

Neglecting legumes may compromise global food and nutritional security

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Abstract

The United Nations declared 2016 as the International Year of Pulses (grain legumes) under the banner ‘nutritious seeds for a sustainable future’. A second green revolution is required to ensure food and nutritional security in the face of global climate change. Grain legumes provide an unparalleled solution to this problem because of their inherent capacity for symbiotic atmospheric nitrogen fixation, which provides economically sustainable advantages for farming. In addition, a legume-rich diet has health benefits for humans and livestock alike. However, grain legumes form only a minor part of most current human diets and legume crops are under-utilized compared with cereals. Food security and soil fertility could be significantly improved by greater grain legume usage and increased improvement of a range of grain legumes. The current lack of coordinated focus on grain legumes may compromise our future food and nutritional security.

Introduction

Unlike other plants, legumes have mastered the art of symbiotic nitrogen fixation, leading to significant advantages for agricultural sustainability, both in developing and developed countries. Recent increases in grain legume yields are only between 0 and 1% per year (Fig. 1) and they currently contribute to only a small portion of our staple food when compared with cereals. For example, the acreage and yield of corn is currently much higher than any of the grain legumes. A shift in land use toward grain legumes and away from livestock would substantially lower the carbon footprint for protein production destined for human consumption. There is significant untapped potential for genetic improvements in legumes which can make a larger contribution to the sustainability of cropping systems. Grain legumes could make a greater contribution to sustainable food production by their highly nutritious seed products and also because of their ability to fix symbiotic nitrogen which provides nitrogen to the legume crop as well as for subsequent crops. In addition to their sustainable and environmental benefits, consumption of grain legumes offers health benefits to humans and livestock. A significant portion of the grain legume crop in Europe and in countries such as Australia (e.g. lupins) is currently used for animal feed, and more than half of grain legume production worldwide is processed (e.g. oils). However, grain legumes are an essential commodity in optimal human diets because their seed structure and composition confers a physiologically favourable matrix in the total diet. This review considers the benefits of legume seeds and products to human health and farming systems and identifies key issues to enable increased production and use of grain legumes.

Role of grain legumes in sustainable agriculture

The beneficial aspects of legumes in sustainable cropping systems have been extensively documented¹. The area planted to grain legumes has gradually increased over the past 50 years, but it is still only a quarter of that planted to cereals (Supplementary Fig. 1). Moreover, while increases in cereal production during the past 50 years have been predominantly due to increases in yield—through changes in agronomic practices and new varieties—increases in grain legume production are mostly due to increases in the land area planted (Supplementary Fig 2). For soybean and the major grain legumes such as chickpea, groundnut and lentil, yield has increased proportionately with land area planted. However, year-on-year increases in soybean yields are slowing while area planted is increasing,

suggesting that more marginal land is being planted and improvements in genetic potential are not keeping pace. In contrast, yields of faba bean and peas are increasing while the area harvested is decreasing (Supplementary Fig. 2), resulting in no net production increases in these two crops.

Intercropping and rotation of grain legumes with cereals or other non-leguminous crops have many benefits, such as enhanced yield, increased nitrogen-use efficiency (NUE), reduced occurrence of disease and, in some cases improved access to other essential elements such as phosphorus. The nitrogen-fixing ability of legumes affords complementarity through natural soil fertilisation. Grain legumes favour reduced greenhouse gas emissions in agricultural cropping systems. For example, greenhouse gas emissions declined by 56% on a per hectare basis when a lupin crop preceded wheat². A global analysis of historical data shows that cereals have greater NUE when a larger proportion of nitrogen inputs come from residues of a preceding legume crop with symbiotic nitrogen fixation, than when from synthetic fertilizer³.

