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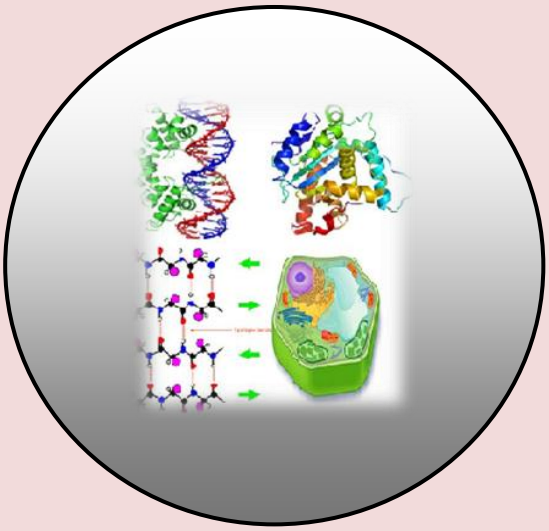

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Effects of Different Moisture Regimes on the Roots Activities of Soybean in Relation to *Bradyrhizobium japonicum* Bacteria

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ABSTRACT

Molecular nitrogen in different ways, such as nitrogen fixation by prokaryotes, lightening and chemical plants to stabilize the soil. In each of three nitrate or ammonium nitrogen is converted into soil. Static electricity does not happen always and everywhere, even in areas of high lightning strike 5 kg per ha of nitrogen in the soil. Costly methods of chemical fertilizer and pollution are the only sustainable way to approach biological nitrogen fixation is safe. Important phenomenon is the world's second fixation in three free-living existence, cooperation and coexistence occurs. Free-living bacteria such R. japonicum nitrogen in the soil without the need to stabilize the plant independently. The contribution of biological nitrogen fixation in the presence of living plant roots or leaves of the plant cells do not do any time. Azospirillum bacteria are the most important companion. Symbionts that live inside cells, like stem or leaf and root nitrogen fixation often do get into root cells. Occupation of useful rhizobium inoculated on the seed coat was known to be low because of their low competition against indigenous rhizobia. This object was to clarify the effect of inoculation method and inoculum density of B. japonicum USDA110 on production of soybean. The results show that Rhizobial-induced chlorosis in soybeans (Glycine max) is caused by a phytotoxin produced in the nodules of the affected plants. The phytotoxin has been isolated from nodules and partially characterized as a low molecular-weight amino compound.
Keywords: Humidity, Rhizobium japonicum and Soybean.

INTRODUCTION

Biological nitrogen fixation (BNF) is one of the most important phenomena occurring in nature, only exceeded by photosynthesis [Vance, 1998, Graham and Vance, 2000].

One of the most common limiting factors in plant growth is the availability of nitrogen [Newbould, 1989]. Although 4/5ths of earth's atmosphere is comprised of nitrogen, the ability to utilize atmospheric nitrogen is restricted to a few groups of prokaryotes that are able to covert atmospheric nitrogen to ammonia and, in the case of the legume symbiosis, make some of this available to plants. Predominantly, members of the plant family Leguminosae have evolved with nitrogen fixing bacteria from the family Rhizobiaceae. In summary, the plants excrete specific chemical signals to attract the nitrogen fixing bacteria towards their roots. They also give the bacteria access to their roots, allowing them to colonize and reside in the root nodules, where the modified bacteria (bacteroids) can perform nitrogen fixation [Vance, 1998, Sadowsky and Graham, 1998, Graham and Vance, 2003]. This process is of great interest to scientists in general, and agriculture specifically, since this highly complex recognition and elicitation is co-ordinated through gene expression and cellular differentiation, followed by plant growth and development; it has the potential to minimize the use of artificial nitrogen fertilizers and pesticides in crop management. This biological nitrogen fixation process is complex, but has been best examined in some detail in the context of soybean-*Bradyrhizobium* plant-microbe interactions.

