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Review

Potential of Purple Non-Sulfur Bacteria in Sustainably Enhancing the Agronomic and Physiological Performances of Rice

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Abstract: Cereal grains and tubers are among the highly consumed staple foods globally; however, due to unfavorable weather conditions and the competition for natural resources, the major staple cereal crops, such as rice, are under production threat. On the other hand, the overuse of chemical fertilizers and pesticides to increase crop yield is deteriorating the growing environment for plants and animals, including humans. As such, sustainable management practices are the key method that can be employed to increase crop production without harming the environment. Plant growth-promoting bacteria (PGPB), such as the purple non-sulfur bacteria (PNSB), have recently gained much attention in crop production due to their ability to accumulate higher-value compounds that are highly beneficial to crops. Some of the major benefits PNSB holds are that it can fix atmospheric nitrogen, solubilize phosphate, remediate heavy metals, suppress methane emissions from waterlogged paddy fields, and assist in carbon sequestration. These benefits allow PNSB to be an important bacterium for improving plant growth and yield much more sustainably while benefiting the environment. This review article discusses the beneficial effects of PNSB on rice crop plants through careful screening of previous work in this area. The review also identifies the research gaps and suggests future research pathways to make PNSB an important bacteria for sustainable rice crop production. The review paper aims for the United Nation's sustainable development goal number two, "Zero Hunger," target 2.4, indicator 2.4.1, "Proportion of agricultural area under productive and sustainable agriculture".

Keywords: carbon sequestration; climate change; heavy metals; photosynthetic bacteria; purple non-sulfur bacteria; sustainable agriculture; zero hunger

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1. Introduction

Agriculture in the 21st century is under pressure due to climate change [1] and the growing world population [2]. According to the United Nations Department of Economic and Social Affairs, Population Division, the world population, currently standing at around 7.8 billion people, will rapidly increase to about 8.5 billion people by 2030 and approximately 9.7 billion people by 2050 [3]. Such an increase in the future world population requires expanding food production to meet the growing demand. However, the current crop production is already under stress due to climate change [4] and increasing human activities. Besides increasing carbon dioxide (CO_2) levels for photosynthesis [5,6] and increasing temperatures in temperate regions [6], the increasing temperatures in non-temperate regions, precipitation frequency and intensity, and extreme weather events will further impact crop yield by lowering crop growth and development [6,7].

Rice, a globally important cereal crop and staple for half of the world population [8–11], is among the other important crops that are threatened by the effects of climate change.

Higher or lower temperatures other than optimum temperature slow down rice's development stage and the time to reach the heading stage [12]. According to Yoshida et al., the reproductive stage in rice is highly susceptible to higher temperatures than the vegetative stage, resulting in lower yields [13]. On the other hand, the soil salinity issue is the second biggest problem in paddy fields [14] that affects the productivity and growth of rice crops [15]. Likewise, heavy metal contamination leads to plant stress affecting agronomic traits, such as the number of panicles per plant, grain fertility, grain yield, and grain size [16–19]. In addition, the overuse of agrochemicals to enhance rice yields leads to soil acidification, destroys food web systems, contributes to water and air pollution, decreases soil fertility, and releases greenhouse gases [20–24]. Methane (CH_4) is the second most important greenhouse gas, with a higher warming potential than carbon dioxide. Paddy fields are the common source of anthropogenic CH_4 emissions, accounting for around 10–20% of emissions [25].

Thus, these issues indicate the need for sustainable management practices to enhance rice production and, at the same time, reduce contribution to climate change. Microorganisms, mainly bacteria, play a vital role in sustainable agriculture with the ability to promote plant growth, reduce plant stress caused by abiotic and biotic factors, nutrient recycling, and manage soil fertility, leading to low usage of chemical fertilizers and pesticides that pose adverse effects on soil or the crops [26]. Purple non-sulfur bacteria are phototropic microorganisms that can enhance plant growth, boost resistance to environmental stress, improve the yield and quality of edible parts, alleviate salinity stress, improve plants' resistance to heavy metal stress, and mitigate greenhouse gas emissions [27]. Therefore, this review paper discusses the importance of using purple non-sulfur bacteria to increase rice crop growth and yield sustainably. The article also seeks to identify the research gaps from previous studies on rice using PNSB and suggest pathways for future research.