Well-grown grain legume crops typically fix between 80 and 120 kg nitrogen/ha. Hence, global nitrogen fixation could account for up to 27 Mt of nitrogen without increasing the area planted to the legumes. Hence, about 9 Mt of soil nitrogen would be available for the following crops, which is equivalent to about 10% of global consumption of nitrogen fertiliser and worth US \$8–12 billion (Box 1). Moreover, the grain protein content of cereal crops following a legume crop is increased and the soil structure and health are improved after growing legumes. Accordingly, nitrogen fixing legumes provide unparalleled sustainable opportunities for minimising future nitrogen fertiliser usage. The inclusion of grain legumes in cropping systems can increase cropping intensity, enhancing annual productivity⁴ as well as increasing diversity and reducing overall risk because the reliance on one or more crops is decreased. While legume crops can favour soil acidification due to an imbalance in cation over anion uptake, this can be managed by varying the legume species used in the crop rotations and by application of lime in the soil. However, the sustainable development of intensive agriculture is limited when grain legumes are intensively cultivated on the same farmland year after year⁵ for example, through the build-up of autotoxins that influence soil microbe communities⁶.

Mitigating the impact of climate change

Future legume production will be influenced by climate change factors such as 1) increased atmospheric CO₂ levels favouring carbon gain because most legumes use C₃ photosynthesis; 2) faster plant developmental rates due to the predicted higher temperatures, which would allow a shorter growing season and reduce exposure to drought that is often experienced at the end of the cropping season; 3) accelerated canopy decay due to extreme temperatures; 4) reduced photosynthetic efficiency, increased pod and flower abortion, and reduced production of reproductive structures due to more frequent droughts; 5) defective pollination due to high temperature-induced pollen sterility; and 6) reduced seed quality⁷. Regional yield changes will depend on the local manifestation of climate change (the interaction between elevated CO₂, high temperature and drought) as well as other factors. Global soybean production already appears to have been influenced by the negative impacts of climate change⁸. Overall, soybean yields declined by 2–4% for every degree rise in temperature during the growing season in the USA between 1994 and 2013 resulting in losses of US\$11 billion⁸. Rising global temperatures could exacerbate heat stress and reduce the areas suitable for bean production⁹. Future climate conditions are predicted to be more favourable to common bean cultivation in the Northern Hemisphere than the Southern Hemisphere¹⁰; new grain legume growing areas should open up in Canada, northern Europe and Russia. For example, pea and faba bean are becoming increasingly important crops in Finland¹¹. Predicted changes in climate should increase yields of dry pea, chickpea, broad bean, lentil, lupin and grasspea in developed countries such as Canada and France but yields will decrease in developing countries in the tropics and sub-tropics such as India, Pakistan and Ethiopia¹².

The yield gap for legume crops in Africa is more than 300%; cowpea yields being only 10–20% of their genetic potential. Moreover, while legume cultivation is an integral part of the Indian agriculture, legume crop production has remained low and unstable, with a yield gap for soybean ranging from 850 to 1320 kg/ha, for groundnut 1180 to 2010 kg/ha, for pigeon pea 550 to 770 kg/ha and 610 to 1150 kg/ha for chickpea. These yield gap analysis of major grain legumes shows that it will be possible to improve productivity by an average 800 kg/ha through improved crop management practices¹³.

Tailoring symbiotic nitrogen fixation

The symbiotic relationship between legumes and *Rhizobium* spp. that facilitates the symbiotic fixation of nitrogen gas from the atmosphere, has both intrinsic scientific interest and widespread implications for agriculture. The mechanisms by which the symbiotic relationship between legumes and *Rhizobia* is initiated and established are well characterised¹⁴. The symbiotic relationship benefits both partners; the plant receives ammonium in return for a supply of dicarboxylic acids that provide an energy source to the bacteria. The bacterial nitrogenase, which catalyses the fixation process, requires a highly reducing environment. Thus, a stable low oxygen environment is achieved within the nodules by the presence of an oxygen diffusion barrier¹⁵. A continual oxygen flux to support bacteroid respiration is facilitated by high concentrations of leghaemoglobin. The nodules deliver reduced nitrogen to the host plant either as amides or ureides depending on the legume species. While the residual nitrogen present in most agricultural soils can have a negative impact on nodule formation and lifespan¹⁶, the sensitivity of this response varies between legume species and needs better characterization. Nitrate acts as a signalling molecule that negatively influences susceptibility to nodulation via nitrate-specific peptide signalling cascades¹⁷. Consequently, one of the challenges facing scientists seeking to expand legume productivity is to maximise symbiotic nitrogen fixation while allowing nitrogen acquisition from the soil. For beneficial nitrogen inputs from legumes in farm rotations, cover crops and as green manures¹⁸ a molecular understanding of the nitrogen sensing components that lead to repression of nodulation is essential. In non-legumes, the molecular mechanisms for sensing soil nitrogen availability are being unravelled and key membrane transporters that can double up as nitrogen sensors have been identified^{19,20}. Similar families of these transporter genes for sensing nitrogen occur in legumes^{19,20}.

