

REVIEW ARTICLE

Genomic Research Favoring Higher Soybean Production

Marcela C. Pagano^{1,*}, Mohammad Miransari^{2,*}, Eduardo J.A. Corrêa³, Neimar F. Duarte⁴ and Bakhytzhan K. Yelikbayev⁵

¹Federal University of Minas Gerais, Belo Horizonte, Minas Gerais, Brazil; ²Department of Book&Article, AbtinBerkeh Scientific Ltd. Company, Isfahan, Iran; ³Empresa de Pesquisa Agropecuária de Minas Gerais EPAMIG-URECO, Pitangui, MG, Belo Horizonte, Brazil; ⁴Instituto Federal de Minas Gerais, Reitoria, Belo Horizonte, Brazil; ⁵Kazakh National Agrarian University, Almaty, Kazakhstan

Abstract: Interest in the efficient production of soybean, as one of the most important crop plants, is significantly increasing worldwide. Soybean symbioses, the most important biological process affecting soybean yield and protein content, were revitalized due to the need for sustainable agricultural practices. Similar to many crop species, soybean can establish symbiotic associations with the soil bacteria rhizobia, and with the soil fungi, arbuscular mycorrhizal fungi, and other beneficial rhizospheric microorganisms are often applied as biofertilizers. Microbial interactions may importantly affect soybean production and plant health by activating different genomic pathways in soybean. Genomic research is an important tool, which may be used to elucidate and enhance the mechanisms controlling such actions and interactions. This review presents the available details on the genomic research favoring higher soybean production. Accordingly, new technologies applied to plant rhizosphere and symbiotic microbiota, root-plant endophytes, and details about the genetic composition of soybean inoculant strains are highlighted. Such details may be effectively used to enhance soybean growth and yield, under different conditions, including stress, resulting in a more sustainable production.

ARTICLE HISTORY

Received: January 15, 2020

Revised: June 10, 2020

Accepted: June 19, 2020

DOI:

10.2174/1389202921999200824125710

Keywords: Gene editing, germplasm, mutants, soybean genome, symbiotic microbes, microbial associations.

1. INTRODUCTION

Interest in the impact of agriculture on the soil organisms [soil biota and micro-biota], affecting the agro-ecosystem functioning and services [1], has increased in recent years [2, 3]. Among the most cultivated crops [maize, rice, wheat], soybean (*Glycine max* (L.) Merr.) is the more investigated leguminous species, establishing a symbiotic association with rhizobia and mycorrhizas. Mutualistic associations, including *Bradyrhizobium japonicum* and arbuscular mycorrhizal (AM) fungi, play a vital role in soybean production [4, 5]. The use of beneficial rhizospheric microorganisms as biofertilizers in agriculture has significantly increased, and the effects of multiple inocula on soybean growth and physiology should be better understood [6].

Soybean (*Glycine max* (L.) Merr) constitutes a major protein source for human and high-quality yield for animal feed [7]. The term soybean refers to the bean from which soy sauce was manufactured. Additionally, the production of important food supplements increases soybean consumption, thus, increasing the demand for more crop production. This

species was originally domesticated in China, with circa 23,000 cultivars in Asia, and then introduced in the USA and Brazil [8, 9].

Soybean, as one of the most important oilseed crops in the world [10], contains the highest protein content (40–42%) compared with the other food crops [11], and among food legumes, it is second only to groundnut in terms of oil content (18 to 22%) [12]. Soybean is used for aquaculture, human diet, and biofuel [13]. Moreover, soy protein helps prevent obesity and muscle fatigue [14].

The increase in the human population is expected to lead to an increase in global crop demand in the future [15-18]; however, agricultural production cannot be sufficient for the estimated demand. Soybean is part of the 16 major crops cultivated worldwide [19]. Thus, urgent need in research for soybean yield is required by policy makers and land managers [13]. Grain legumes have advantages over cereals by associating with N₂-fixing bacteria, a superior agronomic trait for N uptake [20].

Soybean is commonly grown after maize in Canada; however, the greater amounts of maize residues could negatively affect no-tillage soybean production by impacting soil nitrogen and soybean nodulation, soybean emergence, growth, and development, as well as affecting soil physical properties such as moisture and temperature [21, 22]. Soybean is also an important summer crop in Japan that is either

*Address correspondence to these authors at the Federal University of Minas Gerais, Belo Horizonte, Minas Gerais, Brazil;
E-mail: marpagano@gmail.com and Department of Book&Article, AbtinBerkeh Scientific Ltd. Company, Isfahan, Iran; Tel: +98313231755; Fax: +983132504068; E-mail: Miransari1@gmail.com

grown in rotation with winter wheat or left fallow in upland crop rotation systems [22].

With respect to the above-mentioned details and the need for the higher production of soybean worldwide (due to restricted cropping areas), this review is presented. The objective was to investigate the methods, which may enhance the efficiency of soybean production, including its symbioses with *B. japonicum* and arbuscular mycorrhizal (AM) fungi, and hence increase soybean yield production under different conditions, including stress. Among such methods, the use of genomic techniques may improve soybean growth efficiency and subsequent yield production.

1.1. Soybean Production

Soybean yield potential, the maximum yield of a crop cultivar adapted to an environment, with nutrients, non-limiting water, and pests and diseases successfully controlled, needs further examination, especially with regard to climatic and genetic potentials [23, 24]. Thus, due to the limited cultivable lands for soybean production, the need for public, private, and farmer investments to increase soybean yield is unavoidable [13]. The soybean cultivated area has increased by substituting other crops, exploiting pastures or replacing native vegetation, resulting in 36% more production. They explained that the production area has shifted from the USA and Asia to South America (Argentina and Brazil) [25].

The worldwide production of soybean, to more than 50%, was accomplished by the USA until the 1980s; however, since then it has decreased in the USA, while it has increased in Brazil (as the second largest producer followed by Argentina). United States, Brazil, Argentina, China, and India produce more than 92% of the world's soybeans, which is also planted in Africa [9].

In Brazil [Midwest and South regions], soybean accounted for 49% of the grain production area, resulting in technological advances. It is especially related to the cerrado grasslands [the Brazil's savannah], where the cultivation was promoted by the research of the Brazilian Agricultural Research Corporation (Embrapa) with the help of producers, industry, and private research centers [25].

The increase in the average productivity per hectare has approached the major world indices. Soybean cultivation is conducted with some sustainable agricultural practices, such as integrated crop-livestock-system and the use of no-tillage [25]. However, the use of pesticides and genetically modified crops, which convert a crop into herbicide resistant (*e.g.* Roundup Ready soybeans) [26], is increasing. Currently, the main transgenic crops, soybean and corn, followed by canola and cotton, are cultivated in the United States and other few countries [Argentina, Canada, and China]. Genetically modified crops as Roundup Ready soybeans are common in Argentina, the country with the second biggest transgenic area worldwide; however, the environmental impacts of these biotechnologies are little studied [27].

1.2. Soybean N Fixation

Soybean yields with high quality require large amounts of nitrogen (N), which can be applied as fertilizers or biofer-

tilizers. The biological fixation of atmospheric nitrogen (BNF) by the symbiotic soil bacteria, mainly *Bradyrhizobium* (Fig. 1), constitutes a less expensive source of N for soybean production. However, BNF efficiency is determined by many factors, including plant species, rhizobial strains, symbiotic associations, and environmental constraints [9]. Soybean symbiotic association with bradyrhizobium has been researched by different companies, educational centers, and individuals, resulting in the production of more efficient inoculants, which is of high value for the environment and for the sustainability of agro-ecosystems.

The recognition of soil microorganisms as an important component of below-ground biodiversity is not much integrated into policies for the conservation and management of the soil microbiota. In Africa, the increasing benefits of BNF for smallholder farmers were showed, especially due to inadequate quantities of inorganic fertilizers used to enhance soybean production [16]. The higher production of the uninoculated promiscuous soybean genotypes than some of the inoculated ones indicate the complex response to inoculation, suggesting to focus on the selection and breeding of promiscuous soybean varieties (the ones establishing symbiosis with a wide variety of rhizobium strains in the soils) [17]. The investment in the development and production of inoculum is affected by uncertainties resulted from the varied response in many regions and difficulties related to its production / conservation. The development and use of inoculum may be more profitable if they result in higher yield production (yield of three tons per ha is relatively common in Brazil) [16].