2. Purple Non-Sulfur Bacteria (PNSB)

Photosynthetic bacteria (PSB) are procaryotes capable of carrying out photosynthesis by converting light energy into chemical energy. These photosynthetic bacteria can either grow in the presence or absence of oxygen (aerobic and anaerobic conditions) and can either use organic or inorganic substances as an electron donor to fix the atmospheric nitrogen (N_2) and carbon dioxide (CO_2) [28] (Figure 1).

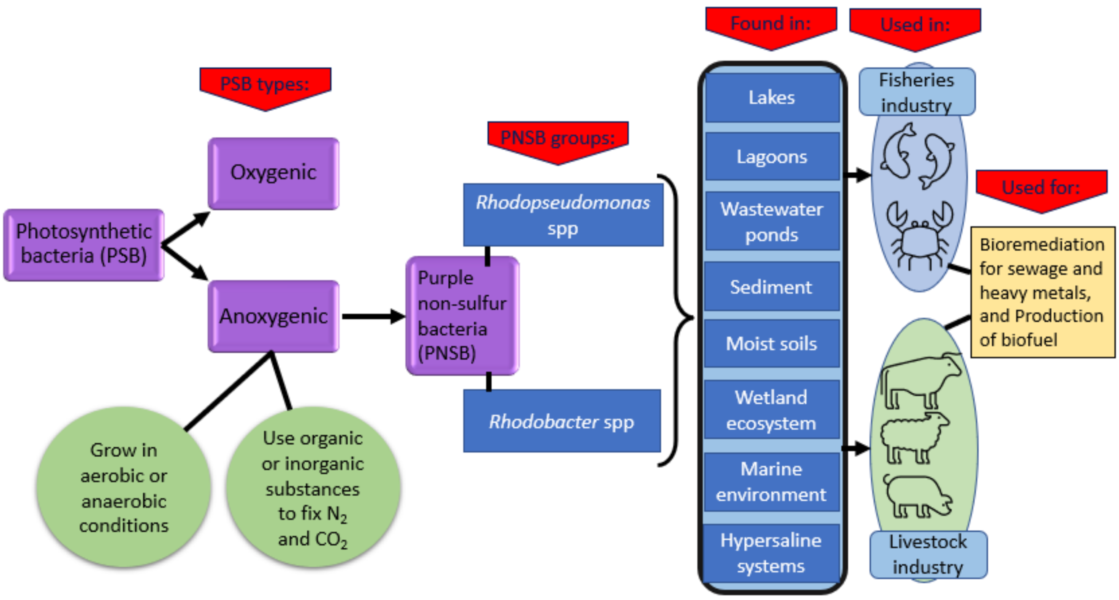

Figure 1. A brief overview of purple non-sulfur bacteria and their benefits to the environment.

The purple non-sulfur bacteria belong to the anoxygenic group of PSB, and their major groups include *Rhodopseudomonas* spp. and *Rhodobacter* spp. [29]. They are naturally present in wastewater ponds, lagoons, lakes, sediments, wetland ecosystems, moist soils, hypersaline systems, and marine ecosystems [30–32]. They possess versatile metabolic pathways [28] and, therefore, are widely used in the livestock and fisheries industries [33], in bioremedial methods for heavy metals and sewage [34,35], and in biofuel production (electricity or photohydrogen) [36]. Studies have also shown that PNSB help boost soil fertility when applied directly to the soil, whereas PNSB applied to plants help improve crop growth and yield.

