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Rhizobia Strain and Host-Legume Interaction Effects on Nitrogen Fixation and Yield of Grain Legume: A Review

Allito B.B.[1], Nana Ewusi-Mensah.[2], Alemneh A.A.[3]
1.Dept. of Plant and Horticultural Science, Hawassa University College of Agriculture, Hawassa, Ethiopia
2.Dept. of Crop and Soil Sciences, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana
3.College of Agriculture and Environmental Sciences, Haramaya University, Harer, Ethiopia.
Corresponding author email: bayoubunkura@gmail.com

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Abstract Though molecular nitrogen represents nearly 80% of the earth's atmosphere, it is chemically inert and cannot be directly assimilated by plants. Only limited numbers of prokaryotes are able to convert the N_2 molecule into a usable form of N through a process known as biological nitrogen fixation. Rhizobia are soil bacteria able to form nodules and establish symbiosis with the roots or the stems of leguminous plants. Nitrogen fixation in legume provides important economic advantages for crop production by reducing the cost of N fertilizer. This review covers contribution of biological nitrogen fixation in agriculture, rhizobia and host-legume related factors influencing symbiotic performance. It highlights the rhizobial strain and host-legume interaction effects on N_2 fixation, soil residual nitrogen, and nitrogen and phosphorus uptake of the plant. The review aims to elucidate the approach for selection of the best rhizobia strain-legume variety combination for maximum nitrogen fixation and yield of grain legume. Variation in nodulation and nitrogen fixation frequently occur in a bacteria strain-legume cultivar specific manner. Genotype of both the host and the competing rhizobia strains have been shown to influence inoculant performance.

Keywords Rhizobia strain; Host-legume; Symbiotic interaction; Nitrogen fixation

Introduction

Grain legumes are a primary source of amino acids providing about a third of all dietary protein (Kudapa et al., 2013) and a third of processed vegetable oil for human consumption (Graham and Vance, 2003). Legumes are second to cereals in providing food for humans worldwide (Kudapa et al., 2013). Being a source of nutritionally rich food, grain legumes complement cereals or root crops, the primary source of carbohydrates. Grain legume crops represent an important component of agricultural food crops consumed in developing countries and are considered a vital crop for achieving food and nutritional security for both poor producers and consumers. Grain legumes are also known to play a pivotal role in nutrient cycling and nutrient enrichment in various cropping systems. They are considered as engines of sustainable farming as they intensify the productivity and interaction of the soil, crop, livestock, people and other components. Improving production of grain legume in smallholder farming systems will lead to improved food security in these systems.

Grain legume also provides essential minerals (Grusak, 2002), and health-promoting secondary compounds that can protect against human cancers (Madar and Stark, 2003), and also protect the plant against the attack of pathogens and pests (Ndakidemi and Dakora, 2003). Furthermore, legume grain has blood cholesterol-reducing effect as well as a hypoglycemic effect, reducing the increase in blood glucose after a meal (Jenkins et al., 2003). Whole-grain is a good source of bioactive proteins, peptides and functional fiber; also it may have beneficial combinations of many micronutrients, antioxidants, vitamin E, polyunsaturated fatty acids and phytochemicals (Liu, 1999). Many of these constituents have been independently associated with reduced risk of coronary artery disease (CAD) (Liu, 1999; Anderson and Hanna, 1999). In addition to reducing insulin resistance, the beneficial effects of whole-grain consumption on lipid peroxidation may be another possible explanation in the significant inverse relation of the whole-grain intake to the risk of CAD. Thus, these protective effects are likely due to multiple mechanisms, such as fiber, antioxidants, and many constituents of grain legumes.

Though grain legumes have several benefits, their productivity is very low and far below the potential production of the species (IFPRI, 2010). This low productivity in grain legumes is often associated with declining soil fertility of the farmland and reduced N_2-fixation. Yield reduction of grain legume can be improved through inoculation of adaptable effective rhizobia (Jida and Assefa, 2014; Desta et al., 2015). Despite the fact that inoculating legumes with rhizobia can achieve substantial increases in nodulation, grain and biomass yield, nitrogen fixation and post-crop soil nitrate levels, there is no doubt that specificity exists between rhizobial strain and the legume variety, and compatibility between the two is essential for successful nodulation and nitrogen fixation (Emam and Rady, 2014).

