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Rhizobia Symbiosis in Legumes and Non-Legumes Crops

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Abstract

Legumes are very important food sources and therefore, the nitrogen fixing ability of legume-rhizobia symbioses have great potential to improve crop yields. Biological nitrogen fixation, an important source of N in terrestrial ecosystems, plays a critical role in terrestrial nutrient cycling and net primary productivity. Symbiotic Nitrogen Fixation is the most effective and economic measures in agriculture to increase crop yield. Currently, symbiotic rhizobia refer to the soil bacteria in alpha and beta-proteobacteria that can induce root nodules on some legumes and a few of non-legumes. Symbiotic nitrogen fixation is part of a mutualistic relationship in which plants provide a niche and fixed carbon to bacteria in exchange for fixed nitrogen. This process is restricted mainly to legumes in agricultural systems, and there is considerable interest in exploring whether similar symbioses can be developed in non-legumes. A biotechnological approach where cereal crops are engineered to fix nitrogen has the potential to reduce fertilizer use in the developed world and greatly reduce the environmental impact. Nitrogen fixation in non-leguminous crops and bacterial associations has been investigated elaborately for their agronomic significance. Three approaches are currently considered as promising such as transfer of nitrogen fixation genes into organelles, root nodulation in cereals and endophytes. Different authors recognized that competent rhizobial strains could be applied to legumes and non-legumes to increase their production. A number of abiotic factors affect symbiotic nitrogen fixation. The most important abiotic factors include water stress, temperature and soil acidity are influenced symbiotic nitrogen fixation. When studying any living organism, it is important to know how each species grows and responds to certain conditions that can be found in their natural environment. Future Prospects in biological nitrogen fixation has focus on efficient strain selection, inoculums production and quality. However, the nitrogen fixation research is the quest for nitrogen fixation in cereals.

Keywords: Nitrogen fixation; Symbiosis; Nodulation; Non-legume; Legumes

Introduction

Nitrogen is one of the most abundant elements in the earth's atmosphere; however, more than 78.08% of the total nitrogen is in the form of nitrogen gas which is unavailable to living organisms, and plays a critical role for plant growth and production. Plants can use nitrogen in the form of ammonium or nitrate ions [**1**]. Biological nitrogen fixation (BNF) is one of the pathways of nitrogen (N) inputs performed by free-living or symbiotic N fixing organisms represents an important source of N in terrestrial ecosystems. The process of converting atmospheric nitrogen gas into these ions is known as nitrogen fixation and it being carried out by nitrogen-fixing microbes such as bacteria and algae [**1**].

Rhizobia are diazotrophic bacteria that fix nitrogen after becoming established inside the root nodules of legumes (Fabaceae). To express genes for nitrogen fixation, rhizobia require a plant host; they cannot independently fix nitrogen, which are part of the α-proteobacteria and β- proteobacteria are the most well-known N- fixing bacterial groups that nodulate mostly legumes. Rhizobia present within soil in two forms: as a free-living saprophyte in the soil in the absence of a suitable host plant and in a symbiotic relationship with leguminous plants. Symbiosis is an interaction between two or more species exchange mutual benefits.

The alpha-rhizobia are the most common legumes microsymbionts, which are distributed in 17 genera of 7 families. Of these 17 genera, Rhizobium, Sinorhizobium and Bradyrhizobium the most common and the majority of the rhizobial species. The α-rhizobia are usually found in common legumes, such as soybean, peanut, chickpea, pea, common bean, alfalfa, mung bean, etc. Beta-Rhizobia (β-rhizobia) are classified in three genera, including Cupriavidus, Paraburkholderia and Trinickia belonging to the family Burkholderiaceae [**2**].

The legume-rhizobial symbiosis starts with a signal exchange between the host plant and its microsymbiont [**3**]. Recognition of compatible bacteria by the host induces cortical cell divisions to form root nodule primordial, and simultaneously initiates an infection process to deliver the bacteria into the nodule cells. Infection of most legumes involves the development of plant-made infection threads that initiate in the root hair [**3**]. This mutualistic relationship is beneficial for both symbiotic partners; the host plant provides the rhizobia with carbon and source of energy for growth and functions while the rhizobia fix atmospheric N2 and provide the plant with a source of reduced nitrogen in the form of ammonium.