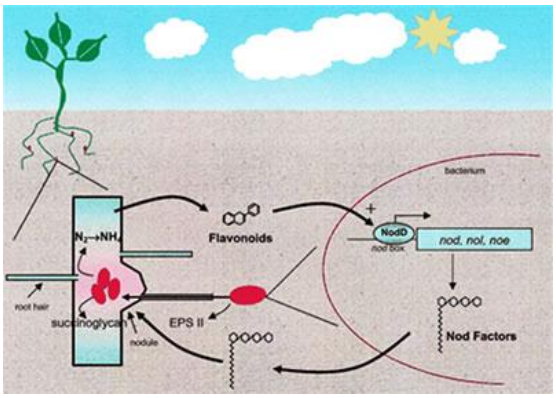

Figure 1. *R. japonicum* in Soybean originated.

Figure 2. Nodule shows healthy rhizobia Soybean originated.

Soybean – The Plant

Soybean (*Glycine max* (L.) Merrill) is a globally important commercial crop, grown mainly for its protein, oil and nutraceutical contents. The seeds of this legume are 40% protein and 20% oil. Each year soybean provides more protein and vegetable oil than any other cultivated crop in the world. Soybean originated in China, where it has been under cultivation for more than 5000 years [Cui et al., 1999].

The annual wild soybean (*G. soja*) and the current cultivated soybean (*G. max*) can be found growing in China, Japan, Korea and the far east of Russia, with the richest diversity and broadest distribution in China, where extensive germplasms are available. The National Gene Bank at the Institute of Crop Germplasm Resources, part of Chinese Academy of Agriculture Sciences (ICGR-CAAS), Beijing, contains close to 24,000 soybean accessions, including wild soybean types. Soybean was introduced into North America during the 18th century, but intense cultivation started in the 1940s – 1950s and now North America is the world's largest producer of soybean [Hymowitz and Harlan, 1983, Qui and Chang, 2010]. Although grown worldwide for its protein and oil, high value added products such as plant functional nutraceuticals, including phospholipids, saponins, isoflavones, oligosaccharides and edible fibre, have gained importance in the last decade. Interestingly, while genistein and diadzein are signal molecules involved in the root nodulation process, the same compounds can attenuate osteoporosis in post-menopausal women. The other isoflavones have anti-cancer, anti-oxidant, positive cardiovascular and cerebrovascular effects [Lui, 2004]. More recently soybean oil has also been used as an oil source for biodiesel [Mandal, 2002, Du et al., 2003, Mushrush et al., 2006, Huo et al., 2009, Pestana-Calsa et al., 2002].

Table 1. Provides the latest statistics on soybean cultivation and production as available at FAOSTAT [FAO, 2009].

	World	Africa	Americas	Asia	Europe	Oceania	Canada
Area harvested (Ha)	102,386,923	1,090,708	78,811,779	19,713,738	2,739,398	31,300	1,476,800
Yield (Hg/Ha)	25,548	13,309	28,864	14,100	17,491	19,042	29,424
Production (Tonnes)	261,578,498	1,451,646	227,480,272	27,795,578	4,791,402	59,600	4,345,300
Seeds (Tonnes)	6,983,352	43,283	4,838,633	1,906,313	193,870	1,252	154,300
Soybean oil (Tonnes)	39,761,852	390,660	24,028,558	12,442,496	2,890,760	9,377	241,300

Soybean is a well-known nitrogen fixer and has been a model plant for the study of BNF. Its importance in BNF led to the genome sequencing of soybean; details of the soybean genome are available at soybase.org (*G. max* and *G. soja* sequences are available at NCBI as well). Although considerable work has been conducted on other legumes with respect to biological nitrogen fixation, we focus only on soybean for this review.