2.1. Plant Growth Promotion and Yield Improvement in Rice by PNSB

Auxins are plant growth hormones that are produced by plants naturally. Indole-3-acetic acid (IAA) is an auxin that assists in plant development and regulates several plant growth and behavioral processes throughout the plant's life cycle [27]. Among other bacteria, four PNSB strains (KK415, TN110, TN217, and TN414) also produce IAA [37], which assists in plant growth and development. IAA produced by PNSB helps to activate cell roots and plant mineral uptake [37], stimulates root formation and seed germination, enhances fructification and vegetative growth, improves biosynthesis of compounds and photosynthesis, and assists in coordinating plant growth under stress conditions [38–43].

Few studies were done on rice to examine the potential of PNSB inoculation on crop growth and yield. A study by Kobayashi & Haque indicated that rice cultivated with *Rhodopseudomonas capsulatus* (*R. capsulatus*) supplied as PNSB powder to soil with 0.5 g of N, P, and K once during the reproductive phase increases the grain yield of rice [44]. The study indicates that the grain yield increase was due to the production of uracil and proline by the PNSB, whereas the soil detoxification by the PNSB led to an increase in soil fertility, thus improving plant growth. Another study on rice using *R. capsulatus* and *Azotobacter vinelandii* (*A. vinelandii*), with 600 mg and 60 mg protein, respectively, in hydroponic growing media, shows that the flowering and panicle formation was shortened to 100 days after germination with increased size and volume of root hairs [45].

Yoshida et al. inoculated *R. capsulatus* in compost at a final concentration of 10^9 cells g^{-1} twice in a field trial, resulting in an increased rice yield and ear number [46]. Soaking rice seedlings for 30 min in *R. capsulatus* cell suspension increases dry weight, plant height, grain yield, and straw and grain nitrogen content [47]. Studies have also shown that inoculating the *R. capsulatus* in the roots of rice seedlings in the hydroponic plant production system increases the shoot dry weight, shoot height, shoot and root nitrogen content, and root number, and decreases the root length and dry weight [48]. On the other hand, a pot experiment by Harada et al. shows that inoculation of PNSB into the waterlogged paddy field soils increases rice grain yield, with the higher grain yield achieved by the combined application of PNSB and rice straw [49]. When rice seeds were coated with an *R. capsulatus* cell suspension (10^8 CFU ml^{-1}) in 10% (*w*/*v*) gum Arabic solution, it led to an increase in shoot weight and height, straw nitrogen concentration, number of productive tillers, grain yield, number of grains per panicle, and grain nitrogen concentration [50].

Finally, inoculating PNSB through a foliar application on rice crop plants under field conditions of a tropical climate significantly improves growth and yield even under cooler temperatures and low light conditions [6]. This effect was shown in the recent study done by Shan et al., indicating that the inoculation of *R. palustris* through foliar application under field conditions improves rice crop tiller number, leaf chlorophyll content, lodging resistance, root length, root dry weight, productive tillers per plant, average grain per plant, grain yield, grain weight, and harvest index.

These studies revealed that PNSB inoculation on plants or soil improves soil fertility and photosynthesis rates, thereby improving plant growth and yield. However, PNSB inoculation alone has little to no effect on plant growth and yield, and as such, fertilizer application is necessary to achieve improved results [50]. Combining *R. capsulatus* with chemical nitrogen fertilizers enhances the usage efficiency of synthetic nitrogen fertilizers.

Likewise, combining *Rhodopseudomonas palustris* spp (*R. palustris)* of PNSB with *Bacillus subtilis* (*B. subtilis*) can further enhance rice yields [51] due to the synergetic effects of their co-inoculation on plant growth. The *R. plaustris* is an important strain of PNSB that is used as a biofertilizer [52], while *B. subtilis* is a biological control agent that protects plants from phytopathogenic organisms [53]. Their combined effects help to improve the growth of various crop plants. However, excessive crop yield losses due to abiotic stress are a major threat to agriculture [54], and findings have shown that the inoculation of PNSB on crops can help alleviate both plant biotic and abiotic stresses [28].

