Purple non-sulphur bacteria (PNSB) are phototrophic microorganisms, which increasingly gain attention in plant production due to their ability to produce and accumulate high-value compounds that are beneficial for plant growth. Remarkable features of PNSB include the accumulation of polyphosphate, the production of pigments and vitamins and the production of plant growth-promoting substances (PGPSs). Scattered case studies on the application of PNSB for plant cultivation have been reported for decades, yet a comprehensive overview is lacking. This review highlights the potential of using PNSB in plant production, with emphasis on three key performance indicators (KPIs): fertilization, resistance to stress (biotic and abiotic) and environmental benefits. PNSB have the potential to enhance plant growth performance, increase the yield and quality of edible plant biomass, boost the resistance to environmental stresses, bioremediate heavy metals and mitigate greenhouse gas emissions. Here, the mechanisms responsible for these attributes are discussed. A distinction is made between the use of living and dead PNSB cells, where critical interpretation of existing literature revealed the better performance of living cells. Finally, this review presents research gaps that remain yet to be elucidated and proposes a roadmap for future research and implementation paving the way for a more sustainable crop production.

Introduction

Agriculture is strongly challenged in the 21st century as a result of the growing world population (FAO, 2009) and the increasing demand for natural resources (Giljum et al., 2015). The rising need for agricultural products results not only in an increase in arable land demand and thus the deforestation of uniquely biodiverse ecosystems (such as Amazon in Brazil) but also an increased consumption of fertilizers (FAO, 2015). In order to sustainably meet the future global food demand, multiple mitigation measures are needed to decrease the impact on the environment (Pikaar et al., 2018). Adopting improved fertilization strategies (i.e. better-quality fertilizers), reducing the stress to plants and environment (e.g. heavy metals) and reducing the environmental impact of crop production (e.g. greenhouse gas emissions) will lead on to meeting this goal. A conventional approach to enhance crop yield at the greatest extent is by using synthetic fertilizers, which contain all necessary nutrients in their inorganic form. When applied to the plant, these inorganic nutrients are readily accessible and thus the remaining quantity either accumulates in the soil, is lost as run-off into the surface water or leaches into the groundwater (Steiner et al., 2007). Avoiding depletion of soil organic carbon (SOC) and too rapid availability, one
can opt for organic fertilizers (Diacono and Montemurro, 2011) typically produced from animal, or plant-based materials, such as blood meal, feather meal and soybean meal. The decomposition and the rate of nutrient release are based on the activity of soil microorganisms, typically rendering a slower release pattern. Nevertheless, it has been documented that the use of conventional organic fertilizers and soil amendments can lead to the accumulation of heavy metals (HMs), such as copper (Cu), zinc (Zn), lead (Pb) and cadmium (Cd) (Diacono and Montemurro, 2011). Apart from stress on the plants, HMs cause detrimental stress on the environment and can potentially be harmful to human health; consequently, novel mitigation strategies should be adopted. Finally, reducing the environmental impact of agriculture would additionally require the reduction of direct (field) and indirect (fertilizer production) emissions, strongly linked to the fertilizer usage efficiency and crop yield.

Microbial biomass presence and/or activity at the soil and rhizosphere can offer advantages at the level of organic matter deposition, stress mitigation and environmental impact. An advantage of using microbes compared to conventional organic fertilizers concerns their production: they can be produced on compact system using recovered resources (Verstraete et al., 2016; Pikaar et al., 2018). Microorganisms typically have a high nitrogen content, which can be slowly released and fertilize the soil (Pikaar et al., 2018). Phototrophic microorganisms have the added value of containing substances that promote plant growth, such as phytohormones and vitamins (Kobayashi and Kobayashi, 1995; Rana et al., 2016). Five groups of bacteria are able to carry out photosynthesis: green sulphur bacteria (GSB), green non-sulphur bacteria (GNSB), purple sulphur bacteria (PSB), purple non-sulphur bacteria (PNSB) and cyanobacteria. The beneficial effect of using cyanobacteria in plant production has been demonstrated (Coppens et al., 2016), while no data were found for the use of GSB or GNSB. In contrast, despite the considerable number of studies on the application of PNSB for plant cultivation, a comprehensive and systematic overview is lacking.

Purple non-sulphur bacteria, classified as α- and β-proteobacteria, are characterized by high diversity in morphological and physiological characteristics. Their metabolism is unique, as they are able to grow in a variety of cultivation modes (Imhoff, 2006): they can derive their energy from light (phototrophic) under anaerobic conditions as well as from chemical molecules (chemotrophic) under aerobic conditions, both with their carbon source either being derived from CO2 (autotrophic) or from organic carbon (heterotrophic). The heterotrophic growth mode results in higher growth rates (1.6–13 day⁻¹) (Madigan and Gest, 1979; Rey et al., 2006) compared to autotrophic (1.0–8.0 day⁻¹) (Madigan and Gest, 1979; Colbeau et al., 1980), and infra-red light can be used as a selectivity tool in the phototrophic growth mode (Hulsen et al., 2014), avoiding the growth of algae. This versatility in metabolic functions as well as their tolerance to extreme conditions allows them to grow on a variety of habitats such as (Imhoff, 2006): (i) stagnant water bodies (lakes, coastal lagoons, wastewater ponds, eutrophic ponds) (Kantha et al., 2015); (ii) sediments; (iii) moist soils (Kantachote et al., 2016; Sakpirom et al., 2017); (iv) paddy fields (Kantachote et al., 2016; Sakpirom et al., 2017); (v) marine environments; (vi) hypersaline environments (Kantachote et al., 2016; DasSarma and DasSarma, 2017); (vii) thermal springs and (viii) cold polar habitats. Thus, they are widely distributed in a variety of environments, with the most commonly encountered genera being Rhodobacter and Rhodopseudomonas (Holguin et al., 2001).

Furthermore, PNSB are capable of executing a variety of useful functions such as: (i) nitrogen (N₂) fixation (Wong et al., 2014; Kantcha et al., 2015); (ii) phosphate solubilization (Koh and Song, 2007; Lee et al., 2008; Rana et al., 2016); (iii) heavy metal remediation (Batool et al., 2017); (iv) methane (CH₄) emission mitigation (Kantha et al., 2015; Sakpirom et al., 2017) and (v) CO₂ sequestration (Tabita, 1995). These traits make PNSB an attractive candidate for multiple applications like use in plant production or as bioremediation agents. In addition, PNSB are known to produce and/or accumulate a diverse range of metabolic products such as: (i) biohydrogen through photofermentative production (Colbeau et al., 1980; Koku et al., 2002) or during N₂ fixation (Basak and Das, 2007); (ii) polyhydroxalkanoates (PHA, including polyhydroxybutyrate PHB) (Melnicki et al., 2009; Wu et al., 2012); (iii) polyphosphate (Lai et al., 2017); (iv) plant growth-promoting substances (PGPSs) (Nunkaew et al., 2014a; Rana et al., 2016); (v) carotenoid pigments (e.g. spirilloxanthin, rhodopin, okeneone and rhodopinal) (Kobayashi and Kobayashi, 1995; Imhoff, 2006); (vi) siderophores (Sasaki et al., 2005); (vii) high amounts of protein (Kobayashi and Kobayashi, 1995); (viii) considerable amounts of essential vitamins (e.g. vitamins B₁₂, B₆, B₁₂, C, E, D and folic acid) (Kobayashi and Kobayashi, 1995) and (ix) compounds with health stimulating benefits, for instance reducing LDL-cholesterol (Ruitang Deng, 2009) or contributing to luminous vibriosis survival (Laranja et al., 2014).

This review presents a critical overview of the past and current research regarding the use of PNSB in the context of plant production. First, the key performance indicators (KPIs) of PNSB regarding plant cultivation and their underlying mechanisms are discussed (section Key performance indicators of PNSB for plant production). Next, section Evaluating use of PNSB as fertilizer, bio-
stimulant and bio-fortifier evaluates and highlights the impact of the PNSB products in plant production, while making a comparison between the use of existing PNSB products (living and dead cells). Section Rice production: harnessing PNSB functionality to its fullest proposes the agricultural application that harnesses the attributes of PNSB at the fullest extent. Finally, this review reveals existing research gaps (section Research gaps and proposed roadmap of PNSB application in plant production) and suggests a roadmap for future research whilst discussing economic aspects.

Key performance indicators of PNSB for plant production

Critical analysis of the existing literature revealed three KPIs of each PNSB product, based on different effects on plants (Fig. 1). These include direct and indirect fertilization as well as biostimulation and biofortification. Furthermore, three categories of PNSB products are distinguished, namely living cells, dead cells and cell-derived products (i.e. PGPS). The KPIs are interwoven with the type of the product as follows: direct fertilization mainly caused by cell decay, therefore, both dead and living cells contribute to this function; indirect fertilization is the result of using living cells where the conversion of nutrients (N and P) into plant-available forms takes place; and biofortification and biostimulation are the result of the supplied PGPS, where increased resistance to biotic and abiotic stresses is observed. Details about the application method of each PNSB product type can be found in the Appendix S1 (section 1).

As shown in Fig. 2, the existing literature mainly focuses on the use of living PNSB cells and less on the use of dead cells, while information regarding the use of extracted PGPS is scarce. Therefore, the latter will not be discussed in the present review (results of all reviewed studies can be found in Appendix S1 in section 2). Furthermore, as can be seen in Fig. 2, there are three distinct effects of the use of PNSB products in agriculture, namely increased productivity, reduced losses due to biotic and abiotic stresses and environmental impacts. The former two concern the useful output of the use of the PNSB products and should be maximized, while the latter aims at the minimization of the harmful environmental output of agriculture. The following section provides an overview of these KPIs of PNSB in agricultural applications.

Fertilization function

The fertilization function can be divided into two categories: direct and indirect. The former concerns the use of living and dead cells, while the latter is the result of the use of living PNSB cells.

Direct fertilization. The use of dead PNSB biomass provides the benefit of a direct process where the only parameter to be considered is the nitrogen/phosphorus/potassium (N/P/K) content, determining the amount of biomass that should be dosed according to the plant's nutrient requirements. This type of microbial fertilizer presents a slow-release pattern, as the dead microbial biomass is decomposed by the autochthonous soil microorganisms, and the gradually released nutrients are utilized by the plant (Coppens et al., 2016). Thereby, synchronous nutrient release and plant nutrient uptake provides superior efficiency (Geng et al., 2015). At the same time, such organic fertilizer with PNSB will potentially improve soil structure and stimulate soil microbial activity (Clark et al., 1998), resulting in sustainable land usage and a diverse ecosystem (Mader et al., 2002). The same effect is presented when living PNSB cells are used, as the decaying cells can provide N/P/K to the plants. While no literature reports on the full nutrient content of PNSB were found, the N/P/K was measured as 8.5/2.4/0.5% in dry weight (DW) (own data for dried biomass of Rhodobacter sp.). Key features include the notably high phosphorus content as compared to microalgae (N/P/K of 8.1/1.3/1.4% DW).