Thus, the process offers an economically attractive and ecologically sound mean of reducing external inputs. Both legumes and rhizobial bacteria are phylogenetically diverse. No single rhizobial strains can form symbiosis with all legumes. This can take place at early stages of the interaction so that the same bacterial strains can infect and nodulate one host plant but not another [**4**]. Nitrogen fixing microorganisms utilize 16 moles of ATP to convert one mole of gaseous nitrogen in plant available form. The energy used in this process comes from the microbial oxidation of organic molecules present in soil, while associative microbes and symbiotic microorganism obtain these

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organic substances from the rhizosphere of host plants [**5**].

Nitrogen fixing prokaryotes (diazotrophs) which are capable of producing the enzyme nitrogenase can fix nitrogen. These diazotrophs can be classified into three types: symbiotic (fixes nitrogen only in specialized organelle, nodules, formed on specific hosts of the Leguminoseae family, which forms symbiotic nodules on a variety of non-leguminous tree and shrub families), endophytic (exists inside the root of the plant of both legumes and non-legumes) and free-living (enhances BNF in the rhizosphere of both legumes and non-legumes).

Symbiotic nitrogen fixation (SNF) has the highest efficiency of BNF, but it is limited to a few genera of the Leguminoseae. While, most of the crop plants are not capable of forming SNF, they are able to benefit from the nitrogen fixed by free-living and associative diazotrophs which exist in the rhizosphere [**6**]. Several mega-grand challenge projects have been commissioned around the world focusing on transfer of the BNF traits from legumes into cereals [**7**]. Most of the attempts to engineer these BNF traits involve transfer of a minimal set of genes from legumes into cereals [**8**].

Different authors recognized that competent rhizobial strains could be applied to legumes and non-legumes to increase their production. According to Abdul (2012), Rhizobium culture significantly affected the growth and yield components of mung-bean. Similarly Mahmoodi reported that the use of appropriate strains of inoculants in nitrogen deficient soils may offer an excellent opportunity for improving legume growth and development.

Other studies have also indicated the contribution of biological nitrogen fixation in the growth promotion of non-leguminous plants through associative interaction with diazotrophs. Rhizobial inoculants have been recognized as endophytes (those microorganisms that live within host plants for at least part of their life and do not cause apparent symptoms of diseases) in the roots of non-legumes. Moreover, Sessitsch reported that rhizobia are now considered rhizobacteria of non-leguminous plants.

Rhizobial symbiosis in legumes

Some microorganisms can fix nitrogen symbiotically by partnering with a host plant. There are several examples of symbiotic nitrogen fixation such as the water fern Azolla's symbiosis with a cyanobacterium, the symbiosis between actinorhizal trees and shrubs, such as Alder (Alnus sp.), with the actinomycete Frankia. One of the well-known symbioses occurs between two partners, legume plants and rhizobia. The rhizobium -legume symbiotic interactions induces specialized organs known as nodules on the roots of their host, and obtains their nutrients from the host plant. Inside nodules rhizobia reduce atmospheric N_2 to NH_3. Nitrogen-fixing bacteria are found in several phyla [**9**], and representatives from most (if not all) of these phyla are known to engage in nitrogen-fixing symbiosis with plants [**10**]. While some bacteria can nodulate a wide range of hosts, most bacteria have strict host selectivity. As such, particular rhizobial species or strains nodulate only a narrow group of legume species or genotypes.

The development of this symbiotic process is complex; the interaction begins with a specific diffusible molecular signal exchange between the legume and the Rhizobium. The roots of the legume plants exude signal compound species-specific flavonoid-type molecules to the bacterial partner. Flavonoids compounds are components used in the chemical communication between legume plants and symbiotic nitrogen-fixing bacteria to form nodules the site of nitrogen fixation process. Nod factors are key symbiotic signals and are indispensable in the specific host-Rhizobium interaction. A bacterial signal molecule (Nod factor) is essential for induction root hair deformation and nodule formation. Lipochitooligosaccharide is produced as a result of expression of bacterial nodulation genes. In addition to these key regulatory molecules, a variety of other compounds, including exopolysaccharides, plant hormones, and vitamins, have been implicated as regulators of the nodulation process.

