Genomic Research Favoring Higher Soybean Production

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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.

Keywords: Gene editing, germplasms, 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
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 biofertilizers. 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.
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, Mn21 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 radiocicolor] 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.
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 N\(_2\)), which compensate for plant selectiveness/promiscuity, survival, and competition with other strains, to infect and fix N\(_2\) [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 N\(_2\) 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 N\(_2\) 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 N\(_2\) fixation and increasing N fertilizer decreases plant N fixation. Moreover, the N\(_2\) 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 N\(_2\) 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 guayamus and Styllosanthes 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 identified 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].

Rodriguez-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 counties such as Pakistan, less amount of soybean yield is produced compared with the other top producer countries. One of the important constrains 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 metallothion. 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 r RNA] [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 HLNAU001 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.
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