrhizal fungus (AMF) or bacteria) and the investigated organs (roots vs. leaf). Also, isoflavonoid biosynthesis up-regulation after PGPB inoculation may function as an antioxidant defense to reduce ROS in *Piper nigrum* under oomycete stress (Umadevi and Anandaraj, 2019), while it may impede nematode replication by influencing the sex ratio and the number of female eggs in *Glycine max* (Wang et al., 2020). Certain molecules have also attracted the attention of several authors. In cucumber, Du et al. (2016) observed that PGPB inoculation under fungus infection increased the expression of enolase (one of the most important enzymes in glycolysis), which may be a key process to generate more energy to cope with stress, and S-adenosylmethionine synthase, involved in the biosynthesis of lignin, glycine betaine and polyamines, which are known to be induced under various

environmental stresses. In *Pisum sativum* seeds, Sistani et al. (2017) observed an overexpression of the triterpenoid soyasapogenol, considered as a defensive compound against pathogens and herbivores, and of late embryogenesis proteins. Also, some authors pointed out that factors of early symbiosis-specific signalling, mainly related to calcium signalling, were clearly overexpressed after AMF and PGPB inoculation under pathogen stress (Schenkluhn et al., 2010). See Table 2 for details.

3.2. Abiotic stress

Abiotic stress (heat, cold, heavy metals, drought, salt, etc.) involves another challenge for agricultural productivity (Hatfield et al., 2011), aggravated in the last decades due to climate change. Salt stress is, up to date, the most studied abiotic stress to detect plant proteome changes after PGPB inoculation (Table 3). High salt concentration is very threatening to plants because it reduces the ability to take up water from the soil, ion imbalance and rise of osmotic pressure (Abideen et al., 2014; Munns and Tester, 2008). Some PGPB properties, like ACC deaminase production, may reduce plant stress under salinity, as demonstrated by Cheng et al. (2012). They found that changes in *Brassica napus* protein relative abundance due to salt exposure were more similar to salt and inoculation with a mutant PGPB with no ACC

Table 3
Research articles that study the effect of PGPB inoculation in plants under abiotic stress. *References selected for further meta-analysis, location of the data within the publication.

Stress and exposure time	Plant species	PGPB	Tissue	Technology	Reference
Drought (10d)	*Capsicum annuum* L.	*Bacillus licheniformis* K11	Root	2D-PAGE MALDI-TOF	Lim and Kim (2013) *Table 2
Cd 5 μM As 10 μM (24d)	*Triticum aestivum* cv. Yangmai 16	*Ralstonia eutropha* Q2-8	Root	iTRAQ nanoLC-MSMS	Wang et al. (2018) *Table S2
Cu natural soil (45d)	*Zea mays*	*Pseudomonas* sp. TLC	Whole plant	2-DE MALDI-TOF	Li et al. (2014) *Table S5
Hypoxia (8d)	*Cucumis sativus* L. cv.	*Pseudomonas putida* UW4	Root	DIGE LTQ- MS/MS	Li et al. (2013) *Table 2
Salt 200 mM (15d)	*Triticum aestivum* L.	*Enterobacter cloacae* SBP-8	Whole plant	MS/MS analysis	Singh et al. (2017) *Table 1
Salt 150 and 300 mM (3w)	*Brassica napus* L. salt-sensitive (Sarigol) and salt-tolerant (Hyola308)	*Pseudomonas fluorescens* FY32	Root	Nano-liquid chromatograph by MS	Banaei-Asl et al. (2015)
Salt 150 and 300 mM (5w)	*Brassica napus* L. salt-sensitive (Sarigol) and salt-tolerant (Hyola308)	*Pseudomonas fluorescens* FY32	Leaf	LC-MS	Banaei-Asl et al. (2016)
Salt 250 mM (4d)	*Brassica napus*	*Pseudomonas putida* UW4	Shoot Root	2-DE MS	Cheng et al. (2012) *Table S2 shoots *Table S3 roots
Osmotic stress (2w)	*Brassica napus*	*Pseudomonas fluorescens* FY32	Leaf	2D-PAGE	Gharelo et al. (2016) *Table 1