Fig. 1. Illustration of the key performance indicators of purple non-sulphur bacteria (PNSB) in plant production, depending on the type of product used (dead cells, living cells or extracted plant growth-promoting substance). The functions supported by each PNSB type are the ones contained in the respective boundaries.
Dead cells

PGPS

et al

available nitrogen form (Franche et al 1978). Nevertheless, some PNSB species in the genera

nitrogenase, which is present in all N₂-fixing bacteria. N₂-fixing microorganisms transform atmospheric molecular nitrogen (N₂), which is biologically unavailable to plants, into ammonia/ammonium (NH₃/NH₄⁺), a plant-available nitrogen form (Franche et al. 2009; Olivares et al., 2013). The enzyme that catalyses N₂ fixation is nitrogenase, which is present in all N₂-fixing bacteria. There are three types of nitrogenase isozymes, namely molybdenum-iron (Mo-Fe), vanadium-iron (V-Fe) and iron-iron (Fe-Fe) nitrogenases (Sakpirom et al., 2017). According to Sakpirom et al. (2017), among 235 tested PNSB isolates, Rhodopseudomonas palustris TN110 possessed all three different nitrogenase genes and presented the best N₂ fixation ability. N₂ fixation by PNSB is most efficient under strict anaerobic conditions, as oxygen inhibits this process (Masepohl and Kranz, 1978). Nevertheless, some PNSB species in the genera Rhodopseudomonas and Rhodobacter are very tolerant to oxygen and fix nitrogen even under micro-aerobic conditions (Larimer et al., 2004; Hoffmann et al., 2014). This largely broadens the application possibilities of PNSB in plant production, for example in paddy fields, which are not strictly anaerobic.

Indirect fertilization. An additional key functionality of living PNSB cells (compared to dead cells) is the enhanced nutrient availability (Fig. 2), due to microbial activities such as nitrogen fixation and chelation of phosphorus.

Biological nitrogen fixation.—Many microorganisms can utilize atmospheric nitrogen to support their growth. The microbes associated with nitrogen fixation can roughly be categorized into two groups, symbiotic and free-living, with PNSB belonging to the latter group (Herridge et al., 2008). N₂-fixing microorganisms transform atmospheric nitrogen (N₂) into plants, into ammonia/ammonium (NH₃/NH₄⁺), a plant-available nitrogen form (Franche et al., 2009; Olivares et al., 2013). The enzyme that catalyses N₂ fixation is nitrogenase, which is present in all N₂-fixing bacteria. There are three types of nitrogenase isozymes, namely molybdenum-iron (Mo-Fe), vanadium-iron (V-Fe) and iron-iron (Fe-Fe) nitrogenases (Sakpirom et al., 2017). According to Sakpirom et al. (2017), among 235 tested PNSB isolates, Rhodopseudomonas palustris TN110 possessed all three different nitrogenase genes and presented the best N₂ fixation ability. N₂ fixation by PNSB is most efficient under strict anaerobic conditions, as oxygen inhibits this process (Masepohl and Kranz, 1978). Nevertheless, some PNSB species in the genera Rhodopseudomonas and Rhodobacter are very tolerant to oxygen and fix nitrogen even under micro-aerobic conditions (Larimer et al., 2004; Hoffmann et al., 2014). This largely broadens the application possibilities of PNSB in plant production, for example in paddy fields, which are not strictly anaerobic.

The N₂ fixation of heterotrophic bacteria can be photo-dependent or photo-independent (Pfenning and Truper, 1989), and the N₂ fixation ability of PNSB is higher under illumination than under dark conditions (Nunkaew et al., 2014a; Wong et al., 2014). Therefore, PNSB supply nitrogen more efficiently to the illuminated habitat zones, where nitrogenase activity is not limited by their chemoheterotrophic metabolism as is the case under dark conditions (Harada et al., 2005).

Purple non-sulphur bacteria are distributed in various habitats exposed to sunlight and atmospheric N₂ (including paddy fields), and their contribution to rendering nitrogen bioavailable to plants has been demonstrated. For instance, when inoculated in a hydroponic nutrient solution lacking a nitrogen source, ammonia was detected in the medium (< 10 μM) (Maudinas et al., 1981). Therefore, PNSB being one of the dominant species in paddy fields (Elbadry et al., 1999a,b) significantly contribute to nitrogen fertility as rice yields can reach values up to 2.0–3.5 ton of nitrogen per hectare using only nitrogen originating from soil organic matter and biological N₂ fixation (Kundu and Ladha, 1997). Gamal-Eldin and Elbanna (2011) demonstrated an improved usage efficiency of a synthetic nitrogen fertilizer when a mixture of synthetic fertilizer and R. capsulatus was used. At the same time, the use of the mixture resulted in higher
grain yield than that obtained from either product (synthetic fertilizer or *R. capsulatus*) when used separately. Biological N2 fixation, apart from supplying essential nutrients to plants, also enhances their nitrogen uptake efficiency (Adesemoye et al., 2008; Wong et al., 2014). For instance, this was validated during rice cultivation in a hydroponic solution inoculated with *R. capsulatus* DSM 155. Specifically, in nitrogen-deficit medium, the nitrogen content of the root increased by 50–65%, illustrating the N2-fixing abilities of PNSB. On the other hand, when the hydroponic solution contained nitrogen, the effect was less substantial (1.3–14% increase) (Elbadry and Elbanna, 1999). Similarly, the nitrogen content of rice straw rose by 9.2% through seed coating with *R. capsulatus* DSM 155 (Gamal-Eldin and Elbanna, 2011). The N2-fixing abilities of *R. capsulatus* DSM 155 were also observed when this PNSB strain was inoculated on the roots of rice seedlings, triggering an increase of rice grain nitrogen content by 7.1% (Elbadry et al., 1999a,b). In this case, the rice straw yield improved by 8.6–24%, with a diminishing effect as the nitrogen content in the fertilizer increased (0–95 kg N ha\(^{-1}\)). Furthermore, the provision of half the amount of recommended synthetic nitrogen fertilizer in combination with PNSB-inoculated seeds resulted in rice grain yields statistically comparable to the addition of the full amount of synthetic nitrogen fertilizer (Gamal-Eldin and Elbanna, 2011). PNSB inoculation could thus result in considerable cost savings due to the reduction of chemical fertilizer use, depending on the required dosage and related production cost for PNSB biomass. Finally, a roughly doubled agronomic nitrogen use efficiency (dry yield per unit of nitrogen supplied) was demonstrated by inoculation with *R. palustris* on pak choi (Wong et al., 2014). Similarly, inoculation with *R. palustris* PS3 increased the nitrogen efficiency of lettuce (17%) and pak choi (22–44%) (Hsu et al., 2015). Hence, the supply of PNSB can enhance the nitrogen efficiency, potentially contributing to a more sustainable agriculture.

Phosphate solubilization.—There is evidence that only about 10–20% of the phosphorus applied to agricultural soils is taken up by plants (Schoumans et al., 2015). The remaining inorganic phosphorus is adsorbed to clay minerals, as well as iron (Fe\(^{3+}\)) and aluminum (Al\(^{3+}\)) ions (at pH < 5.5) or forms crystalline structures with calcium (Ca\(^{2+}\)) and magnesium (Mg\(^{2+}\)) ions (at pH > 6) (Schoumans et al., 2015). As a result, many agricultural soils are phosphorus-saturated, creating a phosphorus reservoir (Tóth et al., 2014) that shall be exploited. An approach to valorize this reservoir is the application of phosphate-solubilizing microorganisms (Qian et al., 2010). These microorganisms, typically including *Pseudomonas* sp. and *Bacillus* sp. (Sharma et al., 2013), can render soil-bonded phosphorus soluble and available to the plants, lowering the need for synthetic fertilizers. Alori et al. (2017) suggest that the principal mechanism of phosphate solubilization is the production of mineral dissolving compounds such as organic acids, siderophores, protons (H\(^{+}\)), hydroxyl ions (OH\(^{-}\)) and carbon dioxide (CO\(_2\)); which result in pH changes or are active as chelating agents. The ability of PNSB for inorganic phosphate solubilization from soil has been demonstrated by several studies, yet the underlying mechanisms remain unknown (Koh and Song, 2007; Lee et al., 2008; Rana et al., 2016). Taking into account that the availability of phosphorus can be the limiting step in plant nutrient uptake (Rodríguez and Fraga, 1999), PNSB with phosphate-solubilizing properties can significantly contribute to an improved plant growth.

*Rhodopseudomonas* sp. produced 64–95 mg l\(^{-1}\) soluble phosphate (21–31 mgP l\(^{-1}\)) from a medium containing 200–800 mg l\(^{-1}\) Ca\(_3\)(PO\(_4\))\(_2\) (40–160 mgP l\(^{-1}\)) (Koh and Song, 2007). Koh and Song (2007) reported that the solubilization was low possibly due to the relatively high pH (6.5–7.0) of the medium. Specifically, it has been reported that the optimal pH value for biological phosphate solubilization is around 4.0 (Whitelaw et al., 1999); nevertheless, this pH value is not probable to occur in natural plant growing environments (Koh and Song, 2007). Rana et al. (2016) tested the solubilization of Ca\(_3\)(PO\(_4\))\(_2\), Mg\(_3\)(PO\(_4\))\(_2\) and Zn\(_3\)(PO\(_4\))\(_2\) by PNSB: *Rhodospirillum rubrum* was able to solubilize these inorganic phosphorus forms with an efficiency of 100%, 100% and 51% respectively. When a mixture of fly-ash (P-rich mineral residue of coal combustion) and *R. rubrum* was tested as a fertilizer mixture, the presence of resp. 20, 10 and 4.0 mg l\(^{-1}\) of Ca\(^{2+}\), Mg\(^{2+}\) and Zn\(^{2+}\) was observed, indicating the solubilization of phosphate without the release of toxic metal ions (Mn, V, Ni, Cd, As, Hg, B, Cu, Co, Cd, Se, Zn, Mo or Pb) (Rana et al., 2016).

**Resistance to stresses**

**Production of plant growth-promoting substances.** Plant growth-promoting substances are extracellular phytohormones that can be produced by PNSB. They contribute to the coordination of diverse physiological processes in plants including growth and development, as well as in the formation of flowers, leaves, roots, stems, pigments and the development and ripening of fruit (Voß et al., 2014). Additionally, they contribute to an increased plant resistance to environmental factors, an induced or suppressed expression of genes and the synthesis of essential compounds such as enzymes, pigments and metabolites (Tsavkelova et al., 2006). PGPSs are produced in each cell of the plant and regulate cellular processes in each cell locally as well as...
in other functional parts of the plant when diffused. Additionally, they are responsible for the differentiation of the cells in each part of the plant (Tsavkelova et al., 2006). The pivotal role of PGPS on plant growth has been well established, and lack of these hormones can cause limited and/or abnormal growth (Fahad et al., 2015).

The most studied PNSB strains (Tables 1 and 2) in regard to their PGPS production potential are able to produce indole-3-acetic acid (IAA) and 5-aminolevulinic acid (ALA). Melatonin, which is synthesized by some PNSB (e.g. R. rubrum) (Manchester et al., 1995), may also be a compound of interest as it is considered to be the first-line defence against oxidative stress in plants (Tan et al., 2013). Even though the ability of plants to absorb exogenous melatonin through their roots is proven (Tan et al., 2007), its role as a PNSB-derived PGPS is unexplored to our knowledge and therefore not further discussed in this review.

