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A seed change in our understanding of legume biology from genomics to the efficient cooperation between nodulation and arbuscular mycorrhizal fungi

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Abstract

Grain legumes play a significant role in global food security. They have an advantage over cereals in that they can form symbiotic associations with nitrogen-fixing bacteria, making them self-sufficient in terms of nitrogen acquisition. In addition to this superior agronomic trait, grain legumes have excellent nutritional properties and are thus widely used as animal feed, as well as in human nutrition. Current global trends towards increased legume consumption and availability of value-added products, as well as legume production in developing countries, require the provision of improved cultivars with better productivity and adaptability. Intensive efforts are thus underway to elaborate genomic resources and gain an improved knowledge base in a number of legume crops. There is also an emerging understanding of the beneficial interactions between legume-associated organisms, particularly rhizobia and arbuscular mycorrhizal fungi, which result in improved nodulation and nutrient acquisition. The emerging focus on legume breeding for high sustainable yields as well as improved biotic and abiotic stress tolerance traits, will serve to close the current gap between grain legume production and demand. With the support from policymakers, this increase in knowledge can be readily translated into increased crop production to meet the demands of an increasing global population.

Key Words: arbuscular mycorrhiza, climate change, genomics nodules, phosphorus, rhizobia, symbiotic nitrogen fixation, QTLs

Introduction

Grain legumes have long been an important human and animal food source, providing a staple source of protein, carbohydrate and fibre for a large proportion of the global population (Foyer et al., 2016). The large and economically important legume family is widely distributed in nature and includes trees, shrubs and perennial herbaceous plants, as well as important annual crops such as soybeans, peas, lentils, chickpeas and peanuts. The legume family is divided into 650 genera with over 18,860 species (Wang et al., 2017). Legumes are the third-largest land plant family, accounting for about 7% of flowering plant species. Most legumes are thought to have originated from a common tetraploid ancestor (called the legume-common tetraploid) about 60 million years ago that helped shape legume genome organization (Wang et al., 2017). Significant progress has been made in the study of legume genomics in recent years as a result of the development of abundant genetic and genomic resources in model legumes, such as M. truncatula and L. japonicus, and in the crop legume soybean (Glycine max, Schmutz et al. (2010).

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Grain legumes are a key feature of cropped and natural ecosystems, because they fix atmospheric nitrogen by intimate symbioses with microorganisms (Doyle, 2011). Nevertheless, global cereal production is about four times that of legumes, with farmers preferring to grow new cereal varieties with higher yields. A much greater knowledge of legume genomics, together with better understanding of the molecular physiology of key traits that underpin legume production under different conditions is required to assist the identification of improved cultivars in legume breeding programs. An intensification of legume breeding will also be necessary to future-proof legumes, so that they can continue to provide cheap and sustainable food sources, particularly in developing countries. The papers published in this Special Issue of Plant, Cell & Environment describe basic and applied research activities that serve to increase our understanding of legume biology, together with the factors that regulate legume growth and yield under different environmental conditions. Particular emphasis is placed on the role of nodulation, symbiotic nitrogen fixation and soil microbial community, as well as developing genomic resources. The manuscripts that comprise this volume also address the challenges imposed by exposure to abiotic and biotic stresses with a view on developing strategies to minimize the impact of changing climate on future legume agriculture.

Achieving high yield stability

Legumes are ideally suited to the task of mitigating many of the agronomic and economic constraints faced by producers, while providing positive impacts on soil health (Jensen et al., 2012; Gresshoff et al., 2015). It is not surprising therefore that legumes are predicted to become increasingly important in ecosystem resilience, poverty reduction and the improvement of human health and nutrition in the coming decades (Ray et al. 2013). However, many crop legumes have a relatively low productivity, which has been caused at least in part by the limited genetic diversity in legume breeding programs. The urgent need for new approaches for the development of high yielding legume cultivars is discussed in detail by **Abdelrahman et al., (2018**). This board overview of the topic considers the application of rapid and cost-effective next generation genomic and transcript profiling technologies to legume crops, and outline some of the significant achievements that have already been made. The availability of suitable germplasm, particularly genetic resources with essential abiotic stress tolerance traits, is critical for current and future legume research and improvement. These challenges are comprehensively reviewed together with novel approaches for the generation of greater forage yields under less favourable growing conditions by **Singer et al. (2018).** Whole-genome sequences for a number of legumes have been obtained, including soybean (Glycine max), chickpea (Cicer arietinum) and common bean (Phaseolus vulgaris). These legume genomes have sizes ranging from ∼400 Mb Medicago) to 1,150 Mb (soybean), housed in between six and 20 chromosomes (Wang et al., 2017). However, a family-level comparative genomics analysis is not yet available. An comprehensive analysis of the RNA-Seq-based high resolution gene expression atlas of chickpea is reported in the paper by **Kudapa et al., (2018)**.