Rhizobia, providing one of the most important macronutrients for plant use, are symbiotic to legumes by the process of BNF. Due to the costly price of nitrate fertilizers to the farmer and also to the environment (the N fertilizers are produced by the consumption of non-renewable fossil energy and release greenhouse gases), the process of BNF can be suitable [28]. However, rhizobia may also affect the growth of economically important non-legume crops (rice or wheat) by acting as non-symbiotic plant growth-promoting bacteria. Thus, rhizobia have been widely researched and studied as models of mutualistic associations affecting crop production in sustainable agriculture [28].

1.3. Soybean Genomic Research

It is important to utilize genomic techniques, which may contribute to the increased production of soybean under different conditions, including stress. For example, the identification of loci, which control the appearance of favorable traits in soybean plants from mutants and germplasms, has significantly increased. The other interesting tool, which may modify soybean genetic properties, is the use of genome editing, which for example, resulted in the production of a soybean plant with a high rate of oleic acid, in 2019 [29].

Fang *et al.* [30] collected the 809 genotypes of soybean, from different parts of the world and phenotyped them for 84 traits. They were able to find 245 important genetic loci, with 95 loci, which were interactive and 14 genes, which controlled the accumulation of fatty acids in soybean. Among the determined loci, 115 controlled 51 traits in the phenotyped soybeans; 23 known loci and 16 unknown loci controlled different traits in the soybean plants.

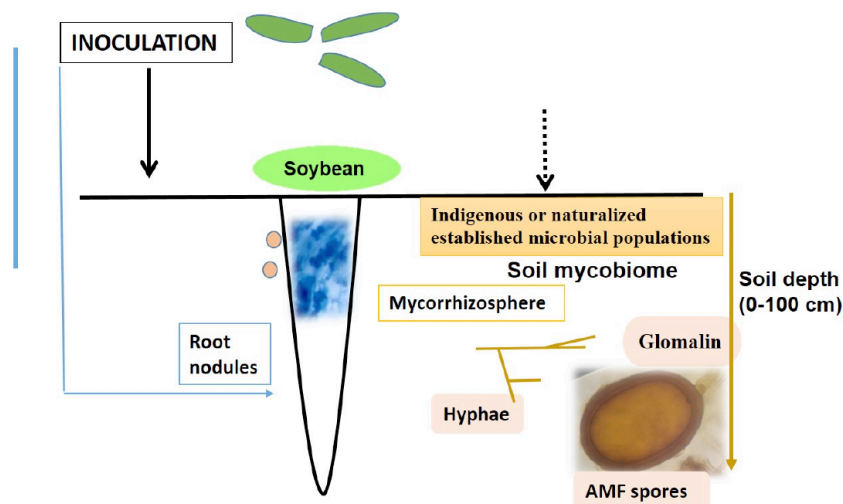


Fig. (1). Rhizobia and mycorrhizal fungal inoculation improve soybean tolerance under stress by modifying plants' genetic potential. (A higher resolution / colour version of this figure is available in the electronic copy of the article).

Zhang *et al.* [31] used genomic techniques to investigate the seed composition (fatty acids, proteins, oils, and amino acids) of 313 soybean germplasms. Accordingly, 87 regional chromosomes were found controlling seed composition. The related genes, found at the major loci, were GmSAT1, SACPD-C, AK-HSDH, and FAD3A with clear functioning and FATB, MtN21 nodulin, and steroid-5-a-reductase controlled N₂ fixation, and the composition of fatty acids and amino acids. The analyses also indicated that such genes had been used for molecular breeding. The authors accordingly indicated that such results could be used for the improvement of soybean nutrition, finding the correlation among different seed components, and providing insight for a better understanding of soybean gene alteration.

1.4. Soybean Microbial Associations

1.4.1. *B. Japonicum*

Beijerinck isolated and cultivated a microorganism [*Bacillus radiocicola*] from the nodules of legumes in the year 1888. Frank [32] renamed it as *Rhizobium leguminosarum* [33], which is retained in Bergey's Manual of determinative Bacteriology [34]. The differentiation of rhizobia is determined on the basis of their growth on a defined substrate, as fast (less than 6 h in selective broth medium) and slow [have mean generation time greater than 6 h] growers [35]. Among 750 genera of legumes containing 16000- 19000 species, only a few have been investigated for their symbiotic association with *B. japonicum* [36].

The establishment of *Bradyrhizobium* was the first accepted change in the rhizobia nomenclature [37]. *Bradyrhizobium* strain that nodulates soybean, characterized as *B. japonicum*, is the first recognized group of *Bradyrhizobium* strains [38]. More recently, *B. japonicum* USDA 110 species name has changed to *B. diazoefficiens* USDA 110 [39], which as a model species of well-studied rhizobia, its molecular genetics, physiology, and ecology have been intensively explored [40].

Soybeans associated with rhizobia, such as *B. japonicum* [*B. diazoefficiens*] and *B. elkanii*, provide about 50 to 60% of

N₂ supplied by BNF in nodules [41, 42]. In general, rhizobia are bacteria classified as *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium* and *Mesorhizobium*, which can survive and reproduce in the soil, and fix atmospheric N₂ inside the nodules developed in roots of their specific legume [43, 44].

Laranjo *et al.* [45] reviewed the rhizobial symbioses focusing on mesorhizobia as legume inoculants. They showed a brief history of rhizobia, their taxonomic diversity, nodulation N₂ fixation genes, and the rhizobial genomes. Moreover, rhizobia include Alphaproteobacteria [Rhizobiales] but some isolates of wild legumes belong to the Betaproteobacteria class [46]. Research indicates that the ability of legumes to be nodulated occurred once or several times during evolution [47]. For a review on the biogeography of nodulated legumes and their N₂-fixing symbionts, the reader can refer to Sprent *et al.* [48].

Dwivedi *et al.* [49] reviewed the development to improve symbiotic N₂ fixation and productivity of grain legumes. Nodules on soybean roots perform symbiotic N₂ fixation, which supply N for plant growth and seed production. Sugiyama *et al.* [11] reported changes in the rhizospheric bacteria and especially *Bradyrhizobium* during soybean growth, suggesting that the plant host could select for their symbionts. In the last years, approximately 19,992 peer reviewed journal papers on soybean production were presented (Table 1). Among the studies on soybean interaction with microorganisms, research on rhizobia predominated (circa 231 papers existing for rhizobia in soybean) over mycorrhizal research (39 articles). Among an increasing number of reviews published on N₂ fixation in legumes, soybean accounts for circa 15 documents in the SCOPUS database [6, 49-51]. Moreover, other articles [51-53] are available.

Dwivedi *et al.* [50] investigated the advances in host plant and rhizobium genomics to enhance symbiotic N₂ fixation in grain legumes. They indicated that soybean genome had been sequenced, and by using the model legumes, 52 genes were identified, which may contribute to finding allelic variations, which affect the agronomically beneficial traits of BNF.

Table 1. Journal articles dealing with soybean production worldwide.

Keywords	Number of Journal Articles
Soybean production	19,992
Soybean production + plant interaction	837
Soybean production + soil interaction	1,126
Soybean production + rhizobia	341
Soybean production + symbiosis	227
Soybean +Arbuscular mycorrhizas	257
Soybean production + <i>Arbuscular mycorrhizas</i>	57

Database survey conducted on October 2019 (SCOPUS).

In Brazil, the strain *B. japonicum* CPAC 15 is widely used in commercial inoculants. The inoculation with efficient strains can considerably increase the yield of important grain legumes worldwide, including soybean in South America as the most representative example [54]. However, the lack of responses to inoculant strains has been attributed to the indigenous or naturalized established population of rhizobia [55]. Thus, in the absence of established populations [areas cropped for the first time], inoculants can colonize the host plant more effectively. At present, a high production can be attained without the dominance of exotic soybean inoculant. However, annual re-inoculation can increase yield [56]. This is due to different known attributes of rhizobial strains, including competitiveness (capacity of the strain to compete against other strains), infectiveness (capacity of forming nodules in stressed environment), and effectiveness (capacity of fixing N₂), which compensate for plant selectiveness/promiscuity, survival, and competition with other strains, to infect and fix N₂ [57].

