EDITORIAL

Nature’s pulse power: legumes, food security and climate change

Global food security requires a major re-focusing of plant sciences, crop improvement and production agronomy towards grain legumes (pulse crops) over coming decades, with intensive research and development to identify climate-resilient species and cultivars with improved grain characteristics. Labs contributing to this special issue have undertaken research and breeding to improve pulse crops, together with innovative production agronomy which contributes to the sustainability of cropping systems. The reviews and research together form an invaluable resource for the research community and policymakers.

The value of pulses in food cultures around the world is well known, and calling them ‘little marvels’ is apt (BBC Radio 4 Food Programme, broadcast in the UK, July 2016), not least because of their significant health benefits (Foyer et al., 2016) (Box 1). However, the use of legumes in agriculture and the genetic improvement of important grain legumes have lagged behind cereal crops. The Food and Agriculture Organization of the United Nations (FAO) facilitated the International Year of Pulses in 2016, focusing on the contribution of pulses to production and dietary diversity to eradicate hunger and malnutrition. This initiative was introduced with objectives to (i) promote the value and utilization of pulses throughout the food system, (ii) raise awareness of their benefits, (iii) foster enhanced research, (iv) advocate for better utilization of pulses in crop rotations, and (v) address challenges in trade. The FAO initiative was also linked to a growing recognition of the contribution of pulses to critical targets under Sustainable Development Goal 2, particularly regarding food access, malnutrition and smallholder incomes, as well as sustainable and resilient agriculture.

Recognizing that increasing the global production of grain legumes has the potential to provide a sustainable solution to food and protein security, significant efforts are currently being made to increase genomic resources and apply innovative breeding techniques to improve the yield and nutritional quality of legume crops, together with enhanced resilience to climate change. Production agronomy and crop rotation approaches could also be intensified to address the associated economic and environmental challenges. The papers presented in this special issue bear testimony to the urgent need for the intensification of basic and applied research into grain legumes, which will form a cornerstone of future food and nutritional security and a global web of biodiversity.

Improved genomic resources and breeding tools

Several papers in the issue highlight the development of genetic resources that will unleash significant untapped potential for genetic improvement. The development of effective phenotyping and breeding approaches is a challenge for the less-well studied grain legumes in particular. Modern breeding efforts to improve yield, disease resistance and quality are constrained by a low level of genetic diversity in breeding programmes. Large genetic diversity exists in seeds of grain legumes held in gene banks, but these are not fully used in active breeding programmes. Cowling et al. (2017) explore the concept of evolving gene banks, applying optimal contribution selection to manage long-term genetic gain and genetic diversity in pre-breeding populations. They simulated pre-breeding using a founder population based on crosses between elite crop varieties and exotic lines of field pea, subjecting the population to 30 cycles of recurrent selection for an index comprising four economically important traits. They conclude that optimal contribution selection provides

| Box 1. Diverse market classes within each grain legume (pulse) species |
| --- |
| Image: Pixabay, CC0 Public Domain. |
the control necessary to actively improve evolving gene banks for economic traits, while maintaining high levels of genetic diversity. This revolutionary plant breeding system will allow breeders to access valuable genes that have been lost through modern breeding programmes. The plant breeding method described by Cowling et al. captures valuable genes from wild relatives and moves them into the breeding programme by crossing the genetically diverse exotic lines with elite lines, creating evolving gene banks. The new rapid-cycle plant breeding method will have long-term benefits for all plant breeders, and could help to adapt and develop climate-ready crops, but the immediate challenge is to validate the results in commercial pulse crops.

