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Advances in the Identification of Novel Factors Required in Soybean Nodulation, a Process Critical to Sustainable Agriculture and Food Security

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Abstract

Nodulation is a process of organogenesis that results from a symbiotic relationship between legume plants and soil-dwelling, nitrogen-fixing bacteria, called rhizobia. The rhizobia are housed in newly formed structures on the host roots, called nodules. Within nodules, the rhizobia fix atmospheric N_2 into useable forms of nitrogen for the plant. This process is highly important to agriculture, as nitrogen is critical for plant growth and development and is typically the main component of fertilizers. Although fertilizers are effective, they are expensive and often pollute, making biological alternatives, such as legume nodulation, attractive for use in agriculture. Nodulation is regulated by the auto regulation of nodulation (AON) pathway, which enables the host plant to balance its needs between nitrogen acquisition and energy expenditure. Current research is elucidating the nodule development and AON signalling networks. Recent technological advances, such as RNA-sequencing, are revolutionizing the discovery of genes that are critical to nodulation. The discovery of such genes not only enhances our knowledge of the nodulation signalling network, but may help to underpin future work to isolate superior legume crops via modern breeding and engineering practices. Here, recent advances using the cutting-edge technique of RNA sequencing to identify new nodulation genes in soybean are discussed.

Global Use of Nitrogen Fertiliser

Approximately half of the world's population is directly reliant upon nitrogen fertiliser use in agriculture for their food supply [1-3]. Taking into account nitrogen fertiliser manufacture, transport and application, the fossil fuel consumed accounts for 50% of fossil fuel use in agriculture, and 5% of the global natural gas consumption annually [4,5]. With the rising cost of fossil fuels, the use of nitrogen fertiliser is becoming increasingly costly for farmers and is often too expensive in developing regions of the world [6]. Not only are nitrogen fertilisers expensive, they are inefficient, with 30-50% of nitrogen fertiliser typically lost to leaching. This run off can cause the eutrophication of waterways and other significant environmental problems [7]. Nitrogen contaminated drinking water can also cause methemoglobinaemia, or "Blue-baby syndrome", a potentially fatal condition in infants [8,9].

The global use of nitrogen fertiliser has been steadily increasing in most continents (Figure 1). Worryingly, this also means an increase in NO_x gases, which are released when nitrogen fertiliser is broken down. These gases contribute to the formation of ground-level ozone, which causes yield reductions. Nitrous oxide (N_2O) is also emitted by breakdown of nitrogen fertilisers [7,10] and is 292 times more active as a greenhouse gas than CO_2 [4]. Agriculture was the main source of anthropogenic N_2O emissions in 2005, making up 60% of the global total [11]. The majority of these emissions resulted from the application of nitrogen fertiliser [11]. By 2050 it is estimated that global nitrogen fertiliser use will increase by 50% in an attempt to boost food production and support a rising population [10]. These numbers have experts calling for agricultural reform to diminish nitrogen fertiliser use.

Legume Crops as a Safe Alternative to Nitrogen Fertiliser

One safe alternative to the use of nitrogen-based fertilisers is to take advantage of biologically-fixed nitrogen. Legumes are able to form a relationship with specialised nitrogen-fixing soil bacteria, called rhizobia. The rhizobia convert atmospheric di-nitrogen into usable forms of nitrogen for the plant, whilst being housed in novel root organs, called nodules. The use of legumes as rotation crops is an important agricultural practice that many experts argue must be increased to help curb nitrogen fertiliser use [2,6,10]. Optimizing biological nitrogen fixation processes, such as nodulation, has the potential to increase crop yields and enhance soil fertility whilst simultaneously reducing farming costs and harmful environmental impacts [1,5,6,12]. However, it is only with an increase in our knowledge of nodulation processes and its genetic basis that we can fully reach this goal.

Nodule Organogenesis

The most common entry point for rhizobia invasion is the region of root where the root hairs are developing, called the Zone of Nodulation (ZON) [13-16]. Rhizobia attach to the root hair, triggering root hair deformation and curling [13,14,17]. This process involves the rearrangement of underlying microtubules which allow bacterial entry and the establishment of tubular structures called the infection threads (IT) [18,19].

Occurring in parallel to rhizobia invasion are inner cellular changes which lead to nodule primordia formation [19]. The ITs full of rhizobia progress towards the nodule primordia. The convergence of the rhizobia in the ITs and the nodule primordia is essential for successful nodule formation. Once the rhizobia reach the developing nodule, they are released from the ITs into specialised structures called symbiosomes, in which they differentiate into bacteroids. Using

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