A successful BNF, thus, is determined by improving rhizobia, host plant, and its environment. The low N contents of most soils and the high price of N-fertilizers have led the farmers to the breeding and selection of more efficient cultivars (under low N conditions) and inoculation with superior strains, which improve N₂ fixation. Additionally, the established populations can evolve and change its effectiveness, which suggests the need to perform continuous monitoring of soil populations [58, 59].

Salvagiotti *et al.* [24] analyzed 637 data sets derived from 108 field studies in 17 countries that included N₂ fixation and N fertilization in soybean. They found that each kilogram increase in N accumulation in above-ground biomass resulted in a mean linear increase of 0.013 Mg soybean seed yield. They concluded that 50-60% of soybean N demand is fulfilled by biological N₂ fixation and increasing N fertilizer decreases plant N fixation. Moreover, the N₂ fixed by soybean is not enough to replace N export from the field with grains. However, properly assessing the real contribution of below-ground N, and its variation, needs more studies. Accordingly, they concluded that the yield response of soybean to N fertilizer is a function of the production environment and abiotic/biotic constraints that decrease crop growth and required N demand. Facing such constraints, the

development of rhizobium inoculums, able to fix N₂ under stress, seems viable to obtain N supply [58, 59].

It has been shown that the efficiency of the symbiotic process depends on many factors related to 1) the plant, 2) the bacteria, 3) the symbiosis, and 4) the environment. The issues of low soil fertility and limited availability of macro- and micro-nutrients can constitute the most important constraints [55]. The response of well-nodulated soybean crops to N fertilization is more likely in the absence of growth constraints and managing yields levels above 4.5 Mg ha⁻¹. Deep placement of [slow-release] fertilizer below the nodulation zone or applying N during reproductive stages in high-yielding environments exemplify encouraging decisions [24].

In central Iowa, USA, Diaz *et al.* [57] investigated the soybean response to inoculation and N application following long-term grass pasture due to the conversion of pastures into soybean fields. They observed that while the seed quality remained the same, rhizobia inoculation increased soybean grain yield, plant dry matter, N concentration, N accumulation, and grain N. In contrast, the fertilizer increased plant dry matter but not grain yield, with or without inoculation. Moreover, there was not any enhancement in plant N or seed quality. Accordingly, they suggested the inoculation of soybean seed (without N fertilizer), when planted after long-term grass pastures.

Cases of legume establishment in countries where there were not any nodulating rhizobia, to inoculate the established crop, were the reasons for the study of rhizobial evolution. The introduction of soybean in Brazil [58] or the implications of biserrula, nodulated by *Mesorhizobium ciceri* (typically known for nodulating chickpea), introduced in Australia, are examples of naturally occurring rhizobia able to evolve and acquire the genes to infect the introduced legume by lateral gene transfer. The detection of rhizobia able to nodulate biserrula, different from the original inoculant in Australian soils, required five years [59].

1.4.2. AM Fungi

With regard to mycorrhizas, Miranda [60, 61] compiled mycorrhizal details in crops from Cerrado. In line with earlier studies, the author showed that soybean could be symbi-

otic to four AMF inoculated species (*Glomus etunicatum*, *Entrophospora colombiana*, *Acaulospora scrobiculata* and *Gigaspora gigantea*) in pots with autoclaved native soil fertilized with P₂O₅ and lime. Accordingly, *G. etunicatum* was the most efficient inoculum followed by *E. colombiana*, increasing soy production by 4 times compared with the uninoculated control. The author also indicated that the plant production in the inoculated pastures [*Andropogon guayanus* and *Stylosanthes guianensis*] were more responsive to inoculation. Usually, the annual soybean crop presents less AMF colonization than maize, thus, crop rotation can benefit soybean association with AMF by twice the percent of colonization in the first year of soybean-maize rotation [60, 61].

Higo *et al.* [23] analyzed the diversity and vertical distribution (100 cm) of AMF under two soybean rotational systems in Japan. They found the influence of crop rotation on AMF communities with specific AMF colonizing soybean. They indicated 16 phylotypes of *Glomus* species predominating in the soybean rhizosphere, depending on crop rotation and soil depth. In Argentina, Grümberg *et al.* [62] showed the significant role of AMF in alleviating drought effects on soybean. They also pointed differences between mixtures of AMF isolates and single strain inoculum, proposing an effective selection of AMF for soybean.

1.5. Soybean Rhizobial Inoculants

1.5.1. *B. Japonicum*

Selection of the most efficient strains of *Bradyrhizobium*, performed for over decades in Brazil [and also in Argentina and other countries in South America] for the inoculation of the exotic soybean, is crucial for the first time of cultivation, as the yearly re-inoculation increases grain yield by 8%. Some researches showed frequent contamination [52].

Hungria *et al.* [52] investigated the details of inoculant preparation, production, and application. They confirmed BNF as crucial to avoid soil degradation negatively affecting crop yield worldwide. Benefits could be enhanced by the presence of efficient and competitive rhizobia in managed soils and better quality and availability of inoculants for legumes. They briefly mentioned the history of rhizobial inoculants and their less quality available products. Moreover, they indicated for the successful inoculation of the host plant, a long-term strain selection can be carried out together with the species, which are environmentally persistent.

Soybean was introduced in Brazil in 1882 and large cultivations were then mounted with bradyrhizobia inoculants from USA; however, a successful strain selection for the natural acid soils took place. The host plant demand for N increased due to the enhanced production of crop yields (in 2003, 2,765 kg ha⁻¹). The inoculated bradyrhizobia are present in most soybean cropped sites; however, more efficient and competitive strains must be selected for covering crop demand. Thus, persistent strains, which result in higher grain yield, have been selected. In commercial production, four strains with high capacity for BNF are commonly used; but the selection program continues to help farm owners. Among those strains, a variant of strains SEMIA 566 and CB 1809 resulted in the highest yield of soybean cultivar BR 133 as well as higher field nodulation from south Brazil. Both

strains did not differ significantly from the fertilized control (200 kg N ha⁻¹) [52].

In general, the number of rhizobia decreases with time, mostly determined by the environmental conditions, soil properties, and the characteristics of the bacterial strain. However, some researches showed persistence of inoculant along 5 to 15 years. Using more efficient inoculants, instead of established *Bradyrhizobium*, is difficult and needs frequent re-inoculations [52]. For example, the supplanting of CPAC 15 strain requires annual re-inoculation, with additional costs. For instance, the strain investigated through molecular methods and the factors, which control rhizobia persistence, must be sought [63].

Other disadvantages are the practices that limit the bacterial number, including 1) the incompatibility of rhizobia, 2) seed-applied pesticides or micronutrients and, 3) the use of small seed size. Due to the use of inoculants near the seed/seedling, they can be applied directly in the soil furrow as a liquid, granules, or peat [and not mixed with fertilizers] [63]. However, the application of higher inocula increases the cost of soil inoculation. For example, in Brazil, broth inoculants applied to the seed, in the furrow or 2.5 cm below the seed, provide more efficient soybean nodulation [63].

One important aspect of the inoculant industry is the rhizobial biodiversity, which is determined by the evaluation of several strain numbers. For example, 56 rhizobia strains were examined for the selection of high temperature-resistant strains for soybean in Iran [64].

Rodríguez-Navarro *et al.* [9] reviewed the soybean interactions with soil microbes, including the agronomical and most relevant genetic aspects of soybean rhizobia. However, they indicated the deficient knowledge of the molecular examinations determining cultivar-strain specificity and nodule occupancy by rhizobia competitors. Thus, different constraints prevent the development of more efficient commercial inoculants and their use for other agriculturally important plants.

Inoculation of soybeans under field conditions has been successful in the USA, Brazil, and Argentina. However, the presence of high populations of indigenous soil rhizobia is considered as an important factor limiting the wider and the more successful use of rhizobial inoculants in some particular areas. In most Chinese soils, more than 105 soybean rhizobia per gram of soil can limit nodule occupancy by the inoculant [9].

1.5.2. *AM Fungi*

The AMF association in soybean was less researched than the rhizobial symbioses. The response of soybean to inoculation with *Glomus* is generally successful; however, inoculation of other genera such as *Gigaspora* proved inefficient [65]. This can be related to the absorption of P by the fungus, which inhibited the activity of plant P transporters. AMF colonization increases micronutrient concentrations in plant tissues. For example, mycorrhizal soybean contains higher Zn levels than P fertilized plants [65].