Like other plants, legumes are paleopolyploids that have undergone several rounds of Whole Genome Duplication (WGD) followed by diploidization during evolution (Zhu et al., 2005)

Repetitive polyploidization not only makes plant genomes complex, but it also confers genomic structural changes that have contributed to plant domestication as well as success (Kellog, 2016). A study on the duplication of genes in soybean and common bean, which share a polyploidy event (~59 MYA), showed that GO terms related to photosynthesis and transcriptional regulation were significantly over-represented among singletons as well as WGD genes (**Xu et al., 2018)**. Moreover, the divergence of gene expression and DNA methylation between WGD-derived paralogs increased with age. The authors suggest that genes, which are not in any ortholog group are derived from divergent and redundant gene copies, in agreement with the neofunctionalization hypothesis (**Xu et al., 2018)**.

Gene co-expression networks in soybean seeds and the specific hub genes involved in seed oil and storage protein accumulation are reported in the paper by **Qi et al. (2018**). This meta-analysis of all publicly available QTL information for soybean seed protein, oil and fatty acids identified some hotspots simultaneously contributing to oil and protein content. Four chromosome segment substitution lines with contrasting oil-protein content were subjected to RNA-seq and gene expression profiling. Dissecting the time-course transcriptome patterns using strand-specific RNA-sequencing of different seed developmental stages identified important candidate genes for seed oil and protein content. This information also enabled construction of two significant co-expression networks and identification of seven hub genes regulating seed oil and protein content in soybean. Another significant outcome from this study is the provision of transcriptome sequences and information on gene regulatory network, which will be useful for further molecular investigations **(Qi et al., 2018).**

Root/soil interactions, symbiotic nitrogen fixation and arbuscular mycorrhiza

Legumes form symbiotic associations with rhizobial bacteria that are housed in specialised organs called nodules (Figures 1). The symbiotic rhizobia fix atmospheric nitrogen and provide host legumes with sufficient reduced nitrogen to support vegetative growth in a manner similar to legumes without nodules but supplied with nitrogen fertilisation (Vanacker et al., 2006). Legumes are therefore less dependent on fertilization than cereals and they can be cultivated on a wide variety of soils. Soil fertility management through either crop rotation or intercropping with legumes has long been an essential resource for farmers who are cannot access and/or afford expensive inorganic fertilizers. The existence of a diverse range of rhizobia has helped legumes adapt to different habitats. Similarly, the diversity and vast geographic distribution of the legumes has shaped the populations of rhizobial in different soils. While extensive efforts have been made to identify soybean nodule-associated Bradyrhizobia and Sinorhizobia with high Symbiotic N_2-fixation (SNF) traits (Figure 2), far fewer studies have been performed on the rhizobial populations associated with other legumes.

SNF not only provides nitrogen in a reduced form but also increases the levels of other nutrients such as phosphate. Agricultural intensification and fertilizer application has led to a large amount of phosphorus being locked in the soil. Legumes are able to mobilize the phosphorus bound in soils by exuding carboxylates such as malonate from the roots. Screening over 250 chickpea genotypes with diverse genetic backgrounds from the world core collection **Pang et al., (2018)** found that leaf transpiration also plays an important role in phosphorus mobilization. Since low inorganic phosphorus is a major constraint to crop productivity worldwide, intensive studies into the roles of plant morphology, particularly root physiology in acquiring phosphorus from the soil are currently underway to provide new markers for breeding programs seeking to improve phosphorus acquisition in legumes. The importance of leaf transpiration-driven mass flow in supporting the growth of the crop on sandy soils low in phosphorus is highlighted in the paper by **Pang et al. (2018)**. The effectiveness of legumes in low-input agriculture is also highly dependent on the C and N losses associated with root turnover, which has impacts on crop productivity, resource dynamics, and long-term soil fertility. The demographic measurement and estimation of root traits in contrasting cultivars of white clover provided by **Scott et al. (2018)** shows that C and N losses were greater from the roots of a larger, faster growing cultivar than from the smaller lower yielding cultivar.