Indole-3-acetic acid (IAA).—Indole-3-acetic acid, or most commonly known as ‘IAA’, belongs to the group of auxins. Auxins are essential for plant development and have a cardinal role in regulating many growth and behavioural processes in the plant’s life cycle. They are responsible for plant cell division, extension and specialization (Tsavkelova et al., 2006). Specifically, IAA plays an important role in the activation of the cell root and the plant mineral uptake (Sakpirom et al., 2017). This PGPS stimulates seed germination and root formation; enhances vegetative growth and fructification; improves photosynthesis, biosynthesis of compounds such as pigments and metabolites; and is responsible for coordinating the plant growth under stress conditions (Tsavkelova et al., 2006; Kazan, 2013; Wani et al., 2016). Research has shown that IAA aids in the plant adaptation to salinity stress, and enhances the root and shoot growth under salinity and heavy metal stress (Sheng and Xia, 2006; Egamberdieva, 2009; Iqbal and Asraf, 2010; Fahad et al., 2015).

Multiple bacteria have been reported to produce IAA through different biosynthesis pathways, with the indole-3-pyruvate and tryptamine pathways identified in Rhodopseudomonas sp., while the produced concentrations vary (Spaepen et al., 2007). In the study of Sakpirom et al. (2017), extracellular production of IAA was found in four PNSB species under micro-aerobic light conditions yielding 0.65–3.6 mgIAA l−1. This variation in produced IAA concentration may lead to a variety of outcomes, ranging from phytostimulation to pathogenesis. For example, the addition of auxin to roots only promotes growth at very low concentrations (0.02–0.18 μgIAA l−1), while being inhibitory at higher concentrations (Davies, 1995). This can inhibit root growth, which may result in poor plant development as the root system has a major role in the water and nutrient uptake. Furthermore, PNSB synthesis of IAA was displayed in species isolated from paddy fields and river sediments, as well as insecticide-tolerant species. The species isolated from paddy fields released IAA in the range 0.65–3.6 mgIAA l−1 in their cultivation medium which was supplemented with 1 mM IAA precursor, tryptophan (Sakpirom et al., 2017). Similarly, Su et al. (2017) found that R. palustris GJ-22 reached an IAA concentration of 30 mgIAA l−1 when the tryptophan (3 mM) was added to the culture medium, which was significantly higher than 15 mgIAA l−1 when no tryptophan was added. Rhodopseudomonas KL9 isolated from river sediments resulted in the highest concentration of 52 mgIAA l−1 with 3 mM tryptophan added (Koh and Song, 2007).

5-aminolevulinic acid (ALA).—5-aminolevulinic acid, also known as ‘ALA’, is a plant growth regulator. Several studies have focused on the effect of ALA on plant growth (Bindu and Vivekanandan, 1998; Akram and Ashraf, 2013; Nunkaew et al., 2014a); however, the mechanisms of ALA-induced growth and yield promotion have not been elucidated yet. When provided at low concentrations to plants, ALA has plant growth-promoting properties (Zhen et al., 2012; Ali et al., 2013). Nevertheless, high ALA levels might cause oxidative stress, thus limiting plant growth (Akram and Ashraf, 2013). Apart from its function as a plant growth promoter, ALA also improves the uptake of minerals and the synthesis of soluble sugars and proteins (Akram and Ashraf, 2013). It is known that ALA is a precursor of the synthesis of chlorophyll, vitamin B12, anti-oxidative enzymes and other metabolites that reduce the adverse effects of various abiotic stress conditions (Wongkantrakorn et al., 2009; Nunkaew et al., 2014b; Sakpirom et al., 2017). Specifically, ALA can increase photosynthesis and therefore promote plant growth at low concentrations of 1–5 mgALA l−1 (Sakpirom et al., 2017). Research has demonstrated that ALA can be used in agricultural applications as a compound to boost tolerance towards salinity (Wongkantrakorn et al., 2009; Naeem et al., 2011; Nunkaew et al., 2014b), drought, temperature and low-light stress in plants (Akram and Ashraf, 2013), as well as a biodegradable herbicide (Sasaki et al., 1994; Sasaki et al., 2002). Furthermore, ALA has shown to improve the ultrastructure of plant cells, leading to less root damage under stress conditions (Ali et al., 2013). The exogenous provision of ALA aids in the accumulation of chlorophyll, resulting in an increase of photosynthetic activity (Bindu and Vivekanandan, 1998; Nunkaew et al., 2014a). Finally, ALA enhances the production of ATP and NADPH, which are essential cofactors for CO₂-fixation (Sun et al., 2019).
| PNSB Product type | Strain | Composition and dosage; frequency | Application method | Soil amount | Common name | Species | Effect | References |
|-------------------|--------|-----------------------------------|--------------------|-------------|-------------|---------|--------|------------|
| Dead (autoclaved) | Rhodopseudomonas <br> KL9 and BL6 | 5 x 10^7 cells; once | Seed inoculation | Soilless cultivation: petri dish | Tomato | SOLANUM LYCopersicon <br> Mill. cv. Poongyoung | Increased seedling dry mass | Koh and Song (2007) |
| Dead (autoclaved) | Rhodopseudomonas <br> sp. KL9 and BL6 | Suspension containing 4 x 10^8 cells; daily for 8 weeks | Soil irrigation | 4 kg sand and soil (1:4 v/v) | Tomato | SOLANUM LYCopersicon <br> Mill. cv. Zeus | Increased shoot and root dry weight; increased formation ratio of tomato fruit from flower; increased fruit yield; increased fresh weight in harvested fruits | Lee et al. (2008) |
| Dead (freeze-dried) | Rhodobacter sphaeroides NR3 | 2.5 or 1.25 g PNSB; once or split over ten times | Supplied as PNSB powder on soil | 15 kg | Tomato | SOLANUM LYCopersicon <br> Mill. | Increased quality of tomato fruit; increased ascorbic acid content; one-time application promoted malic acid content; ten-time application promoted phosphoric acid content | Kondo et al. (2010) |
| Dead (65°C heat-killed) | Rhodopseudomonas palustris PS3, YSC3 and YSC4 | 50% of standard amount of chemical fertilizer + R. palustris strain suspension (1.20 x 10^9 CFU); weekly for 4 weeks | Soil application | 0.3 kg | Pakchoi | Brassica rapa sp. chinensis | Insignificant effect | Wong et al. (2014) |
| Living | Rhodopseudomonas palustris | 1–5 ml of suspension; every 2 days for 30 days | Foliar spray | 1 kg soil containing 1 g fertilizer (N/P/O/K 15/15/15) | Pakchoi | Brassica rapa ssp. chinensis | Enhanced photosynthesis; increased crop yield | Xu et al. (2016) |
| Product type  | Strain                                | Composition and dosage; frequency | Application method | Soil amount | Common name | Species     | Effect                                                                 | References         |
|---------------|---------------------------------------|-----------------------------------|--------------------|-------------|-------------|-------------|----------------------------------------------------------------------|--------------------|
| Living        | *Rhodopseudomonas palustris* PS3 and BCRC16408, *R. palustris* suspension<sup>b</sup> to achieve $3.5 \times 10^{10}$ CFU in 50% Hoagland solution; weekly for 17 days | Hydroponics                      | Soilless cultivation | Pakchoi     | *Brassica rapa* ssp. *chinensis* | Improved nitrogen usage efficiency of vegetables; reduced nitrate concentration in the plant | Hsu et al. (2015)  |
|               |                                       |                                   |                    |             | Lettuce     | *Lactuca sativa* ssp. *Crispa* | Improved nitrogen usage efficiency of vegetables; enhanced plant growth; reduced nitrate concentration in the plant |                    |
|               |                                       |                                   |                    |             | Mustard     | *Brassica campestris* | Under blue light (470 nm): increased root growth; increased leaf number; increased chlorophyll and carotenoid contents | Kondo et al. (2004) |
| Dead (freeze-dried) | *Rhodobacter sphaeroides*<sup>d</sup> | 0.1 g l<sup>−1</sup> PNSB cells in 10% Hoagland solution; daily<sup>a</sup> | Soil irrigation    | N.A.        | Mustard     | *Brassica campestris* | Under 20% blue (470 nm) – 80% red (660 nm) light: increased average weight of crop; increased leaf number | Kondo et al. (2008) |
| Dead (freeze-dried) | *Rhodobacter sphaeroides* NR3 | 0.28; 0.56 and 1.12 g PNSB per pot; once | Supplied as PNSB powder on soil | N.A.        | Mustard     | *Brassica campestris* | Promoted root growth; increased chlorophyll and carotenoid contents | Kondo et al. (2008) |
|               |                                       | 0.4; 0.8 and 1.6 g PNSB per pot; once |                    |             | Spinach     | *Spinacia oleracea* | Promoted shoot growth; increased carotenoid content; increased chlorophyll content when sterilized soil was used |                    |
| Living        | *Rhodopseudomonas* sp. (ISP-1)        | i. Leaves sprayed with 3.0 $\times 10^{11}$ cells; daily for 8 days (total amount of 2.4 $\times 10^{12}$ cells); ii. soil irrigated with 3.0 $\times 10^{12}$ cells; once (total amount of 3.0 $\times 10^{12}$ cells); iii. leaves sprayed with 1.5 $\times 10^{11}$ cells; daily for 8 days; and soil irrigated with 1.5 $\times 10^{12}$ cells; once (total amount of 2.7 $\times 10^{12}$ cells) | i. Foliar spray; leaves (S); ii. rhizosphere irrigation; soil (I); iii. foliar spray + rhizosphere irrigation leaves and soil (S+I) | Stevia      | *Stevia rebaudiana* | Enhanced growth; S was more effective; S+I increased yield; soil dehydrogenase activity, shoot biomass, chlorophyll content in new leaves; and soluble sugar in old leaves were | Wu et al. (2013)   |
| PNSB | PNSB product application modalities | Plant and performance |
|------|------------------------------------|------------------------|
| Living | Rhodopseudomonas palustris | Composition and dosage; frequency | Soil irrigation | Field experiment | Common name | Species | Effect | References |
| | | Suspension containing 10^9 cells; five times | Soil | Stevia | Stevia rebaudiana | Slightly increased leaf dry weight; slightly increased yield | Xu et al. (2018) |
| Dead (autoclaved) | Rhodopseudomonas palustris GJ-22 | R. palustris suspension to soaking wet (density of 6x10^7 CFU ml^-1); once (seeds); daily for 7 days (leaves) | Seeds; leaves | Tobacco | Nicotiana tabacum L. cv. Samsun NN | Insignificant effect | Su et al. (2017) |
| Living | Rhodopseudomonas palustris | Suspension containing 5 x 10^10 cells; once | Soil irrigation | Tobacco | Nicotiana tabacum L. cv. Yunyan 85 | Increased growth and seed germination; increased root and shoot length; increased plant dry weight; induced virus resistance capability against tobacco mosaic virus | Hua et al. (2014) |
| Living | N.A. | One litre of 20% (v/v) PNSB cell suspension water diluted; every 10 days for 3 months | Soil irrigation | Mandarin | Citrus spp. | Increased number of fruit per tree; increased fruit weight; increased fruit sugar content; increased fruit carotenoid pigments | Kobayashi and Tchan (1973) |
| Living | N.A. | Fifty fold diluted culture with OD652 = 0.3; twice | Soil application | Persimmon | Diospyros kaki | Increased fruit yield; increased fruit quality (sugar and carotenoid content) | Kobayashi and Kobayashi (1995) |
| Living | Mixed culture of Rhodospirillaceae | Fifty fold diluted culture on leaves and young fruit | Foliar spraying on leaves and young fruit | Grape vine | Vitis vinifera | Increased fruit-to-flower ratio; increased weight per fruit; Increased fruit yield; | Shi et al. (1995) |
| Living | Rhodopseudomonas palustris | Four R. palustris suspensions: 8.25 x 10^{12}; 9.90 x 10^{12}; 1.24 x 10^{13} and 1.65 x 10^{13} cells; in four doses | Spraying at casing soil | 40 kg | | | |
| Living | Agaricus bisporus | Increased mushroom yield; increased number of harvested mushrooms | | | | | Han (1999) | Mushroom |
| Product type | Strain                                      | Composition and dosage; frequency | Application method | Soil amount | Common name | Species             | Effect                                                                 | References       |
|--------------|--------------------------------------------|-----------------------------------|--------------------|-------------|-------------|---------------------|------------------------------------------------------------------------|------------------|
| Living       | *Rhodobacter sphaeroides* Tx25326          | R. sphaeroides suspension (2.01 × 10^8 CFU and 1800 ml deionized water); once for 31 days | Soil submerged in suspension | N.A.        | Wheat       | Triticum aestivum L. | Decreased adverse effects from Cd toxicity; decreased Cd exchangeable phases; reduced Cd accumulation in leaves and root (53 and 67% respectively) | Fan et al. (2012) |
| Living       | *Rhodopseudomonas palustris*               | R. palustris suspension containing 2.0 × 10^10 MPN; twice | Foliar spray (leaves) | N.A.        | Chinese dwarf cherry | Prunus humilis Bunge | Increased fresh weight and leaf area; increased net photosynthetic rate (Pn); improved antioxidant capacity | Yin et al. (2012) |
| Living       | *Rhodopseudomonas sp.* (ISP-1)            | i. Leaves sprayed with 3.0 × 10^11 cells; daily for 8 days (total amount of 2.4 × 10^12 cells); ii. soil irrigated with 3.0 × 10^11 cells; once (total amount of 3.0 × 10^12 cells); iii. leaves sprayed with 1.5 × 10^11 cells; daily for 8 days; and soil irrigated with 1.5 × 10^12 cells; once (total amount of 2.7 × 10^12 cells) | i. Foliar spray: leaves (S); ii. rhizosphere irrigation: soil (I); iii. foliar spray + rhizosphere irrigation leaves and soil (S+I) | N.A.        | Stevia       | Stevia rebaudiana     | Enhanced growth; S was more effective; S+I increased: yield; soil dehydrogenase activity, shoot biomass, chlorophyll content in new leaves; and soluble sugar in old leaves were | Wu et al. (2013) |
| Living       | *Rhodopseudomonas palustris* CS2; *Rhodopseudomonas faecalis* SS5 | Seeds inoculated with PNSB cells suspended in water (0.5 optical density at 600 nm); once | Seeds              | N.A.        | Bean        | Vigna mungo         | Increased shoot and root length (without and with As stress); increased wet and dry weight (without and with As stress); increased resistance towards As stress | Batool et al. (2017) |