Other researchers, such as Minhoni *et al.* [66], examined the AMF symbiosis in soybean. They observed that the increased levels of P fertilization decreased root colonization

with *G. macrocarpum*. Moreover, inoculation with AMF can improve soybean tolerance against drought and avoid the premature nodule senescence induced by such stress [67]. The combined use of AMF and rhizobia at appropriate rates may increase plant growth and resistance to pathogens [68] by increasing nodulation and N₂ fixation [69]. In the future, it is likely that microbial inoculants, including mycorrhizal fungi, will also be used as an important component in sustainable agriculture.

1.5.3. Co-inoculation

Due to their effects on plant growth and yield production, the rhizospheric ecology, including the interactions among the microorganisms and the environment surrounding roots [70], is of major interest to agronomists. It is crucial to use and develop technologies, including the use of microorganisms, which make the understanding of such interactions possible. Legumes are interactive with their rhizospheric microbes, especially the rhizobia [71]. Thus, the microbiota, present in the legume rhizosphere, can have several benefits and result in the recycling, mineralization, and uptake of nutrients. Moreover, microbes are able to produce plant growth regulating substances, such as amino acids, vitamins, and phytohormones [72, 73].

The estimation of crop loss from pathogens is not much documented; however, it includes from 7 to 15% of crop loss related to major world crops [wheat, rice, potato, maize, and soybean] resulted from fungi and bacteria [74]. Soil bacteria, PGPR, are capable of promoting plant growth in endophytic, or symbiotic association as well as free-living microorganisms, by enhancing plant nutrient uptake or production of plant hormones, or also by alleviating the biotic stresses, including the pathogens [72, 73].

Interestingly, inoculation of plants with soil bacteria other than rhizobia has also been the center of attention during recent times. Inoculation of *Azospirillum* is capable of increasing plant growth and seed yields by, for example, the production of plant hormones and the enhancement of phosphate uptake by plant roots. The co-inoculation with *Azospirillum* and rhizobia can improve nodulation and N fixation [9].

Co-inoculation of three *Bacillus* strains, isolated from the nodules of vigorous field-grown soybean, with *B. Japonicum*, has been indicated by research [75], which resulted in the increased nodulation and plant total biomass, including root growth, total N, and grain yield [76]. They suggested a selected strain (*B. thuringiensis* NEB17) for use as a plant growth promoting bacteria (PGPR) to increase soybean yield production under cool and short growing conditions. It is because suboptimal root zone temperatures inhibit nodulation and N fixation by soybean, and PGPR can alleviate such stress.

In Asian countries such as Pakistan, less amount of soybean yield is produced compared with the other top producer countries. One of the important constraints of soybean production, especially in the arid and semi-arid areas of the world, is the decreased fertility of soil due to intensive cropping. Accordingly, BNF related research may present more possibilities to increase crop yields. Compared with the use of P₂O₅ chemical fertilization, the inoculation of soybean

seeds with N₂-fixing and P-solubilizing bacteria resulted in higher yield [77]. Moreover, several species of *Pseudomonas sensu*, belonging to rRNA group I, can solubilize phosphate *in vitro* [78].

In their experiments of soy co-inoculation, [79, 80], higher levels of phytohormones, including auxins and gibberellins, were produced by the *Pseudomonas* strain 54RB, than the *Bradyrhizobium japonicum* strain TAL 377, with a P solubilization index of 4.1. The strain, with the highest amount of phytohormones, also resulted in the highest growth and yield [79, 80]. The dual inoculation of *Bradyrhizobium-Pseudomonas*, combined with the use of triple super phosphate (P₂O₅), was the most efficient treatment enhancing plant growth and yield parameters, including plant height, number of pods, and grain yield of soybean. They concluded that co-inoculation with the use of P₂O₅ was more effective in increasing grain yield of soybean (between 12 and 38% as compared with only P₂O₅) both under controlled and field conditions. It is also known that higher P uptake and N accumulation has resulted in mycorrhizal plants. Soybean can establish tripartite symbiotic associations with rhizobia and AMF [81]; however, there is little research on plant growth, or root architecture as well as on N and P availability affected by such type of symbiosis.

Wang *et al.* [82] also tested how co-inoculation with AMF and rhizobia may affect soybean growth, specifically root architecture and availability of N and P in a field experiment. They found the positive effects of AMF colonization on root architecture. They observed that under P-deficient conditions, a soybean genotype with deep roots was more responsive due to its greater rate of AMF colonization and higher nodulation under high P compared with the shallow root genotype. They observed that the N and P status determined the synergistic association between rhizobia and AMF affecting soybean growth. Soybean growth was positively affected by co-inoculation with rhizobia and AMF under P and/or N deficient conditions [increased shoot dry weight, along with plant N and P content were observed]. The effects of co-inoculation were correlated to root architecture, as co-inoculation was more effective on the deep root genotype compared with the shallow root genotype.

It is known that inoculation with efficient rhizobia at ordinary doses does not increase the seed yield of soybean considerably because the inoculated rhizobium would not be able to efficiently inoculate the host plant, which is mostly due to the presence of less efficient native rhizobia [83]. Accordingly, to increase the seed yield by rhizobial inoculation, the bacterial rate of inoculation must increase, which is a function of different parameters, including the bacterial strains and inoculation methods [84].

A large number of useful strains had been isolated from mutagenized and recombinant rhizobia to find the most efficient and competitive strains [85, 86]. One important aspect determining the successful colonization of the legume rhizosphere by an inoculated strain of *Bradyrhizobium* is its ability to effectively compete with the indigenous microorganisms for organic compounds produced by the root. The population of indigenous bacteria, as well as their growth rate, influence the colonization.

Sakamoto *et al.* [87] analyzed and compared (with control (uninoculated) roots) the transcriptions of soybean genes, which are differentially activated during the single and combined symbiosis of rhizobia and mycorrhizal fungi. The soybean plants were inoculated with the microbial inoculants for 6 weeks and the transcription analysis of their roots was then determined by the oligo DNA method. The co-inoculation with rhizobia and mycorrhizal fungi resulted in the highest nodule number and soybean growth. The single and combined inoculation of the microbes resulted in the up- (187, 441 and 548) and down-regulation (119, 1439, and 1298) of host genes.

According to the results, during the single and combined inoculations, 34 of the genes were up-regulated, affecting the activation of transcription factors in the families of MYB and bHLH, membrane transporters, and type 1 metallothionein. However, during the combined symbiosis, 56 genes of the host plant were upregulated, resulting in the activation of the proteins controlling the metabolism of phenylpropanoid, carbonic anhydrase, and nodulin proteins. The up-regulation of nodulin genes, during the mycorrhizal symbiosis, possibly resulted in the increased number of the nodules and subsequent host plant growth. The authors accordingly indicated that the presence of mycorrhizal fungi, during the tripartite association of the soil microbes with the soybean host plant, can importantly affect BNF and the growth of the host plant [87].

1.6. Soybean Microbial Genomic Research

It is known that the land use system intensely affects biodiversity, and such changes in composition or species diversity of aboveground communities can affect soil communities [63, 64]. The interest in BNF and rhizobial symbioses was revitalized due to the need for sustainable agricultural practices. Different researches have compared the genetic and phenotypic diversity between rhizobium species, enabling the researchers to study the evolutionary interactions among the known species [46].

The progress in molecular genetics of rhizobia has highlighted some new knowledge related to these plant symbionts. The isolation of mesorhizobia from chickpea (*Cicer arietinum*), the most important legume known to be nodulated by *Mesorhizobium* species, has been shown in different researches [46, 47]. In the review by Laranjo *et al.* [47], the rapid evolution of *Mesorhizobia* was shown. They mentioned the lateral transfer of chromosomal symbiosis islands in the field from a soybean inoculant *B. japonicum* strain to both a *B. elkanii* and a *S. fredii* strains, as the first research indicating such type of transfer between different rhizobial genera. In *Mesorhizobium* strains, symbiosis genes are found in chromosomal symbiosis islands and only rarely in plasmids [47].

The classification of rhizobia is based on the sequencing of genes for 16S or small subunits of ribosomal RNA [SSU rRNA] [88]. Four species in *Bradyrhizobium* are correctly recognized: *B. japonicum*, *B. elkanii*, *B. liaoningense*, and *Bradyrhizobium* sp. [35-41]. The new species shall not be given to *Bradyrhizobium* but the plant host name shall be written in

parenthesis, as proposed by Young [43]. A more recent overview of the classification of rhizobia presented by Willems [44] shows the history of the rhizobia, now divided into several genera.

