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Foyer, CH orcid.org/0000-0001-5989-6989, Nguyen, H and Lam, H-M (2019) Legumes-The art and science of environmentally sustainable agriculture. Plant, Cell and Environment, 42 (1). pp. 1-5. ISSN 0140-7791

https://doi.org/10.1111/pce.13497

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Legumes- the Art and Science of Environmentally-Sustainable Agriculture

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Abstract

Symbiotic nitrogen fixation, which is carried out by the legume-rhizobia partnership is a major source of nitrogen acquisition in natural ecosystems and in agriculture. The benefits to the plant gained through the rhizobial-legume symbiosis can be further enhanced by additions associations of the legume with arbuscular mycorrhiza. The progressive engagement of the legume host with the rhizobial bacteria and mycorrhizal fungi requires an extensive exchange of signalling molecules. These signals alter the transcriptional profiles of the partners, guiding and enabling extensive microbial and fungal proliferation in the roots. Such interactions and associations are greatly influenced by environmental stresses, which also severely limit the productivity of legume crops. This special issue provides new insights into the mechanisms that underpin sustainable symbiotic partnerships, as well as the effects of abiotic stresses, such as drought, waterlogging and salinity on legume biology. The requirement for germplasm and new breeding methods is discussed as well as the future of legume production in the face of climate change.

Key Words: arbuscular mycorrhiza, drought, heat, symbiotic nitrogen fixation, flooding, root architecture, seed traits

Introduction

Leguminous plants have specialized organs called nodules that contain symbiotic bacteria that fix atmospheric nitrogen and provide the host plant with reduced nitrogen in exchange for carbon metabolites. Legumes have traditionally played a significant role in agriculture, providing economic benefits that are particularly important in low-input subsistence agriculture. However, while legumes are still often used in crop rotation systems or in intercropping, the use of legumes in agriculture has declined over recent decades. This can be attributed to the increased usage of nitrogen-rich fertilizers in agriculture. While this practice is required to meet the needs of consumers in rapidly growing economies, it is not sustainable not least because intensive nitrogen fertilization has had a negative impact on the environment. The success of future agriculture depends on achieving an appropriate balance between environmental sustainability and yield-associated economic constraints. One economically-efficient solution to protect soil quality in a sustainable manner is not only to return to legume-based conservation agriculture (Stagnari et al., 2017) but also to simultaneously develop improved legume varieties and more effective rhizobial strains, which can be introduced across different cropping systems. The aim of this special issue is to provide a synergistic collation of current knowledge on priority areas within legume research.

Enhancing stress tolerance

Several manuscripts in this volume highlight the importance of shoot processes, particularly photosynthesis (Basu et al., 2019), root architecture and the genetic control of lateral root number (Prince et al., 2019) and seed traits (Paganao et al., 2019) in the survival of abiotic stress conditions. For example, developing crops with better root systems is widely accepted to be an important strategy to ensure crop sustainability and productivity, particularly under stress conditions.

Existing genetic variation in legumes can readily be used to address the challenges of climate uncertainty. The genetic diversity required to understand the mechanisms that determine root system architecture (RSA) was attained in the study reported by Prince et al., (2019), which involved 397 soybean accessions. A genome-wide association mapping approach was used to detect genetic loci for RSA. Of the candidate genes that were identified Glycine Lateral Root 1 (GLR1) was found to control lateral root number (LRN). The allelic variants of this locus increased LRN through regulation of cortex cell shape and size. Moreover, soybean accessions with the specific allelic variants of this locus showed improved root branching ability in water-limited and optimal field conditions (Prince et al., 2019).

A better understanding of the photosynthetic carbon metabolism is essential to design yield improvement strategies in crops. Basu et al. (2018) studied the genetic basis of photosynthetic efficiency (PE) and seed yield (SYP) in chickpea using an integrated genomic approach. Studies combing QTL mapping, molecular haplotyping and haplotype-specific gene expression identified two superior haplotypes for each chlorophyll a/b binding protein-coding sequence and its interacting TOC1 gene that regulate both PE and SYP traits in chickpea. The higher heritability of these trait-associated molecular signatures suggests their broad practical applicability in genetic enhancement studies. The production of high quality seeds is essential for successful crop production, particularly in challenging environments. The characterization of novel germination markers such as those identified by the application of histone deacetylase inhibitors in Medicago truncatula are thus of fundamental importance (Pagano et al., 2019). In addition, the integrity of the seed testa membrane was found to be important in the survival of seedlings exposed to the stress caused by waterlogging (Zaman et al., 2019).