deaminase production, than it was to exposure to salt and the wild-type PGPB with ACC deaminase production. On the other hand, Banaei-Asl et al. (2015) found these main groups significantly overexpressed in canola inoculated with *Pseudomonas fluorescens*: secretion-associated RAS super family 1, dynamin-like protein, histones, and proteins related to amino acid metabolism and the tricarboxylic acid cycle. Also, Banaei-Asl et al. (2016) highlighted that the abundance of copper/zinc superoxide dismutase 1 was significantly increased in inoculated plants under severe salt stress. It is known that within cells, SOD constitutes the first line of defense against reactive oxygen species. Prashanth et al. (2008) have reported that halophytic plants like mangroves have a high level of SOD activity. They also showed that transgenic rice plants with a cDNA encoding a cytosolic Cu/Zn SOD from a mangrove plant were more tolerant to salinity and drought stress in comparison to the un-transformed control plants (Prashanth et al., 2008). This example emphasizes the importance of antioxidant systems to face stress. Singh et al. (2017) suggested that bacterial inoculation enhanced the ability of wheat plant to combat salt stress via regulation of transcription factors, promoting antioxidative activity, induction of defense enzymes, lignin biosynthesis, and acceleration of protein synthesis. Begum et al. (2019) showed that PGPB-inoculated switchgrass under cadmium stress conditions notably increased the expression of *HSP70* and *HMA3* genes, especially in the first days after Cd exposure, which prevent the accumulation of nascent proteins as aggregates, and confirm the appropriate folding of proteins while transferring them to their destination. Other authors have revealed that major overexpressed proteins in maize and wheat exposed to heavy metals and inoculated with PGPB were related to cell-wall biosynthesis and defense efficacy (Li et al., 2014; Wang et al., 2018). Other sources of stress have been also considered (Table 3). Lim

and Kim (2013) evaluated the effect of PGPB inoculation in pepper proteome when it was exposed to drought, which clearly showed a 1.5x induction of stress proteins (*Cadhn, VA, sHSP, CaPR-10*), compared to non-inoculated pepper. On the other hand, Li et al. (2013) focused on *Pseudomonas* effects on cucumber under hypoxic conditions, and Gharelo et al. (2016) did on canola under osmotic stress. See Table 3 for details.