The efficiency of BNF depends on climatic factors such as temperature and photoperiod [Shiraiwa et al., 2006], the effectiveness of a given soybean cultivar in fixing atmospheric nitrogen depends on the interaction between the cultivar's genome and conditions such as

soil moisture and soil nutrient availability [Sridhara, 1995, Jung et al., 2008] and the competitiveness of the bacterial strains available, relative to indigenous and less effective strains, plus the amount and type of inoculants applied, and interactions with other, possibly antagonistic, agrochemicals that are used in crop protection [Campo and Hungria, 2004]. The most important criteria, however, is the selection of an appropriate strain of *B. japonicum* since specific strains can be very specific to soybean cultivar, and subject to influence by specific edaphic factors [Hughes and Herridge, 1989, Alves et al., 2003, Abaidoo et al., 2007]. Under most conditions, soybean meets 50-60 % of its nitrogen demand through BNF, but it can provide 100 % from this source [Salvagiotti et al., 2008].

Bradyrhizobium japonicum

B. japonicum, is a gram negative, rod shaped nitrogen fixing member of the rhizobia and is an N2-fixing symbiont of soybean. *B. japonicum* strain USDA110, was originally isolated from soybean nodules in Florida, USA, in 1957 and has been widely used for the purpose of molecular genetics, physiology, and ecology, owing to its superior symbiotic nitrogen fixation activity with soybean, relative to other evaluated strains. The genome sequence of this strain has been determined; the bacterial genome is circular, 9.11 Million bp long and contains approximately 8373 predicted genes, with an average GC content of 64.1% [Kaneko et al., 2002a, Kaneko et al., 2002b]. Initially attached to the root-hair tips of soybean plants, rhizobia colonize within the roots and are eventually localized within symbiosomes, surrounded by plant membrane. This symbiotic relationship provides a safe niche and a constant carbon source for the bacteria while the plant derives the benefits of bacterial nitrogen fixation, which allows for the use of readily available nitrogen for plant growth. Inoculation of soybean with *B. japonicum* often increases seed yield [Ndakidemi et al., 2006].

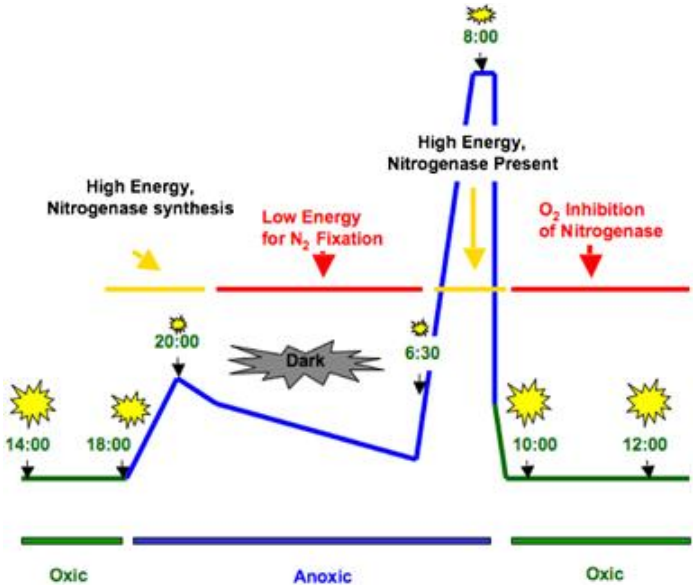

Figure 3. Conceptual model depicting changes in nitrogenase activity over the diel cycle. The figure depicts the relative nitrogenase activity, light conditions, the O_2 status and the energetics of the mat over the diel cycle.

B. japonicum synthesize a wide array of carbohydrates, such as lipopolysaccharides, capsular poly saccharides, exopoly saccharides (EPS), nodule polysaccharides, lipo-chitin oligosaccharides, and cyclic glucans, all of which play a role in the BNF symbiosis.