As one of the five major crops, soybean is the most widely planted and highest-yielding grain legume (Foyer et al., 2016). The comprehensive overview of current genomic resources from functional sequences to epigenomics provided by Li et al. (2017) discusses the value of improving the soybean resilience to different climate change scenarios. High-throughput genomic technologies including genome sequencing, genome re-sequencing (DNA-seq) and transcriptome sequencing (RNA-seq) are being applied to a range of legumes. New insights into the giant faba bean (Vicia faba) genome are provided by Cooper et al. (2017) who used a combination of DNA-seq and RNA-seq to improve genomic resources in soybean. Using RNA-seq analysis, Du et al. (2017) present interesting new data on the regulatory networks that control seed set and seed size in soybean and identify hub genes that control these processes.

Adapting to climate change through crop resilience

The genetic and biotechnology resources that are currently being applied to drought and water-logging are described by Valliyodan et al. (2017), within the context of existing QTLs and breeding approaches. The effects of terminal drought leaf parameters, seed set and pod abscisic acid concentrations are reported in chickpea (Pang et al., 2017). Moreover, the crucial importance of root trait variability and its role in facilitating stress tolerance in chickpea is reported (Chen et al., 2017). The depletion of soil water often brings the added burden of salt stress to limit plant productivity. The beneficial effects of sucrose infusion at the reproductive stage of chickpea production are presented by Khan et al. (2017), together with evidence that salt-stressed chickpea is carbon-limited. Hence the provision of sucrose improves vegetative and reproductive growth in plants exposed to high salt (Khan et al., 2017).

Another study in this issue presents novel findings showing that a drought-responsive legume, miR1514a, triggers phased siRNA formation through modulation of a NAC transcription factor (Sosa-Valencia et al., 2017).

The mechanisms that underpin drought tolerance in legumes are further elaborated by an innovative analysis of root xylem plasticity and its role in improving water use efficiency in soybean plants subjected to water stress (Prince et al., 2017). These and other papers in this special issue not only highlight the importance of the availability of water to legume agriculture, but also demonstrate that both drought and flooding pose some of the greatest challenges to the current and future production of soybean and forage legumes (Striker and Colmer, 2017). Their comprehensive analysis of the diversity in forage legumes for flooding tolerance will be of particular interest to those engaged in gaining a deeper understanding of the physiology of stress tolerance in legumes. It is also of practical use to researchers and agronomists engaged in forage plantings in flood-prone areas. Data for some key species are provided, in which current eco-physiological understanding is limited. Suggestions for future areas of priority in this important group of plants include the central importance of understanding anoxia tolerance in roots, the ability to maintain symbiotic nitrogen fixation during waterlogging in the field, and identification of traits conferring the ability to recover after water levels subside (Striker and Colmer, 2017).

Different aspects of reproductive physiology are described in well-considered and thought-provoking reviews by Cao et al. (2017) and Ozga et al. (2017). Cao et al. examine the dependence of soybean flowering and stem growth habits on day length, highlighting the interplay between photoperiod and miRNA-mediated flowering modules in soybean. Meanwhile, Ozga et al. cast the net beyond soybean to explore how hormones integrate high-temperature stress during reproductive development in grain legumes, from meiosis to flowering, fruit set and seed maturation. Moreover, a gene expression atlas is described for pigeon pea (Pazhamala et al., 2017), together with the application of this knowledge to deduce novel information regarding the genes associated with pollen fertility and seed formation.

Some grain legume species such as faba bean and pigeon pea (Cajanus cajan) have outcrossing characteristics, and rely to some extent on pollination by animal vectors. Climate change and associated extreme weather events such as sudden episodes of high temperature during flowering can affect reproductive success in grain legumes, directly through physiological damage and indirectly by affecting plant–pollinator interaction. Bishop et al. (2017) report a substantial increase in the level of outcrossing in faba bean by insect pollinators following heat stress both in a controlled environment and under field conditions. Stoddard, in his Insight article, discusses the ability of faba bean to self-pollinate in the absence of bee activity, known as ‘autofertility’ (Stoddard, 2017). It is argued that reliance on wild pollinators is a risky strategy when also affected by climate change. Thus the provision of honey bees may be increasingly required for adequate pollination of faba bean crops in the future.