Of the 300,000 plant species living in the world today that are exposed to soil microorganisms, only legumes have evolved nitrogen-fixing nodules. However, the at least part of genetic platform that facilitates the legume-rhizobia interaction is conserved with other symbioses²¹. The opportunity for establishing agriculturally-relevant rhizobial symbioses on non-legume species, particularly cereals is attractive. However, we currently know little about the drivers controlling nodulation opportunities, particularly amongst diverse soil rhizobial populations. The management of rhizobial populations under hostile soil conditions remains a challenge particularly in new or expanded cropping areas²². In addition, our current understanding of the regulation of nodule lifespan is superficial. Nodule senescence is a complex and programmed process that is controlled both by developmental

factors and environmental triggers. Activation of the senescence program can lead to premature loss of nitrogen-fixing activity, increased proteolysis and ultimately the death of the infected cells²³.

Global grain legume production in 2013 was 399 Mt, with soybean (278Mt) contributing a significant portion to the agricultural exports of the Americas" (Fig. 2). However, legume crop yields tend to vary more than cereal crops²⁴ largely due to environmental constraints such as drought^{25,26}, which limits symbiotic nitrogen fixation^{27,28}. However, nitrogen fixation is extremely tolerant to soil drying in cowpea²⁹. The incorporation of improved drought tolerance and nitrogen fixation traits into elite lines of grain legumes will generate high-yielding cultivars that can be grown on marginal land.

New technologies for legume improvement

Grain legumes have underpinned the development of genetics. The common garden pea was used by Gregor Mendel to demonstrate the ‘particulate nature of inheritance’ in 1865³⁰. Nevertheless, many grain legume breeding programs suffer from low genetic diversity and low rates of genetic progress. Chickpea experienced several bottlenecks during and after domestication and consequently has limited genetic diversity in the crop gene pool³¹ and in the case of soybean, five introductions accounted for 55% of the pedigree in public soybean cultivars in the USA in the 1990s³². Genetic improvement of peas was accelerated by early generation selection based on the animal model³³. Such methods could contribute to sustainable genetic improvement of the world’s grain legume crops, and help to bridge the gap between grain legumes and their wild and landrace relatives (Fig. 3). When combined with genomics-assisted breeding³⁴, it will be possible to unlock valuable genes such as tolerance to drought and heat stress in wild legumes, and move them efficiently into cultivated varieties³⁵. Rapid introgression of these important genes is a major challenge facing grain legume breeders, who need to accelerate grain legume genetic improvement to meet the expectations of the 2009 Declaration of the World Summit on Food Security, which stated that a 70% increase in agricultural output was required by 2050 to keep pace with population increase, while adapting to climate change through sustainable use of genetic resources for food and agriculture.

The importance of biodiversity in seed banks has been recognized and much attention

has been paid to rice and other cereal crops³⁶. To promote and optimise cultivation of legumes, germplasm collections are important genetic resources and large genetic and phenotypic variation exists in the world collections (Table 1, Fig 4). It is therefore important to have a systematic inventory of germplasm centres and their collections. Most of the publicly available information can be found in GENESYS (Global Portal on Plant Genetic Resources; www.genesys-pgr.org). In addition to major CGIAR Institutes listed in Table 1, significant numbers of grain legume germplasm are conserved in various national genetic resource centres. Germplasm from China can be accessed via the Chinese Crop Germplasm Resources Information System (www.cgris.net/cgris_english.html) and the Crop Germplasm Resources Platform under the Ministry of Science and Technology, P.R. China. The National Institute of Agrobiological Sciences (NIAS) Genebank(www.gene.affrc.go.jp/databases_en.php?section=plant) holds the largest germplasm database in Japan. The germplasm from India can be accessed through the National Bureau of Plant Genetic Resources (NBPGR) database (http://www.nbpgr.ernet.in/PGR_Databases.aspx). This germplasm list is not exhaustive, because information is often hard to retrieve and several accessions are duplicated across genetic resource centres. Moreover, the format of the data could be further standardized to facilitate the users.