2.2. PNSB Helps Alleviate Plant Stress in Rice

The production of reactive oxygen radicals higher than the usual amount in plants is a result of the stresses caused by environmental changes [55–59]. As a plant goes through abiotic stresses caused by air pollution, drought, extreme temperature change, heavy metals, herbicides, nutrient deficiencies, salinity, and UV radiation, they accumulate reactive oxygen species (ROS) [60–64], which are free radicals and non-radical molecules [65]. These include hydrogen peroxide (H_2O_2), hydroxyl radicals (OH), perhydroxyl radical (HO_2), and superoxide radical anions (O_2^-) [27,66]. Antioxidant enzymes, such as ascorbate peroxidase, catalase, glutathione reductase, and superoxide dismutase, detoxify the overproduced ROS. However, under extreme saline conditions, the antioxidant enzyme activity is reduced [27], leading to the overproduction of ROS [67] and causing damage to lipids, proteins, macromolecules, and carbohydrates [66]. Therefore, these antioxidant enzymes need to be provided to plants externally, or their synthesis needs to be promoted [27] for direct scavenging of free radicals to increase antioxidative defenses. One of the sustainable ways to promote plant growth and productivity even under abiotic stress conditions is by using microbial biostimulants [54].

The 5-aminolevulinic acid (5-ALA) is one of the promising biostimulants [68] and vital antioxidant promoters [69] that shields the photosynthesis apparatus during stress conditions [70] by acting as a shielding mechanism against ROS. The 5-ALA boosts the tolerance of plants toward salinity [71–73], temperature, drought, low-light stress [74], and biodegradable herbicides [75,76] (Figure 2). On the other hand, as a growth regulator, 5-ALA also regulates plant growth and development at different growth stages [77]. The exogenous application of 5-ALA also assists in chlorophyll accretion, thereby increasing photosynthetic activity in plants [72,78]. The 5-ALA is also responsible for enhancing the production of the essential cofactors of CO_2 fixation—ATP and NADPH [70]—and microorganisms can be an important source of 5-ALA for plant production due to the higher price of the commercially produced 5-ALA [72]. The PNSB species *R. palustris*, *Rhodovulum*, and *R. sphaeroides* produce 5-ALA [37,72,79], a plant growth regulator that assists in plant growth and yield and alleviates various abiotic stresses in plants [80].

Kantha et al. studied rice inoculated with *R. capsulatus* under salt stress conditions and concluded that using PNSB product can reduce the inhibition of rice husk carrier and rice straw and increase root dry weight, root length, shoot dry weight, and plant height [81]. On the other hand, Kantachote et al. applied 0.75 kg ha^{-1} of *R. palustris* spp of PNSB product fortnightly during the vegetative stage and weekly during the reproductive and maturation phase of rice, revealing that the PNSB has the potential to mitigate salt stress conditions in rice and increase the grain yield and grains per panicle [82].

Moreover, toxic molecules such as amines, hydrogen sulfide, etc., found in soil are metabolized by the PNSB, leading to soil detoxification, thereby helping improve soil fertility and plant growth conditions [44] (Figure 3). PNSB uses a variety of mechanisms, such as absorption on extracellular polymeric substances (EPS) bound to the outer surface of the cells, within cell accumulation, conversion of toxic to non-toxic compounds through redox transformation, and conjugation in the siderophores, to alleviate stress caused by heavy metals [37,83–85].