Bacteria produce polysaccharide degrading enzymes, such as polygalacturonase and carboxymethyl cellulase, cleave glycosidic bonds of the host cell wall at areas where bacteria are concentrated, creating erosion pits in the epidermal layer of the roots, allowing the bacteria gain entry to the roots [Mateos et al., 2001]. The energy source for *B. japonicum* is the sugar trehalose, which is taken up readily and converted to CO_2 [Salminen and Streeter, 1986, Müller et al., 2001, Streeter and Gomez, 2006, Sugawara et al., 2010]. On the other hand UDP-glucose is taken up in large quantities but metabolized slowly, like sucrose and glucose. Promotion of plant growth causes more O_2 to be released and more CO_2 to be taken up [Mateos et al., 2001].

Lipo-chitooligosaccharide (LCO) from *Bradyrhizobium japonicum*

As mentioned earlier in this review, the process of nodulation in legumes begins with a complex signal exchange between host plants and rhizobia. The first step in rhizobial establishment in plant roots is production of isoflavonoids as plant-to-bacterial signals; the most common in the soybean-*B. japonicum* symbiosis being genestin and diadzein [Rao and Cooper, 1994].

Some recent literature has also shown that jasmonates can also cause *nod* gene activation in *B. japonicum* although the strain specificities are very different from those of isoflavonoids such as genistein [Mabood et al., 2006a, Mabood et al., 2006b, Mabood et al., 2006c, Mabood et al., 2006d]. LCOs are oligosaccharides of β-1,4-linked N-acetyl- D-glucosamine coded for by a series of *nod* genes and are rhizobia specific [Spaink et al., 1995, Perret et al., 2000]. The nod DABCIJ genes, conserved in all nodulating rhizobia [Spaink et al., 1995, Kamst et al., 1998, Vazquez et al., 1993] are organized as a transcriptional unit and regulated by plant-to-rhizobia signals such isoflavanoids [Carlson et al., 1994, Schultze M, Kondorosi, 1996, Schultze and Kondorosi, 1998]. Nodulation and subsequent nitrogen fixation are affected by environmental factors. It has been observed that, under sub-optimal root zone temperatures (for soybean 15-17 ºC), pH stress and in the presence of nitrogen, isoflavanoid signal levels are reduced, while high temperature (39 ºC) increases non-specific isoflavanoid production and reduces *nod* gene activation, thereby affecting nodulation [Bai et al., 2002a]). Our laboratory has isolated and identified the major LCO molecule produced by *B. japonicum* 532C as Nod Bj V (C18:1, MeFuc) [Prithiviraj et al., 2000]. This Nod factor contains a methyl-fucose group at the reducing end that is encoded by the hostspecific *nodZ* gene [López-Lara et al., 1995], which is an essential component for soybean-rhizobia interactions. LCOs also positively and directly affect plant growth and development in legumes and nonlegumes. The potential role of LCOs in plant growth regulation was first reported by Denarie and Cullimore [Denarie and Cullimore, 1993]). Nod genes A and B from *R. meliloti*, when introduced into tobacco, altered the phenotype by producing bifurcated leaves and stems, suggesting a role for *nod* genes in plant morphogenesis [Schmidt et al., 1993]. The development of somatic embryos of Norway spruce is enhanced by treatment with purified Nod factor from *Rhizobium* sp. NGR234. It has been suggested that these Nod factors can substitute for auxin and cytokinin like activities in promoting embryo development, and that the chitin core of the nod factor is an essential component for regulation of plant development [Dyachok et al., 20002, Dyachok et al., 2002]. Some of the LCO induced enod genes in non-legumes seem to encode for defense related responses, such as chitinase and PR proteins, peroxidase [Cook et al., 1995] and enzymes of phenylpropanoid pathway, such as L-phenylalanine ammonia-lyase (PAL) [Inui et al., 1997].