Biological N_2 Fixation (BNF) in Agriculture

The earth's atmosphere contains the largest global pool about 10^{15} tons of dinitrogen (N_2) gas, and the N_2 cycle involves the transformation of 3×10^9 tons of N_2 per year on a global basis (Postgate, 1982). Although N_2 represents almost 80% of the earth's atmosphere (Abd-Alla et al., 2014), it is not useful to most organisms unless it is converted into a reduced form either biologically by bacteria or abiologically by lighting or industrial processes. Nitrogen reduction is a very complex mechanism not yet fully elucidated (Franche et al., 2009). The result of net reduction of molecular nitrogen to ammonia is generally accounted for by the following equation:

$$N_2 + 8H^+ + 8\ e^- + 16\ Mg\ ATP \rightarrow (nitrogenase) \rightarrow 2NH_3 + 2H^+ + 16MgADP + 16Pi$$

Figure. 1 presents N_2-fixation and N_2 fixing agents in agriculture and terrestrial natural systems. BNF is the process whereby a number of bacteria species use the enzyme nitrogenase to convert atmospheric N_2 into ammonia (NH_3). It occurs in almost every ecosystem, and accounts for ~1.4 x 10^{11} kg N yr^{-1} entering terrestrial systems, with ~76 % of the N added to natural ecosystems while the remaining goes into agroecosystems (Galloway et al., 2004). The world production of fixed N from chemical fertilizer accounts for about 25%, whereas BNF accounts for about 60% (Zahran, 1999).

Nitrogen (N) is an essential plant nutrient and one of the key drivers of global agricultural production. Between 150 and 200 million tons of mineral N are required each year by plants in agricultural systems to produce the world's food, animal feed and industrial products (Unkovich et al., 2008). To meet those requirements, close to 100 million tons of N are fixed annually via the industrial Haber Bosch process. However, the use of nitrogenous fertilizers has resulted in unacceptable levels of water pollution and the eutrophication of lakes and rivers (Al-Sherif, 1998). BNF is considered to be more ecofriendly than industrial N fixation because the NH_3 produced in the former process is readily assimilated into organic form by the plant (Valentine et al., 2011) and therefore would be ideal for sustainable agriculture. It is an efficient source of nitrogen for resource poor farmers who are using little or no fertilizer, and plays a key role in sustainable grain legumes production. Approximately 2 tons of industrially-fixed N is needed as fertilizer for crop production to equal the effects of 1 ton of N biologically fixed (Abd-Alla et al., 2014). Given the high cost of fertilizer in developing countries and the limited market infrastructure for farm inputs, current research and extension efforts have been directed to integrated nutrient management, in which legumes play a crucial role (Chianu et al., 2008). More focus has been given to the symbiotic associations as they have the greatest quantitative impact on the nitrogen cycle.

Legumes are very important both ecologically and agriculturally because they are responsible for a substantial part of the global flux of N_2 to fixed forms. Increased plant protein levels and reduced depletion of soil N reserves are obvious consequences of legume N_2 fixation. Among the flowering plant families, Leguminosae is the third largest represented by about 730 genera with more than 19,320 species (Lewis et al., 2005). Most species of the Leguminosae form symbiotic associations with rhizobia. Therefore, they are an essential part of the terrestrial N cycle and used to sustain ecosystem functioning (Sprent, 2001). Legumes are grown for production of food and oil, fiber, fuel, timber, medicines, forages, biodiesel fuel, and chemicals.

Grain legumes are an integral part of African farming systems, covering usually large parts of the farmlands in the regions (Akibode, 2011). For legume-based farms, the effectiveness of the fertility maintenance depends upon the balance of N-fixing legumes and N-depleting non-legumes in the rotation. The amount of N_2 fixed by a legume crop varies widely because it depends on the rhizobial strain, legume genotype and the environment. Assessing BNF is essential to manage N turnover in the soil and maximize crop yields while minimizing losses of reactive N to the environment (Lupwayi et al., 2011). Thus, quantifying BNF is a key factor for both economic viability and environmental performance of low-input farming systems. In spite of several reviews examining BNF by crops and pasture legumes (Herridge et al., 2008; Jensen et al., 2010; Unkovich et al., 2010; Yang et al., 2010; Unkovich, 2012), there is still a strong need to estimate different rhizobia strains and host-legume interaction effect on N fixation in order to achieve full environmental potential and resource benefits of protein crops.