NA, not available.

Soil irrigation = irrigation of soil with suspension of cells in water.

a. Irrigation quantity and frequency not available.
b. Amount of cells contained in the suspension not specified.
c. Extracted from natural environment.
d. Cultivation method not available.
e. *Rhodopseudomonas palustris* BCRC16408 did not result in plant performance enhancement.
f. Inoculation 60th, 67th, 74th and 81st day after seedling transplanting.
g. This mushroom is included in this review since its cultivation is similar to that of plants.
| PNSB   | PNSB product application modalities | Plant and performance | Reference                   |
|--------|------------------------------------|-----------------------|-----------------------------|
| **Dead (freeze-dried)** | Rhodopseudomonas capsulatus | Amount containing 0.5 g of N, P and K; once during reproductive stage | Increased rice grain yield | Kobayashi and Haque (1971) |
|        |                                    | Supplied as PNSB powder on soil | ssp. japonica               |                            |
| **Living** | Rhodopseudomonas capsulatus B10 | Azotobacter vinelandii and R. capsulatus cells (600 mg and 60 mg protein respectively) in growing medium for rice cultures; once | Flowering and panicle formation about 100 days after germination (despite the absence of N source in the rhizosphere); enhanced number and size of root hairs; increased shoot height; increased shoot dry weight; increased shoot N content | Maudinas et al. (1981) |
| **Living** | Rhodopseudomonas capsulatus | 610 kg ha⁻¹ compost inoculated with R. capsulatus at final concentration of 10⁸ cells g⁻¹; twice | Increased plant height and dry weight; increased grain yield; increased grain and straw N content | Elbadry et al. (1999a,b) |
| **Living** | Rhodobacter capsulatus DSM 155 | R. capsulatus cell suspension in phosphate buffer (pH 7.0) and 10% (w/v) gum Arabic solution; once | Increased shoot height; increased shoot dry weight; increased shoot N content; increased root length and dry weight; increased root number; increased root N content | Elbadry and Elbanna (1999) |
| **Living** | Rhodobacter capsulatus DSM 155 | 600 ml nutrients solution inoculated with R. capsulatus (final concentration of 2.2 × 10⁷ cells ml⁻¹); once | Increased shoot height; increased shoot dry weight; increased shoot N content; increased root length and dry weight; increased root number; increased root N content | Elbadry and Elbanna (1999) |
| **Living** | Rhodopseudomonas palustris KN122 | R. palustris cells dispersed into sterile distilled water (1st (day 0): 1.7 × 10¹¹ cells pot⁻¹; 2nd (day 43); 5.0 × 10⁸ cells pot⁻¹; 3rd (day 86): 5.1 × 10¹⁰ cells pot⁻¹); once (day 0) or thrice (days 0, 43 and 86) | Increased plant height; increased grain yield | Harada et al. (2005) |
| Product type | Strain | Composition and dosage; frequency | Application method | Soil amount | Plant and performance | Reference |
|--------------|--------|----------------------------------|-------------------|-------------|-----------------------|-----------|
| Living       | *Rhodobacter capsulatus* DSM 155<sup>1</sup> | *R. capsulatus* cell suspension (<span class="math" role="math" aria-label="10<sup>6</sup> CFU ml<sup>-1</sup> in 10% (w/v) gum Arabic solution; once</span>) | Seed coating | Field trial | cv. Giza 177 | Increased shoot height and weight; increased straw N content; increased number of productive tillers; increased number of grains per panicle; increased grain yield; increased grain N content | Gamal-Eldin and Elbanna (2011) |
| Living       | *Rhodopseudomonas palustris* TK103, PP803, and P1 | One gram of each PNSB product<sup>2</sup> in 3 l water (without and with salt stress); once | Soil application | 0.5 kg | ssp. indica cv. Pathumthani | Reduced inhibition of rice straw and rice husk carrier; increased root dry weight (without and with salt stress); increased root length and shoot dry weight under salt stress; *R. palustris* PP803 increased plant height under salt stress | Kantha et al. (2015) |
| Living       | *Rhodopseudomonas palustris* TN114, PP803 and TK103<sup>3</sup> | 0.75 kg ha<sup>-1</sup> of each PNSB product<sup>2</sup>; every 2 weeks during vegetative stage; every week during reproductive and maturation stages | Soil | Field trial | cv. KDML 105 in organic field; cv. RD 41 in saline field; Organic paddy field: only TN114 increased grain yield; decreased CH<sub>4</sub> flux | Saline paddy field; increased grain yield; increased grains per panicle; decreased CH<sub>4</sub> flux | Kantachote et al. (2016) |
| Living       | *Rhodospirillum rubrum* ATCC 11170 | Bacterized according to ISTA protocol; once | Seeds | Field trial | N.A. | Promotion of sprout growth; increased vigour-index; increased plant survival on fly-ash; suppressed toxic metal ion release from fly-ash | Rana et al. (2016) |
Since the commercially available ALA is very expensive for most agricultural applications, the use of ALA-producing microorganisms is viewed as a promising economically viable option for plant cultivation (Nunkaew et al., 2014a).

Two ALA biosynthetic pathways are known in bacteria, namely the five-carbon and the ALA synthase pathway (Avissar et al., 1989). In PNSB, the synthesis of ALA is performed by the latter pathway, in a reaction catalysed by ALA synthase that condenses glycine with succinyl-CoA (Beale, 1990; Sasaki et al., 1990). PNSB have been demonstrated to produce ALA under saline or heavy metal stress conditions. For instance, PNSB isolates from paddy fields and Cd/Zn contaminated soils produced 0.23-5.0 mg ALA l\(^{-1}\) under micro-aerobic light conditions (Kantha et al., 2010; Nunkaew et al., 2014a; Sakpirom et al., 2017). The production of ALA can also be promoted by adding the precursor molecules glycine and succinate to the cultivation medium. In the study of Su et al. (2017), concentrations reached 7.9 mg ALA l\(^{-1}\) when the precursors were added compared to 4.5 mg ALA l\(^{-1}\) in absence of precursors.

**Mechanisms responsible for abiotic and biotic stress resistance.** Salinity.—Increased salinity has detrimental effects on plant endogenous metabolic processes, such as phytohormone production and photosynthetic activity (Nunkaew et al., 2014a). Reactive oxygen species (ROS) are by-products of aerobic metabolism, formed in the shoot of the plant. These include the superoxide radical anion (\(O_2^-\)), hydrogen peroxide (H\(_2\)O\(_2\)) and hydroxyl radical (OH). Their production increases under salinity stress (Ashraf and Harris, 2004), and ROS can have a detrimental oxidative effect if accumulated. Detoxification of ROS occurs through the production of anti-oxidative enzymes (e.g. ascorbate peroxidase, catalase, glutathione reductase and superoxide dismutase). However, the activity of these enzymes is reduced under extremely saline conditions. Generally, plants producing higher amounts of anti-oxidative enzymes are more resistant to oxidative damage induced from ROS (De Azevedo Neto et al., 2006). In case the plant is unable to produce sufficient amounts of antioxidants, they should either be provided externally, or their synthesis should be promoted. One of these antioxidant promotors is ALA, which acts as a protective mechanism against ROS (Zhen et al., 2012). The treatment with ALA protects the photosynthetic apparatus under stress conditions (Sun et al., 2009). For instance, rice under salt stress that was pre-treated with ALA (0.13–0.33 mg\(_{\text{ALA}}\) l\(^{-1}\)) presented increased activities of ascorbate peroxidase (126–282%), catalase (950–1067%), glutathione reductase (116–165%) and superoxide dismutase (404–572%) (Nunkaew et al., 2009).
Carotenoids are key non-enzymatic plant antioxidants (Ashraf, 2009). The effect of PNSB on carotenoids varies, ranging from up to 138% increase in spinach provided with dried PNSB cells (Kondo et al., 2008), until a 27% decrease in rice cultivated under stress conditions (Nookongbut et al., 2018) (for more information refer to Tables S5 and S8). The effect on other important antioxidants, including tocopherols and flavonoids (Ashraf, 2009), is to our knowledge unexplored.