Rhizobial symbiosis in non-legumes

Nitrogen-fixing microbial associations with cereals have been of intense interest for more than a century. Works on rhizobia interaction with non-legumes has been done progressively and it has been demonstrated that rhizobia can associate with roots of non-legumes also, without forming true nodules, and can promote their growth. The need for an improved means of delivering nitrogen to cereals and other non-legume crops is crucial for the future of sustainable agriculture. Three approaches are currently considered as promising.

Transfer of nitrogen fixation (nif) genes into organelles

A direct approach to engineering nitrogen fixation in non-legumes is the introduction of nitrogenase-encoding bacterial nif genes into plants. The introduction of nitrogenase-encoding bacterial nif genes into non-legumes is challenging due to the complex nature of nitrogenase biosynthesis and the extreme sensitivity of nitrogenase to the presence of oxygen. Extensive genetic and biochemical studies have identified the common core set of genes products required for functional nitrogenase biosynthesis. The direct transfer of nitrogen fixation (nif) genes to the plant has the advantage of having germ line transmission therefore the technology will be in the seed. Achieving this goal will require engineering the complete biosynthetic pathway of the nitrogenase enzyme into cereals. Nitrogen fixation in non-leguminous crops and bacterial associations has been investigated elaborately for their agronomic significance. For example, associative nitrogen fixation in sugarcane, sweet potato and paddy rice are agronomically significant. Active expressions of the di-nitrogenase reductase-encoded gene (nifH) phylogenetically similar to those of Bradyrhizobium spp. and Azorhizobium spp. were abundantly found in the nitrogen-fixing sugarcane stems, sweet potato stems, and storage tubers .

Root nodulation in cereals

The second approach envisions the development of legume like root-nodule symbioses (RNS) in cereal crops. During bacterial recognition of a suitable plant host, rhizobia and legumes undergo signaling crosstalk, whereby the plant secretes flavonoids that trigger the bacteria to secrete nodulation (Nod) factors that promote nodule formation within the plant. Recently, Myc factors, which are part of the crosstalk between 70 to 90% of terrestrial plants (including cereals) and arbuscular mycorrhiza endosymbiotic fungi, were discovered to be very similar structurally to Nod factors.

Moreover, in legumes, these same genetic components play a critical role in aiding initial stages of root-nodule symbioses (RNS) development as well. Thus, genetic elements that participate in promoting both arbuscular mycorrhizae symbiosis (AMS) and root-nodule symbioses (RNS) development constitute the "common symbiosis pathway" (CSP). Current lines of research in cereals are making use of functionally conserved genetic constituents of the common symbiosis pathway (CSP) as a foundation to extend genetic networks to assemble a complete signaling pathway to support legume-like RNS in cereal crops.

Endophytes

Endophyte has been known for long that some nitrogen-fixing endophytic bacteria form nodule-independent association with cereal crops. One of the potent approaches for increasing biological N_2 fixation in cereals is to enhance associative or endophytic root colonization by desirable bacteria. The inoculation of non-legumes, especially cereals, with various non-rhizobial diazotrophic bacteria has been undertaken with the expectation that they would establish themselves intercellularly within the root system, fixing nitrogen endophytically and providing combined nitrogen for enhanced crop production. Azorhizobium caulinodans is known to enter the root system of cereals, other non-legume crops and Arabidopsis, by intercellular invasion between epidermal cells and to internally colonize the plant intercellularly, including the xylem. A particularly interesting, naturally occurring, non-nodular xylem colonizing endophytic diazotrophic interaction with evidence for endophytic intracellular symbiotic nitrogen fixation, without the need for nodulation is that of Gluconacetobacter diazotrophicus in sugarcane.

A rhizosphere-associated nitrogen fixation can occur in different ways. They may be endophytic, which reside in the internal tissue of the plant when a lack of Nod genes, which results in a Nod factor-independent infection process, and rhizospheric, which reside within the rhizosphere.

Effect of inoculation of rhizobia on non-legumes crops

Following section highlights the improvement of growth and yield parameters of different non-legumes upon inoculation with rhizobia. Several studies indicate that rhizobia may act as natural elicitor for improving the growth and yield of rice. Growth stimulation of rice followed by inoculation with rhizobium has been reported by many workers.