Whole genome sequencing has become an affordable and powerful tool to delineate genomic information of core germplasm³⁷. Genomic information can be used to generate high resolution genetic maps for important agronomic traits, develop molecular markers for breeding, and identify important genes for crop improvement³⁴. High-resolution genetic maps are available for 10 legumes with *de novo* sequence information and low-resolution maps available for all but Bambara bean, tepary bean, and lima bean. The establishment of genetic resources and grain legume genome sequencing together accelerated the development of genomics-assisted breeding strategies toward crop improvement (Fig 5).

Global cereal production has almost tripled over the past 50 years but grain legume production has only increased by about 60%. The relatively low rate of yield improvement in grain legumes versus cereals is at least partly explained by low genetic diversity in grain legume breeding programs³⁸. It is important to increase genetic diversity in elite breeding programs if we are to capitalize on biotechnology for legume yield improvement. Genomic selection relies on allelic diversity in the breeding population for complex traits, and may

improve long-term genetic progress if accompanied by high effective population size with minimal inbreeding³⁹. Selection for complex traits was shown to be more efficient when based on genomic relationship information in animals⁴⁰. For grain legumes, many of which are self-pollinating crops, genomic selection offers the prospect of accelerating genetic progress for yield⁴¹. Advanced phenotyping technologies are available to measure morphological and physiological traits⁴². High-throughput image-based phenotyping platforms will make significant impact in plant phenomics⁴³. Accurate physiological phenotyping on specific and well defined traits can contribute towards improved breeding outcomes⁴⁴.

Bringing in orphans

Orphan crops, including legumes, are minor crops with regional importance that have been largely neglected by researchers and industry due to limited economic importance in the global market. However, many people, particularly in developing countries, rely on these crops not only as food and feed crops but also for their daily healthcare needs despite advancements in modern medicine. They often fill ecological niches, unoccupied by major crop plants, resulting in a greater genetic diversity and plasticity. Orphan food legumes such as cowpea, grass pea, the ‘Dolichos’ bean, the Tepary bean and the marama bean are usually grown in arid regions, often on marginal land unsuitable for major crop species. They have heat-and drought-tolerance traits, high nutritional value and are extensively used by subsistence farmers. Cowpea is particularly valuable to humans who have limited access to animal protein. The seeds have a high protein content of 25% of dry weight and the leaves are also consumed. The protein content of cowpea leaves consumed annually in Africa and Asia is equivalent to the amount in 5 million tons of dry cowpea seeds which equates to about 30% of total food legume production in lowland tropics⁴⁵. The ‘Dolichos’ bean, one of the most ancient legume crops among cultivated plants, is grown as a multipurpose crop pulse, vegetable and forage. The bean is a major protein source in diets in the southern states of India. The Tepary bean originated from dry subtropical areas of Mexico and the southwestern United States. Tepary bean is well adapted to drought and high- temperature stresses; the major drought stress adaptation mechanisms are deep rooting for more water uptake, small leaves for reduced water use and less stomatal conductance⁴⁶. The oil-rich marama bean, a perennial legume of Southern Africa growing in the Kalahari Desert, can be more nutritious than soybean⁴⁷. A major drawback of all these legume crops, or potential crops like

marama bean, is inefficient harvesting techniques due to the shape and density of branches, being ground creepers occupying large areas with limited seed yield and low propagation rates. Therefore, the promise of orphan legume crops remains largely unexplored, even though they may represent a treasure trove of undiscovered and potentially unique traits due to their great genetic diversity.