4. Proteomic meta-analyses

4.1. Zea mays and PGPB

Maize is the most studied crop in the literature consulted for this review. A protein-protein interaction map for the DEPs identified in *Z. mays* plants after PGPB inoculation was constructed, using the published data from references in Table 1 and STRING database (Fig. 2). The resulting STRING map disclosed one main node and two secondary nodes. Interacting proteins in the first node were mainly related to (1) glucose metabolism processes (B4FTJ6, mitochondrial phosphate carrier protein 3 mitochondrial; P19023, ATP synthase subunit beta, mitochondrial; B4FZUB, malate dehydrogenase; Q08062, malate dehydrogenase, cytoplasmic; P08735 and Q09054, glyceraldehyde-3-phosphate dehydrogenase subunit 1 and 2, cytosolic, respectively; C0PD27, isocitrate dehydrogenase) and (2) photosynthesis metabolism (P16243, NADP-Dependent malic enzyme, chloroplastic; Q7SIC9, transketolase, chloroplastic; B4FQ59, phosphoribulokinase; P05348 and O24574, ribulose bisphosphate carboxylase small chain, chloroplastic; P09315, glyceraldehyde-3-phosphate dehydrogenase A, chloroplastic). These results highlight, on one hand, the role of different isoforms of
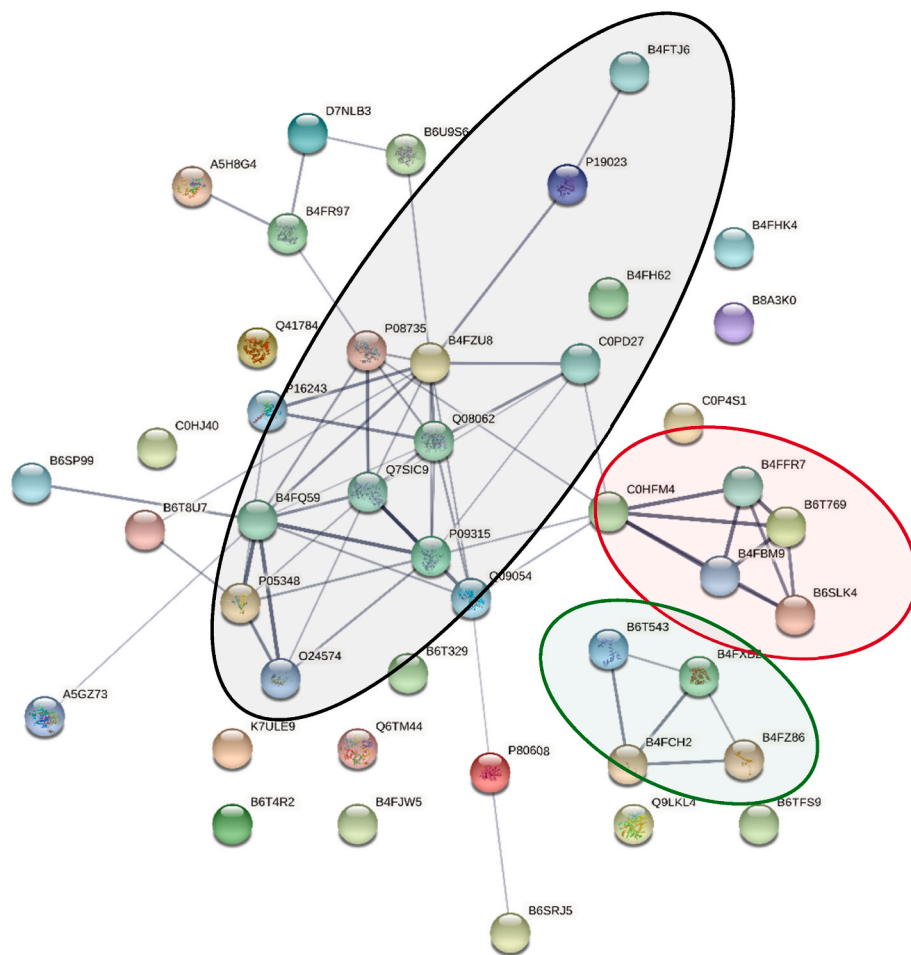

Fig. 2. Protein-protein interaction network from proteins with altered expression after the inoculation of PGPB on *Zea mays* (data from references in Table 1). The nodes (circles) represent proteins and networks edges are functional associations (threshold 0.4, medium confidence interval). The thickness indicates the strength of data support. Three clusters are represented: cluster 1 in black, cluster 2 in red and cluster 3 in green. Proteins that do not belong to clusters include BSU9S6 (APx1-cytosolic ascorbate peroxidase); D7NLB3 (peroxidase 2); A5H8G4 (peroxidase 1); B4FR97 (putative cinnamyl alcohol dehydrogenase 6); Q41784 (tubulin beta-7 chain); C0HJ40 (phenylalanine ammonia-lyase); B6SP99 (photosynthetic NDH subunit of subcomplex B 1 chloroplastic); B6T8U7 (sterile alpha motif (SAM) domain-containing protein); K7ULE9 (extensin-like protein); Q6TM44 (germin-like protein); B6T329 (endonuclease 2); P80608 (cysteine synthase); B6SRJ5 (bifunctional 3-phosphoadenosine 5-phosphosulfate synthetase 2); Q9LKL4 (lipoxygenase); B6TFS9 (14-3-3-like protein A); C0P4S1 (peroxidase); B4FH62 (NAD(P)-binding Rossmann-fold superfamily protein); B8A3K0 (glutathione transferase6); B4FHK4 (natterin-4). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