According to Gutierrez and Martinez, (2001) reported that increased in maize yield upon R. etli inoculation. Similarly, while testing nine different rhizobial strains for their growth promotion effects with six different non-leguminous plants in laboratory and greenhouse experiments reported that the rhizobial strain PAR-401 was the best for Zea mays and increased shoot and root dry weight of plants.

Furthermore, Hoflich (2000) conducted a series of experiments under greenhouse and field conditions to see the growth stimulating effects of rhizobia. He reported that R. leguminosarum bv. trifolii strain R39 promoted the shoot growth of maize grown in greenhouse experiments whereas in field experiments. A recent report demonstrated that an indigenous maize landrace, characterized by an extensive development of aerial roots that secrete large amounts of mucilage, can acquire 28–82% of its nitrogen from atmospheric dinitrogen. Although the Sierra Mixe maize landrace is unique in the large quantity of mucilage produced, other cereal crops secrete mucilage from underground and aerial roots and we hypothesize that this may represent a general mechanism for cereals to support associations with microbial diazotrophs. A key feature of the Sierra Mixe maize landrace mucilage is the abundance of sugars that potentially serve as a source of energy for the diazotrophs.

The aerial root mucilage was found to maintain oxygen levels below 5% at a depth of 8 mm, suggesting that the mucilage could sustain a micro aerobic environment compatible with nitrogenase activity . Azoarcus sp. Strain BH72, a mutualistic endophyte of rice, is of agro-biotechnological interest because it supplies biologically fixed nitrogen toits host and colonizes plants in remark high numbers without eliciting disease symptoms. Used four (BHUE-2, 3, 4 and 5) isolates of rhizobia for rice plant growth response studies under laboratory and greenhouse conditions. All four isolates gave a positive response in enhancing the plant growth measured in terms of plant height and shoot dry weight.

Similarly, tested six rhizobial strains isolated from a wide range of legume hosts to determine their growth promoting activities in lowland rice in a potted soil supplemented with varied amounts of mineral N and reported that inoculation with R.leguminosarum bv.trifolii E11Rhizobium sp. IRBG74, and Bradyrhizobium sp.

The growth promotion ability of rhizobial inoculant with wheat has been viewed by some researchers under greenhouse conditions. For example, conducted greenhouse experiments and reported that the strain of R. leguminosarum bv. trifolii R39, isolated from red clover nodules, promoted the shoot growth of wheat. Whereas, isolated one hundred strains of R. leguminosarum bv. trifolii from the roots of wheat cultivated in rotation with clover in two different regions of Morocco. I summarized rhizobia species in Table 1 that promote growth and yield components of the non-legumes.

Effect of symbiotic nitrogen fixation on legumes crop production

Better alternative strategies of replacing depleted soil nitrogen through by BNF using leguminous crops. Beneficial soil microorganisms that can increase soil fertility and crop yield. As the combined effect of rhizobium inoculation (EAL-1018) and boron brought significantly difference on nodule number, nodule dry weight, biomass yield and grain yield compared to the control. Similarly, reported the inoculation of legumes with efficient rhizobia is believed to increases the yield and yield components of legumes while maintaining soil health. It is also supposed to be eco-friendly practices used for improvement of N fixation resulted in increased shoot growth, number of pods and grain yield of faba bean. also reported application of N fertilizer and inoculation of rhizobium increased seed yield ha^{-1} of common bean.

Inoculation of faba bean with rhizobia increased hundred seed weight by 11.44%, number of pods per plant from 7 to 13.08, nodules dry weight by 34.04%, 82% increase of nodules per plant compared to un-inoculated plant. Similarly, Endrias reported that rhizobium inoculation increases hundred seed weight (28.76 g) Compared to un-inoculated treatments (26.57g). Inoculation of legume with specific strain of rhizobium is well known for its ability to increase N_2 fixation, plant yield and also improve the seed quality. reported that, combined application of NP fertilizer with Rhizobium inoculation provided highest plant height. also found that Rhizobium inoculation increased plant height of mung bean and groud nut, respectively. Moreover biological nitrogen fixation improved the fertility gradient of the experimental soil.

Table 1: Rhizobia Species In Commercially Available Inoculants For Legume Crops In Ethiopia.

