Soybean interactions with soil microbes, agronomical and molecular aspects

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Abstract – Soybean, Glycine max (L.) Merrill, is one of the most important food crops in the world. High soybean yields require large amounts of N fertilizers, which are expensive and can cause environmental problems. The industrial fixation of nitrogen accounts for about 50% of fossil fuel usage in agriculture. In contrast, biological fixation of N2 is a low-cost source of N for soybean cropping through the symbiotic association between the plant and soil bacteria belonging to the genera Bradyrhizobium and Sinorhizobium, which are collectively called “soybean rhizobia”. In general, symbiotic nitrogen fixation in crop legumes not only reduces fertilizer costs but also improves soil fertility through crop rotation and intercropping. Biological nitrogen fixation is due to symbioses between leguminous plants and species of Rhizobium bacteria. Replacing this natural N source by synthetic N fertilizers would cost around 10 billion dollars annually. Moreover, legume seed and foliage have a higher protein content than that of non-legumes, and this makes them desirable protein crops. There is a wide knowledge of the industrial elaboration and use of commercial soybean inoculants based on bradyrhizobia strains. At present, the technology to prepare different types of inoculants, either solid or liquid, is sufficiently developed to meet market requirements, although further research and investments are still required to improve the symbiotic efficacy of rhizobial inoculants. Inoculation of soybeans under field conditions has been successful in the USA, Brazil and Argentina, which are the world leaders in soybean cultivation in terms of acreage and grain yields. There are, however, limitations to a wider use of rhizobial inoculants: the size of indigenous soil rhizobial populations can prevent the successful use of inoculants in some particular areas. For example, many Chinese soils contain more than 108 soybean rhizobia per gram of soil, which imposes a serious barrier for nodule occupancy by the soybean rhizobia used as an inoculant. The use of inoculants based on soil bacteria other than rhizobia has also increased in the last decades. An example is the genus Azospirillum, which can be used for its capacity to increase plant growth and seed yields through different mechanisms, which include the production of plant hormones and the increase in phosphate uptake by roots. In addition, co-inoculation with Azospirillum and rhizobia enhances nodulation and nitrogen fixation. Although less developed, it is expected that inoculants based on mycorrhizal fungi will also play a relevant role in sustainable agriculture and forestry. In spite of any possible limitations, the use of inoculants appears compulsory in a frame of sustainable agriculture, which seeks to increase crop yields and nutrient-use efficiency while reducing the environmental costs associated with agriculture intensification. This review also summarizes some of the most relevant genetic aspects of soybean rhizobia in relation to their symbiosis with soybeans. They can be listed as follows: (1) legume roots exude flavonoids, which are able to activate the transcription of nodulation (nod, nol, noe) genes; (2) expression of nodulation genes results in the production and secretion of lipo-chitin oligosaccharide signal molecules, called LCOs or “Nod factors”, which activate nodule organogenesis in the legume root; (3) LCOs induce numerous responses of the legume roots, such as hair curling and the formation of nodule primordia in the inner or outer cortex; (4) the function of many soybean rhizobia nod genes is known and the chemical structure of the LCOs produced has been determined; (5) in addition to LCOs, different soybean rhizobia surface polysaccharides are required for the formation of nitrogen-fixing nodules; (6) surface polysaccharides might act as signal molecules or could prevent plant defense reactions. Cyclic glucans, capsular polysaccharides and lipopolysaccharides appear to play relevant roles in the soybean nodulation process since rhizobial mutants affected in any of these surface polysaccharides are symbiotically impaired. Present knowledge of the molecular bases determining cultivar-strain specificity and nodule occupancy by soybean rhizobia competitors is clearly insufficient. This lack of information is a serious barrier for developing strategies aimed at improving nodulation and symbiotic nitrogen fixation of commercial inoculants. In spite of these difficulties, recent studies have shown that the signaling pathway involved in triggering nodule organogenesis is independent of that operating in bacterial entry through infection thread formation. These facts might offer new insights for improving symbiotic nitrogen fixation and also for the feasibility of transferring nodule organogenesis, a first step in expanding this symbiotic interaction into other agriculturally important species.