GAPDH (glyceraldehyde-3-phosphate dehydrogenase), which are known to be involved in metabolic pathways to neutralize ROS. In particular, GAPDH may be translocated to the cell nucleus, where its DNA binding properties increase the transcriptional regulation of genes related to malate valves. Export of excess NAD(P)H through the malate valves will allow for the continued production of ATP trough an increment of electron pressure in the chloroplast (Scheibe, 2004; Holtgrefe et al., 2008; Selinski and Scheibe, 2019), in favor of plant growth (Gururani et al., 2015; Jorrín-Novo et al., 2009). GAPDH is also known to be involved in glycolysis. However, the protein interaction map generated (Fig. 2) shows a direct relationship of GAPDH with the enzyme malate dehydrogenase, involved in gluconeogenesis and Krebs cycle, which provides the plant with reducing power. This suggests a main function of GAPDH in ROS scavenging in response to PGPB inoculation, rather than glycolysis. On the other hand, relevant overexpressed proteins in maize were the isocitrate dehydrogenase and malate dehydrogenase enzymes, involved in the Krebs cycle and the glyoxylate cycle, allowing the use of fatty acids reserves and ATP production (Minárik et al., 2002; Zhang et al., 2010). Also, several proteins related to the Calvin cycle, such as ribulose biphosphate carboxylate (Spreitzer, 2003) or phosphoribulokinase (Miziorko, 2000) were overexpressed in maize as a response to PGPB inoculation. In the second node, proteins were associated to (3) translation activity (C0HFM4, B4FFR7, B6T769 and B4FBM9, 60 ribosomal protein subunit L13a-1, L24-2, L7A and L3-1, respectively; B6SLK4, elongation factor 1-beta). Overexpression of ribosomal proteins and elongation factors suggests that PGPB inoculation leads to an increment of protein synthesis in maize, either related to plant structure and growth, or to metabolism and signaling (Fu et al., 2012). The third node was related to (4) nucleotide metabolism (B6T543, B4FXB2 and B4FCH2, histone subunit H2A; B4FZ86, histone subunit H3). In this line, Yadav et al. (2022) also proposed that differential expression of histone proteins after PGPB inoculation might contribute towards improved grain and biofortification in wheat. Multiple epigenetic mechanisms, including histone modification, DNA methylation, and small RNA molecules, act interactively and redundantly to regulate gene expression in plants (Lei and Berger, 2020), which could be exploited to improve crop production (Corbin, 2020). Interestingly, Lv et al. (2022) demonstrated that the model plant *A. thaliana* with dysfunctional histone demethylase IBM1 substantially reshaped the root microbiota and showed a stronger immune response to pathogens. This idea has been also supported by Knaack et al. (2022), who showed that changes in chromatin accessibility altered the early stages of the dynamic process of symbiosis in *M. truncatula*. Our results were also confirmed after an enrichment analysis with g:Profiler (Fig. 3), which highlighted terms related to photosynthetic carbon fixation, carbon metabolism, and glyoxylate and dicarboxylate metabolism ($p <$ 0.05, Fig. 3). Altogether, these results showed that inoculation of PGPB alters processes in *Z. mays* at the proteome level related to ROS reduction, energy metabolism and epigenetic regulation of transcription,

which may explain the influence of PGPB in increasing maize growth and yield (Lipková et al., 2021; Amezquita Aviles et al., 2022).