Rhizobia

BNF is carried out by a small number of diazotrophic prokaryotic microorganisms, belonging to a wide range of eubacteria and archaebacteria. Diazotrophs are usually divided into free-living and symbiotic forms, though some cyanobacteria are able to fix N either independently or in symbiotic association. Symbiotic diazotrophs include a number of genera of the Rhizobiaceae, which form symbiosis with legumes (Unkovich et al., 2008), where nitrogen fixation takes place in specialized organs, the nodules. These soil bacteria are called rhizobia. Most of rhizobial species form nodules on legume roots, but some like *Azorhizobium caulinodans, Azorhizobium dodereinereae* and *Azorhizobium oxalatiphilum* are able to form both root and aerial (stem) nodules (Dreyfus et al., 1988). *Azorhizobium caulinodans* ORS571 also shows N_2 fixing ability in the free living state that most of the other rhizobia do not (Dreyfus et al., 1983).

Because of their ecological and economic importance, the diversity and taxonomy of rhizobia have been extensively studied. In 1982, two groups of root nodule bacteria were described: fast growing types assigned the generic name *Rhizobium* and slow growing types referred to as *Bradyrhizobium* (Jordan, 1982). In 1996, seventeen species, in four genera (*Rhizobium*, *Bradyrhizobium*, *Sinorhizobium* and *Mesorhizobium*) were described (Young and Haukka, 1996). Currently, rhizobia include at least 14 genera comprising more than 98 species (Weir, 2013).

On the basis of the 16S ribosomal DNA sequence, rhizobia species belong to three main distinct phylogenetic subclasses: α, β and γ-*Proteobacteria* (Table 1). The majority of species belong to the α-*Proteobacteria* which comprises more than 95 species grouped in 11 genera: *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, Azorhizobium, Ensifer (formerly *Sinorhizobium*), *Methylobacterium*, *Devosia*, *Microvirga*, *Ochrobactrum, Phyllobacterium* and *Shinella* (Zakhia et al., 2004). Two genera, *burkholderia* and *Cupriavidus* (formerly *ralstonia*) (Moulin et al., 2001) belong to the β- *Proteobacteria* (Nogom, 2004) whereas one genus belong to the γ-*Proteobacteria* (Benhizia et al., 2004). Han et al. (2005); Liu et al. (2005); Velázquez et al. (2005); Pulawska et al. (2012) revealed that some species previously named *Agrobacterium* are able to nodulate leguminous plants, and hence included in genus *Rhizobium*, namely *R. radiobacter*, *R. rhizogenes*, *R. rubi*, *R. vitis* and *R. nepotum*. Increase in advanced study of legume's new species in different geographical regions opens new perspectives to isolate and characterize more rhizobial species/strains.

Rhizobium-Legume Symbiosis

The interaction between legume and rhizobia leads to the development of a nitrogen fixing symbiosis (Ohyama et al., 2009). The legume-rhizobia symbiosis is the single most important source of biologically fixed nitrogen in agricultural systems (Graham and Vance, 2000). Between one-third and one-half of the total N added to agricultural land is attributable to the legume-rhizobia symbiosis (Herridge et al., 2008). Sprent (2001) documented species in the legume family that have the ability to form intimate intracellular associations with diverse rhizobial species. Generally, the relation between rhizobia and legume is a selective one: each rhizobia species has a distinct host range allowing nodulation of a particular set of leguminous species, and each leguminous species

Table1 List of rhizobial species nodulating legumes

Class: Alphaproteobacteria; Order: Rhizobiales

Genus: *Rhizobium*

R. leguminosarum, *R. galegae*, *R. Tropici*, *R. endophyticum*, *R. Phaseoli*, *R. fabae*, *R. etli*, *R. undicola*, *R. gallicum*, *R. giardinii*, *R. hainanensis*, *R. Huautlense*, *R. Mongolense*, *R. yanglingense*, *R. larrymoorei*, *R. indigoferae*, *R. sullae*, *R. loessense*, *R. cellulosilyticum*, *R.miluonense*, *R. multihospitium*, *R. oryzae*, *R. pisi*, *R. mesosinicum*, *R. alamii*, *R. alkalisoli*, *R. tibeticum*, *R. tubonense*, *R. Halophytocola*, *R. radiobacter*, *R. rhizogenes*, *R. rubi*, *R. vitis*, and *R. nepotum*

Genus: *Ensifer*

E. meliloti, *E. Fredii*, *E. sahelense*, *E. terangae*, *E. Medicae*, *E. arboris*, *E. kostiense*, *E. xingianense (Formerly:Sinorhizobium xingianense)*, *E. adhaerens*, *E. kummerowiae*, *E. Americanum*, *E. mexicanus*, *E. numidicus*