Evolutionary adaptation and the selection pressures driven by climate change are comprehensively discussed in the review by Mousavi-Derazmahallehever (2019). These authors consider the genomics approaches that have led to recent discoveries relating to adaptive genes in legumes. Individual mechanisms that allow survival of extremes of water availability are reported in several manuscripts. For example, the ectoapyrases, otherwise known as ecto-NTPDases that function to decrease levels of extracellular ATP and ADP are shown to be important in drought tolerance (Veerappa et al., 2019), as are the micro RNAs, miR398 and miR2119 in controlling superoxide dismutase and alcohol dehydrogenase mRNAs (De la Rosa, et al., 2019). The role of AOX of the alternative oxidase (AOX) in legumes is considered in relation to plant growth and performance is discussed in the paper by Sweetman et al., (2019). These authors discuss the composition and expression of the different AOX genes, describing the multiple AOX2 isoforms that are found in legumes in contrast to most other species, where AOX1 isoforms are predominantly expressed, usually in a stress-induced manner (Sweetman et al., 2019). Protein phosphorylation is shown to be an important control of the dehydration response in chickpea (Barua, et al., 2019). These authors have used phosphoproteomics to analyze the stress-induced dehydration-induced changes in global phosphorylation patterns of nuclear proteins (Barua, et al., 2019). In addition, Song et al., (2019) identified novel interactors and potential phosphorylation substrates for the GsSnRK1 kinase in soybean.

High daytime temperatures have a negative impact on the reproductive success of soybean and other legumes. The identification and characterization of high-temperature-tolerant genotypes is therefore particularly important. The study reported by Djanaguiraman et al., (2019) showed that increases in the daytime temperatures from gametogenesis to full bloom in field-grown soybeans were shown to decrease pod-set in a range of soybean genotypes because of decreased pollen viability. These authors identified soybean genotypes in a high-throughput phenotypic screen (Djanaguiraman et al., 2019).

Various regions are likely to experience an increase in flood events owing to changing climate patterns (Pedersen et al., 2017). Flooded soils typically become anoxic and root oxygen deficiency is a major stress for plants. In contrast with the depletion of oxygen, ethylene and carbon-dioxide increase in flooded soils (Ponnamperuma, 1984). Indeed carbon-dioxide can accumulate to above several kPa, with possible adverse effects on root metabolism, although knowledge is scant on this condition (Greenway et al., 2006). Munir et al. (2018) evaluated the responses of two cool-season grain legumes, chickpea (Cicer arietinum L.) and faba bean (Vicia faba L.), to root-zone treatments of carbon-dioxide and ethylene. Carbon-dioxide inhibited root respiration and reduced growth. Ethylene increased the gas-filled porosity of roots; this phytohormone is well-known to induce formation of aerenchyma in various species (Yamauchi et al., 2018). The present study showed faba bean developed substantially greater root gas-filled porosity than chickpea, in response to ethylene. Although high carbon-dioxide partially inhibited root extension in both species, severe hypoxia was more damaging. Faba bean was more tolerant than chickpea to growth in an oxygen-deficient root-zone, highlighting the importance of choosing which grain legume species to grow as crops in flood-prone fields.

Soil waterlogging poses a severe threat to the yields of major legume crops including pea, chickpea, and mungbean that are particularly susceptible to this stress. Zaman et al. (2018) evaluated the germination ability of three contrasting pea genotypes under different waterlogging duration and conducted RNAseq and gene expression studies to identify differentially expressed candidate genes and related stress tolerance mechanisms. In summary, the authors suggest two contrasting tolerance mechanisms related to pea germination under waterlogging stress. One of them is the quiescence strategy where the seed reserve energy is preserved during waterlogging and the second one is the escape strategy where rapid germination utilizing energy from both protein and lipid metabolism during waterlogging stress. Further investigations of the genes associated with these mechanisms is required to effectively utilize them in the future breeding program for crop improvement.