4.2. PGPB effect in plants under biotic stress

Plants under biotic stress inoculated with PGPB showed significant differences in the proteome and overrepresented proteins were analyzed (Table 2). An integrative enrichment analysis was performed with DEPs after plant-PGPB-pathogen interaction (Fig. 4). The most important GO term was "glycolytic process" which included, among others, glyceraldehyde-3-phosphate dehydrogenase, fructose-biphosphate aldolase or triosephosphate isomerase enzymes. Together with enzymes included in the term "tricarboxylic acid cycle", they are involved in energy generation, needed to cope with biotic stresses (Du et al., 2016; Kwon et al., 2016). Also, they are linked to the activation of carbohydrate metabolism, allowing the production of new tissues and modulation of cell division (Eveland and Jackson, 2012). Other important GO term that arose in our analysis were "protein folding", "response to cadmium ion" and "proteosomal ubiquitin-independent protein catabolic process" (Fig. 4). Increased demand for protein folding may be related to heat shock proteins (HSPs). HSPs are molecular chaperones whose most important role is the cellular trafficking, assembly and disassembly, folding and misfolding of damaged proteins and proteasome targeting. This means that they play an important role during plant development to protect cells in response to environmental pathogens (Huang and Xu, 2008; Waters, 2013). The proteasome protein degradation systems of eukaryotic cells not only remove misfolded and defective proteins, but also control various cellular pathways through the selective elimination of short-lived regulatory proteins, and it has been extensively studied as the target of pathogenic proteins (Banfield, 2015). Actually, it has been demonstrated that proteasome activity is strongly induced in defense priming and SAR (systemic acquired resistance) in *A. thaliana* (Üstün et al., 2016). Finally, the term "response to cadmium ion" could be explained because molecular responses to heavy metal excess in sensitive plants can resemble elicitor-induced defense reactions (Morkunas et al., 2018). An example of the cross-talk between heavy metal stress and biotic stress responses is the study by Llugany et al. (2013), who showed that Cd accumulation in *Thymus praecox* induced salicylic acid production, which was also induced in response to the presence of the plant pathogen *Erysiphe cruciferarum*. Jasmonic acid is one of the typical phytohormones induced as a result of cell damage by pathogens, but it has been found that Cu and Cd also induce this phytohormone expression in both *A. thaliana* and *Phaseolus coccineus* (Maksymiec et al., 2005). On the other hand, plants may use the accumulation of metals like Ni, Cd or Zn as a mechanism of defense against herbivory (Morkunas et al., 2018). Hence, it could also explain the induction of Cd response in plants against an herbivore pathogen. A third hypothesis may be in line with several authors studies that demonstrate that plant protection against pathogens may be facilitated by the
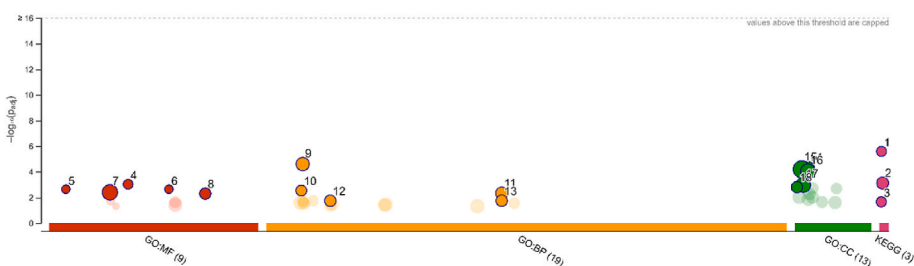