Genus: *Shinella*

S. kummerowiae

Genus: *Mesorhizobium*

M. loti, M. Huakuii, M. ciceri, M. tianshanense, M. mediterraneum, M. plurifarium, M. amorphae, M. chacoense, M. septentrionale, *M. temperatum*, *M.* thiogangeticum, *M. albiziae*, *M. caraganae, M. gobiense, M. tarimense, M. australicum, M. opportunistum, M. metallidurans, M. alhagi Alhagi, M. camelthorni, M. abyssinicae, M. muleiense, M. hawassense, M. qingshengii, M. robiniae, M. shonense, M. shangrilense, M. silamurunense, M. tamadayense*

Genus: *Phyllobacterium*

P. trifolii

Genus: *Microvirga*

M. lupini, M. lotononidis, M. zambiensis

Genus: *Azorhizobium*

A. caulinodans, A. Dobereinereae, A. oxalatiphilum

Genus: *Methylobacterium*

M. nodulans

Genus: *Ochrobactrum*

O. cytisi, O.lupini

Genus: *Devosia*

D. neptuniae

Genus*: Bradyrhizobium*

B. japonicum, *B. elkanii*, *B. liaoningensese*, *B. yuanmingense*, *B. betae*, *B. canariense*, *B. iriomotense*, *B. jicamae*, *B. lablabi*, *B. huanghuaihaiense*, *B. cytisi*, *B. daqingense*, *B. denitrificans*, *B. Oligotrophicum*, *B. pachyrhizi*

Class: Beta Proeobacteria; Order: Burkholderiales

Genus: *Burkholderia*

B. caribensis, B. cepacia, B. tuberum, B. phymatum, B. nodosa, B. sabiae, B. mimosarum, B. rhizoxinica, B. diazotrophica, B. endofungorum, B. heleia, B. symbiotica

Genus*: Cupriavidus*

C. taiwanensis

Class: Gamma-Proteobacteria; Order: Pseudomonadales

Family: Pseudomonaceae

Pseudomonas sp.

Source: Barrada and Fikri-Benbrahim (2014)

nodulates only with a certain range of rhizobia. However, a complex association between legume and rhizobia has been found and many leguminous species can nodulate with distinctive rhizobial species in different geographical regions (Han et al., 2005). Development of functional nodules requires spatially controlled activities of genes and gene products of both partners (Oldroyd et al., 2001). For a successful infection, a compatible pairing of legume cultivar and rhizobial strain is required.

The symbioses between rhizobia and legume plants are mainly a mutualistic interaction (Lindström and Mousavi, 2010). However, it seems that there are cases where these partnerships can also be considered as parasitic when they form ineffective symbiosis with legumes, in which the rhizobia get a continuous nutrient supply while they fix little or do not fix nitrogen for the host plant. These types of situations may occur when multiple rhizobial strains compete for the same plant and when the strains infect non-specific hosts promiscuously. Rhizobial strains can form effective symbioses when they interact with their own specific host legumes (Denison and Kiers, 2004). For example, *Rhizobium leguminosarum* strains isolated from nodules of native legumes in New Zealand were found to form ineffective nodules, while they still