The presence of PNSB in saline paddy fields (3.0–4.0 mS cm⁻¹) is an indication that these microorganisms can tolerate saline conditions (Nunkaew et al., 2012). Tests with isolated strains indicate that this tolerance can be attributed to the binding of Na⁺ with the extracellular polymeric substances (EPSs) produced by PNSB (Nunkaew et al., 2015), and prove the concurrent production of ALA under these conditions (Nunkaew et al., 2014a). It has been demonstrated that exogenous supply of low concentrations of ALA (0.01–30 mgₐₐ₁⁻¹) can reduce the injurious effect of salinity stress on plants (Wongkantrakorn et al., 2009; Naeeem et al., 2011). Nunkaew et al. (2014a) tested two *R. palustris* strains for their ALA production under saline conditions (induced *in vitro* with 0.25% NaCl), and they observed a production of 1180–1705 mg l⁻¹ ALA. When cultivated in a saline paddy field, the maximum ALA levels produced by *R. palustris* TK103, PP803 and P1 ranged between 1.4 and 1.7 mgₐₐ₁⁻¹, resulting in increased growth and yield parameters (Kantha et al., 2015). Inoculation with PNSB presents positive effects on plant growth under saline conditions, specifically on fresh and dry plant and root weight, chlorophyll content and grain yield (Gamal-Eldin and Elbanna, 2011; Nunkaew et al., 2014a; Kantha et al., 2015; Kantachote et al., 2016), approaching the values recorded for unfertilized plants grown without salinity stress (Nunkaew et al., 2014a). The increased root development (Kantha et al., 2015) is a great advantage especially under salinity stress, as a high root density can mend the vital functions of rice plants and enhance the grain yield (Mishra and Salokhe, 2011). This ability renders PNSB as eligible for agricultural applications in saline environments.

Heavy metals.—Purple non-sulphur bacteria are able to reduce plant stress caused by the presence of HM through a variety of mechanisms, such as accumulation inside the cell, adsorption on EPS bound to the cell’s outer surface, conjugation in the siderophores and conversion to less toxic compounds through redox transformations (Panwichian et al., 2011; Batool et al., 2017; Sakpirom et al., 2017; Nookongbut et al., 2018). The latter has been demonstrated to be a more effective mechanism for HM stress mitigation in plants than the former two. The speciation of metals in the soil plays a major role, as the exchangeable phases are highly absorbed by the plants (Geebelen et al., 2003; Fan et al., 2012). At the same time, the accumulation of metals in plants is highly related to their bioavailability. Hence, the reduction of exchangeable species decreases the bioavailability and therefore the inhibiting effect (Fan et al., 2012). For instance, the increased root length (33%), when both *R. palustris* CS2 and *R. faecalis* SS5 were supplied (compared to 25–26% for the individual strains), was attributed to the decreased bioavailability of As present in the soil, due to the simultaneous oxidation of As(III) and reduction of As(V) maintaining thus the redox cycle (Batool et al., 2017). Finally, Nookongbut et al. (2018) argued that the reduction of HM stress to plants by PNSB is a combination of sequestration in siderophores, EPS binding, as well as the enhancement of photosynthesis and activity of antioxidant enzymes through the use of the produced IAA and ALA.

Diseases.—Plant diseases, viral or microbial, can cause severe damage to crops. The exposure to certain stimuli can enhance the disease resistance potential, and plants that have been exposed to these biotic or abiotic stimuli in the past can rapidly respond to the exposure to a virus by setting off robust defence responses (Conrath et al., 2006; Pastor et al., 2013). This induced resistance can be catalytic for the plant’s survival, especially when triggered prior to infection (Choudhary et al., 2007). In this context, PNSB produce IAA, ALA and siderophores, which are compounds that can induce systemic resistance against viruses (Pieterse et al., 2014). Foliar fertilization using PNSB has been reported to be efficient in suppressing plant viral diseases such as tobacco mosaic virus (TMV) (Su et al., 2017).

Environmental benefits

Heavy metal bioremediation. Although PNSB have been reported to remove metals from wastewaters (Bai et al., 2008), they are rarely used for the bioremediation of soil, as they are usually obligate anaerobes and require a lower redox potential (Fan et al., 2012). Hence, the best practice is the isolation of strains from environments with conditions similar to the envisaged application. For instance, Fan et al. (2012) isolated *R. sphaeroides* from HM-containing oil field injection water, for bioremediation of Cd from soil. The treatment resulted in a lower Cd concentration in the root and leaves of wheat (67% and 53% reduction resp.) (Fan et al., 2012). Moreover, Panwichian et al. (2011) tested *Rhodobium marinum* NW16 and *R. sphaeroides* KMS24 for their removal potential regarding HM (Cd⁰, Cu²⁺, Pb⁰ and Zn²⁺) from
contaminated shrimp pond water under micro-aerobic, light and aerobic, dark conditions. The results showed that bio-adsorption by EPS had a greater HM removal efficiency (91–97%) compared to accumulation in the cell (14–75%). Finally, the acid sulphate soil isolates Rhodopseudomonas spp. VNW64 and VNS89 reduced Al$^{3+}$ up to 63% and remediated the mixture of Al$^{3+}$ and Fe$^{2+}$ up to 88% (Khuong et al., 2017).

**Greenhouse gas emission mitigation.** Apropos of the greenhouse gas (GHG) emissions, plant cultivation can be a net source or a net sink, depending for instance on the balance between methane (CH$_4$) emissions from rice cultivation and the CO$_2$ uptake by plants (Tubiello et al., 2014). In order to reach the longed-for climate stabilization, GHG sources should be minimized, while carbon sequestration should be maximized (Powlson et al., 2011). The potential PNSB contribution to the latter is discussed in section Increased soil fertility.

Purple non-sulphur bacteria can thrive in environments with micro-aerobic and anaerobic zones, containing biodegradable compounds. Given that methanogenic archaea grow in similar conditions, these environments are prone to CH$_4$ formation. Considering that CH$_4$ is a GHG with an effect on global warming 21 times that of CO$_2$, the mitigation of CH$_4$ emissions is of imperative importance. It is estimated that 26% of the total CH$_4$ emissions of 550 Tg year$^{-1}$ originate from wetlands and paddy fields, while the latter contribute to roughly 10% of the total emissions (53 Tg year$^{-1}$) (Cao et al., 1998). PNSB have the ability to mitigate CH$_4$ emissions in paddy fields by suppressing the growth of methanogenic archaea (Harada et al., 2005; Nunkaew et al., 2014a; Kantha et al., 2015; Sakpirom et al., 2017). Given that (i) both methanogens and PNSB compete for the same carbon sources, (ii) PNSB can additionally use CO$_2$ as carbon source and (iii) the presence of light gives a great advantage to PNSB, the latter can become dominant in paddy fields (Nunkaew et al., 2014b). Several PNSB strains have shown the potential to totally eliminate CH$_4$ produced under paddy field conditions, while also reducing the CO$_2$ emissions by up to 47% in laboratory scale experiments (Kantha et al., 2015; Sakpirom et al., 2017). The latter was ascribed to the potential use of CO$_2$ as carbon source by PNSB (Kantha et al., 2015).

**Evaluating use of PNSB as fertilizer, bio-stimulant and bio-fortifier**

Critical analysis of the existing literature revealed the different functions of each PNSB product type (Fig. 2), resulting in various effects and interactions with plants. More specifically, the dead cells mainly deliver nutrients, while living cells additionally convert nutrients into plant-available forms and continuously supply PGPS. This results in the most prominent impact, promoting increased plant growth performance, while suppressing abiotic and biotic stress, as well as reduction of GHG emissions. This section provides a critical comparison of the functionalities of each type of PNSB product.

A systematic analysis and a comparison are made for all results found in literature, and the five major agricultural topics are discussed (Fig. 2). For overall plant growth performance and fruit quality and yield, the comparison is made between the two most occurring PNSB product types: dead cells and living cells. An overview of these data can be found in Tables 1 and 2, and a visual representation is shown in Figs 3 and 4. Over one-third of the available literature regarding the use of PNSB for plant production concerns rice cultivation (Table 2). The three other topics (abiotic stress resistance, biotic stress resistance and environmental benefits) will only discuss living cells, since no literature was available for dead cells. It should be noted that details about the reference fertilizer, as well as the frequency of fertilization and amount of fertilizer used, can be found in Appendix S1 in section 4. Furthermore, it is recommended to verify the apparent trends as systematically as possible in view of a high methodological variability.

**Fertilization function**

This section presents the effects of the use of PNSB products with emphasis on: (i) overall plant growth performance showing the effects on the whole plant,
including shoot and root and (ii) yield and quality of the edible plant biomass, where the effect on crop/produce is discussed. It should be noted that some of the observed effects might not be strictly due to fertilization (nutrient supply) but biostimulation and/or biofortification can have contributed to the result. This distinction is made to facilitate the understanding of the effects on the different categories.

**Overall plant growth performance.** The comparison of dead and living cells for the different KPI within plant performance is illustrated in Fig. 3. For overall plant growth performance, four KPIs were chosen: shoot dry weight, shoot length, root dry weight and total chlorophyll content. For all KPI, mostly positive effects are seen compared to the control. Overall, the living cells show a larger variability in the positive direction compared to the dead cells, while the median is also higher for each KPI for living cells, meaning that more than 50% of the results were more positive compared to dead cells.

In accordance with the meta-analysis showing that living biomass had a more positive effect on plant growth performance, tests under the same crop growth conditions showed a better performance of dosing an equal amount of living biomass. Specifically, when Koh and Song (2007) inoculated with living cells of *Rhodopseudomonas* sp. BL6 and KL9 to tomato seeds, they observed a 7.6–32% increase in germination percentage, as opposed to the application of autoclaved cells. This showed that germination is more affected by bacterial metabolism than by plant-available nutrients contained in the bacterial cells (Koh and Song, 2007). The positive effects of PNSB metabolites on plant growth were further observed during hydroponic tests. Shoots of rice seedlings cultivated in a nutrient solution inoculated with *R. capsulatus* DSM 155 were up to 75% taller, and significantly heavier (up to doubled dry weight) compared to uninoculated controls (Elbadry and Elbanna, 1999). Moreover, the addition of living PNSB had notably better effects on tomato plant growth compared to the same amount of autoclaved cells (47–121%, 18–35%, 12–79% increase in shoot dry weight, shoot length and root dry weight as compared to 2.8–34%, 0% and 0–26% for autoclaved biomass) (Lee et al., 2008). Heat-killed or autoclaved cells of *R. palustris* did not display any notable effects on the growth of pak choi at soil application (Wong et al., 2014), nor on the growth of tobacco during soil application (Hua et al., 2014) or foliar fertilization (Su et al., 2017). In contrast, the same

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amount of living cells presented significant positive effects on plant growth (Hua et al., 2014; Wong et al., 2014; Su et al., 2017) (see sections 3.1 and 3.2 in Appendix S1). The effectiveness of dead cells is attributed to the fact that their use promotes the activity of soil microbes which use the PNSB biomass nutrients for their own growth, therefore, demonstrating similar properties with organic fertilizers. This was indicated by Kondo et al. (2008), where the use of sterilized soil resulted in a lower increase in fresh and dry shoot weight, as well as length and carotenoid content of spinach, compared to the use of non-sterilized soil. Therefore, it can be concluded that the use of dried PNSB promotes the activity of soil microbes, which produce elevated amounts of PGPS (Kondo et al., 2008), indirectly displaying the effects of living PNSB biomass.