Fig. 3. Functional enrichment analysis using g:GOSt multiquery Manhattan (g:Profiler) for the differentially expressed proteins obtained after inoculation with PGPB in *Zea mays* (data from references in Table 1). X-axis groups the data by the gene ontology terms (GO molecular function, GO:MF; GO cellular component, GO:CC; GO biological process, GO:BP) and the KEGG Reactome (KEGG). The y-axis shows the adjusted enrichment p-values in negative log10 scale. Each circle represents a GO term, and circle sizes represent the corresponding term size. Numbers from 1 to 18 stand for the terms with the most significant p-value. Unnumbered circles are the unselected terms, with a less significant p-value. 1 carbon fixation in photosynthetic organism; 2 carbon metabolism; 3 glyoxylate and dicarboxylate metabolism; 4 protein domain specific binding; 5 and 6 glyceraldehyde-3-phosphate dehydrogenase; 7 oxidoreductase activity; 8 NAD binding; 9 generation of precursor metabolites and energy; 10 glucose metabolic process; 11 ATP metabolic process; 12 purine nucleoside diphosphate metabolic process; 13 ADP metabolic process; 14 chloroplast; 15 cytoplasm; 16 plastid; 17 cytosol; 18 nucleosome.
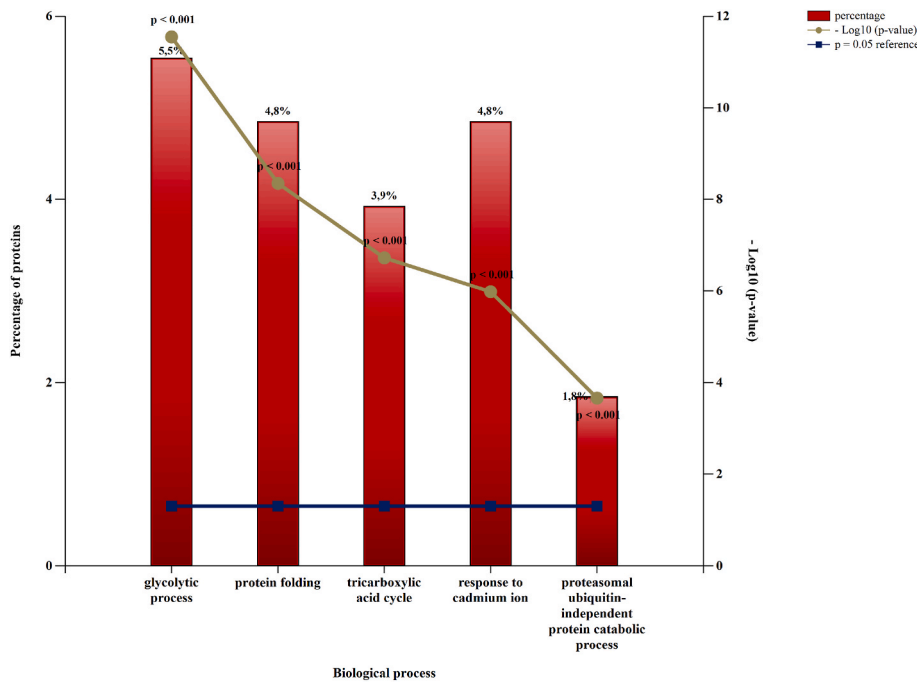
Fig. 4. Functional enrichment analysis using FunRich (http://www.funrich.org) for biological processes of proteins under biotic stress in plants inoculated with PGPB. Enrichment was performed using the DEPs published in references from Table 2. The individual GO terms were set according to the *p*-value (green), the percentage of proteins for each GO term (grey) and the reference (*p*= 0.05, blue). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Fig. 5. Functional enrichment analysis using FunRich (http://www.funrich.org) for biological processes of proteins under abiotic stress in plants inoculated with PGPB. Enrichment was performed using the DEPs published in references from Table 3. The individual GO terms were set according to the *p*-value (green), the percentage of proteins for each GO term (grey) ant the reference (*p*= 0.05, blue). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
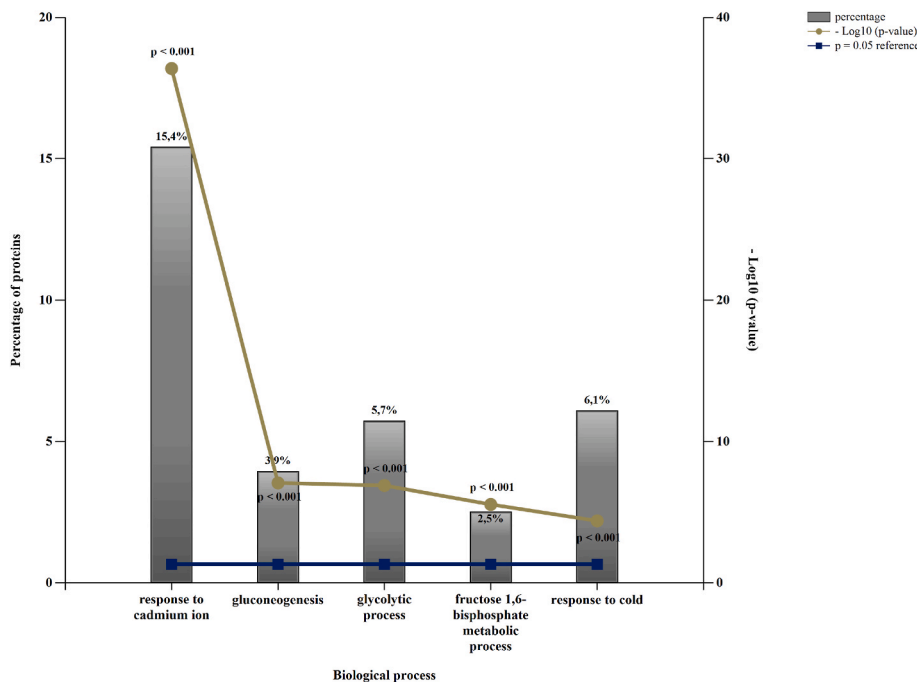
exposure to previous abiotic stress, including the case of cadmium- and fungal pathogen-treated plants (reviewed in Romero-Puertas et al., 2021).