Crops	**Type of inoculants(Rhizobium)**
Faba Bean, Lentil and Field Bean	*Rhizobium leguminosarum*
Chick Pea	*Mesorhizobium cicero*
Soy Bean	*Bradyrhizobium japonicum*
Common Bean	*Rhizobium leguminosarum phaseoli*
Cowpea	*Bradyrhizobium elkani*
Alfalfa	Rhizobium meliloti
Fenugreek	*Rhizobium spp*. Strain RGFUI
Groundnut	*Rhizobium spp*

Factors affecting symbiotic nitrogen fixation

Several environmental conditions are limiting factors to the growth and activity of the N_2-fixing plants. When studying any living organism, it is important to know how each species grows and responds to certain conditions that can be found in their natural environment. Ascertaining how bacteria respond to environmental signals, or stressful conditions, is a vital part to understanding how those microbes live, thrive and survive. Every bacterium has optimum conditions that make this process easier, however in order to survive in a changing environment the bacteria must be able to adapt.

In the Rhizobium-legume symbiosis, the process of N_2 fixation is strongly related to the physiological state of the host plant. Therefore, a competitive and persistent rhizobia strain is not expected to express its full capacity for nitrogen fixation if limiting factors Nodulation and biological nitrogen fixation are sensitive to environmental stressful conditions, which may cause inhibition of initial steps of bacterial infection in roots. The most important abiotic factors include temperature, soil moisture, soil acidity, and availability of nitrogen in the soil.

Soil temperature

Soil temperature inhibits legume BNF through its control on nodulation, nodule establishment, and nitrogenase activity when it is either too high or too low. According to, Nitrogenase activity increased with temperature in all mosses, and the temperature optimum was between 20^{0}C and 30^{0}C for all mosses. Similarly, reported that high soil temperature is one of critical factors which can prevent the development of a nitrogen-fixing association between the two symbiotic partners especially in arid and semi-arid regions. The survival of rhizobia in soil is more affected by high temperatures than by low temperatures because it can be deleterious. Most rhizobia have an optimum growth temperature at 28-31°C and many of them are unable to grow at 38°C.

High temperature can induce an inhibiting effect on bacterial adherence to root hairs, on bacteroïd differentiation, on nodule structure and on legume root nodule's functioning. At low temperatures, the cellular membrane rigidity presents a major problem for bacteria, in addition to a decreased rate of enzymatic reactions and the instability of single stranded DNA and RNA. It appears that every legume and rhizobium combination has an optimum temperature relationship, which is around 30°C for clover and pea, between 35 to 40°C for soybean, peanut and cowpea, and between 25 to 30°C for common bean. Moreover, Temperature has a marked influence on survival and persistence of rhizobial strains in soils. For example, cowpea rhizobia from the hot dry Sahel-savannah of West Africa grow at 37°C, and more than 90% of the strains isolated from this region grew well to 40°C.

Soil moisture

Water, and its availability, is one of the most vital environmental factors to affect the growth and survival of micro-organisms. The specific activity of nodules was negatively impacted by water stress during drought. Based on the reaction catalyzed by nitrogenase, under drought stress and water logging condition, which could be caused by reduced carbon supply from the plant via a decrease in sucrose synthase activity, by lower O_2 concentration, which restricts respiration efficiency. Numerous studies have addressed the impact of drought on each component involved in N_2 fixation. They revealed that under drought, the formation of new nodules is depressed, the size of the nodules is decreased, and the specific activity of the nodules is reduced reported that when water stress occurs later during the reproductive stage, the ability of plants to recover from the water deprivation period is greatly reduced. Because of preferential allocation of photosynthetic to reproductive organs during this stage, this presumably results from less photosynthesis being available for vegetative organs including roots and nodules. Similarly reported that the negative impact of water stress was larger when stress was applied at vegetative (-70%) compared to reproductive (-30%) stages. Flooding reduced BNF by 40% relative to the non-flooded control with highest effect when applied during vegetative stage (-82%).

Drought effects on rhizobial persistence and survival in the soil, on root-hair colonization and on infection by rhizobia can consequently limit the nodulation. However, some rhizobial species have shown an ability to tolerate and survive in drought conditions. The efficiency of these rhizospheric bacteria to persist in severe water deficit conditions can be used to ameliorate drought impact on plants and to help them to tolerate stress by producing physical and chemical changes.