Yield and quality increase of edible plant biomass. The use of PNSB enhances both quantity and quality of harvested crops. The effect on the yield and quality of edible plant biomass was also quantified based on four KPIs: fruits per flower, number of fruit/grain/edible leaves (the more general term 'crops' is used for conciseness) per plant, average fresh weight per crop and crop yield (Fig. 4). The majority of the results have positive outcome when dead or living PNSB cells were dosed compared to the control. For instance, autoclaved *Rhodopseudomonas* sp. BL6 and KL9 cells significantly promoted the average tomato fruit yield (42–50% increase) while inoculation with the same amount of living BL6 and KL9 enhanced the yield by 21–98% (Lee et al., 2008). Furthermore, there is smaller variability between the outcomes compared to the results for overall plant growth (Fig. 3), with the exception for the crop yield, which also shows more extreme outliers for living cells. There is no straightforward trend showing an overall better performance of dead or living PNSB cells regarding KPI for edible plant biomass.

A general remark is that, in most cases, the yield is increased by the elevated number of fruits or grains rather than a higher individual crop weight. For instance, Kobayashi and Kobayashi (1995) reported a 16% rise in persimmon fruit yield due to 34% more fruits, whereas the average weight per fruit decreased by 14%. Elbadry et al. (1999a,b) demonstrated a 30% higher rice grain yield, but the weight of individual grains decreased by 9.1%. This indicates that PNSB products enhance the new grain formation rather than the individual grain weight increase, as shown by the 3.9% rise in the number of grains per panicle (Elbadry et al., 1999a,b). An increase in grain yield was observed in all cases (19–33%), attributable to the higher number of productive tillers, with a most notable effect when nitrogen fertilizer was not provided (Elbadry et al., 1999a,b). Han (1999) ascribed the increased numbers and yield of mushroom1 (7.4–26% and 10–22% resp.) to the enhanced nutrient provision as well as to the ALA contained in the suspension. No significant effect was observed regarding the size of the mushrooms, with the latter indicating that the PNSB stimulated the formation of more primordia (cells in the earliest stage of development). In another study, inoculation with *R. palustris* KN122 improved the rice grain yield (8.9–24%), whereas the grain weight was not affected by the treatment (Harada et al., 2005). Nevertheless, there is a limited number of studies reporting elevated fruit weight (Kobayashi and Tchan, 1973; Shi et al., 1995; Lee et al., 2008). Specifically, the use of PNSB biomass resulted in higher number of mandarin fruits per tree (9.1%), fruit yield (27%), as well as the average weight per fruit (17%) compared to the control (Kobayashi and Tchan, 1973). When Shi et al. (1995) used foliar spray containing mixed PNSB cultures on grapes, they observed a 2.5% rise in the average fruit weight. More importantly, the ratio of fruits per flower increased by 1.9%, which is important as the flowers of this plant commonly die due to weakness of the plant and nutrient limitation (Shi et al., 1995). Similarly, Lee et al. (2008) observed that the provision of *Rhodopseudomonas* sp. KL9 doubled the weight of harvested tomatoes, while the formation ratio of tomato fruit from flower also increased (14–89%).

It has been demonstrated that PNSB, apart from increasing the quantity, can also improve the quality of the harvested edible plant biomass. It was demonstrated that dead PNSB cells perform equally as well as conventional inorganic fertilizers ((NH₄)₂SO₄) in terms of tomato quality increase (Brix sugar content, titrable acidity, carotenoid and citric acid content) (Kondo et al., 2010). Moreover, Kobayashi and Tchan (1973) reported that the use of living PNSB resulted in sweeter mandarin fruit (5.8% higher sugar content) and more attractive visual appearance due to 20% more carotenoids. The taste as well as the appearance of persimmon fruit improved, as indicated by an elevated sugar and carotenoid content (15% and 20% increase resp.) (Kobayashi and Kobayashi, 1995). Similarly, the use of *R. sphaeroides* NR3 enhanced the carotenoid content of spinach (14–138%) and mustard spinach (4.1–21%) (Kondo et al., 2008). Lee et al. (2008) concluded that a significant increase in lycopene content (1.7–48%) of tomato fruit was the result of the stimulation of tomato plant metabolism from the symbiosis with *Rhodopseudomonas* sp. BL6 and KL9. Additionally, the use of *Rhodopseudomonas* sp.

1Mushrooms are included in this review since their cultivation is similar to that of plants.
(ISP-1) resulted in 77–116% more soluble sugars in stevia leaves, 30–91% rise in chlorophyll a and 29–82% chlorophyll b, while the stevioside content rose up to 69% (Wu et al., 2013). The nitrogen content of rice grains was 7.1% higher due to the inoculation with \textit{R. capsulatus} DSM 155 (Elbadry et al., 1999a,b). Finally, inoculation with \textit{R. palustris} PS3 reduced the nitrate content of the nitrate-rich vegetables pak choi (20–50%) and lettuce (27%) (Hsu et al., 2015). This could have a potentially positive effect on high nitrate diets (e.g. Mediterranean, Japanese) since the high dietary nitrate intake is often associated with health risks (Lidder and Webb, 2013).

\textbf{Resistance to stress}

This section discusses the enhanced resistance to stresses (abiotic and biotic), induced by the supply of living PNSB cells.

\textbf{Resistance to abiotic stress.} Research shows that the use of PNSB in plant cultivation can reduce the yield losses due to abiotic stresses and/or diseases. For instance, the lack of light during the dark months negatively affects plant growth and crop yield. Kondo et al. (2004) noted that the use of dried \textit{R. sphaeroides} can compensate for the lack of the full light spectrum on the growth of mustard spinach. It was observed that the average weight of the vegetable increased by 17% during the 20% blue – 80% red light treatment, while the crop quality significantly increased with the PNSB product under blue light as indicated by the elevated chlorophyll a (61%) and chlorophyll b (39%) content. Finally, Wong et al. (2014) found that the effect of living PNSB fertilization on old seeds of pak choi was higher than on new seeds, indicating that this is a good technique to avoid the costly damage of stored seeds.

The adverse effects of salinity stress on plants have been successfully minimized by applying living PNSB, as demonstrated with experiments using rice plants. For instance, coating with \textit{R. capsulatus} DSM 155 resulted in 18–33% higher rice grain yields (\textit{Oryza sativa} L. cv. Giza 177) during cultivation in a saline paddy field (Gamal-Eldin and Eibanna, 2011). At the same time, the use of living PNSB in saline paddy fields has been reported to enhance all plant growth parameters (Kantha et al., 2015). Specifically, Kantha et al. (2015) inoculated \textit{R. palustris} TK103, PP803, and P1 in rice plants (\textit{Oryza sativa} L. subsp. indica) under salt stress. The root dry weight and length as well as the shoot length and dry weight increased (210–250%, 80–105%, 36–45% and 73–115% resp.). \textit{R. palustris} PP803 most efﬁciently limited the negative effects of salinity stress on rice plants (highest increase for all growth parameters). Similar results were reported by Kantachote et al. (2016), where during the cultivation of rice in saline ﬁelds, the shoot height and panicle weight increased by 4.1–10% and 21–33%, while the number of rice grains per panicle and rice grain yield were elevated (8.4–18% and 5.2–9.0% resp.) using a mixed carrier inoculated with \textit{R. palustris} TN114, PP803 and TK103 in a saline paddy ﬁeld (\textit{Oryza sativa} L. cv. RD 41). These results indicate that under salinity stress, PNSB fertilization enhances the grain production rather than the plant growth (Kantachote et al., 2016).

Stress due to the presence of metals can also be mitigated using living PNSB, as reported in experiments performed on wheat and bean plants. Fan et al. (2012) treated Cd-contaminated soil with \textit{R. palustris}, and the Cd bioremediation efficiency was tested by planting wheat seeds (\textit{Triticum aestivum} L.). No significant improvement of plant growth was observed, with the level of inhibition being a function of the Cd concentration; however, the Cd accumulation in roots and leaves decreased by 67% and 53% resp. (Fan et al., 2012). Batool et al. (2017) used the As-resistant \textit{R. palustris} CS2 and \textit{R. faecalis} SS5 on bean plants (\textit{Vigna mungo}) cultivated in As-contaminated soil. \textit{R. palustris} CS2 and \textit{R. faecalis} SS5 were able to tolerate resp. 150 and 100 mM As(V) and Cr, Ni and Zn at a concentration of 1.0 mM, while they could not tolerate Cu, Cd and Co. \textit{R. palustris} CS2 reduced As(V) to As(III) whereas \textit{R. faecalis} SS5 oxidized As(III) to As(V). It should be noted that As is mainly found in two forms: arsenate (As (V)) and arsenite (As(III)) (Oremland and Stolz, 2003), with the latter being roughly 100 times more toxic compared to As(V) (Jain and Ali, 2000). \textit{R. palustris} CS2 presented the highest As(V) reduction potential of 63%, while SS5 showed the highest As(III) oxidation potential of 96% (providing 10 mM As(V) and 5 mM As(III)). A significant enhancement of growth was observed in plants inoculated with the individual PNSB, under As exposure (25–26% and 31–33% increase in root and shoot length), while the effect was greater when a mixture of both strains was used (33% and 37% increase resp.). Moreover, the inoculation with \textit{R. palustris} of tobacco plants cultivated in As-contaminated soil increased shoot height (14%), as well as root and shoot dry weight (32% and 6.8%) (Hua et al., 2014). Furthermore, the yield increased as shown by the elevated leaf number (20%) and leaf dry weight (42%). Importantly, the As concentration of the plant decreased by roughly 15% with the largest effect presented in the root concentration (43% decrease), however, the As concentration in the leaves was not significantly affected. Similarly, \textit{R. palustris} C1 and \textit{Rubrivivax benzoatilyticus} C31 reduced the accumulation of As in rice plants (\textit{Oryza sativa} ssp. indica) while the mixture of strains enabled the highest reduction (up
to 65\% (Nookongbut et al., 2018). Most importantly, even though the control plants contaminated with a mixture of \text{As(III)} and \text{As(IV)} as well as the ones inoculated with the individual strains did not survive, the mixture of PNSB enabled their growth. This potentially renders the synthetic community suitable for real application in fields where both As species exist.