The salt stress-induced changes in gene expression profiles were studied, together with physiological metabolic adjustments to salinity in the paper by Liu et al. (2019). These authors identified both rapid physiological responses and longer term metabolic adjustments. Salt stress tolerance was linked metabolic responses and Na^+, K^+, or Cl^- accumulation in Vicia faba (Ricter et al., 2019). Untargeted metabolomics profiling using UPLC-HRMS, a method that allows high-throughput parallel analysis of metabolites using the same sample, was used to identify pools of metabolites that might be associated with the underlying metabolic and physiological adjustments of chickpea to drought stress (Khan et al., 2019).

Exposure to drought and/or heat stress decreased both the yield of lentil seeds and their nutritional quality (Sehgal, et al., 2019). However, these authors identified a drought-tolerant lentil genotype that exhibited cross tolerance to heat stress. Understanding how heat stress influences reproductive organs is critical to improving grain legume yields in future climates. The study reported by Jiang et at al., (2019) shows that heat stress exposure in pea leads to a greater inhibition of pollen development and viability than of ovules. A heat tolerant pea genotype was found to exhibit a more stable lipid composition in the stamens.

Optimizing legume-rhizobia symbiosis while avoiding pathogens

Legumes are able to form symbiotic associations with rhizobia, which are nitrogen fixing bacteria. The bacteria are housed in a specialized organs called nodules, in which the concentration of oxygen is very low, allowing the enzyme nitrogenase to fix atmospheric nitrogen gas. The study by Gil-Diez, et al. (2019) highlights the importance of molybdate transporter (MtMOT)1.2 for the synthesis of the nitrogenase iron-molybdenum cofactor and nitrogenase activity in M. truncatula. These authors demonstrate that nitrogenase activity was adversely affected in the mot1.2-1 mutants compared with wild-type (Gil-Diez, et al., 2019)

The initiation and decision-making steps that define the plant-microbial interactions require considerable inter-species crosstalk based on chemical signals and communication. The initial recognition in the rhizosphere requires the release of a range of plant metabolites including flavonoids, strigolactones and N-acetylglucosamine as well as microbial nod factors, which are lipochitooligosaccharides. The nod factors are recognised by the plant LysM receptors kinases. The resultant extensive reprogramming of gene expression in both partners facilitates the exchange of beneficial exchange of metabolites and forms the basis of sustained symbiosis. The legume host tightly controls the number of nodules it forms in symbiosis with its nitrogen-fixing rhizobial partner. This enables the plant to balance its need to acquire nitrogen with its ability to expend resources developing and maintaining nodules. To achieve this, the plant uses a number of molecular mechanism that are outlined here in detail by Ferguson et al. (2019). This includes the Autoregulation of Nodulation (AON) pathway, in addition to the nitrogen-regulation and stress-regulation of nodulation pathways. To initiate the AON and nitrogen-regulation pathways, the host plant produces highly specific CLE peptide hormones in response to compatible rhizobia bacteria or the soil nitrogen content, respectively. In this issue, Hastwell et al. (2019) have investigated the posttranslational modifications of these peptides using a unique petiole feeding technique to deliver synthetic peptides into recipient plants. Using these methods, these authors demonstrate that a triarabinose building block attached to a central proline residue of the peptide is critical to achieve maximum nodule-suppressing activity. Perception of the nodule-suppressing CLE peptides triggers the regulation of downstream factors that act to control further nodule development (reviewed by Ferguson et al., 2019). The interactions between legumes and different symbiotic partners is not mutually exclusive. Moreover, tripartite associations between legumes, rhizobia and mycorrhiza are frequently beneficial as illustrated by the reports of Kafle et al., (2019), who explored carbon allocation and the availability of resources in M. truncatula. Such tripartite interactions led to synergistic growth responses and stimulated the phosphate and nitrogen uptake of the plants, which allocated more carbon to rhizobia under nitrogen demand, but more carbon to the fungal partner when nitrogen was available (Kafle et al., 2019). These changes in carbon allocation were accompanied by changes in the expression of sucrose transporters, providing insights into how the host plant controls carbon allocation to different root symbionts in order to maximize its symbiotic benefits. Watts-Williams et al., (2019) also report the effects of arbuscular mycorrhiza on plant growth and gene expression. In this study of twenty geographically-diverse M. truncatula accessions inoculated with the AMF Funneliformis mosseae, a diverse range of responses in plant physiology and gene expression were observed amongst the accessions compared to the mock-inoculated plants. (Watts-Williams et al., 2019).