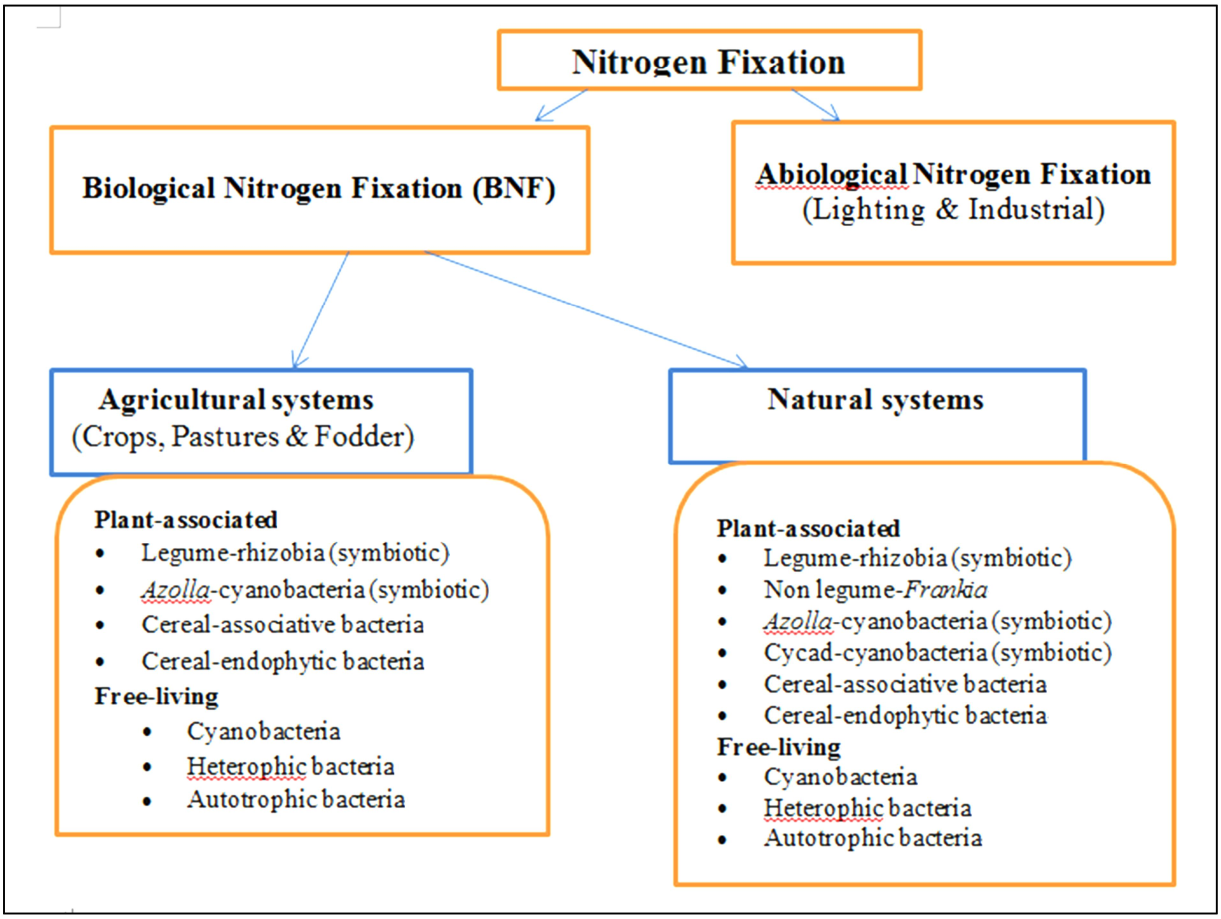

Figure 1 Nitrogen fixation and N_2-fixing agents

reserved the ability to form an effective symbiosis with classical host plants (pea, bean and clover) (Weir, 2006). *Rhizobium galegae* strains isolated from *Galega orientalis* or *Galega officinalis* form effective symbioses with their original hosts, whereas strains isolated from *G. officinalis* form ineffective nodules on *G. orientalis* and vice versa (Andronov et al., 2003).

Rhizobia often fail to fix nitrogen when they encounter atypical hosts. When rhizobia isolated from one host species are inoculated onto different legumes, invariably only a subset of such cross-inoculated strains can nodulate the novel host, and only a smaller subset efficiently fix nitrogen on the novel host. This pattern suggests that many rhizobia that have been identified as ineffective might be highly effective if inoculated onto a more suitable host. Host-symbiont mismatches might be widespread in agricultural settings where plants, bacteria, and even soils are transported among sites. On the other hand, though rhizobia are defined by their ability to infect legumes, studies of multiple rhizobial lineages have revealed that much diversity within these groups is represented by strains that do not exhibit the ability to infect legumes (Sachs et al., 2010). The N_2-fixing symbiosis on N fixation is characterized by legume x rhizobium specificity. Some host varieties are superior to others in their ability to fix N_2, and in turn, some rhizobil strains have similar superior capability. One hypothesis that has been posed in many studies is that the appearance of rhizobial exploitation is the result of mismatched host-symbiont pairs (Sachs et al., 2010; Friesen, 2012).

Factors Affecting Symbiotic Nitrogen Fixation (SNF)

SNF efficiency depends on rhizobial strain, plant host, environmental factors, soil and their interaction. A number of biotic and abiotic factors affect SNF. The most important abiotic factors include drought, salinity, waterlogging, temperature, soil acidity, inadequate mineral nutrition and mineral toxicities (Zahran, 1999; Abdel-Latef and Ahmed, 2015) and biotic factors such as competition of ineffective indigenous rhizobia, insect pest and diseases (Serrage and Adu-Gyamfi, 2004; Gommaa et al., 2006; Sofy et al., 2014). These factors can interpose survival of rhizobia in the soil, the infection process, nodule growth and nodule functioning and SNF (Serrage and Adu-Gyamfi, 2004).