**Resistance to biotic stress.** Living PNSB have the capacity to suppress plant diseases, as demonstrated through experiments with rice and tobacco plants (Tables 1 and 2). Specifically, this was validated by Rana et al. (2016) who reported that \textit{R. rubrum} resulted in total elimination of disease incidence in rice (\textit{Oriza sativa} L.). Similarly, during experiments with tobacco plants, Su et al. (2017) used \textit{R. palustris} GJ-22 foliar spray against of tobacco mosaic virus (TMV), which is registered as one of the ‘top 10’ economically important plant viruses (Ryicki, 2015). This treatment presented similar performance to a commercially available disease resistance inducer [i.e. BTH or benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester]. Specifically, under axenic conditions, \textit{R. palustris} GJ-22 colonized the rhizosphere of tobacco plants (\textit{Nicotiana tabacum} L. cv. Samsun NN) and exhibited enhanced virus-resistance-inducing capacity against TMV, while the produced PGPS resulted in enhanced seed germination (2\%), growth performance and resistance to TMV. Likewise, under field conditions, the PNSB foliar spray enhanced the activities of defensive enzymes and protected the tobacco plants against TMV. Specifically, the use of \textit{R. palustris} GJ-22 presented similar results to the provision of BTH, with 74\% and 70\% lower TMV accumulation for BTH+ and GJ-22-treated leaves. GJ-22 cells increased the yields by 30–32\% while BTH resulted in lower values (10–12\%). The first-class tobacco leaves increased by 28–40\% with GJ-22, whereas the BTH spray enhanced the yield of leaves by roughly 23\%. The disease severity lowered to resp. 12–13\% and 11–12\% with GJ-22 and BTH, while the corresponding values were 25–26\% for the control (water). It should be noted that the same amount of autoclaved \textit{R. palustris} GJ-22 did not present any significant effect regarding growth parameters and resistance to TMV (Su et al., 2017). Finally, it was demonstrated that the inoculation of \textit{R. faecalis} increased the antifungal activity of several strains belonging to the \textit{Bacillus} genus against the root rot fungus \textit{Helicobasidium mompa} using disk placement tests (We et al., 2016).

**Environmental benefits**

**Sustainability of PNSB production.** A superiority of PNSB products compared to conventional fertilizers is the possibility of utilizing inexpensive feedstock and/or waste(water) as sources of carbon and nutrients to produce biomass (Nasseri et al., 2011). This means that PNSB products can be produced on nutrient-rich agro-industrial or process liquid side-streams (e.g. potato cutting-waters). These side-streams are often treated without generating a recovery product with distinctive value and/or demand, further contributing to an increased pressure on natural resources. The pressure on P, for example, has been steadily enlarging (Verstraete et al., 2016). Phosphate fertilizers are made from apatite, a group of phosphate minerals identified as one of the 20 critical raw materials in Europe (European Commission, 2017). More specifically, apatite is expected to be depleted in 50–100 years if the rate of consumption remains the same as nowadays (Cordell et al., 2009). Finally, given that the microbial product is entering the food chain only indirectly (i.e. use as fertilizer), system operation in strictly axenic conditions is not required therefore facilitating the overall handling (Pikaar et al., 2018).

**Increased soil fertility.** The maintenance of soil fertility is important for sustainable land use, supply of nutrients that are vital for plant growth and the stimulation of the active and diverse ecosystems (Clark et al., 1998; Mäder et al., 2002). This results in an appropriate soil structure and permits the organic material decomposition through natural processes (Mäder et al., 2002). PNSB products supply the soil with nutrients in their organic form, resulting in the enhancement of soil quality, through the provision of SOC, in contrast to synthetic fertilizers. Given that the intensification of agriculture has dramatically decreased the SOC content of agricultural land (Lal, 2004), PNSB products can contribute to the restoration of soil quality. Finally, PNSB are able to convert atmospheric CO\textsubscript{2} into biomass (Kantha et al., 2015) and can contribute to the targeted yearly 0.4\% increase in soil carbon stocks, which is expected to contribute to food security and climate stabilization (Vermeulen et al., 2019).

**Heavy metal bioremediation.** There is evidence that PNSB have the ability to resist and bioremediate HM, including Cd, Zn, Al, Fe and As. This ability was demonstrated by Sakiprom et al. (2017), where \textit{R. palustris} TN110 and \textit{Rubrivivax gelatinosus} TN414 were isolated from Cd and Zn contaminated paddy fields. \textit{R. palustris} TN110 removed resp. 84\% and 55\% of Cd and Zn (initial concentration of 262 mg l\textsuperscript{-1}), while for \textit{R. gelatinosus} TN414, the removals reached the values of resp. 72\% and 74\% (initial concentration of 23 mg l\textsuperscript{-1}). The HM resistance of these strains
Rice production: harnessing PNSB functionality to its fullest

As discussed in the previous section, PNSB have the ability to enhance plant growth performance, increase crop yield and quality, reduce the adverse effects of salinity and HM stress, increase the resistance of plants towards diseases, bioremediate HM and mitigate GHG emissions (Fig. 5). The combination of these effects leads to the most promising application, being the use in paddy fields for rice cultivation. Growth performance enhancement, crop yield and quality increase, as well as disease resistance are effects non-exclusive to paddy fields, and have been thoroughly elaborated in sections Fertilization function and Resistance to biotic stress. Therefore, they will not be discussed here. It should be stressed though, that there is more than one capability of PNSB enabling these effects. For instance, Kantachote et al. (2016) concluded that the increased rice plant growth performance (cultivated in paddy field) could be attributed to (i) the lower concentration of H2S, which is an inhibiting compound for plant growth due to its use as electron donor by some PNSB strains (Harada et al., 2001b), in addition to (ii) N2 fixation, as well as (iii) the production of phytohormones.

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It is of key importance that paddy fields provide favourable conditions for PNSB growth, due to the combination of an anaerobic environment containing acetate which originates from rice straw degradation (reaching mM levels) (Conrad, 2007) and sunlight. In the study of Kantachote et al. (2016), all PNSB strains proliferated in both organic and saline fields, as indicated by the increase of 1 log CFU g\(^{-1}\) compared to the control. This gives PNSB the advantage of potentially outcompeting native microbes and allotting their positive effects on rice plants throughout their growth. It should be noted that PNSB are inherently present in paddy fields, nevertheless, their number depends on the field conditions (Elbadry et al., 1999a,b). Specifically, Elbadry et al. (1999a,b) reported that PNSB populations increase after rice pre-transplanting, reaching their maximum numbers at tillering stage and declining until the time of harvest. It is therefore suggested here, that PNSB inoculation at an early stage of the rice production cycle can result in beneficial for rice production effects. An interesting remark is that PNSB inoculation had a more prominent effect on the (PNSB) population contained at the outer soil layer (0–1 cm depth) in the case where rice straw was not applied (rice straw application is a common practice to enhance soil fertility during rice cultivation) (Harada et al., 2005). Specifically, in the study of Harada et al. (2005), the uninoculated control had PNSB populations of \(10^5\)–\(10^6\) most probable number (MPN) g\(^{-1}\) soil DW whereas the inoculation resulted in \(10^8\) MPN g\(^{-1}\) soil DW. On the other hand, the uninoculated control containing rice straw had PNSB populations comparable to that of inoculated pots (\(10^7\) and \(10^8\) MPN g\(^{-1}\) soil DW respectively). These results illustrate that, when straw is applied, PNSB populations naturally increase around the surface soil. As indicated by the larger PNSB populations on bulk soil (4–6 cm) in the latter case (\(10^5\)–\(10^6\) compared to \(10^5\)–\(10^5.1\) MPN g\(^{-1}\) soil DW), when PNSB are inoculated under these conditions, part of the community moves in the deeper soil levels resulting in a more prominent positive effect on plant growth enhancement (Harada et al., 2005).

Furthermore, when similar experiments were performed under non-saline and saline conditions, the increase in growth and yield parameters was higher under salinity stress, indicating a beneficial effect of produced phytohormones under these conditions (Gamal-Eldin and Elbanna, 2011; Kantachote et al., 2015; Kantachote et al., 2016). This is a promising ability, especially considering that saline fields are annually increasing by 10%, with 20% of the worldwide cultivated land already suffering from high salinity (Shrivastava and Kumar, 2015). Kantachote et al. (2016) noted that there was no difference in PNSB populations between organic and saline fields, indicating that the binding of Na\(^+\) from the produced EPS may be an effective mechanism to increase PNSB survival in saline soil.

Several experiments revealed the ability of PNSB to bioremediate HM such as Cd, Zn (Panwician et al., 2011; Sakpirom et al., 2017), Al, Fe (Khuong et al., 2017) and As (Batrool et al., 2017). Cd and Zn are commonly found in areas with intensive mining (Li et al., 2014; Xu et al., 2014). Taking into account that paddy fields close to the aforementioned areas are still in use (Xu et al., 2014), the concentrations of these HM are building up. Al and Fe are basic components of acid sulphate soils which are used for rice cultivation in Asiatic countries (Panhwar et al., 2016). This type of soil causes drastic reduction of rice yields, mainly due to metal toxicity, and are expected to have a major effect in the future food security. Furthermore, As is a toxic HM naturally occurring or released by industrial processes. When plants are grown in As-contaminated waters, the growth and yields are reduced as a result of toxicity (Li et al., 2007). As-resistant PNSB have the ability to oxidize and reduce As in addition to adsorb and desorb it, as a defence mechanism against As toxicity (Stolz et al., 2006; Nookongbut et al., 2016). It is recognized that paddy fields are amongst the areas that suffer the most from increasing As accumulation (Meharg and Rahman, 2003). Therefore, rice cultivation in paddy fields is often limited due to HM contamination, and thus, PNSB can play an important role in their bioremediation.

Paddy fields have been identified as one of the major contributors of CH\(_4\) emissions (Yagi and Minami, 1990). Specifically, it is estimated that about 10% of the total annual CH\(_4\) budget originates from rice cultivation (Cao et al., 1998). This CH\(_4\) source is particularly important, as the rice produced in paddy fields is a major component of the global economy and nutrition. CH\(_4\) production in paddy fields is enhanced by the addition of straw, which is a common technique to increase soil fertility in flooded paddy fields (Harada et al., 2005; Nunkaew et al., 2014a; Kantha et al., 2015; Sakpirom et al., 2017). Straw is metabolized to acetic acid by anaerobic microbes and is subsequently converted to CH\(_4\) (Conrad, 2007). Studies performed under mimicked paddy field conditions prove the potential of PNSB to suppress the growth of methanogens in paddy fields (Harada et al., 2003; Nunkaew et al., 2014a; Kantachote et al., 2016; Sakpirom et al., 2017). As explained in section Greenhouse gas emission mitigation, due to their suitability for PNSB growth, paddy field conditions may result in higher growth rates for PNSB compared to methanogens, enabling them to eventually outcompete the methanogens (Harada et al., 2001a). Moreover, PNSB have the ability to reduce CO\(_2\) emissions (Kantha et al., 2015; Sakpirom et al., 2017), even when paddy fields are characterized by high salinity or are
contaminated with HM. The rechanneling of organics into PNSB biomass (rather than CH₄ and CO₂) was demonstrated during tests with paddy soil incubated with rice straw under illuminated conditions, where the MPN of PNSB cells reached values of 1.0 × 10¹⁰ MPN g⁻¹ soil DW whereas the corresponding value for unilluminated assays was 4.0 × 10⁸ MPN g⁻¹ soil DW (Harada et al., 2005).

Research gaps and proposed roadmap of PNSB application in plant production

Even though the use of PNSB appears to be a promising approach for many applications, there is still a plethora of questions to be answered. This section discusses the key research gaps that emerged from reviewing existing literature and proposes a roadmap for future research and implementation. It should be stressed that the analysis of the existing literature revealed the need for a more comparable design of experiments and standardized measurement of key parameters, to facilitate systematic comparison and more generically valid findings.