4.3. PGPB effect in plants under abiotic stress

Functional enrichment analysis was carried out with DEPs (Table 3) under different abiotic stresses (Fig. 5). The main GO term was "response to cadmium ion", even though only one of the studies included in the analysis applied this pollutant (Table 3). Cd is a non-essential, extremely polluting heavy metal for plants (Xu et al., 2015), and has a long half-life in the environment (Verma et al., 2017). This

would make necessary a plant response to Cd presence in soil, even at very low concentrations. Interestingly, another important GO term was related to plant response to cold (Fig. 5), despite no studies have been carried under cold stress in our meta-analysis (Table 3). It should be noted that DEPs found for this GO term, like G-phosphogluconate de-hydrogenase, sucrose synthase or annexin D1, are involved in other abiotic stresses such as osmotic stress, heat, drought or hypoxia (Uni-ProtKB 2021a; 2021b; 2021c). These results support the idea that a significant overlap between pathways, as shared and general stress-responsive genes, appears to be commonly involved in responses to multiple stresses (Morkunas et al., 2018). The following three GO terms were related to metabolic pathways, "glycolytic process",

"gluconeogenesis" and "fructose 1,6-bisphosphate metabolic process". Glycolysis is the catabolic process of converting glucose into energy, while gluconeogenesis is the formation of glucose from non-glucolytic precursors. Both processes share the metabolite fructose 1,6-bisphosphate. Thus, these glucose metabolism processes seem to be essential to cope with abiotic stress, as it has been shown that an increase in supplemented energy when plants are facing abiotic stress is required and rapidly achieved through changes in carbohydrate metabolism (Bolton, 2009; Li et al., 2013).

5. Perspectives of the field

After reviewing literature, we found that there are still quite a few gaps that need to be addressed to deepen into the knowledge of plant proteome response to PGPB inoculation. For example, more studies should be developed in the whole plant. Despite PGPB may colonize the rhizosphere, it has been shown that they may have an impact on photosynthetic machinery. Some PGPB are also able to colonize inner plant tissues and have direct effects in various parts of the plant. In this line, it would be also interesting to have more data on proteomic plant response to endophytes, as they appear to activate protein-kinase cascades and plant seems to be able to regulate colonization based on their needs. A broader range of studies under biotic and abiotic stress would be desirable too. For example, current climate change scenario is bringing extreme short hot and cold events, soil salinization, droughts, etc. And it would be important to clearly establish intensity, duration, and frequency of stress, plant species, and other environmental conditions, because effects may vary depending on these factors (Omae and Tsuda, 2022).