It is estimated that crops grown on 90% of arable lands experience one or more environmental stress (Abdel-Latef and Ahmed, 2015). All are interconnected in the control of N_2 fixation, and hence none of them could be considered in isolation. It is also difficult to isolate the effects of such factors on the success of inoculation from their effects on symbiosis functioning and nitrogen-fixation. Rhizobial populations vary in their tolerance ability to major environmental factors (Biswas et al., 2008). The existence of genetic variability in tolerance to most stress factors has been shown in both legume host plants and their respective rhizobial strain (Hungria and Vargas, 2000). This suggests the possibility of overcoming the environmental constraints limiting SNF potential. Optimal performance of the N-fixing symbiosis depends upon selection of both symbiotic partners for adaptation to the target environment (Sessitsch et al., 2002).

The SNF process also depends on the occurrence and survival of *Rhizobium* in soils and their efficiency (Adamovich and Klasens, 2001). One of the most common factors limiting a legume's ability to fix N_2 is the absence of sufficient numbers of efficient and effective rhizobia in the soil (Unkovich et al., 2008). Fortunately, strains of rhizobia can be introduced into soil relatively simply by inoculation. Inoculation can lead to the establishment of large rhizobial population in the rhizosphere and improved nodulation (Boahen, 2008). An emerging paradigm suggests that agronomists must factor in natural selection on both crop plants and their symbionts to optimize crop production. Santos *et al.* (1999) explained that when rhizobia are applied in agricultural settings, the inoculum strains must be able to thrive in soil under the varied conditions of the field. This means that the inoculum strains must be able to compete with indigenous rhizobia for nodulation, efficiently escape from senescent nodules, and persist in the soil in order to infect the next season of cultivated hosts.

Inoculation with highly effective N-fixing rhizobial strain requires survival and establishment in the soil environment. An effective and persistent rhizobial strain has several advantages, and is preferable to the repeated inoculation in the subsequent season. To be established in the field, introduced rhizobial strain must coexist with competitors and predators, and maintain itself during period of low nutrient availability. It is possible to change the established rhizobial strain by new rhizobial strain when the inculated rhizobial strain loss its nitrogen fixing capacity suffering genetic change, or when the host legume cultivar is changed. During the introduction of new rhizobial strains it may create competition barrier. However, competition from indigenous rhizobia is not necessarily the major determining factor for lack of response to inoculation; rather the presence of an adequate soil population to meet the N_2 fixation requirements of the host is the primary reason for failure of crops to respond inoculation (Thies *et al.*, 1991). Osunde et al. (2003) stated that the presence of a large indigenous population of compatible rhizobia does not necessarily preclude response to inoculation, provided the inoculant rhizobial strains are competitive and highly effective.

Inoculation Response and Promiscuity of Nodulation

Rhizobia inoculants have been used to address the problems of soil fertility and inadequate fertilizer application in grain legume production. Application of effective rhizobial strains as biofertilizers to improve legume production is an important approach in sustainable agriculture (Saharan and Nehra, 2011). Researches on use of rhizobia inoculants for production of grain legume showed it is a cheaper and usually more effective agronomic practice for ensuring adequate N nutrition of legumes, compared with the application of N fertilizer (Chianu et al., 2008). Inoculation with compatible and appropriate rhizobia is critical for sustained yield in farmlands where N supply limits production of grain legume (Abd-Alla *et al.*, 2014). According to Odame (1997), inoculation is needed in all agricultural lands deficient in N and where N supply is a key limiting factor in crop production. For legume crops to effectively add nitrogen to a cropping system, they must have appropriate rhizobia partners. The capacity of nitrogen fixation in differing rhizobia strains varies (Albareda et al., 2008). Differences between *Bradyrhizobium* strains regarding their effectiveness with different soybean genotypes have been reported (Tien et al., 2002; Mahna et al., 2006). Similarly, Annapuma and Krishnan (2003) revealed that compatibility of *Sinorhizobium fredii* with soybean is strain and cultivar dependent. Hence, matching rhizobial strains to host legumes is the most important factor in maximizing N fixation and productivity of grain legume.

Researches have demonstrated enormous potential for developing effective N-fixing inoculants to enhance N fertility in grain legume production. Inoculating legumes with adaptable and effective species of specific rhizobia increase the success of their establishment, nodulation, biomass and N yields (Adamu et al., 2001; Habtegebrail and Singh, 2006). Variations in nodulation and N_2-fixation efficiency frequently occur in a bacteria strain-legume cultivar specific manner (Sanginga et al., 2000). Ampomah et al. (2008) evaluated the ability of five isolates from cowpea to nodulate and effectively fix nitrogen on groundnut (*Arachis hypogeae*), mungbean (*Vigna radiata*), and soybean (*Glycine max*). Except for cowpea where all the isolates were symbiotically effective, there was variation in the symbiotic effectiveness of the isolates among the different host-legume varieties. Genotype of both the host and the competing rhizobia strains have been shown to influence the outcome. Genetic variation for N_2-fixation ability has been reported involving both the legume and rhizobium components of the symbiotic association (Sanginga et al., 2000).