Research, development and demonstration

The research gaps arisen through reviewing the existing literature can be divided in two categories: (i) PNSB production and (ii) application (Fig. 6). Regarding production, parameters to be taken into account include the selection of a suitable PNSB product (strain, microbial consortium or extracted compound), the cultivation conditions and the downstream processing. Given the generic nature of the latter two, they will not be elaborated in the present review. Concerning the application, two parameters will be discussed, namely (i) plant selection and (ii) application modalities. Even though plant selection will not be further elaborated, it should be noted that more trials are required in order to establish the plant types for which PNSB products are suitable. As can be seen in Fig. 6, the selection of a suitable product for each application is an iterative process, requiring a strong link between research (phase A) and valorization (phase B).

PNSB strain selection. Choosing a strain for a specific application is not straightforward, as many criteria need to be met. For example, Maudinas et al. (1981) inoculated R. capsulatus B10 in a hydroponic medium (deprived of a nitrogen source), and this strain alone was unable to sustain plant growth in such a system. On the other hand, Elbadry and Elbanna (1999) used R. capsulatus DSM 155 in a similar experiment, where normal plant growth was observed. Parameters to be considered during strain selection include the ability to grow under micro-aerobic conditions (Kantha et al., 2015), the potential to produce IAA and ALA, to fix nitrogen, and to produce soluble phosphate (Koh and Song, 2007; Lee et al., 2008). Furthermore, the carbon assimilation profiles give an indication about the
spectrum of plant metabolites that can be used from each microbe, indicating the suitability as plant growth-promoting rhizobacteria (Wong et al., 2014). Depending on the envisaged application, the extent of limiting the adverse effects of abiotic stresses plays an important role, as well as the HM bioremediation potential (Sakpirom et al., 2017). The isolation from environments with conditions similar to the envisaged application seems to be a promising approach (Fan et al., 2012; Sakpirom et al., 2017). In the study of Sakpirom et al. (2017), only seven from 235 PNSB isolates showed Sakpirom et al. (2017). In the study of Sakpirom et al. (2017), only seven from 235 PNSB isolates showed CH4 emissions, illustrating the complexity of only four strains were able to remove HM and reduce CH4 emissions, illustrating the complexity of finding promising strains. The authors of this study stated that finding promising strains for field applications, both extensive and intensive efforts are required (Sakpirom et al., 2017). This is in agreement with the findings of Lo et al. (2018), who performed a whole-genome sequencing and analysis of R. palustris strains PS3 and YSC3 isolated on paddy soils. Even though both strains contained genes associated to plant growth-promoting functions, the strain YSC3 did not enhance plant growth, which led to the conclusion that responses towards and interactions with plant hosts are essential. Furthermore, given that the combination of strains leads to better results than individual strains (Batrool et al., 2017), research should focus on the use of synthetic communities to achieve the highest potential efficiency. For instance, the combination of R. capsulatus with A. vinelandii (Maudinas et al., 1981) as well as R. palustris CS2 with R. faecalis (Batrool et al., 2017) resulted in better fertilization performance than application of individual strains. Mixed cultures outperform monocultures for a combination of diverse abilities, such as plant growth promotion, bioremediation of HM and GHG mitigation.

The unknown potential of PNSB-derived products. The limited amount of studies and parameters tested concerning the use of cultivation supernatants or extracted PGPS does not enable the complete evaluation of this product (Appendix S1 in section 2). Even though the application of ALA-containing PNSB cultivation supernatant restored the rice plant growth to the level of unfertilized plants not exposed to salinity stress, it resulted in lower growth performance than comparable dosage of commercially available ALA, indicating the presence of growth-inhibiting compounds (Nunkaew et al., 2014a). Apart from the inhibiting effect of these compounds when applied in their biomass-free form during batch tests, there is no evidence of their effect when accumulated in the field. Consequently, further research is required to establish the type of these inhibiting compounds and the mechanism of their production, as well as to elucidate their mechanism of action.

Application modalities. This literature review revealed that the required frequency and dosage of application remain yet undefined. For instance, the use of dried R. sphaeroides NR3 on spinach increased the yield (68%) when supplying 1.6 g dry PNSB cells, while the lower dosages did not have any effect (Kondo et al., 2008). On the other hand, the yield of mustard spinach increased (7.0%) only at the lowest dosage (0.28 g dry PNSB) (Kondo et al., 2008). Furthermore, Kondo et al. (2010) reported that the amount and times of application had no effect on fresh weight, Brix sugar content, titrable acidity, carotenoid and citric acid content, while they affected ascorbic, malic and phosphoric acid content of tomato fruit. Regarding the use of living cells, results show that weekly application of living PNSB on soil is sufficient to maintain the microbial populations for four (Lee et al., 2008) to 8 weeks (Wong et al., 2014) or for at least 17 days in a hydroponic system (Hsu et al., 2015), indicating that they can sustain their beneficial effects on plants. The large variation in frequency and dosage of application (Tables 1 and 2) did not enable making conclusions. Therefore, the effect of these parameters on plants, fruit and crops needs to be elucidated.

In addition, the reviewed studies did not present a clear pattern regarding the effect of each application method, due to the variability of the determined parameters. For example, Maudinas et al. (1981) inoculated R. capsulatus and A. vinelandii in a hydroponic nutrient solution (lacking a nitrogen source) for rice seedling growth (Oryza sativa L. cv. Delta). Normal growth, flowering and panicle formation were observed in 40% of the plants, indicating bacterial N2 fixation. Nevertheless, R. capsulatus alone was unable to sustain plant growth in such a system, as indicated by the signs of nitrogen deficiency in all plants and the fact that only 10% of the plants had formed panicles at the time of harvesting. On the other hand, Elbadry and Elbanna (1999) noted normal plant growth in similar experiments. Another example concerns the use of carrier material. When Harada et al. (2005) inoculated R. palustris KN122 at the flood-water of rice plants (Oryza sativa L. cv. Nipponbare), with and without the addition of rice straw, the shoot dry weight was not affected by the treatments. It was also observed that the total number of tillers and number of productive tillers was not affected by the inoculation when straw was not used, while they increased by 10–30% and 15% resp. when straw was supplied (Harada et al., 2005).

Furthermore, foliar spray of PNSB cells is a promising method to enhance photosynthesis as well as
increase the glucoside content of stevia plants (Wu et al., 2013). However, the most significant effect was observed by the combination of foliar spray and irrigation, rather than each method individually, due to the combination of plant growth-promoting effects of the two different application modes (Wu et al., 2013). Consequently, further research should be performed to establish the optimal fertilization strategy. Furthermore, foliar fertilizers containing PNSB are reported to contribute to disease resistance through the successful colonization of the phyllosphere (Su et al., 2017). Even though disease suppression through the use of microbes is theoretically an attractive solution, in reality, the alteration of environmental conditions due to the presence of viruses hinders the application potential (Atehnkeng et al., 2016; Cray et al., 2016). Given that studies using PNSB are scarce, no conclusion could be drawn about the optimal application method to promote disease resistance. Furthermore, no data were found regarding the effect of using PNSB products on microbial or parasitic plant diseases. Therefore, studies should focus on the effect of different PNSB application methods on the suppression of plant diseases.

The reviewed literature did not present a clear pattern regarding the effect of PNSB use on plant or/crop pigmentation. For instance, the use of dried PNSB yielded 23–54% higher chlorophyll content in mustard spinach (Kondo et al., 2004, 2008), while similar treatments had no positive effect on the chlorophyll content of spinach (Kondo et al., 2004). Additionally, the use of live PNSB increased the chlorophyll content of stevia by 30–88% (Wu et al., 2013), whereas similar treatment did not present a significant effect on Chinese dwarf cherry (4.8% increase) (Yin et al., 2012). In addition, there are no available data regarding the long-term effect of the use of PNSB in HM-contaminated fields, as well as whether the HM content in the crop is reduced through the treatment. Finally, as highlighted by Pikaar et al. (2018), elaborated field trials are required in order to establish whether the use of microbial products can increase the SOC of agricultural soils.

From research to implementation: Reflections on shelf life and application methods

To our knowledge, currently no PNSB products are available on the global market. Whereas the parameters to be considered during the production of bacterial inoculants have been summarized in the past (Bashan et al., 2014), an important remark concerning the industrialization of PNSB products concerns the costs of their production. Given their importance, the economic aspects are discussed separately (section A preliminary cost effectiveness analysis on PNSB).

A key concern at the distribution level is the shelf life of living inocula. Even though there are no available data regarding PNSB products, there is evidence that the shelf life of these liquid cultures is longer than 2 years at temperatures below 20°C (Catroux et al., 2001), and they can even tolerate temperatures up to 55°C (Mahdi et al., 2010). Future studies could focus on optimizing preservation conditions, through slowing down decay rates.

Finally, several application methods suggested in literature (Appendix S1 in section 1) are suitable for small-scale cultivation due to their labour-intensive nature, which can be translated to increased costs. For instance, seedling dipping in PNSB products requires a considerable amount of effort, whereas soil application, foliar spraying and seed coating seems to be possible on a large-scale due to the similar equipment already available. Therefore, further investigations are required in order to target potential consumers of each product type.

A preliminary cost effectiveness analysis on PNSB

A preliminary cost effectiveness analysis was performed by comparing the price (cost and profit margin) for delivering the different functionalities of PNSB with the current market price of products with comparable properties. Parameters contributing to the production costs include the cultivation medium and the need to provide sterile conditions. Concerning the former, as explained in section Sustainability of PNSB production, PNSB can be produced on recovered resources such as wastewaters (Verstraete et al., 2016). Therefore, they can contribute to resource recovery through the immobilization of nutrients from anthropogenic sources (i.e. wastewaters) (Hülsen et al., 2014; Alloul et al., 2019), while eliminating the need for external nutrient supply. Given that PNSB use the infra-red light spectrum, coating the reactors with a membrane permitting the penetration of this light spectrum would facilitate selective growth (Alloul et al., 2019), however, increasing the investment costs. Nevertheless, provided that selective production in raceway ponds can be established, this would lower the overall costs. Given the forthcoming related innovations, these two parameters are not considered in the present cost analysis.

To our knowledge, only, Alloul et al. (2019) reported estimated production costs for photoheterotrophic PNSB production under European conditions. This economic estimation was based on a closed photobioreactor fed with recovered resources (brewery effluent) and included harvesting and downstream processing with ultrafiltration, centrifugation and spray drying as to obtain a biomass powder (i.e. dead cells). A production cost of €10.0 kgDw⁻¹ was estimated, which is comparable to the cost of producing dried microalgae (€12.6 kgDw⁻¹).
Purple non-sulphur bacteria present promising results in plant cultivation as they combine multiple functions: direct and indirect fertilization, biostimulation and biotechnology as they combine multiple functions: direct and indirect fertilization, biostimulation and biofortification as well as demonstrating environmental benefits. Paddy fields provide favourable conditions for these photosynthetic bacteria to grow (photoheterotrophically, micro-aerobically), therefore, allowing them to unfold their full potential in enhancing rice plant growth, harvest yield and quality, reinforcing the resistance to environmental stresses while reducing environmental footprint of rice production. However, the synergies involved are not yet fully understood. Further research is required to establish the optimal strain (or microbial consortium), frequency, formulation and dosage of each application and evaluate the effect of the PNSB metabolites on plant growth and environmental parameters. Answering these questions should pave the way for the use of PNSB products in a variety of agricultural applications leading to a better and more sustainable food production.

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Conflict of interest

None declared.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details regarding the application methods of PNSB, effects of PNSB on plant cultivation, and economic aspects of PNSB production addressed in the review.

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