Evidence suggests that tripartite interactions between legumes and their root symbionts i.e. rhizobia and arbuscular mycorrhizal fungi (AMF) are critical for the production of high yielding grain legumes. The development of improved legumes therefore requires knowledge of how associations with rhizobia and other soil organisms, particularly AMF, benefit plant growth and development. Future legume cultivars will have to be well-nodulated by compatible rhizobia that are able to reduce atmospheric nitrogen to ammonia at high rates. A key problem in all legume biology is that strains of rhizobia with high SNF rates (i.e. effective strains) are not always competitive for colonization and nodulation of the host legume. They are often outcompeted for nodule occupation by strains that are already resident in soil and that are less effective at SNF. It is therefore crucial to isolate and characterize highly effective strains that are also competitive for nodulation. Legumes also form associations with intracellular symbiotic AMF, which can enhance nodulation, bacteroid development, and symbiotic nitrogen fixation. For example, nodulation of the Brazilian legume tree Piptadenia gonoacantha was shown to be modified by the presence of AMF (**Bournaud et al., 2018**). These authors present evidence showing that nodulation of P. gonoacantha was not dependent on the presence of AMF. However, nodule effectiveness and plant growth were dependent on the presence of specific combinations of rhizobial strains and AMF. In addition, an interdependency for the establishment and/or functioning of symbioses was also demonstrated in Piptadenia (Bournaud et al., 2018). Similarly, the presence of the mutualistic fungus, Phomopsis liquidambari increased the symbiotic efficiency of Bradyrhizobium in peanut, as discussed by **Zhang et al., (2018).** These authors show that auxin signalling is enhanced in the presence of Phomopsis liquidambari leading to increased nodulation and SNF. Recruitment of auxin signalling pathways therefore plays a central role in mediating this important interplay between the plant host and associated bacteria and fungi (**Zhang et al., 2018**).

The signalling pathways that allow the associations between plants and their rhizobia and beneficial fungal partners share a number of common features including regulation by phytohormones such as auxin and cytokinin. A new technique allowing simultaneous imaging of plant hormone outputs in soybean is reported in the paper by **Fisher et al. al (2018**). This technique offers non-invasive imaging of large organs by combining 3-D imaging using multiphoton microscopy with image analysis tools. The technique allowed the authors to accurately detect individual nuclei, quantify hormone outputs, and calculate relative ratios of auxin and cytokinin outputs in each nucleus.

The signalling molecule nitric oxide (NO) is produced in nodules by the enzyme nitrate reductase (NR) and the mitochondrial electron transport chain of the plant cells, and by the periplasmic nitrate reductase (Nap) and the respiratory nitrite reductase (NirK) of the bacteroids. NO is required for a number of nodule functions, its interactions with leghaemoglobin being critical for regulating infection, particularly at the early stages of the plant–rhizobia interaction. NO has dual functions in mature and senescent nodules. Low NO concentrations are required to maintain nodule functions. However, too much NO can lead to inhibition of nitrogenase activity and lead to the production of nitrating molecules that can alter the activity of essential nodule proteins such as glutamine synthetase and legheamoglobin through tyrosine nitration or heme nitration. Several studies have examined NO production in nodules. In a comprehensive and timely review of the topic, **Berger et al., (2018)** discuss the complexities of NO production in nodules, together with the role of the NO/reductive haemoglobin (phytoglobin) cycle in the maintenance in the redox and energy balance of the nodules.

Enhancing stress tolerance and seed quality

Abiotic environmental stresses substantially impact on agricultural production worldwide (Parkash Dhankher and Foyer, 2018). Climate-associated yield instabilities are higher in grain legumes and broad-leaved crops than in autumn-sown cereals (Reckling et al., 2018). An intensification of efforts to uncover important genes and mechanisms involved in stress tolerance that can be used for targeted crop improvement (Li et al., 2017; Qi et al., 2014). Plants face with a wide range of abiotic and biotic stresses in the field, many of which are experienced simultaneously (Parkash Dhankher and Foyer, 2018). Of these stresses, drought, particularly when experienced at flowering and pod set, is one of the most important constraints to legume yields. Drought stress alone is expected to limit the productivity of more than half of the arable land on earth over the next 50 years (Mancosu et al., 2015). Differentially expressed candidate genes from a "QTL-hotspot" region associated with the drought stress response in chickpea are described in the paper by **Kudapa et al., (2018**). In the field, however, crops experience extreme weather events such as flooding as well as drought. Plant responses to such large variations in water availability are controlled by multiple genes that can be mapped as quantitative trait loci (QTLs). QTLs associated with root system architecture and waterlogging tolerance in soybean are described in the paper by (**Ye et al., 2018**). This study not only highlights the plasticity of the root response but also identifies new genetic resources to improve waterlogging tolerance. Root system architecture is considered to be important for the ability of plants to explore the environment in order to obtain essential nutrients and water, and to withstand stress. Machine learning was used to improve the phenotyping of root traits in sixteen European faba bean cultivars in the study reported in the paper by **Zhao et al., (2018).** Results from supervised hypothesis-driven approaches were compared with those from unsupervised clustering approaches and used to provide guidelines for enhancing the phenotyical analysis of root systems.