Inoculation response also varies with degree of promiscuity of legume species. The International Institute of Tropical Agriculture (IITA) developed promiscuous soybean varieties, which are capable of establishing symbiotic relationship with indigenous brandyrhizobia, as a practical alternative to inoculation by African farmers (Dashiell et al., 1983). The resulting soybean varieties form significantly more nodules in un-inoculated native soils than traditional varieties (Kasasa et al., 1998). Contrarily, Sanginga et al. (2000) found that promiscuous soybean is incapable of nodulating effectively with indigenous rhizobia in all locations in the moist savanna zone of Nigeria. As the promiscuous varieties have shown inconsistence in nodulation, it may be safer to rely on effective inoculant strains rather than breed for the ability to nodulate with indigenous rhizobial strains of unknown potential.

Muhammad (2010) observed the response to inoculation by promiscuous soybean varieties. Solomon et al. (2012), Argaw (2014) found significant interactions between soybean variety and inoculation status for all traits scored regardless of promiscuity. Understanding the rhizobia-legume interaction is important for the development of rhizobial strains and legume cultivars with high N_2-fixation potential. Simultaneous selection for the optimal combination of the rhizobium and the host usually results in more effective symbiosis and better growth of the host plant. Breeding programs can help to develop crop varieties that nodulate under targeted environment. Molecular soil microbiology together with screening genotypes and classical breeding techniques will increase productivity of symbioses and eventually result in maximum economic yields of crop plants (Rengel, 2002). Efforts to develop rhizobial inoculants also need to be accompanied by research that facilitates their efficient use that is relevant to resource-poor farmers.

Nitrogen and Phosphorus Uptake

Nutrients are essential components required by living plants for normal growth and development. Plants require 17 essential elements of which carbon, hydrogen, and oxygen are derived from the atmosphere and soil water (Uchida, 2000) whereas the rest are obtained from the soil mineral, soil organic matter and organic or inorganic fertilizers (Roy et al., 2006; Ndakidemi et al., 2011). Each nutrient is needed in different amounts by the plant, and varies in how mobile it is within the plant. Nutrient uptake by plants depends mainly on the quantity, concentration and activities in the root zone soil as well as the capacity of soil to replenish the concerned nutrients in the soil solution (Makoi et al., 2013).

Nitrogen (N) and phosphorus (P) are chief elements that are richly available in the atmosphere and soil respectively, but inaccessible forms to plants (Acharya et al., 2012). These elements are often limiting factors for plant growth and development (Shu-Jie et al., 2007). The majority of soils in Africa have low levels of nitrogen and phosphorus and hence the capacity to support plant growth such as leguminous crops is limited (Tairo and Ndakidemi, 2013). The supply of these mineral nutrients is vital in enhancing legume growth and development. Nitrogen is required by plant for proper growth and development as it is necessary for the formation of amino acids which are building blocks of protein. Besides, N is a necessary component of several vitamins in legumes (Uchida, 2000). Phosphorus is considered to be an essential component in plant bioenergetics of the living cell (Hüttemann et al., 2007). It is also vital for development of new tissue and the transfer of the genetic information within the plant (Rausch et al., 2001).

Rhizobia are known to have a constructive influence on the real chemistry of soil nutrients and thus promote nutrients uptake (Lugtenberg and Kamilova, 2009). Makoi et al. (2013) revealed that improved uptake of N and P following inoculation with efficient strains of *Rhizobium.* Nyoki and Ndakidemi (2014) found that *B. japonicum* inoculants supplemented with phosphorus in cowpea improved the uptake of N and P. Similarly, Jida and Assefa (2014); Desta et al. (2015) revealed inoculation improve nodulation and nutrient uptake of faba bean. Microbial inoculants have become promising solution to some of the problems associated with intensive agriculture by enhancing nutrient availability and uptake, and ultimately enhanced yield.