Grain legumes such as cowpea have potential uses in the cosmetic, food, textile and pharmaceutical sectors with their therapeutic properties⁴⁸. Cowpea is a source of vitamins and minerals such as folic acid, vitamins A and B, thiamine, niacin and the water-soluble vitamins riboflavin, pyridoxine and folic acid, as well as minerals such as calcium, zinc, potassium, iron and phosphorous and other trace elements⁴⁹. Cowpea proteins have high lysine contents and are potentially an excellent supplement for cereal-based diets⁵⁰. The marama bean serine protease inhibitor that prevents elastase activity provides a safe and natural trypsin and elastase inhibitor (United States Patent 5869063). Elastase is part of the chymotrypsin-like clan and an important role has been suggested for human elastase in various inflammatory disorders, including pulmonary emphysema, sepsis, arthritis, nephritis and certain skin diseases⁵¹. These inhibitors, therefore, have the potential to be therapeutic candidates for these diseases and as an additive in creams for skin treatments.

Nutrition and health

Legumes hold a near-unique position among foodstuffs because of their health determinant properties (Fig. 6)⁵². For example, all-cause mortality increased by 113% for Chinese women on a legume-free diet and by 30% for Chinese men⁵³. Moreover, the mortality hazard ratio declines by 7–8% in older people globally for every 20 g increase in daily grain legume intake⁵². The first study to assess the link between the Mediterranean diet and health, which included a 20 g intake of legumes per day, found a 10% reduction in all-cause mortality⁵⁴.

Legumes offer a food-based solution to decreasing risk of certain diseases such as pre-diabetes⁵⁵ and diabetes management as well as diabetes-associated complications, especially cardiovascular disease⁵⁶. Since diabetes is a major risk factor for several cancers and neurodegeneration, the future health of ageing populations may be dependent on a food system that provides legumes in an affordable, palatable and sustainable way. Most benefits from legumes are achieved at an intake of about 30 g per day, but lesser amounts are also beneficial.

Lupin-enriched foods

Flour made from lupin grains contains about 45% protein and 30% fibre, and is a minor food ingredient in baking. However, this novel food ingredient can partially replace wheat flour to increase protein and fibre. Lupin-enriched foods, such as bread, pasta and biscuits, are palatable and acceptable to consumers. In clinical trials, lupin flour-enriched bread greatly reduced appetite and energy intake, suppressed plasma ghrelin, an orexigenic hormone that stimulates appetite, and reduced post-meal glucose and insulin responses⁵⁷. These results suggest that bread with lupin-kernel flour has the potential to influence appetite and reduce energy intake and glucose control. In contrast to the findings in an acute setting, consumption of lupin-enriched bread over 16 weeks did not alter body weight or body composition of participants who replaced 15–20% of their usual daily energy intake with lupin kernel-enriched bread compared to white bread (control) in an *ad libitum* diet⁵⁸. Nevertheless, lupin bread reduced 24-hour and awake systolic blood pressure (3.0 mm Hg and 3.1 mm Hg, respectively) and pulse pressure (3.5 mm Hg and 4.6 mm Hg) relative to controls⁵⁹. While a lupin-rich diet did not significantly influence body weight, body composition or cardiovascular risk factors in overweight men and women⁶⁰, the 24-h ambulatory systolic and diastolic blood pressures of participants had reduced with the lupin diet by 12 months. Additionally, fasting insulin concentrations and homeostasis model assessment (HOMA) scores, used as measures of insulin resistance, were significantly lower at 4 and 12 months. Fasting insulin concentrations declined by 16 and 21% and HOMA scores by 30 and 33% at 4 and 12 months, respectively⁶⁰.

The positive findings on blood glycaemic response in normoglycaemic individuals suggest that lupin foods could benefit patients with Type 2 diabetes. The acute effects of a lupin-based beverage on glucose and insulin responses in Type 2 diabetic subjects were determined in a randomised, controlled, cross-over trial, in which participants consumed a beverage containing 50 g glucose (control), or 50 g glucose plus lupin kernel flour with 12.5 g fibre and 22 g lupin protein, or 50 g glucose plus 12.5 g fibre and 22 g protein from soya isolates⁶¹. Post-beverage glycaemic responses were significantly lower in participants following intake of the lupin beverage than the control beverage over a 4 h period following consumption.