Bradyrhizobium elkanii [41] has phenotypic and genetic characters, which define a number of groups within the soybean nodulating bradyrhizobia. This group of *Bradyrhizobium* dominates ecosystems in Australia and central South America, in association with the native legumes in acidic soils [40]. *B. liaoningense* species presented extra slow-growing soybean rhizobia that form a coherent DNA-DNA hybridization group [42]. Moreover, some *Bradyrhizobium* strains, known as *Bradyrhizobium* sp., do not nodulate soybeans [43].

Shi *et al.* [89] isolated *B. japonicum* HLNEAU001 from soybean fields (45.75° N, 126.53° E). The authors accordingly analyzed 215 cores of soybean germplasm from Northeast China for nodule traits containing 0-95 nodules. The analysis indicated that *B. japonicum* HLNEAU001 is highly similar to *B. japonicum* USDA6 *B. diazoefficiens* USDA110, and 30 germplasm of soybean were analyzed for each strain. Interestingly, the new *B. japonicum* strain was able to make more nodules than the other two strains. The comparison of the genome sequence of the strains indicated that the three strains had 5790 core genes. The authors indicated that type III, IV, and VI produced proteins that resulted in the differences of nodulation among the different strains. The new isolated strain was able to fix N in symbiotic association with soybean under cold conditions, which is of significance for the sustainable production of soybean.

CONCLUSION

Some of the latest, related to genomic research favoring soybean production, worldwide, has been reviewed. Preserving agro-ecosystem services can be decisive to buffer the negative effects of global change. The symbiotic associations of soybean with AMF and rhizobia have greater potential as biofertilizers but, further studies are required to understand the full symbiotic and non-symbiotic microorganisms. For instance, *Glomeraceae* predominate in the soybean rhizosphere worldwide; however, AMF communities can change with plant cover, crop rotation, and soil depth. According to the literature, few rhizobia can survive under unfavorable conditions of soil and bio inoculants of rhizobia strains efficiently improve soybean growth and productivity. Finally, it was shown that soybean proper production could play a crucial role in the future, but more research is required in the rhizobial genomes and soybean microbiome. Soybean genome research and gene editing are among the most important methods, which can be used to enhance soybean growth and its symbiotic associations with beneficial soil microbes. Meanwhile, if the genetic structure of soil microbes is also modified, it would be possible to improve the symbiotic interactions of soybean with soil microbes and increase crop yield under different conditions, including stress.

CONSENT FOR PUBLICATION

Not applicable.

FUNDING

None.

CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

ACKNOWLEDGEMENTS

The authors would like to thank very much AbtinBerkeh Scientific Ltd. Company (<https://AbtinBerkeh.com>), Isfahan, Iran, for editing the manuscript, and revising it according to the journal's format.

REFERENCES

- [1] Wall, D.H.; Nielsen, U.N. Biodiversity and ecosystem services: is it the same below ground? *Nat. Edu. Knowledge*, **2012**, 3(12), 8.
- [2] Pagano, M.C.; Schalamuk, S.; Cabello, M.N. Arbuscular mycorrhizal parameters and indicators of soil health and functioning: applications for agricultural and agroforestry systems. In: *Soil Microbes and Environmental Health*; Miransari, M., Ed.; Nova Science Publishers: New York, USA, **2011**, pp. 267-276.
- [3] Pagano, M.C.; Covacevich, F. Arbuscular Mycorrhizas in Agroecosystems. *Mycorrhizal Fungi: Soil, Agriculture and Environmental Implications*; Fulton S.M., Ed; Nova Science Publishers: New York, **2011**, pp. 35-65.
- [4] Pagano, M.C. *Mycorrhiza: Occurrence in Natural and Restored Environments*; Nova Science Publishers: New York, **2012**.
- [5] Simard, S.; Austin, M.E. The role of mycorrhizas in forest soil stability with climate change. *Climate change and variability*. Simard, S., Austin, M. E., Ed; **2010**, pp. 275-302. <http://dx.doi.org/10.5772/9813>
- [6] Miransari, M.; Riahi, H.; Eftekhari, F.; Minaie, A.; Smith, D.L. Improving soybean (*Glycine max* L.) N₂ fixation under stress. *J. Plant Growth Regul.*, **2013**, 32(4), 909-921. <http://dx.doi.org/10.1007/s00344-013-9335-7>
- [7] FAO (Food and Agriculture Organization). **2003**. <http://apps.fao.org>
- [8] López-López, A.; Rosenblueth, M.; Martínez, J.; Martínez-Romero, E. Rhizobial symbioses in tropical legumes and non-legumes. *Soil Biology and Agriculture in the tropics, Soil Biology*; P. Dion, Ed; **2010**, 21, pp. 163-184. http://dx.doi.org/10.1007/978-3-642-05076-3_8
- [9] Rodríguez-Navarro, D.N.; Oliver, I.M.; Contreras, M.A.; Ruiz-Sainz, J.E. Soybean interactions with soil microbes, agronomical and molecular aspects. *Agron. Sustain. Dev.*, **2011**, 31(1), 173-190. <http://dx.doi.org/10.1051/agro/2010023>
- [10] Cattelan, A.J.; Dall'Agnol, A. The rapid soybean growth in Brazil. *OCL*, **2018**, 25(1), 1-12.
- [11] Sugiyama, A.; Ueda, Y.; Takase, H.; Yazaki, K. Cotton-groundnut intercropping system: a pragmatic approach for increasing edible oilseeds production in India. *Proc. Natl. Acad. Sci. India Sect. B Biol. Sci.*, **2015**, 87(3), 761-767.