Grain legume species also have mechanisms to allow recovery of phosphorus from unavailable forms. One mechanism is the exudation of organic acids from legume roots which decreases the pH in the soil surrounding the roots and releases phosphorus. Several organic acids are exuded with malate and citrate by faba bean (Nuruzzaman et al., 2005a) and soybean (Nwoke et al., 2008), respectively. Grain legumes can also release phosphatase enzymes into the soil to breakdown organic material that contains phosphorus (Gilbert et al., 1999). The third mechanism is a contact reaction between the root surface and the insoluble phosphorus adjacent to the root (Ae and Shen, 2002). Faba bean appears to be one of the most promising of several legumes to express the advantage in phosphorus recovery (Nuruzaman et al., 2005b). However, the extent of the benefit of legume phosphorus acquisition to the cropping system is highly dependent on the soil type and the soil environment (Jones et al., 2003)

Residual N

Part of the symbiotically fixed N in a legume crop is available to subsequent crops through the decomposition and mineralization of the legume residues. The legume residues can supply more mineral N to succeeding crops than cereal residues due to their relatively high N contents and relatively low C:N ratio as compared to cereal residues. Cereals cropped in sequence with legumes derive N benefits compared with cereal monoculture. Nitrogen benefits in legume-cereal rotation have been attributed entirely to the transfer of biologically fixed N (Munyinda *et al.,* 1998). Others have expressed the view that N benefits may be due to a combination of legume N-sparing and the transfer of fixed N (Keatinge *et al.,* 1998).

Grain legumes cause significant and positive yield effects on subsequent non-legume crop when compared with rotations with non-legumes (Adeleke and Haruna, 2012). Maize yields increase when grown in crop rotations with soybeans compared to maize grown after maize (Carsky et al., 1997). Agro-economic studies of mung bean-wheat and fallow-wheat cropping systems revealed that wheat growth, development and yield differ significantly when followed after mung bean crop as compared to fallow (Asim et al., 2006). Many factors have been hypothesized to explain these results including enhanced N availability following grain legume and other rotational effects such as reduction of disease and pest, and higher mycorrhizal colonization rate and diversity. However, to determine N contribution of legume to subsequent or associated crop reliable estimates of N_2 fixation and residual soil N are required.

Crop rotations involving legumes were reported to reduce the rate of applied nitrogen fertilizer in succeeding crop. N derived from legume rhizodeposits contributed to an increase of 35 – 44% in residual N content in soil and constituted 79 – 85% of the below-ground N of plants at maturity (Mayer *et al.,* 2003). Jensen (1996) reported that 47% of the total below-ground N derived from plants originated from root depositions. Khan et al. (2003) found below-ground N constituted 24 % of total plant N for faba bean and 68 % for chickpea. In the field, below-ground N represent around 30% of plant N, and rhizodeposited N often accounted for 88–97% of below-ground N (Fustec et al., 2010). The influence of legume material on soil N availability and crop yields has also been reported (Collins et al. 2007; Schellenberg et al. 2009). Most estimates of N_2 fixation are based solely on above ground plant biomass, but as most of this N is removed in grain, the importance of belowground deposition of fixed N in maintaining the soil-N balance may not be ignored. Quantifying N in legume root systems is fundamental to understanding its effects on soil mineral N fertility and supply of N to crops in legume-based rotations (Khan et al., 2002) to determine the rate of N fertilizer application to succeeding crops.

Conclusion

Legumes are very important both ecologically and agriculturally because they are responsible for a substantial part of the global flux of N_2 to fixed forms. For legume-based farms, the effectiveness of fertility maintenance depends upon the balance of N-fixing legumes and N-depleting non-legumes in the rotation. Nitrogen fixation efficiency depends on rhizobial strain, plant host, environmental factors, soil and their interaction. All are interconnected in the control of N_2 fixation and yield of grain legumes. Variation in nodulation and N_2-fixation efficiency occur in a rhizobial strain-legume cultivar specific manner. Matching rhizobial strains to host legumes is the most important factor in maximizing the productivity of grain legumes. Rhizobia are also known to have a constructive influence on the real chemistry of soil nutrients and thus promote nutrient uptake. Properly quantifying rhizobial strain and host-legume interaction effects in diverse agro-ecologies is essential to identify effective and efficient combinations for host-cultivar specificity recommendation.

Integration of grain legumes into cropping systems has been adopted in many regions. This gives better economic returns to the farmers, as well as contributing towards maintaining soil fertility. Owing to a sustained rise in per capita income, growing population and changing lifestyles, the demand for grain legumes and their products has been growing rapidly in the world. With the generation and transfer of effective technologies for different production environments, it is expected that grain legume production will continually increase worldwide following its demand in the future.

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