These studies consistently demonstrate that lupin-enriched foods reduce blood pressure and glycaemic responses, providing strong evidence that lupin-enriched food may have

cardiovascular benefits, particularly in patients with diabetes who are at a significantly increased risk of cardiovascular disease. Moreover, lupins have negligible anti-nutritional properties and can be consumed with minimal cooking as snack foods⁶².

Conclusions and perspectives

Legumes have been included in cropping systems for hundreds of years, especially in rotation with other crop species. A boost in grain legume production is urgently needed to oppose the static or declining production trends especially in developing countries, despite increasing global demand. The international year of pulses (grain legumes) in 2016 provides an excellent opportunity to reflect on the status of global grain legume production, consumption and potential opportunities for future expansion. Our current overreliance on a handful of major staple crops has inherent agronomic, ecological, nutritional and economic risks and devalues the contributions made by under-utilized legumes. Intake of a diverse array of legumes is important in the human diet. Moreover, many underutilized legume crops are already an essential source of vitamins, micronutrients and protein for large parts of the developing world and, thus, a valuable component for nutritional security. Frequently, underutilized legume crops are not always grown as a commodity, but harvested from unimproved land races or wild populations. The inherent adaptability and stress tolerances of these nutritious and energy sufficient species could play an important role in ensuring food security in the face of climate change for populations living in marginalized regions. The transfer of technologies related to grain legume production to resource-poor rural communities could be hastened with more participatory approaches¹.

The current use of nitrogen fertilisers in agriculture is ~110 million tonnes pa, with the majority directed to cereal production. Only 30-50% of applied nitrogen is used by the intended crop and excess nitrogen fertilization has negative impacts on climate change and biodiversity. The ability of legumes to fix atmospheric nitrogen through symbiosis with rhizobia has enormous largely untapped potential for sustainable agriculture, plant diversity and enhancement of primary production with reduced fertiliser use, benefits that may also extend to phosphorus-poor soils⁶³. Recent increasing nitrogen fertilizer costs are focussing more attention on improving efficiency in cropping systems. Attempts to create nitrogen-fixing cereals are underway but grain legumes currently receive less research and development attention. Legumes lag behind cereals in terms of area expansion and productivity gains, despite increasing global demand. This lag may be due in part to unstable

grain legume prices due to high variability in their yields and high competition from high-yielding cereal crops. In addition, government price support policies exist, particularly in developing countries, as well as insufficient inputs into breeding and agronomic technologies required to improve yields.

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Author contributions

CHF co-created the network, discussed the idea, organised the content and edited the final article before submission, H-M Lam discussed and contributed to the content, prepared Fig. 2, Table 1 and the associated webpage, highlight and cover design. RV provided information concerning genetics and breeding. HTN discussed and contributed to the content and coordinated the genetic and breeding topics including figures and table. KHMS co-created the network, discussed the idea, contributed to various sections, figures and edited the final version. TDC discussed the content, contributed to the section on sustainable agriculture, contributed edits to several sections, and gave suggestion on figures. WC wrote parts of the main text, contributed citations and edited tables and figures. HB discussed the content, prepared Fig. 1 and Supplementary Figures, and contributed to the sustainable agriculture section TAM, discussed the idea, provided Fig 6 and contributed to the section on nutrition and health. JMH assisted in the production of Fig 6 and contributed to the section on nutrition

and health. JWC produced Fig 3 and finalised the references. T M contributed to the section on symbiotic nitrogen fixation. KK contributed to orphan legume section, JV contributed to orphan legume section. CC organized orphan legume section and reviewed final version. JAO discussed the idea and provided information concerning genetics and breeding. MLW contributed to the section on nutrition and health. YL discussed the idea and contributed to the section on sustainable agriculture. HS discussed the idea and helped to edit the content before submission. KS discussed the idea and helped to edit the content before submission. JY discussed the idea and helped to edit content before submission. NF contributed to section on climate change, BNK contributed to sections focussed on legume nitrogen fixation and helped to edit the content before submission. F-LW produced Fig. 3 and highlight and cover design. BV contributed to abiotic stress information, citations and genomics-assisted breeding figure. MC co-created the network, prepared Box 1, discussed the idea and edited the figures before submission.