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1. INTRODUCTION

1.1. Brief history of world soybean production

The soybean [Glycine max (L.) Merrill] is one of the most important food crops in the world. High soybean yields require large amounts of nitrogen (N). The least expensive source of N for soybean is biological fixation of atmospheric N\(_2\) by the symbiotic association between the plant and soil bacteria belonging mainly to the genus *Bradyrhizobium*. The efficiency of the biological fixation of the atmospheric N\(_2\) process depends on many factors related to the plant, to the bacteria, to the symbiosis, and to the environment. Problems of low soil fertility and limited availability of macro- and micronutrients are also among the most important constraints (Campo et al., 2009).

By whom, when, where and how the soybean crop was domesticated in China and disseminated throughout the world is a fascinating story (Hymowitz and Shurtleff, 2005). Because the soybean is one of humanity’s food crops, the history and literature describing the origin of soybean cultivation is full of errors and myths. In fact, soybean is not one of the world’s oldest domesticated crops and there are no archaeological records that suggest the soybean has been cultivated in China for more than 5000 yr. The current oldest reliable record for soybean in China goes back to the 11th century BC or perhaps a little earlier.

The earliest known introduction of the soybean into America was by Samuel Bowen in 1765. He introduced Chinese vetches (soybean) into the Colony of Georgia. Henry Yonge, the Surveyor General of Georgia from 1766 on, cultivated soybean at the request of Bowen and one year later he received a royal patent for making soy sauce from soybean growing in America. The term “soybean” was probably coined to refer to the bean from which soy sauce was produced.

In 1712 the German botanist Kaempfer brought soybean to Europe. Soybean was exhibited in the Botanical Garden of Paris in 1739 and in the British Royal Botanic Gardens in 1790. Soybean cropping was initiated in other countries in Europe (1875–1877) as a result of its successful exhibition at an International Exposition in Vienna in 1873. Although it was not cropped in Brazil until the 1960s, at present Brazil is the second largest soybean producer after the United States of America. Soybean cropping was spread through Africa during the twentieth century.

1.2. The importance of soybean cultivation today

The US soybean harvest reached over 10 million tons (Mt) in the early 1950s and it is now 70–75 Mt a year, almost half of the global total. Soybeans are the country’s second most valuable crop, close behind corn, and worth nearly three times as much as wheat. Soybean acreage represents more than 15% of all arable land. Brazilian production, stimulated by exports, has grown even faster: the area planted with soybeans has expanded more than sixty-fold since the late 1950s and the total national production in 2007 reached 61 Mt. In the same year, Argentina with acreage of about 18 Mha harvested 47 Mt, relegating the Chinese harvest to fourth place. The Japanese now grow a mere 3% of what they consume.

In Europe acreage dedicated to soybean is less than 1Mha (ca. 840 000 ha). Italy (with 44.5%), France (29%) and Romania (22%) occupy the leading positions. Grain yields vary between 3300 and 2500 kg/ha in Italy and France, respectively. Table I summarizes the total acreage, production and value of soybean, corn and wheat crops of the United States of America during the period 2006–2008. Table II shows the production of the leading soybean countries as well as the main sources of protein meal consumption. Interestingly, although many fishes are close to extinction due to overfishing, fish protein meal consumption is only 3% of that derived from soybean.

This review is mainly focussed on the description of applied and fundamental aspects of rhizobia species able to form nitrogen-fixing nodules on soybean roots. Other soil microorganisms that, through their interaction with soybean roots, show a positive effect on plant growth will be briefly mentioned. Information about the plant side can be found at the website “http://www.wsrr2009.cn/en/index.asp”, which includes The Proceedings of the VIII World Soybean Research.