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Review

The value of biodiversity in legume symbiotic nitrogen fixation and nodulation for biofuel and food production

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ABSTRACT

Much of modern agriculture is based on immense populations of genetically identical or near-identical varieties, called cultivars. However, advancement of knowledge, and thus experimental utility, is found through biodiversity, whether naturally-found or induced by the experimenter. Globally we are confronted by ever-growing food and energy challenges. Here we demonstrate how such biodiversity from the food legume crop soybean (*Glycine max* L. Merr) and the bioenergy legume tree *Pongamia* (*Millettia pinnata*) is a great value. Legume plants are diverse and are represented by over 18,000 species on this planet. Some, such as soybean, pea and medics are used as food and animal feed crops. Others serve as ornamental (e.g., wisteria), timber (e.g., acacia/wattle) or biofuel (e.g., *Pongamia pinnata*) resources. Most legumes develop root organs (nodules) after microsymbiont induction that serve as their habitat for biological nitrogen fixation. Through this, nitrogen fertiliser demand is reduced by the efficient symbiosis between soil *Rhizobium*-type bacteria and the appropriate legume partner. Mechanistic research into the genetics, biochemistry and physiology of legumes is thus strategically essential for future global agriculture. Here we demonstrate how molecular plant science analysis of the genetics of an established food crop (soybean) and an emerging biofuel *P. pinnata* feedstock contributes to their utility by sustainable production aided by symbiotic nitrogen fixation.

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Global nitrogen condition

Nitrogen fixation is the capture of literally unlimited atmospheric nitrogen gas (N_2) to form ammonia (NH_3), which is readily available for assimilation by plant and microbes. The biological process is broadly distributed but always relies on prokaryotic organisms such as *Klebsiella*, *Azotobacter*, *Frankia* or *Rhizobium* bacteria. It is mimicked by the industrial Haber–Bosch process developed about 100 years ago, leading to the present day industrial fertiliser industry. This process is globally essential for modern agricultural production, but has negative aspects caused by a large dependence on fossil fuel, related CO_2 release and increasing production costs, fertiliser run-off and associated pollution caused by eutrophication, and nitrous oxide (N_2O) release (a major ‘Greenhouse Effect’ gas; Gresshoff, 2014).

Biological nitrogen fixation by free-living soil bacteria is significant; indeed, so is the associative nitrogen fixation involving non-legume plants such as sugarcane. Nitrogen fixation has a strong impact on elemental stoichiometries as outlined by Carnicer et al. (2015) in this issue. However, plant productivity is limited and its large scale utility, as compared to ecological impact, is even sometimes questioned as environmental factors control the apparent efficiency. In contrast symbiotic nitrogen fixation as seen in root nodules of legume plants, is more tightly associated with plant productivity and yield.

Numerous legume species are used in modern agriculture and silviculture as the nitrogen fixing benefit of the legume–rhizobia symbiosis is globally distributed (from Arctic tundra to tropical rain forest). Indeed both soybean (*Glycine max* L. Merr.) and common bean (*Phaseolus vulgaris* L.), as well as chickpea (*Cicer arietinum* L.) and cowpea (*Vigna unguiculata* L.), are major food and feed sources. Forage legumes such as clover (*Trifolium* species) and medics (*Medicago* species) globally contribute to nitrogen input into animal protein. About 200 million tons of nitrogen are added to the biosphere annually by symbiotic nitrogen fixation of legumes (Graham and Vance, 2003). About one third of all the nitrogen atoms in a human (or whichever other mammal) was captured from the air by the nitrogen fixing symbiosis of legumes. Legumes also appear as tree species, many of them used ornamentally (such as Leopard tree; *Caesalpinnea ferrea*) or as timber crops (such as blackwood; *Acacia melanoxylon*). One tree species of current importance is the legume *Pongamia pinnata* L. Pierre (aka *Milletia pinnata*), which serves as a biofuel feedstock (Scott et al., 2008; Biswas et al., 2013) for the production of transport biodiesel, and aviation jet fuel (Klein–Marcuschamer et al., 2013; Gresshoff, 2014).

For both pongamia and soybean the ability to fix nitrogen is seen as a major economic and ecological benefit. However, note that most nodulated legumes, as verified by both soybean and pongamia in our laboratory, grow larger and yield more when supplied with nitrogen fertiliser! In other word, nodulation and symbiotic nitrogen fixation are fine, but come at a cost to the plant. Of course, when integrating the environmental and economic costs of fertiliser supply and comparing these against the yield depression, the overall picture seems to favour the symbiotic relation, especially as future supplies of fossil fuel energy for synthesis of nitrogen fertiliser are destined to become limiting. Available biodiversity in both species, even if induced experimentally by mutagenesis as in soybean (see Carroll et al., 1985a,b), adds to their potential in the agriculture of the future, which needs to address limitations of growing space, increased demand from an increasing global population and depleting energy reserves (especially crude oil and natural gas).