Figure legends

Figure 1. Increase in total world production (a) and yield (b) of dry grain legumes compared to cereals.

Cereals include wheat, rice, barley, maize, rye, oats and millet, and grain legumes includes 11 of the 12 major categories of grain legume in FAO data: bambara bean; broad bean and faba bean; chickpea; cowpea; groundnut; lentil; lupin; string beans and miscellaneous grain legumes; pea; *Phaseolus* spp.; pigeonpea. All production values are dry clean weights, excluding pod weights. Production of string beans were neither dried nor shelled so data were excluded. Data for groundnuts in shells were converted using 70% in FAO data. Miscellaneous grain legumes include *Dolichos* spp. (lablab or hyacinth bean), *Canavalia* spp. (jack or sword bean), *Psophocarpus tetragonolobus* (winged bean), *Cyamopsis tetragonoloba* (guar bean), *Stizolobium* spp. (velvet bean) and *Pachyrhizus erosus* (yam bean). *Phaseolus* spp. includes *Phaseolus vulgaris* (kidney, haricot, common bean), *Phaseolus lunatus* (lima, butter bean), *Phaseolus angularis* (adzuki bean), *Phaseolus aureus* (mungo bean, golden, green gram), *Phaseolus mungo* (black gram, urd), *Phaseolus coccineus* (scarlet runner bean), *Phaseolus calcaratus* (rice bean), *Phaseolus acutifolius* (moth bean) and *Phaseolus acutifolius* (tepariy bean). Data source: FAO, <http://faostat3.fao.org/compare/E>, accessed 05/01/2016.

Figure 2: World grain legumes production in 2013.

a. 121 Mt of grain legumes (excluding soybean) were produced globally in 2013. Data comprises the grain legumes as cited in **Fig 1** plus string bean. Production of the 12 categories are presented in the inset of **Fig 2a** as a stacked column graph by the ten net highest-producing countries: **1.** bambara bean, **2.** broad bean and faba bean, **3.** chickpea, **4.** cowpea, **5.** groundnut, **6.** lentil, **7.** lupin, **8.** miscellaneous grain legumes, **9.** pea, **10.**

*Phaseolus*spp., 11. pigeonpea, 12. string bean. Of these, the top three grain legumes (excluding soybean) were groundnut (42.8 Mt), chickpea (13.3 Mt) and pea (11.5 Mt). *Phaseolus*spp. are a significant category of grain legumes by production (23.7 Mt).

b. Global soybean production. Global production was 278 million tons (Mt) in 2013, accounting for 70% of global grain legumes produced. The top five soybean producing countries were the USA (91.4 Mt), Brazil (81.7 Mt), Argentina (49.3 Mt), China (12.0 Mt) and India (11.9 Mt). Data source: FAO, www.faostat.fao.org, accessed 30/01/2016. The maps were generated using R ver. 3.1.3 (R Core Team 2015) with extension packages, *rworldmap*⁶⁴ and *RColorBrewer*⁶⁵. Countries indicated in white are where data are unavailable.

Figure 3: Taxonomic relationships within the Papilionideae family showing the two major clades of cultivated legume; the cool season Hologalegina (blue) and the warm season Phaseoloids (light green) using methodology, adapted from Lavin et al., (2005)⁶⁶.

Clades are denoted by coloured circles and corresponding labels at nodal points. *Arabidopsis thaliana* has been included as an out-group from which the phylogeny was rooted. Genus abbreviations: *Ara.*, *Arabidopsis*; *Arc.*, *Archis*; *Lup.*, *Lupinus*; *Lot.*, *Lotus*; *Med.*, *Medicago*; *Cic.*, *Cicer*; *Vic.*, *Vicia*; *Lat.*, *Lathyrus*; *Pis.*, *Pisum*; *Caj.*, *Cajanus*; *Gly.*, *Glycine*; *Dol.*, *Dolichos*; *Pha.*, *Phaseolus*; *Vig.*, *Vigna*. ● denotes forage species, included due to their value as model legumes (i.e. not pulse crops). Ma denotes evolutionary age in millions of years, according to Gepts et al. (2005)⁶⁷. The tree was constructed in MAFFT⁶⁸ using maturase K protein sequence similarity. Tree visualization was performed in FigTree⁶⁹.