Seed germination and seedling establishment is enhanced in soybean, common bean, maize, rice, canola, apple and grapes, accompanied by increased photosynthetic rates [Zhang and Smith, 2001]. Hydroponically grown maize showed an increase in root growth when LCO was applied to the hydroponic solution [Souleimanov et al., 2002a, Souleimanov et al., 2002b] and foliar application to greenhouse grown maize resulted in increases in photosynthetic rate, leaf area and dry matter [Khan, 2003]. Foliar application to tomato, during early and late flowering stages, increased flowering and fruiting and also fruit yield. An increase in mycorrhizal colonization (*Gigaspora margarita*) was observed in *Pinus abies* treated with LCO [Oláh et al., 2005]. Recent research in our laboratory, on soybean leaves treated with LCOs under sub-optimal growth conditions, revealed the up-regulation of over 600 genes, many of which are defense and stress response related, or transcription factors, microarray results show that the transcriptome of the leaves is highly responsive to LCO treatment at 48 h post treatment. These results suggest the need to investigate more carefully the mechanisms by which microbe-to-plant signals help plants accommodate abiotic and biotic stress conditions.

MATERIALS AND METHODS

RhiZobial Strains: Strains of *Rhliobiurnt japonicihll* used in these experiments were numbers 38. 61. 73, 76, 94, 117 and 119 from the 3Ilb series of the USDA Rhizobilmn strain collection. Strains 61, 73, 76, and 94 have been observed to include chlorosis in some varieties of soybeans (2), while strains 38, 117, and 119 have not been observed to induce chlorosis in any soybean variety (Ura Mae Means, private communication) Media. The bacteria were cultured in 4 nutrient media having the following compositions: A) Synthetic; 10 g of mannitol, 0.48 g of NH\NO,, 0.11 g of CaCl.,, 0.25 g of MgSO4, 1.21 g of Tris buffer [Tris-(hydroxymethyl) amino methane], 0.04 g of KHPO,1, 0.1 mg of thiamine chloride, 0.5 lug of biotin, 1.0 mg of FeCl. 6HO, 0.1 mg of MnSO4, and 0.1 mg of Na., MoO4 per liter; B) yeast extract medium, mannitol, CaCL, MgSO4, and Tris buffer in the amounts shown above plus the extract from 5 g.

Culture Condition: For most experiments the rhizobia were cultured at 280 in 300 ml of medium contained in 500-nil Erlenmeyer flasks on a reciprocal shaker. Ten-liter cultures, contained in 20 liter carboys, were forcibly aerated with filtered air and stirred with magnetic stirrers. Growth was monitored by measuring OD at 425 mu. The cells were harvested and washed by centrifugation, lyophilized, and weighed. Concentrations of toxin are expressed as asparagines equivalents; however, since the 2 compounds may not be equivalent in their molar color yield with ninhvdrin estimated values for the toxin are only relative. Reference standards for Y were prepared from purified preparations of Y, using a molecular weight of 208 (Owens, unpublished data). For purification of the toxin and unknown Y. the cellular extract from 100 liters of culture is chromatographed on a 15- by 600-mm (100 cc) column of sulfonic acid resin in the NH4, form (4). After washing with 1 liter of water, the column is eluted successively with 1.5 liters of 0.002 N. 1 liter of 0.0033 N, and 1 liter of 0.006N NH4OH (2 ml per min, 20 ml fractions).

RESULTS AND DISCUSSION

In the work reported here Rhizobiumzi strain 94 synthesized and accumulated the phytotoxin when cultured in synthetic, yeast extract, and yeast extract plus casamino acids media, but not when cultured in synthetic medium supplemented with casanmino acids.

These results suggest that the proportion of nutrients in the medium, and not the presence or absence of certain nutrients, is a critical factor in determining whether toxin is produced by rhizobial strains having the genetically potential to do so. A somewhat different nutritional aspect is presented by the finding that only 2 of the 4 chlorosis inducing strains produced detectable quantities of the toxin in yeast extract.