Legume nodule formation and subsequent nitrogen fixation

The subject has been broadly researched and significant knowledge exists (Oldroyd et al., 2011; Geurts and Bisseling, 2002;

Caetano–Anollés and Gresshoff, 1991; Pueppke, 1996; Gresshoff, 1993; Ferguson et al., 2010; Stacey et al., 2006; Biswas and Gresshoff, 2014). The modes of nodule formation are diverse (determinate, coralloid and indeterminate nodule types, stem nodulation, microsymbionts with or without symbiotic plasmids, etc.), but seem to have common mechanistic ‘overtones’. These are quickly reviewed here.

Essentially the ‘*Rhizobium*’ bacteria (mainly called *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Photorhizobium* and *Azorhizobium*) respond to phenolic legume exudates composed of flavonoid substances such as the isoflavones genistein and daidzein (signals in soybean) and the flavone 7,4’ dihydroxyflavone (DHF; signal in white clover) by initial chemotactic attraction, followed by synthesis of a ‘return signal’ called the lipochito-oligosaccharide “Nod Factor” (Dénarié et al., 1996). It is an oligomer of *N*-acetylglucosamine, similar to the insect exoskeleton component ‘chitin’, but shorter, decorated by small side groups including a major fatty acid (C16 and C18), fucose, sulphate and further acetyl groups; the modifications are symbiosis-specific so that the Nod factor from *Rhizobium leguminosarum* (the pea microsymbiont) differs structurally from that from *Bradyrhizobium japonicum* (the soybean microsymbiont). Nod factors usually are about 1500 Da in size and act at extremely low levels (nanomolar). Indeed even non-legume plants have been shown to respond to them, not with a nodulation response, but rather a pathogenesis-type response (Liang et al., 2013), as the *N*-acetyl glucosamine (five subunit) backbone alone is a strong chitin-like elicitor to many plants.

Nod factors are perceived at the legume root epidermis by a receptor complex involving two LysM type receptor kinases (NFR1 and NFR5, or equivalents in other legumes). These transmit an unknown signal to the root hair nucleus leading to ionic fluctuations and subsequent (usually delayed within 15 min) calcium ion spiking (Oldroyd et al., 2011). Several genes, as designated in Fig. 1, are known to be involved as a result of induced, loss-of-function mutations in *G. max* (soybean), *Lotus japonicus*, *Pisum sativum* (pea), and *Medicago truncatula* that eliminate the capability to nodulate.

The initial visible Nod factor response is root hair curling and subsequent infection thread formation by which the rhizobia enter the root hair cell through redirected tip growth and new cell wall formation (the infection thread). This allows bacteria to be released into newly induced cortical cell divisions (nodule primordia) for further infection and eventual nodule formation. Xylem-pole localised pericycle divisions, normally limited to lateral root induction, occur concurrently and allow development of nodule vascular connections (see Ferguson et al., 2010).

The central nodule tissue is inhabited by invading rhizobia, now called bacteroids, to form the nitrogen-fixing region. In determinate nodules of soybean about 25,000 bacterial cells per infected cell develop into bacteroids (shaped like the rod-like vegetative cell; Gresshoff and Rolfe, 1978). In indeterminate-type nodulating legumes, such as pea, medics and clovers, through incomplete cell divisions, bacteroids further differentiate into larger cells with about 750–1000 bacteroids found per infected cell (Gresshoff et al., 1977).

Fixed nitrogen (NH_3) is exported from the symbiosome membrane-enclosed bacteroid into the plant cytoplasm for subsequent assimilation by glutamine synthetase (GS) into glutamine (Padilla et al., 1987); this is further transported to the plant via the xylem or converted to nitrogen transport molecules like ureides in soybean, and then transported. Optimal nitrogen fixation rates were detected for field-grown soybean at about 400 kg N/ha/year; usual levels are around the 100 kg N/ha/year level.

To gain new insights into the processes underlying legume nodule initiation and regulation of nodule number (and thus nitrogen fixation potential), EMS induced mutations were produced in soybean into the mid-1980s (Mathews et al., 1989; Carroll et al.,

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