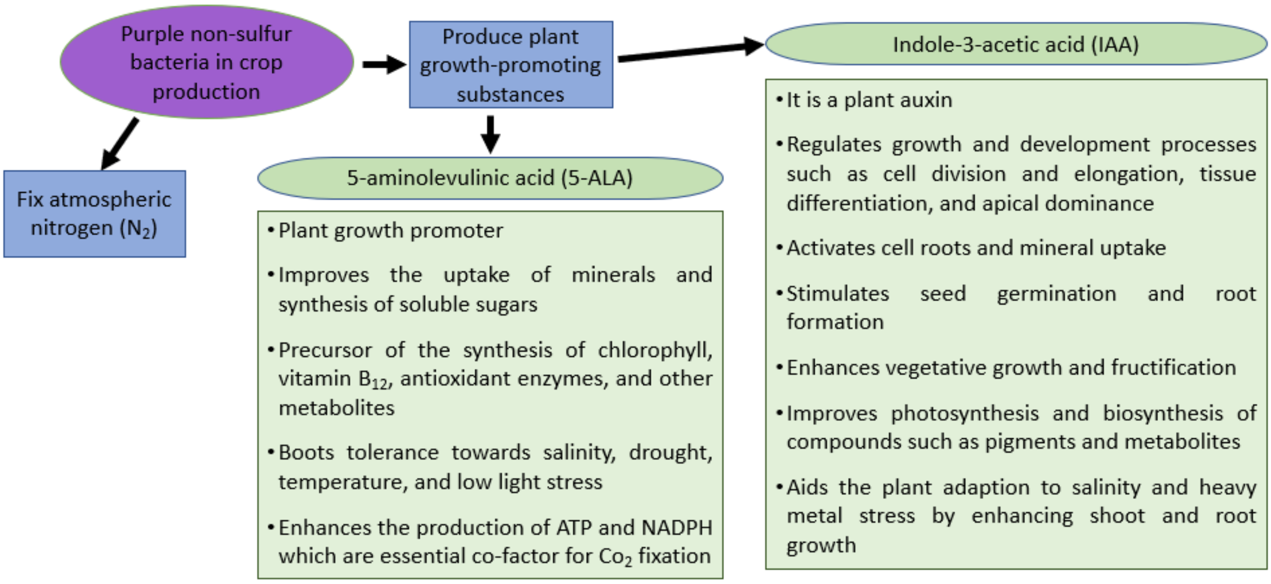

Figure 2. The plant growth-promoting substances produced by the purple non-sulfur bacteria to enhance plant growth and yield.