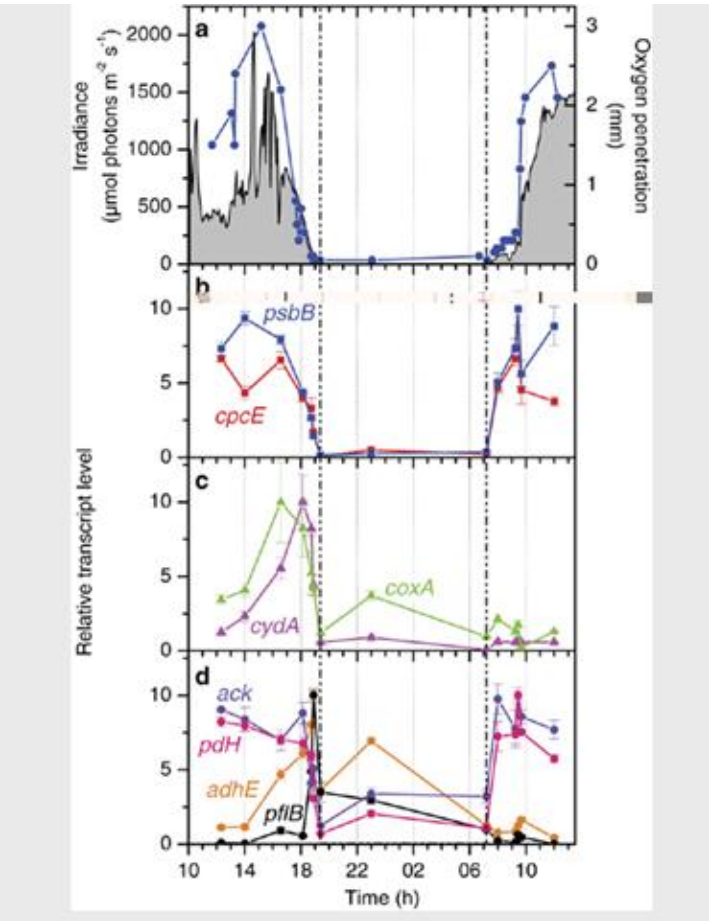

Figure 4. Real-time reverse transcriptase (RT)-PCR (qPCR) analysis of relative transcript levels from genes involved in energy metabolism in *Synechococcus* ecotypes. (a) Curves showing the light intensity and O_2 penetration in the mats over the diel cycle, this data, the same as in Figure 1, provide a reference for evaluating the transcript data presented in the remaining panels. The levels of transcript encoding proteins with (b) photosynthetic (*psbB*, *cpcE*), (c) respiratory (*cydA*, *coxA*) and (d) fermentation functions (*pflB*, *pdH*, *adhE*, *acs*) measured over the diel cycle. Error bars on graphs indicate the mean ±s.d.

A chiorosis-inducing phytotoxin, formerly known to be produced only in soybean nodules, was found to be synthesized by several strains of *Rhivobium japonicumn* in pure culture. Two of the strains have not been observed to induce chlorosis in soybeans, while 2 chlorosis-inducing strains failed to produce detectable quantities of the toxin in pure culture. Production of the phytotoxin is a selected strain was greatly affected by the culture medium. Maximum production per unit volume of culture was obtained with cells grown in yeast extract medium supplemented with casamino acids and harvested at the end of the logarithmic phase of growth.

Procedures for isolating milligram quantities of the phytotoxin are described. Inoculation with efficient rhizobia at the ordinary dose does not increase appreciably the seed yield of soybean because the occupation ratio of the inoculated rhizobial strains in the nodules is very low due to competition with less efficient indigenous rhizobia. In order to increase the seed yield by rhizobial inoculation, the occupation ratio of the inoculated strains must be increased. The increase of the occupation ratio has been examined from various viewpoints such as improvement of inoculation method. For the screening of efficient and competitive strains, a large number of useful strains had been isolated from mutagenized and recombinant rhizobia.

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