- [12] Singh, R.J.; Alam, N.M.; Kumar, S. Bt Cotton-groundnut intercropping system: a pragmatic approach for increasing edible oilseeds production in India. *Proc. Natl. Acad. Sci., India, Sect. B Biol. Sci.*, **2017**, 87(3), 761-767. <http://dx.doi.org/10.1007/s40011-015-0643-5>
- [13] Masuda, T.; Goldsmith, P.D. World soybean production: area harvested, yield, and long-term projections. *Int. Food Agribus. Manag. Rev.*, **2009**, 12(4), 143-161.
- [14] Agyei, D.; Potumarthi, R.; Danquah, M.K. Food-derived multifunctional bioactive proteins and peptides: Applications and recent advances. *Biotechnology of Bioactive Compounds: Sources and Applications*; Gupta, V.K.; Tuohy, M.G.; O'Donovan, A.; Lohani, M., Eds.; Wiley-Blackwell: Chichester, **2015**, pp. 507-524. <http://dx.doi.org/10.1002/9781118733103.ch20>
- [15] The Economist. The miracle of the cerrado: Brazil has revolutionised its own farms. *Can it do the same for others?*, **2010**. Available from: <http://www.economist.com/node/16886442>
- [16] Chianu, J.N.; Huising, J.; Danso, S.; Okoth, P.; Chianu, J.N.; Sanginga, N. Financial value of nitrogen fixation in soybean in Africa: increasing benefits for smallholder farmers. *J. Life Sci.*, **2010**, 4(6), 50-59.
- [17] Mpeperekwi, S.; Javaheri, F.; Davis, P.; Giller, K.E. Soybeans and sustainable agriculture: 'Promiscuous' soybeans in southern Africa. *Field Crops Res.*, **2000**, 65(2-3), 137-149. [http://dx.doi.org/10.1016/S0378-4290\(99\)00083-0](http://dx.doi.org/10.1016/S0378-4290(99)00083-0)
- [18] Tilman, D.; Balzer, C.; Hill, J.; Befort, B.L. Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Acad. Sci. USA*, **2011**, 108(50), 20260-20264. <http://dx.doi.org/10.1073/pnas.1116437108> PMID: 22106295
- [19] Foley, J.A.; Ramankutty, N.; Brauman, K.A.; Cassidy, E.S.; Gerber, J.S.; Johnston, M.; Mueller, N.D.; O'Connell, C.; Ray, D.K.; West, P.C.; Balzer, C.; Bennett, E.M.; Carpenter, S.R.; Hill, J.; Monfreda, C.; Polasky, S.; Rockström, J.; Sheehan, J.; Siebert, S.; Tilman, D.; Zaks, D.P.M. Solutions for a cultivated planet. *Nature*, **2011**, 478(7369), 337-342. <http://dx.doi.org/10.1038/nature10452> PMID: 21993620
- [20] Foyer, C.H.; Nguyen, H.T.; Lam, H.-M.A. A seed change in our understanding of legume biology from genomics to the efficient cooperation between nodulation and arbuscular mycorrhizal fungi. *Plant Cell Environ.*, **2018**, 41(9), 1949-1954. PMID: 30520104
- [21] Wingeyer, A.B.; Amado, T.J.C.; Pérez-Bidegain, M.; Studdert, G.A.; Varela, C.H.P.; Garcia, F.O.; Karlen, D.L. Soil quality impacts of current south American agricultural practices. *Sustainability*, **2015**, 7(2), 2212-2242. <http://dx.doi.org/10.3390/su7022213>
- [22] Vanhie, M.; Deen, W.; Lauzon, J.D.; Hooker, D.C. Effect of increasing levels of maize (*Zea mays* L.) residue on no-tillsoybean (*Glycine max* Merr.) in Northern production regions: a review. *Soil Tillage Res.*, **2015**, 150, 201-210. <http://dx.doi.org/10.1016/j.still.2015.01.011>
- [23] Higo, M.; Isobe, K.; Yamaguchi, M.; Drijber, R.A.; Jeske, E.S.; Ishii, R. Diversity and vertical distribution of indigenous arbuscular mycorrhizal fungi under two soybean rotational systems. *Biol. Fertil. Soils*, **2013**, 49(8), 1085-1096. <http://dx.doi.org/10.1007/s00374-013-0807-5>
- [24] Salvaggiotti, F.; Cassman, K.G.; Specht, J.E.; Walters, D.T.; Weiss, A.; Dobermann, A. Nitrogen uptake, fixation and response to fertilizer N in soybeans: a review. *Field Crops Res.*, **2008**, 108, 1-13. <http://dx.doi.org/10.1016/j.fcr.2008.03.001>
- [25] MAPA. *Ministério da Agricultura, Pecuária e Abastecimento*, **2015**. <http://www.agricultura.gov.br/>
- [26] Sobolevsky, A.; Moschini, G.; Lapan, H. Genetically modified crops and product differentiation: trade and welfare effects in the soybean complex. *Am. J. Agric. Econ.*, **2005**, 87(3), 621-644. <http://dx.doi.org/10.1111/j.1467-8276.2005.00752.x>
- [27] Castro, G.S.A.; Crusciol, C.A.C. Yield and mineral nutrition of soybean, maize, and Congo signal grass as affected by limestone and slag. *Pesqui. Agropecu. Bras.*, **2013**, 48(6), 673-681. <http://dx.doi.org/10.1590/S0100-204X2013000600013>
- [28] Ho, Y. Plant-microbe ecology: interactions of plants and symbiotic microbial communities. *Plant Ecology-Traditional Approaches To Recent Trends*, IntechOpen, **2017**, pp. 93-119.
- [29] Li, M.W.; Wang, Z.; Jiang, B.; Kaga, A.; Wong, F.L.; Zhang, G.; Han, T.; Chung, G.; Nguyen, H.; Lam, H.M. Impacts of genomic research on soybean improvement in East Asia. *Theor. Appl. Genet.*, **2020**, 133(5), 1655-1678. <http://dx.doi.org/10.1007/s00122-019-03462-6> PMID: 31646364
- [30] Fang, C.; Ma, Y.; Wu, S.; Liu, Z.; Wang, Z.; Yang, R.; Hu, G.; Zhou, Z.; Yu, H.; Zhang, M.; Pan, Y.; Zhou, G.; Ren, H.; Du, W.; Yan, H.; Wang, Y.; Han, D.; Shen, Y.; Liu, S.; Liu, T.; Zhang, J.; Qin, H.; Yuan, J.; Yuan, X.; Kong, F.; Liu, B.; Li, J.; Zhang, Z.; Wang, G.; Zhu, B.; Tian, Z. Genome-wide association studies dissect the genetic networks underlying agronomical traits in soybean. *Genome Biol.*, **2017**, 18(1), 161. <http://dx.doi.org/10.1186/s13059-017-1289-9> PMID: 28838319
- [31] Zhang, J.; Wang, X.; Lu, Y.; Bhusal, S.J.; Song, Q.; Cregan, P.B.; Yen, Y.; Brown, M.; Jiang, G.L. Genome-wide scan for seed composition provides insights into soybean quality improvement and the impacts of domestication and breeding. *Mol. Plant*, **2018**, 11(3), 460-472. <http://dx.doi.org/10.1016/j.molp.2017.12.016> PMID: 29305230