Neglected orphan crops

As a protein staple in the diet of many of the world’s poorest, pulses are nature’s gemstones because they are protein packed and nutritious. However, in many cases relatively little is known about the biology of the plethora of ‘orphan’ legume crops that contribute to human and animal diets. Cullis and Kunert (2017) address the issue of under-utilized grain
legumes directly, highlighting the considerable but neglected opportunities to advance grain legume agriculture by developing the existing germplasm. They recognize the investments of organizations such as the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), International Centre for Agriculture Research in the Dry Areas (ICARDA) and the Kirkhouse Trust, as well as initiatives to develop genomic data for these underused crops, but emphasize the need for crop physiology and production agronomy to support future crop development. Moreover, Kim and Cullis (2017) describe the chloroplast genome of marama (Tylosema esculentum) for the first time.

Interactions with the soil microbiome

Many unique functions of grain legumes take place beneath the soil. These plants offer the promise of more sustainable use of nitrogen fertilizers in crop systems through their ability to fix atmospheric nitrogen in symbiotic root nodules. The process of bacteroid infection in legume roots that culminates in the formation of symbiotic nodules is summarized by Ibañez et al. (2017). Highlighting the differences between root-hair entry and intercellular invasion, these authors explore the evolution of this process. Nodulation, however, is suppressed in soils replete with nitrogen, for example in farms with a long history of nitrogen fertilization. This phenomenon is explored by Murray et al. (2017), who provide a comprehensive overview of emerging knowledge on nitrogen sensing in legumes and explore the complexity of physiological and molecular signalling and responses. With a key focus on the role of nitrate and other transporters in sensing of nitrogen availability, Murray et al. (2017) consider how the signalling activities of such transporters might influence nodulation.

Crops of ancient origin come of age

The importance of legumes in current and future agriculture cannot be overemphasized. Moreover, grain legumes form a minor part of current human diets, yet they are a vital source of plant-based protein and amino acids for people around the world, a versatile ingredient in human diets with a long shelf-life. The FAO recommends that they are eaten daily as part of a healthy diet to prevent and manage chronic disease, and to address growing global obesity issues (fao.org/pulses-2016). Prepare for more from these little marvels in the future.

Acknowledgements

We thank the Worldwide Universities Network (WUN) for financial support for the Grain Legumes Network, many members of which have contributed papers to the special issue.

Key words: Crop resilience, food security, genomics, grain legumes (pulse crops), legume breeding, orphan crops, RNA sequencing, symbiotic nitrogen fixation.

Michael J. Considine1,2, Kadambot H.M. Siddique1,* and Christine H. Foyer1,3,#

1 The UWA Institute of Agriculture, The University of Western Australia, Australia, LB 5005, Perth WA 6001, Australia
2 Department of Agriculture and Food Western Australia, South Perth WA 6151, Australia
3 Centre for Plant Sciences, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK
* UN FAO Special Ambassador for the International Year of Pulses 2016: www.fao.org/pulses-2016/en/
# Correspondence: c.foyer@leeds.ac.uk

References

Bishop J, Jones HE, O’Sullivan DM, Potts SG. 2017. Elevated temperature drives a shift from selfing to outcrossing in the insect pollinated legume, faba bean (Vicia faba). Journal of Experimental Botany 68, 2055–2063.
Cao D, Takeshima R, Zhao C, Liu B, Jun A, Kong F. 2017. Molecular mechanisms of flowering under long days and stem growth habit in soybean. Journal of Experimental Botany 68, 1873–1884.
Chen Y, Ghanem ME, Siddique KHM. 2017. Characterising root trait variability in chickpea (Cicer arietinum L.) germplasm. Journal of Experimental Botany 68, 1987–1999.
Cooper J, Wilson M, Derks M, Smit S, Kunert K, Cullis C, Foyer CH. 2017. Enhancing faba bean (Vicia faba L.) genome resources. Journal of Experimental Botany 68, 1941–1953.
Cowling WA, Li L, Siddique KHM, Henryon M, Berg P, Banks RG, Kinghorn BP. 2017. Evolving gene banks: improving diverse populations of crop and exotic germplasm with optimal contribution selection. Journal of Experimental Botany 68, 1927–1939.
Cullis C, Kunert KJ. 2017. Unlocking the potential of orphan legumes. Journal of Experimental Botany 68, 1895–1903.
Du J, Wang S, He C, Zhou B, Ruan Y-L, Shou H. 2017. Identification of regulatory networks and hub genes controlling soybean seed set and size using RNA sequencing analysis. Journal of Experimental Botany 68, 1955–1972.