Soil pH

Agricultural soils are either alkaline or acidic that effect on rhizobia growth, survival and subsequent formation of nitrogen-fixing symbiosis with a legume host. Each rhizobium has its own optimum pH, under which it grows at its best. Although neutral conditions are generally optimum for bacteria, different species of rhizobium display varying degrees of pH resistance as measured by their ability to grow. Soil acidity has long been known to decrease symbiotic nitrogen fixation in legumes, negatively affecting growth and yield, especially in plants depending exclusively on symbiosis to acquire nitrogen. Rhizobia can be more sensitive to acidic condition than their legume host. According to Foster, (2000) recorded that S. meliloti was viable only below to pH 5.5. Similarly reported that mutants of R. leguminosarum have been able to grow at a pH as low as 4.5. The higher nodulation rate was observed at pH 4.0, and nodule number was similarly decreased at pH 5.5 and 7.0. Nitrogenase activity was higher at pH 4.0, and lower at pH 7.0, while at pH 5.5. suggested this approach in a way of afterward identification of tolerant bacteria, where the target should be on specific gene expression under acidic condition in order to improve plant-bacterial interaction. Moreover, have been identified 20 genes in R. leguminosarum that are responsible for acid stress namely as act genes (acid tolerance).

Alkalinity stress can also retard rhizobium from growing and subsequent establishment of a viable nitrogen-fixing symbiosis with a legume host. Therefore, it makes good sense agriculturally to select rhizobial isolates that are tolerant of alkaline conditions as well as capable of nodulating legumes. The negative effect of the alkaline soil's conditions is the unavailability of essential minerals for both rhizobia and host plant such as iron and manganese. Rhizobiumetli strains EBRI 2 and EBRI 26 are more competitive than strain CIAT 899G in soils with high salt or alkaline conditions.

Availability of Nitrogen in the soil

The availability of nitrogen in the soil suppresses both nodulation and nitrogen fixation by reducing root hair and their curling. Fixed nitrogen in excessive amount reduces synthesis of leghemoglobin which leads to lower nodule activity. When large amounts of nitrogen are applied, the plant literally slows down the nitrogen fixation process. Some studies using several legume species like soybean, have reported a significant decline in legume BNF with inorganic N fertilization. High soil N availability can reduce or even suppress BNF by reducing %.

Nitrogen increases were the only factor that decoupled host and symbiont fitness response. We highlight that, any factor that increase the availability of soil nitrates should exhibit a similar pattern, considering that both soil N and BNF are complementary. In general, plant growth is greatly influenced by soil mineral N, and in N-fixing plants, as soil mineral N levels increase, BNF rates decrease and the uptake of mineral N increases.

Summary and conclusion

This review covers contribution of biological nitrogen fixation in agriculture, rhizobia and host-legume and non-legumes related factors influencing symbiotic performance. Symbiotic N_2 fixation is one of the biological processes important for development of sustainable agriculture by which the atmospheric N_2 is converted to ammonia with the aid of a key enzyme called nitrogenous. Up scaling available symbiotic nitrogen fixation measured values obtained from natural ecosystems, we estimate in the range of 52 – 130 Tg N year^{-1}) for BNF in natural terrestrial ecosystems.

Over the last several years, research and technical advances have provided a better understanding of rhizobial strains association and promotion in non-legumes crop plants. These advances could be applied to agricultural systems to enhance production by increasing crop growth through combinations of biological nitrogen fixation. There has been a biotechnological interest to promote associative nitrogen fixation in non-legume crops. Three approaches are currently considered as promising such as transfer of nitrogen fixation genes into organelles, root nodulation in cereals and endophytes.

Nitrogen fixation efficiency depends on rhizobia strain, plant host, environmental factors and their interaction. All are interconnected in the control of N_2 fixation and yield of grain crops. Matching rhizobia strains to host legumes is the most important factor in maximizing the productivity of crops. Environmental condition such as temperature, soil moisture and pH of soil had a significant influence in nitrogen fixation.

Future Prospects in biological nitrogen fixation has focus on efficient strain selection, inoculum production and quality, plant breeding for nitrogen fixation can be improved upon, and associative (endophytic) nitrogen fixation clearly is of importance. However, the nitrogen fixation research is the quest for nitrogen fixation in cereals. The transfer to an expression of the nif genes in transgenic cereal plants and the transfer of the ability to fix nitrogen symbiotically.

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