Climate change is predicted to the likelihood of infestation by pests and pathogens, which will decrease crop yields and enhance the risk of famine (Long, Marshall-Colon, & Zhu, 2015). Intensive efforts are therefore underway to enhance the sustainability of crop yields through improved biotic and abiotic stress tolerance traits (Parkash Dhankher and Foyer, 2018). This requires a deep understanding of molecular, metabolic and physiological responses of plants to attack by pests and pathogens. Changes in the metabolite profiles of different varieties of common beans to infection by the pathogenic fungus Sclerotinia Sclerotiorum were documented in the study reported by **Robison et al. (2018),** who reported that stem resistance was associated with phyoalexin production, while changes in lipid metabolism altered susceptibility.

Manipulation of cell wall components and lignin can have marked effects on disease resistance (**Gill et al. 2018**). Transcript and metabolite profiling techniques were used to show that improved Fusarium resistance was linked to increased accumulation of flavonoids. These studies show that decreases in caffeoyl-CoA O-metyltransferase activity in alfalfa (Medicago sativa) not only altered lignin production but also enhanced disease resistance in the study reported by (Gill et al. 2018). The resultant increase in availability of cell wall polysaccharides facilitated better isoflavonid production in the transgenic alfalfa lines leading to enhanced resistance.

The blight caused Ascochyta rabiei is a major production constraint in chickpea. A modified version of QTL-seq, multiple QTL-sequencing, was performed by using two mapping populations segregating for blight resistance is in chickpea (**Kumar et al. 2018**). Genetic analysis of one intraspecific and another interspecific mapping population identified three QTLs and helped narrow down a major QTL to a ‘robust region’ with four genes. Further molecular analysis suggested that CaAHL18 is the potential candidate gene associated with Ascochyta blight resistance in chickpea. The composition of cell wall polysaccharides is also important in determining the cooking time and cooking performance of grain legumes such as chickpeas. The composition, structure, abundance and location of cell wall polysaccharide in chickpea cotyledons is described in the paper by **Wood et al. (2018),** who provide evidence that environmental as well as genetic factors determine cotyledon composition.

Plant growth and stress tolerance are controlled by the programmed expression of different suites of genes in response to metabolic/developmental cues and environmental triggers. In particular, the transcriptional control of stress responsive genes is crucial to survival in a hazardous environment that poses biotic and abiotic threats. The APETALA2/ethylene response factor (AP2/ERF) superfamily not only plays important roles in plant development but also regulates the transcription of biotic and abiotic stress response genes. The functional characterization of one of the cold responsive ERFs (MfERF1) isolated from Medicago falcate is reported in the paper by **Zhuo et al. (2018**). These authors confirm the role of MfERF1 in freezing and chilling tolerance through regulation of polyamine turnover, proline accumulation and increased antioxidant defences (**Zhuo et al., 2018**).

Environmental stresses not only limit plant growth and crop yields, but they can also adversely affect the nutritional quality of the grains, limiting their end-use and value as food and feed. One example is the stress-induced accumulation of alkaloids in lupins. Quinolizidine alkaloids (QA) are considered to be produced in lupin leaves and transported to the seeds during grain filling. Cultivar-specific responses to drought and high temperature stresses were reported to be accompanied by changes the expression of genes underpinning the QA pathway and grain QA levels in three narrow-leafed lupin varieties (**Frick et al., 2018**). The authors also identified a cultivar which did not show enhanced QA accumulation in responses to these stresses.