Also, it would be useful to design studies with different plant species of the same genus, or even different plant genotypes of the same species, to unravel whether the genetic constitution of the plant is a decisive factor in their response to PGPB. Indeed, it has been demonstrated that the same PGPB strain may cause different effects in different crops. This is important to design biofertilizers, as not all PGPB would be optimal for all plants. Of great importance would also be the design of experiments where plants (or PGPB) are genetically modified with specific key mutations, to reveal the importance of targeted pathways. This approach may solve to a certain extent the problem of establishing direct cause and effect in PGPB effect on stress plant tolerance. If bacteria induce certain proteins, how can one tell whether the changes are a direct response to the bacteria (e.g. oxidative stress-related proteins could be in this category) or if changes in the same functional group of proteins are protecting from abiotic stress. All these studies would result in a higher volume of plant proteome data and using meta-analysis studies would help to go further into the search for reliable and predictive biomarkers, which should be strongly validated across species. They may be used to elucidate the most optimal PGPB inoculants for agriculture or phytoremediation, for example. Finally, there may be a need to extend the use of modern techniques among proteomic approaches. 60% of the consulted bibliography used gel-dependent techniques, mainly 2-DE. Although gel-free methods are trying to outpace gel-based methods, this tool is still being used in proteome studies. It is a mature approach to screen the protein expression at the large scale, it is cheaper, and it allows to identify small changes in the volume of proteoforms and isoforms, or evaluate post-translational modifications. However, they have known limitations such as the use of narrow pH and M_r range gels (Rodríguez-Vázquez et al., 2022). From 2015, modern gel-free techniques like iTRAQ HPLC, LC-MS/MS or LTQ Orbitrap MS have gained more popularity because of their accuracy and reliability. Advances in mass spectrometry-based proteomics (bottom-up and top-down methodologies) have provided in-depth information on the characterization and quantification of the protein components of biological systems (Oliveira et al., 2014; Liu et al., 2019; Timp and Timp, 2020). However, these techniques present several issues, such as quantification of proteins at low abundance level, high dynamic range or reduction of the number of missing values, among others (Chen et al., 2020; Lee et al., 2020; Rodríguez-Vázquez et al., 2022). Hence, the combination of techniques, 2-DE-MS and gel-free methods may be a robust tool to quantify and characterize the highest number of proteins. Altogether, proteome analysis of plant response to PGPB is a field in which a great deal remains to be done in order to draw robust conclusions.

6. Conclusions

The study of the proteome may be a useful technology to unravel key mechanisms in plants responses to PGPB inoculation. In this review, we covered a selective list of related studies in the last decade. We observed that effects of PGPB in plant growth were highly related to over-expression of ROS-reduction proteins, promotion of the photosynthetic machinery and its associated pathways (like Calvin cycle), direct effects on plant transcription (histones and chromatin organization), cell architecture, energy metabolism (tricarboxylic acid and glyoxylate cycle) and protein extrusion (directly related to nutrient uptake). A meta-analysis of *Z. mays* growth under PGPB inoculation showed three main nodes related to glucose metabolism, photosynthesis, translational activity (ribosomal proteins) and nucleotide metabolism (histones), which may explain plant growth and crop productivity observed in inoculated *Z. mays*. Also, authors have demonstrated that PGPB inoculation when plants are exposed to pathogens (fungi, nematodes, viruses and bacteria) and abiotic stress (heavy metals, salt, osmotic or hypoxic) induced the expression of ROS-reduction related proteins, HSP for protein processing and proteasomes. Integrative functional enrichment analyses highlighted processes related to response to cadmium or cold, suggesting an overlap between pathways and defense genes as general and shared stress-responsive genes, which appears to be commonly involved in responses to multiple biotic and abiotic stresses. However, proteome analysis of plant response to PGPB is a field in which a great deal remains to be done in order to draw robust conclusions.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

No data was used for the research described in the article.

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