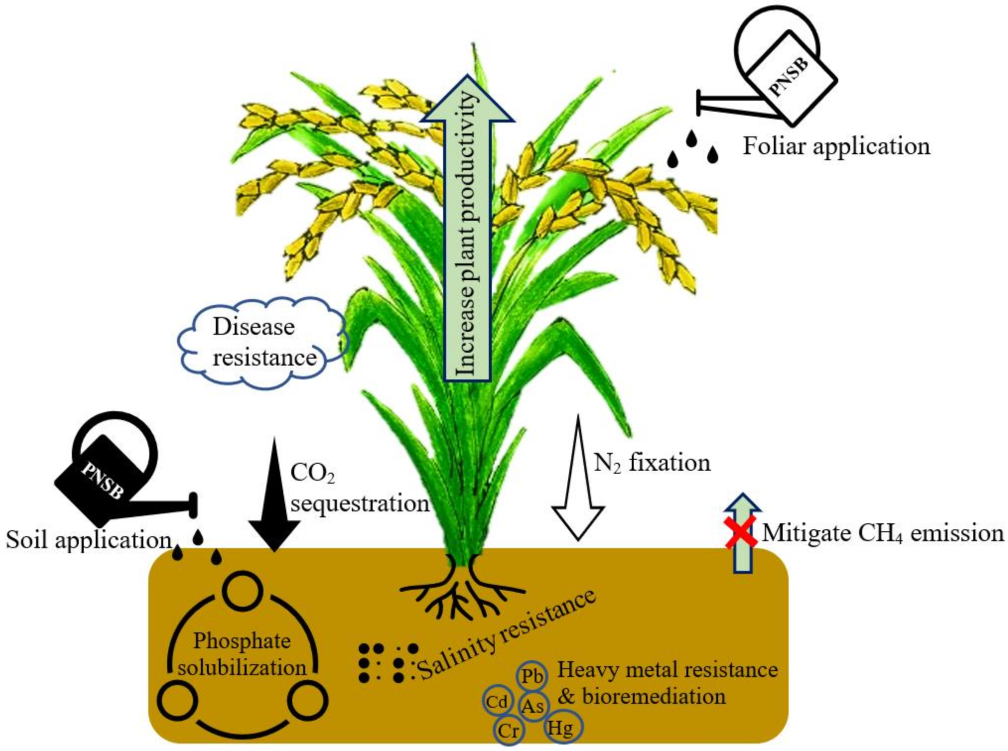

Figure 3. Summary of the benefits purple non-sulfur bacteria provides to the rice ecosystem when applied to soil or foliar.

A study by Nookongbut et al. reveals that the *R. palustris* spp of PNSB can reduce arsenic (As) stress in rice crops by reducing As accumulation, leading to an increased shoot and dry root weight, increase in shoot height, and enhanced photosynthesis rate [84]. The study also concluded that reducing As accumulation in plants makes it possible for rice farmers to produce safer rice for consumption from contaminated paddy fields. Another study showed that the *R. palustris* spp of PNSB has the potential to immobilize the lead (Pb) and cadmium (Cd) metals [86], which otherwise, when present in excessive amounts, can inhibit photosynthesis and respiration, thereby reducing rice crop productivity [87].

The study by Yoshida et al. showed that *R. capsulatus* spp of PNSB inoculation increases rice yield and ear number and can decrease the damage from hydrogen sulfide (H_2S) [46].

So far, studies on abiotic stress mitigation using PNSB show impressive results. However, more work is needed to prove these results under different growing conditions and soil types. Since rice is grown under field conditions, the performance of this bacteria in mitigating biotic and abiotic stresses should also be studied under field conditions. PNSB has also shown other benefits to the environment and human health, such as the potential to reduce methane (CH_4) emissions from the paddy fields, helping ease the problem of global warming (Figure 3).

2.3. PNSB Inoculation Reduces CH_4 Emissions from Rice Fields

Two common problems of waterlogged rice fields (organic or saline) are low productivity and CH_4 emissions [82]. Carbon dioxide (CO_2) and CH_4 are among the most significant greenhouse gasses since the 20th century, contributing to global warming and climate change. As indicated earlier, CH_4 holds a 20–25-times greater potential for global warming than CO_2. Waterlogged rice fields are among the most important anthropogenic sources of CH_4, with around 60 Tg of CH_4 year^{-1} contributing to global CH_4 emissions [88].

The study by Kantachote et al. showed that applying 0.75 kg ha^{-1} of *R. palustris* spp of PNSB on rice fortnightly during the vegetative stage and weekly during the reproductive and maturation phase increased not only the grain yield and grains per panicle but also decreased the CH_4 flux [82]. The PNSB competes with the methane-producing bacteria for a similar substrate and lowers the CH_4 emission by suppressing the methanogens population in the rice field. However, only a single study has been conducted to assess the effectiveness of PNSB in mitigating the CH_4 emission from rice fields; therefore, further research is needed to verify these results.

3. Research Gap

Even though research on rice using PNSB has been done, the frequency and dosage of PNSB on rice crop plants are still unclear due to the variations in the results obtained from various research [27]. For example, inoculation of *R. capsulatus* with *A. vinelandii* in the nutrient solution deficient in nitrogen for rice seedling growth shows normal growth and panicle and flowering formation in 40% of the plants, indicating bacterial nitrogen fixation [45]. However, it was clear that *R. capsulatus* alone cannot support plant growth, as revealed by the low nitrogen content in plants and 10% panicle formation before harvest. No such results were obtained in a similar study by Elbadry and Elbanna [48]. In another example, Harada et al. inoculated *R. palustris* KN122 in the waterlogged pots containing rice seedlings with and without using the rice straw, and the results show that the treatment did not affect the shoot dry weight [49]. However, previous studies have shown that growth and nitrogenase activity is promoted by including rice straw in the waterlogged soil of paddy fields [89–91] since it provides a better surface area for bacteria to colonize. In another study, the total number of tillers and the number of productive tillers were unaffected when inoculation was done without rice straw; however, the total number of tillers and productive tillers increased by 10–30% and 15%, respectively, when rice straw was used.