* Correspondence: c.foyer@leeds.ac.uk
Foyer CH, Lam H-M, Nguyen HT, et al. 2016. Neglecting legumes has compromised human health and sustainable food production. Nature Plants 2, 16112.

Ibañez F, Wall L, Fabra A. 2017. Starting points in plant-bacteria nitrogen-fixing symbioses: intercellular invasion of the roots. Journal of Experimental Botany 68, 1905–1918.

Khan HA, Siddique KHM, Colmer TD. 2017. Vegetative and reproductive growth of salt-stressed chickpea are carbon-limited: sucrose infusion at the reproductive stage improves salt tolerance. Journal of Experimental Botany 68, 2001–2011.

Kim Y, Cullis C. 2017. A novel inversion in the chloroplast genome of marama (Tylosema esculentum). Journal of Experimental Botany 68, 2065–2072.

Li M-W, Xin D, Gao Y, Li K-P, Fan K, Muñoz NB, Yung W-S, Lam H-M. 2017. Using genomic information to improve soybean adaptability to climate change. Journal of Experimental Botany 68, 1823–1834.

Murray JD, Cheng-Wu L, Chen Y, Miller AJ. 2017. Nitrogen sensing in legumes. Journal of Experimental Botany 68, 1919–1926.

Ozga JA, Kaur H, Savada RP, Reinecke DM. 2017. Hormonal regulation of reproductive growth under normal and heat-stress conditions in legume and other model crop species. Journal of Experimental Botany 68, 1885–1894.

Pang J, Turner NC, Khan T, Du Y-L, Xiong J-L, Colmer TD, Devilla R, Stefanova K, Siddique KHM. 2017. Response of chickpea (Cicer arietinum L.) to terminal drought: leaf stomatal conductance, pod abscisic acid concentration, and seed set. Journal of Experimental Botany 68, 1973–1985.

Pazhamala LT, Purohit S, Saxena RK, Garg V, Krishnamurthy L, Verdier J, Varshney RK. 2017. Gene expression atlas of pigeonpea and its application to gain insights on genes associated with pollen fertility implicated in seed formation. Journal of Experimental Botany 68, 2037–2054.

Prince SJ, Murphy M, Mutava RN, Durnell LA, Valliyodan B, Grover Shannon J, Nguyen HT. 2017. Root xylem plasticity to improve water use and yield in water-stressed soybean. Journal of Experimental Botany 68, 2027–2036.

Sosa-Valencia G, Palomar M, Covarrubias AA, Reyes JL. 2017. The legume miR1514a modulates a NAC transcription factor transcript to trigger phased RNA formation in response to drought. Journal of Experimental Botany 68, 1819–1821.

Stoddard FL. 2017. Climate change can affect crop pollination in unexpected ways. Journal of Experimental Botany 68, 1819–1821.

Striker GG, Colmer TD. 2017. Flooding tolerance of forage legumes. Journal of Experimental Botany 68, 1851–1872.

Valliyodan B, Ye H, Song L, Murphy M, Grover Shannon J, Nguyen HT. 2017. Genetic diversity and genomic strategies for improving drought and waterlogging tolerance in soybeans. Journal of Experimental Botany 68, 1835–1849.