- [32] Frank, B. Über die Pilzsymbiose der Leguminosen. *Ber. Dtsch. Bot. Ges.*, **1889**, 7, 332-346.
- [33] Fred, E.B.; Baldwin, I.L.; McCoy, E. *Root nodule bacteria and leguminous plants. University of Wisconsin Studies in Science No.5*; University of Wisconsin: Madison, **1932**.
- [34] Holt, J.G.; Krieg, N.R.; Sneath, P.H.A.; Staley, J.T.; Williams, S.T. *Bergey's manual of Determinative Bacteriology*; Williams and Wilkins Press: Baltimore, **1994**.
- [35] Elkan, G.H. Taxonomy of the rhizobia. *Can. J. Microbiol.*, **1992**, 38(6), 446-450.
<http://dx.doi.org/10.1139/m92-075>
- [36] Allen, O.N.; Allen, E.K. *The Leguminosae*; University of Wisconsin Press: Madison, Wis., **1981**.
<http://dx.doi.org/10.1007/978-1-349-06142-6>
- [37] Jordan, D.C. Transfer of *Rhizobium japonicum* Buchanan 1980 to *Bradyrhizobium* gen. nov. a genus of slow growing root nodule bacteria from leguminous plants. *Int. J. Syst. Bact.*, **1982**, 32(1), 136-139.
<http://dx.doi.org/10.1099/00207713-32-1-136>
- [38] Young, J.A.W.; Haukka, K. Diversity and phylogeny of rhizobia. *New Phytol.*, **1996**, 133(1), 87-94.
<http://dx.doi.org/10.1111/j.1469-8137.1996.tb04344.x>
- [39] Delamuta, J.R.M.; Ribeiro, R.A.; Ormeño-Orrillo, E.; Melo, I.S.; Martínez-Romero, E.; Hungria, M. Polyphasic evidence supporting the reclassification of *Bradyrhizobium japonicum* group Ia strains as *Bradyrhizobium diazoefficiens* sp. nov. *Int. J. Syst. Evol. Microbiol.*, **2013**, 63(Pt 9), 3342-3351.
<http://dx.doi.org/10.1099/ijs.0.049130-0> PMID: 23504968
- [40] Sprent, J.I.; Ardley, J.; James, E.K. Biogeography of nodulated legumes and their nitrogen-fixing symbionts. *New Phytol.*, **2017**, 215(1), 40-56.
<http://dx.doi.org/10.1111/nph.14474> PMID: 28211601
- [41] Kuykendall, L.D.; Saxena, B.; Devine, T.E.; Udell, S.E. Genetic diversity in *Bradyrhizobium japonicum* Jordan. 1982 and a proposal for *Bradyrhizobium elkanii* sp. nov. *Can. J. Microbiol.*, **1992**, 38(6), 501-505.
<http://dx.doi.org/10.1139/m92-082>
- [42] Xu, L.M.; Ge, C.; Cui, Z.; Li, J.; Fan, H. *Bradyrhizobium liaoningense* sp. nov., isolated from the root nodules of soybeans. *Int. J. Syst. Bacteriol.*, **1995**, 45(4), 706-711.
<http://dx.doi.org/10.1099/00207713-45-4-706> PMID: 7547289
- [43] Young, J.P.W. Phylogenetic classification of nitrogen-fixing organisms. *Biological Nitrogen Fixation*; Stacey, G. Burris and Evans H.J. Eds.; Chapman and Hall, New York, USA., **1991**, pp. 43-86.
- [44] Willems, A. The taxonomy of rhizobia: An overview. *Plant Soil*, **2006**, 287(1-2), 3-14.
<http://dx.doi.org/10.1007/s11104-006-9058-7>
- [45] Cooper, J.E. Early interactions between legumes and rhizobia: disclosing complexity in a molecular dialogue. *J. Appl. Microbiol.*, **2007**, 103(5), 1355-1365.
<http://dx.doi.org/10.1111/j.1365-2672.2007.03366.x> PMID: 17953546
- [46] Denison, R.F.; Toby Kiers, E. Why are most rhizobia beneficial to their plant hosts, rather than parasitic? *Microbes Infect.*, **2004**, 6(13), 1235-1239.
<http://dx.doi.org/10.1016/j.micinf.2004.08.005> PMID: 15488744
- [47] Laranjo, M.; Alexandre, A.; Oliveira, S. Legume growth-promoting rhizobia: an overview on the Mesorhizobium genus. *Microbiol. Res.*, **2014**, 169(1), 2-17.
<http://dx.doi.org/10.1016/j.micres.2013.09.012> PMID: 24157054
- [48] Sprent, J.I. Evolving ideas of legume evolution and diversity: a taxonomic perspective on the occurrence of nodulation. *New Phytol.*, **2007**, 174(1), 11-25.
<http://dx.doi.org/10.1111/j.1469-8137.2007.02015.x> PMID: 17335493
- [49] Parniske, M. Uptake of bacteria into living plant cells, the unifying and distinct feature of the nitrogen-fixing root nodule symbiosis. *Curr. Opin. Plant Biol.*, **2018**, 44, 164-174.
<http://dx.doi.org/10.1016/j.pbi.2018.05.016> PMID: 30071473
- [50] Dwivedi, S.L.; Sahrawat, K.L.; Upadhyaya, H.D.; Mengoni, A.; Galardini, M.; Bazzicalupo, M.; Biondi, E.G.; Hungria, M.; Kaschuk, G.; Blair, M.W.; Ortiz, R. Advances in host plant and rhizobium genomics to enhance symbiotic nitrogen fixation in grain legumes. *Adv. Agron.*, **2015**, 129, 1-116.
<http://dx.doi.org/10.1016/bs.agron.2014.09.001>
- [51] Uchida, Y.; Akiyama, H. Mitigation of postharvest nitrous oxide emissions from soybean ecosystems: A review. *Soil Sci. Plant Nutr.*, **2013**, 59(4), 477-487.
<http://dx.doi.org/10.1080/00380768.2013.805433>
- [52] Hungria, M.; Loureiro, M.F.; Mendes, I.C.; Campo, R.J.; Graham, P.H. Inoculant preparation, production and application. *Nitrogen fixation in agriculture, forestry, ecology, and the environment*; Werner, D.; Newton, W.E., Eds.; Kluwer: Dordrecht, **2005**, pp. 223-253. a
http://dx.doi.org/10.1007/1-4020-3544-6_11
- [53] Hungria, M.; Franchini, J.C.; Campo, R.J.; Graham, P.H. The importance of nitrogen fixation to soybean cropping in South America. *Newton, W. E. (Org.). Nitrogen fixation in agriculture: forestry ecology and environment*; Werner, D., Ed.; Kluwer Academic Publishers: Dordrecht, **2005**, pp. 25-42. b
http://dx.doi.org/10.1007/1-4020-3544_3
- [54] Keyser, H.H.; Li, F. Potential for increasing biological nitrogen fixation in soybean. *Plant Soil*, **1992**, 141, 119-135.
<http://dx.doi.org/10.1007/BF00011313>
- [55] Hungria, M.; Mendes, I.C. Nitrogen fixation with soybean: the perfect symbiosis? *Biological Nitrogen Fixation*; de Bruijn, F.J., Ed.; Wiley: Hoboken, **2015**.
<http://dx.doi.org/10.1002/9781119053095.ch99>
- [56] Campo, R.J. Silva, Araujo R.; Hungria, M. Molybdenum-enriched soybean seeds enhance N accumulation, seed yield, and seed protein content in Brazil. *Field Crops Res.*, **2009**, 110(3), 219-224.
<http://dx.doi.org/10.1016/j.fcr.2008.09.001>
- [57] Diaz, D.A.R.; Pedersen, P.; Sawyer, J.E. Soybean response to inoculation and nitrogen application following long-term grass pasture. *Crop Sci.*, **2009**, 49(3), 1058-1062.
<http://dx.doi.org/10.2135/cropsci2008.08.0510>
- [58] Barcellos, F.G.; Menna, P.; da Silva Batista, J.S.; Hungria, M. Evidence of horizontal transfer of symbiotic genes from a *Bradyrhizobium japonicum* inoculant strain to indigenous diazotrophs *Sinorhizobium (Ensifer) fredii* and *Bradyrhizobium elkanii* in a Brazilian Savannah soil. *Appl. Environ. Microbiol.*, **2007**, 73(8), 2635-2643.
<http://dx.doi.org/10.1128/AEM.01823-06> PMID: 17308185
- [59] Nandasena, K.G.; O'Hara, G.W.; Tiwari, R.P.; Sezmiş, E.; Howieson, J.G. *In situ* lateral transfer of symbiosis islands results in rapid evolution of diverse competitive strains of mesorhizobia suboptimal in symbiotic nitrogen fixation on the pasture legume *Biserrula pelecinus* L. *Environ. Microbiol.*, **2007**, 9(10), 2496-2511.
<http://dx.doi.org/10.1111/j.1462-2920.2007.01368.x> PMID: 17803775
- [60] Miranda, J.C.C. *Cerrado, Micorriza Arbuscular ocorrência e manejo. Embrapa*; Planaltina, **2008**.
- [61] Miranda, J.C.C.; Vilela, L.; Miranda, L.N. Dynamics and contribution of arbuscular mycorrhiza in culture systems with crop rotation. *Pesqui. Agropecu. Bras.*, **2005**, 40(10), 1005-1014.
<http://dx.doi.org/10.1590/S0100-204X2005001000009>
- [62] Grümberg, B.C.; Urcelay, C.; Shroeder, M.A.; Vargas-Gil, S.; Luna, C.M. The role of inoculum identity in drought stress mitigation by arbuscular mycorrhizal fungi in soybean. *Biol. Fertil. Soils*, **2015**, 51(1), 1-1.
<http://dx.doi.org/10.1007/s00374-014-0942-7>
- [63] Palleroni, N.J. Present situation of the taxonomy of aerobic pseudomonads. *Pseudomonas: Molecular Biology and Biotechnology*; Galli, E.; Silver, S.; Witholt, B., Eds.; American Society for Microbiology: Washington, DC, **1992**, pp. 105-115.
- [64] Rhamani, H.A.; Saleh-Rastin, N.; Khavazi, K.; Asgharzadeh, A.; Fewer, D.; Kiani, S.; Lindstrom, K. Selection of thermotolerant bradyrhizobial strains for nodulation of soybean (*Glycine max* L.) in semi-arid regions of Iran. *World J. Microbiol. Biotechnol.*, **2009**, 25, 591-600.
<http://dx.doi.org/10.1007/s11274-008-9927-8>
- [65] Raaijmakers, J.M.; Paulitz, T.C.; Steinberg, C.; Alabouvette, C.; Moëgne-Loccoz, Y. The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. *Plant Soil*, **2009**, 321(1-2), 341-361.
<http://dx.doi.org/10.1007/s11104-008-9568-6>
- [66] Minhoni, M.T.A.; Cardoso, E.J.B.N.; Eira, A.F. Efeitos da adição de fosfato de rocha, bagaço de cana-de-açúcar, fosfato solúvel e fungo micorrízico no crescimento e na absorção de nutrientes por plantas de soja. *Rev. Bras. Ciênc. Solo*, **1993**, 17, 173-178.