Moreover, limited studies under field conditions have been conducted to understand the effectiveness of PNSB inoculation on rice crops. Compost inoculation of *R. capsulatus* resulted in increased ear number, rice yield, and decreased damage from hydrogen sulfide (H_2S) [46]. Likewise, soil application of *R. palustris* fortnightly during the vegetative stage and weekly during the reproductive phase of the rice crops increased grain yield and grain per panicle and a decreased CH_4 flux under saline conditions [82]. Another study shows that the seeds were coated with *R. capsulatus* before transplanting in the field, resulting in improved shoot height, shoot weight, number of productive tillers, straw, grain nitrogen content, number of grains per panicle, and grain yield [50]. Each of these field-based studies used different strains of PNSB, which becomes difficult when comparing the results and deciding which species of PNSB are exceptionally effective. On the other hand, these studies used different sets of parameters for the experiment, which becomes challenging when comparing results. Therefore, further research under field conditions is greatly needed to understand the effectiveness of these PNSB strains in successfully developing biofertilizers for rice crops.

Besides, in recent years, plant diseases, either microbial or viral, have been shown to cause profound crop losses [27]. PNSB induces systematic resistance against viruses through the compounds they produce, i.e., 5-ALA, IAA, and siderophores [92]. This effect was shown in the study that investigated the effectiveness of PNSB in suppressing plant diseases, such as the tobacco mosaic virus (TMV) in tobacco plants [93]. The research concluded that PNSB, through foliar application, was able to successfully suppress the problem of TMV in tobacco plants grown under field conditions. From this study, we assume that PNSB also has the potential to control rice crop diseases when inoculated through foliar application. However, no such research has been conducted to investigate these effects under field conditions or controlled environments. As such, further experiments must be undertaken to recognize the effectiveness of PNSB in controlling rice diseases, which could help reduce our dependency on chemical pesticides.

Furthermore, studies done to investigate the effectiveness of PNSB in mitigating abiotic stress, i.e., heavy metal and salinity stress in rice crops, proved successful [72,84]. However, these studies were done in a controlled environment and do not exhibit a clear picture of the effectiveness of PNSB in mitigating abiotic stress in rice crops under field conditions. On the other hand, the results of these studies do not agree with each other, leaving a gap for further investigation. As such, further studies are needed to understand the effectiveness of PNSB in mitigating abiotic stress in rice crops under field conditions. Finally, since most of these experiments were done once, there is also a need to repeat these studies to prove the effectiveness of these results, especially under field conditions (normal growing conditions for rice crops).

4. Conclusions and Future Research Needs

This review shows an urgent need to increase rice yield due to the higher demand, which will significantly increase in the coming years with an increase in the global population. However, in an era of climate change, it is vital to employ sustainable management practices to improve rice growth and yield. One of the sustainable ways is to use the PGP bacteria, such as the PSB, of which the PNSB can be a suitable candidate to help increase yield by improving soil fertility, alleviating abiotic stresses, and eliminating methane emissions from waterlogged fields. However, the application rate and the application method of these PNSB for rice production (same for other crops) is still unclear, as shown from the results (incomparable results) of the previous studies. It is also unclear which species of PNSB can be used to get the most benefits out in the rice field. Therefore, further research on application methods, application rate, and suitable PNSB species for successful crop production needs to be identified to create a suitable biofertilizer to help improve the growth and yield of crops. Additionally, detailed research needs to be done under field conditions to recognize the effectiveness of this bacteria in enhancing the productivity of the field crops, such as rice, which was lacking in previous studies.

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