Appropriate changes in cellular antioxidants are required to buffer stress-induced changes in the production of reactive oxygen species (ROS), which function as signalling molecules in the plant development and stress response networks. Changes in ROS production occur at different stages of in the development of plant organs. In seeds ROS are produced during dormancy release and germination. Although seeds are well equipped to survive the oxidative stress caused by enhanced ROS production, they cannot retain their viability indefinitely and eventually deteriorate, partly as a result of the accumulation of carbonylated proteins, which impairs function and stability. Seed quality and viability during storage depend upon the initial quality of seed and the manner in which the seeds are dried and stored. In a study reported by **Satour et al. (2018)** the patterns of carbonylated proteins were compared in maturing Medicago truncatula seeds that had either been desiccated naturally or prematurely dried,. The authors discuss the possibility that one of these proteins called PM34 could be used as a marker of seed quality. Since legume seed quality and deterioration during storage can be a major constraint to profitable grain legume production, having reliable markers quality and viability is crucial to the industry.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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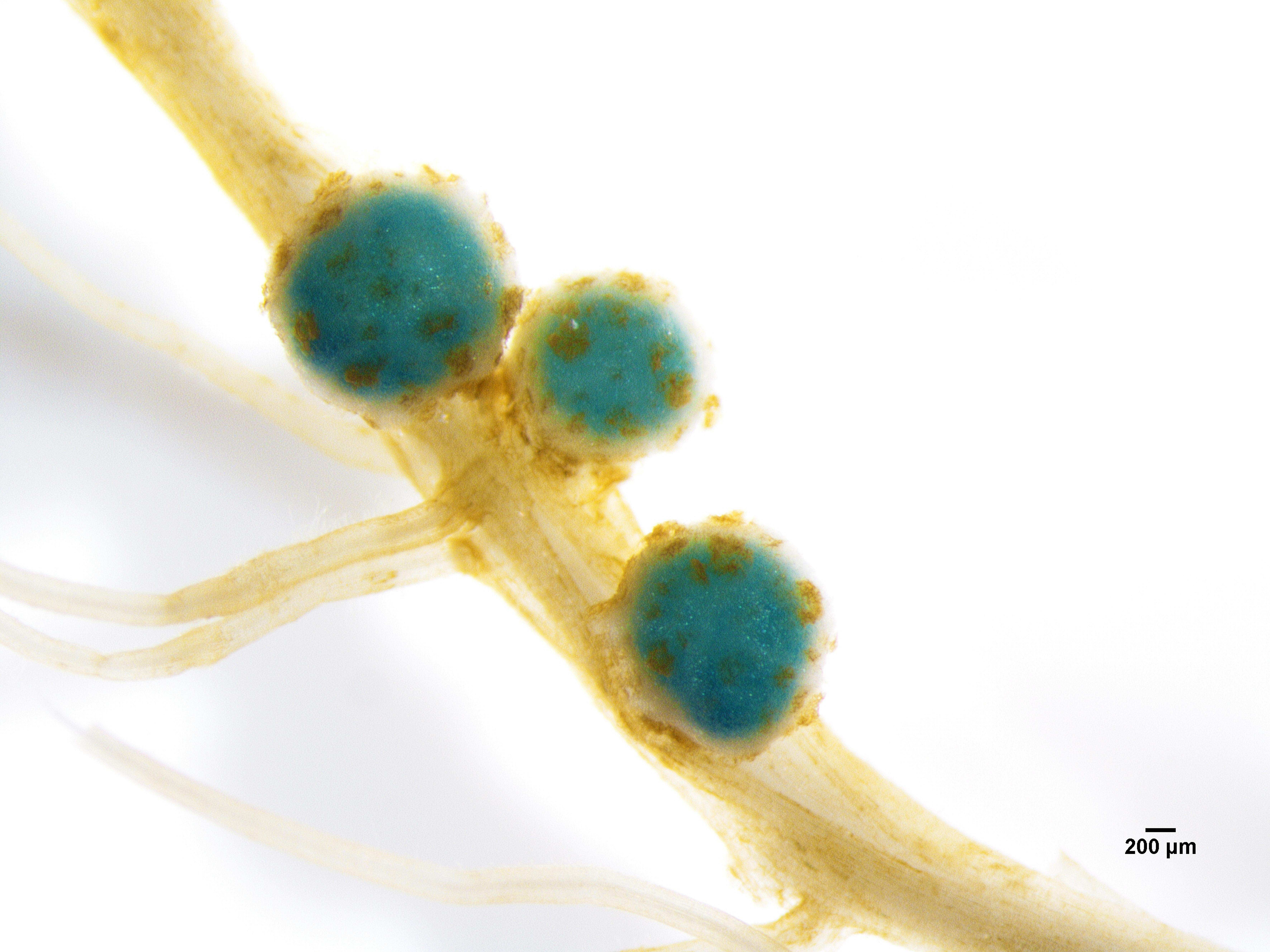
Legends to Figures

Figure 1. Root system of pea (Pisum sativum) inoculated with compatible Rhizobium leguminosarum exhibiting mature nodule structures.

Figure 2. Mature nodules on a transgenic soybean (Glycine max) root expressing a GUS reporter gene driven by a nodule-specific promoter. Roots and nodules were fixed in 0.5% paraformaldehyde buffer and incubated overnight in X-Gluc staining buffer.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