- [67] Porcel, R.; Barea, J.M.; Ruiz-Lozano, J.M. Antioxidant activities in mycorrhizal soybean plants under drought stress and their possible relationship to the process of nodule senescence. *New Phytol.*, **2003**, *157*(1), 135-143.
<http://dx.doi.org/10.1046/j.1469-8137.2003.00658.x>
- [68] Aysan, E.; Demir, S. Using arbuscular mycorrhizal fungi and *Rhizobium leguminosarum*, biovar Phaseoli against *Sclerotinia sclerotiorum* (Lib.) de bary in the common bean *Phaseolus vulgaris* L. *Plant Pathol. J.*, **2009**, *8*, 74-78.
<http://dx.doi.org/10.3923/ppj.2009.74.78>
- [69] Barea, J.M.; Azcón, R.; Azcón-Aguilar, C. Mycorrhizosphere interactions to improve plant fitness and soil quality. *Antonie van Leeuwenhoek*, **2002**, *81*(1-4), 343-351.
<http://dx.doi.org/10.1023/A:1020588701325> PMID: 12448732
- [70] Contreras-Cornejo, H.A.; Macías-Rodríguez, L.; del-Val, E.; Larsen, J. Ecological functions of Trichoderma spp. and their secondary metabolites in the rhizosphere: interactions with plants. *FEMS Microbiol. Ecol.*, **2016**, *92*(4), fiw036.
<http://dx.doi.org/10.1093/femsec/fiw036> PMID: 26906097
- [71] Cao, Y.; Halane, M.K.; Gassmann, W.; Stacey, G. The role of plant innate immunity in the legume-rhizobium symbiosis. *Annu. Rev. Plant Biol.*, **2017**, *68*, 535-561.
<http://dx.doi.org/10.1146/annurev-arplant-042916-041030> PMID: 28142283
- [72] Miransari, M.; Abrishamchi, A.; Khoshbakht, K.; Niknam, V. Plant hormones as signals in arbuscular mycorrhizal symbiosis. *Crit. Rev. Biotechnol.*, **2014**, *34*(2), 123-133.
<http://dx.doi.org/10.3109/07388551.2012.731684> PMID: 23113535
- [73] Miransari, M. Plant growth promoting rhizobacteria. *J. Plant Nutr.*, **2014**, *37*(14), 2227-2235.
<http://dx.doi.org/10.1080/01904167.2014.920384>
- [74] Strauss, S.L.; Kluepfel, D.A. Anaerobic soil disinfestation: a chemical-independent approach to pre-plant control of plant pathogens. *J. Integr. Agric.*, **2015**, *14*(11), 2309-2318.
[http://dx.doi.org/10.1016/S2095-3119\(15\)61118-2](http://dx.doi.org/10.1016/S2095-3119(15)61118-2)
- [75] Dashti, N.; Zhang, F.; Hynes, R.; Smith, D.L. Plant growth promoting rhizobacteria accelerate nodulation and increase nitrogen fixation activity by field grown soybean (*Glycine max* (L.) Merr.) under short season conditions. *Plant Soil*, **1998**, *200*, 205-213.
<http://dx.doi.org/10.1023/A:1004358100856>
- [76] Xie, Z.P.; Staehelin, C.; Vierheilig, H.; Wiemken, A.; Jabbouri, S.; Broughton, W.J.; Vogeli-Lange, R.; Boller, T.; Xie, Z.P. Rhizobial nodulation factors stimulate mycorrhizal colonization of undulating and non-nodulating soybeans. *Plant Physiol.*, **1995**, *108*(4), 1519-1525.
<http://dx.doi.org/10.1104/pp.108.4.1519> PMID: 12228558
- [77] Ramesh, A.; Sharma, S.K.; Yadav, N.; Joshi, O.P. Phosphorus mobilization from native soil P-pool upon inoculation with phytate-mineralizing and phosphate-solubilizing *Bacillus aryabhatai* isolates for improved P-acquisition and growth of soybean and wheat crops in microcosm conditions. *Agric. Res.*, **2014**, *3*(2), 118-127.
<http://dx.doi.org/10.1007/s40003-014-0105-y>
- [78] Kwak, Y.; Jung, B.K.; Shin, J.H. Complete genome sequence of *Pseudomonas rhizosphaerae* IH5T (=DSM 16299T), a phosphate-solubilizing rhizobacterium for bacterial biofertilizer. *J. Biotechnol.*, **2015**, *193*, 137-138.
<http://dx.doi.org/10.1016/j.jbiotec.2014.11.031> PMID: 25483321
- [79] Abd-Alla, M.H.; El-Enany, A.W.E.; Nafady, N.A.; Khalaf, D.M.; Morsy, F.M. Synergistic interaction of *Rhizobium leguminosarum* bv. viciae and arbuscular mycorrhizal fungi as a plant growth promoting biofertilizers for faba bean (*Vicia faba* L.) in alkaline soil. *Microbiol. Res.*, **2014**, *169*(1), 49-58.
<http://dx.doi.org/10.1016/j.micres.2013.07.007> PMID: 23920230
- [80] Li, S.M.; Li, L.; Zhang, F.S. Enhancing phosphorus and nitrogen uptake of faba bean by inoculating arbuscular mycorrhizal fungus and *Rhizobium leguminosarum*. *J. China. Agric. Uni.*, **2004**, *9*, 11-15.
- [81] Afkhami, M.E.; Almeida, B.K.; Hernandez, D.J.; Kieseewetter, K.N.; Revellini, D.P. Tripartite mutualisms as models for understanding plant-microbial interactions. *Curr. Opin. Plant Biol.*, **2020**, *56*, 28-36.
<http://dx.doi.org/10.1016/j.pbi.2020.02.003> PMID: 32247158
- [82] Wang, X.; Pan, Q.; Chen, F.; Yan, X.; Liao, H. Effects of co-inoculation with arbuscular mycorrhizal fungi and rhizobia on soybean growth as related to root architecture and availability of N and P. *Mycorrhiza*, **2011**, *21*(3), 173-181.
<http://dx.doi.org/10.1007/s00572-010-0319-1> PMID: 20544230
- [83] Yan, J.; Chen, W.; Han, X.; Wang, E.; Zou, W.; Zhang, Z. Genetic diversity of indigenous soybean-nodulating rhizobia in response to locally-based long term fertilization in a Mollisol of Northeast China. *World J. Microbiol. Biotechnol.*, **2017**, *33*(1), 6.
<http://dx.doi.org/10.1007/s11274-016-2170-9> PMID: 27848139
- [84] Kalita, M.; Malek, W. Root nodules of *Genista germanica* harbor Bradyrhizobium and Rhizobium bacteria exchanging nodC and nodZ genes. *Syst. Appl. Microbiol.*, **2020**, *43*(1), 126026.
<http://dx.doi.org/10.1016/j.syapm.2019.126026> PMID: 31706562
- [85] Kanehara, K.; Minamisawa, K. Complete genome sequence of *Bradyrhizobium japonicum* J5, isolated from a soybean nodule in Hokkaido, Japan. *Genome Announc.*, **2017**, *5*(6), e01619-e16.
<http://dx.doi.org/10.1128/genomeA.01619-16> PMID: 28183772
- [86] Htwe, A.Z.; Yamakawa, T. Enhanced plant growth and/or nitrogen fixation by leguminous and non-leguminous crops after single or dual inoculation of *Streptomyces griseoflavus* P4 with Bradyrhizobium strains. *Afr. J. Microbiol. Res.*, **2015**, *9*, 2337-2344.
<http://dx.doi.org/10.5897/AJMR2015.7796>
- [87] Sakamoto, K.; Ogiwara, N.; Kaji, T.; Sugimoto, Y.; Ueno, M.; Sonoda, M.; Matsui, A.; Ishida, J.; Tanaka, M.; Totoki, Y.; Shinozaki, K.; Seki, M. Transcriptome analysis of soybean (*Glycine max*) root genes differentially expressed in rhizobial, arbuscular mycorrhizal, and dual symbiosis. *J. Plant Res.*, **2019**, *132*(4), 541-568.
<http://dx.doi.org/10.1007/s10265-019-01117-7> PMID: 31165947
- [88] Saïdi, S.; Ramirez-Bahena, M.H.; Santillana, N.; Zúñiga, D.; Álvarez-Martínez, E.; Peix, A.; Mhamdi, R.; Velázquez, E. *Rhizobium laguerreae* sp. nov. nodulates *Vicia faba* on several continents. *Int. J. Syst. Evol. Microbiol.*, **2014**, *64*(Pt 1), 242-247.
<http://dx.doi.org/10.1099/ijs.0.052191-0> PMID: 24067731
- [89] Shi, Y.; Li, J.; Wang, J.; Zhu, R.; Li, S.; Li, Q.; Chen, L.; Zhu, J.; Zou, J.; Wang, J.; Chang, H. Nodulation and genomic capacity of a novel high-latitude *Bradyrhizobium japonicum* HLNEAU001. *J. Soil Sci. Plant Nutr.*, **2019**, *19*(2), 277-289.
<http://dx.doi.org/10.1007/s42729-019-00027-w>