The authoritative review by Wille et al., (2019) summarizes our current knowledge of resistance mechanisms against soil-borne pathogens in grain legumes, providing evidence for genetic variation for rhizo-sphere-related traits. The role of root exudation in microbe-mediated disease resistance and elaborates is considered together with how such traits can be incorporated in resistance breeding programmes. These authors suggest that the whole plant should be considered as a holobiont in future breeding strategies seeking to improve complex legume defence mechanisms.

Breeding for improved traits and sustainable yield in Legumes

Legume breeding is often constrained by a narrow germplasm base within breeding programmes. A good example is narrow-leafed lupin, which was domesticated during the 20th Century from very few landrace and wild ancestors. In Europe and Australia, breeders independently found mutations which eliminated vernalisation response in narrow-leafed lupin, and these mutations predominate in breeding programs in Europe and Australia to this day. Researchers in Australia have shown that these two mutations were caused by similar deletions in the promotor region of LanFTc1, a major flowering time gene in narrow-leafed lupin (Taylor et al. 2019). These deletions are associated with altered responsiveness to vernalisation, flowering time, and expression of LanFTc1 in the absence of vernalisation. A third smaller deletion, reported in Taylor et al. in this issue, results in a unique intermediate phenotype which may be valuable for breeding purposes and expanding the agronomic adaptation of lupin to new and existing production regions. Additionally, the insertion/deletion (INDEL) variant series may also help to increase knowledge of how signalling within the vernalisation pathway is mediated at a molecular level in legumes.

Prospects and applications of legume production in Africa

Grain legumes have traditionally played a key role in African agriculture because they provide a natural fertilization to small scale farmers and an inexpensive source of protein to the African consumer. Using current data from the Food and Agriculture Organization (FAO) of the United Nations the production of soybeans (Glycine max Merr.) and other legume crops in Africa was modelled (Foyer et al., 2019). This analysis predicts that soybean is poised to dominate future legume production across Africa. Intensification of production may serve to reduce the regions' dependence on soybean imports, thus generating new economic opportunities through the development of soybean-based supply chains across different regions, producers and consumers. However, the successful production of soybean across Africa will require not only an intensive research and development effort, but also the backing of effective extension services, as well as food chain and marketing assurance and government policy incentives.

Microelement deficiencies are among the most common and devastating global nutritional problems, posing serious health challenges across vast sectors of the African population. Micronutrient deficiencies have increased in recent decades due to a decrease in quality of the diets of the poorest people, both in developing and developed countries, even in areas where food is not limiting. The problem is further aggravated by widespread poverty, which makes it difficult for the vast majority to access the more expensive but nutrient-rich animal-based and fortified products. While supplementation is effective for easy-to-reach groups and relatively low cost, this strategy is not sustainable in the long term and it does not build resilience in a population. Moreover, supplementation requires an elaborate and costly distribution network but it often misses the hard-to-reach vulnerable groups and the rural poor Supplementation strategies have therefore only achieved modest success, even in African countries that have appropriate legislation and processing capacities. Legumes are major sources of dietary protein, particularly in the developing economies, and they have a significant for nutritional trait improvement. The biofortification potential of legumes, which offer a diversity of micronutrients and amino acids is discussed in the review by Rehman et al., (2019), who provide a comprehensive review of the challenges and breeding approaches that are being used for the nutritional enhancements of legumes. These authors highlight the potential of the legume microbiome in the agronomic trait improvement.

ACKNOWLEDGEMENTS

We thank the Worldwide University Network (WUN) for financial support for the Legumes consortium, many members of which have contributed papers to this special issue. CF thanks BBSRC (UK) for financial support (BB/N004914/1).

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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