Figure 4: Major strategies in genomics-assisted crop improvement for grain legumes.

Large-scale germplasm stored in different genebanks can be characterised into smaller sets such as a core/mini-core germplasm set. Such small sets of germplasm can be characterised

extensively for traits of interest. Subsequently, specialised genetic stocks such as a mini-core collection (diverse set), bi-parental and multi-parent mapping populations and mutant populations can be developed. Subjecting the populations to Whole Genome Sequencing (WGS)/Genotyping-By-Sequencing (GBS)/ -array-based genotyping together with phenotyping for traits of interest can provide Quantitative Trait Loci (QTLs), Quantitative Trait Nucleotides (QTNs), superior alleles and haplotypes. In the end, modern breeding approaches such as Marker Assisted Selection (MAS), Marker-Assisted Backcrossing (MABC) and Genomic Selection (GS) can be deployed for integrating/accumulating superior alleles. QTNs can be edited through genome editing approach called Promotion of Alleles through Genome Editing (PAGE). Candidate genes identified by using -omics approaches can be deployed in genetic engineering approach. By using one or more of the approaches mentioned above, cultivars with improved yield and nutritional quality can be developed.

Figure 5. Phenotypic variability in chickpea germplasm conserved at ICRISAT, India.

Figure 6: The human health benefits of grain legumes.

- a. Common grain legumes in the human diet. b. Lupin as an example of processed staple foods. c. Passion for Pulses⁷⁰. d. Key benefits of dietary grain legumes on human health.

Supplementary Figures

Supplementary Figure 1: Relationship between changes in yield and world area harvested for dry grain legumes compared with cereals over the past 50 years. Increased production of grain legumes is associated with expansion of land area planted to the crops compared with

cereals whose increased production is due to yield improvements while land area has remained the same. Data are for the legume and cereal species detailed in Fig. 1. Data source: FAO <http://faostat3.fao.org/compare/E>, accessed 05/01/2016.

Supplementary Figure 2: Relationship between changes in yield and world area harvested for different grain legumes over the past 50 years. Most increases in yield are associated with expansion of land area planted to the crops. Data are for the legume and cereal species detailed in Fig. 1. Data source: <http://faostat3.fao.org/compare/E>, accessed 5/1/2016.

Table 1. Genetic and genomic resources of grain legumes important to global food and nutrition security

Common name	Scientific name	Number of accessions ^a	Main holding institutes ^b	Genome size (Mb) ^c	No. of chromosomes (haploid)	Ploidy	Breeding System ^d	De novo genome sequencing ^e
Adzuki bean	<i>Vigna angularis</i>	9978	B (54%), N (24%), H (16%)	528	11	2	ib	V
Bambara beans	<i>Vigna subterranea</i>	2183	I (94%)	864	11	2	ib	Not available
Black gram	<i>Vigna mungo</i>	1668	N (51%), P (18%), K (13%)	528	11	2	ib	Not available
Mung bean	<i>Vigna radiata</i>	23646	B (28%), N (28%), G (18%), P (17%)	509	11	2	ib	S, V
Cowpea	<i>Vigna unguiculata</i>	42281	I (38%), P (20%)	576	11	2	ib	Q
Broad bean Faba bean	<i>Vicia faba</i>	30073	M (33%), B (16%), A (12%)	12797	6	2	ob	Not available
Chickpea	<i>Cicer arietinum</i>	76192	F (27%), G (19%), M (19%), P (10%)	912	8	2	ib	S, T
Common bean	<i>Phaseolus vulgaris</i>	102732	C (30%), P (13%)	576	11	2	ib	S, Y
Tepary bean	<i>Phaseolus acutifolius</i>	1257	P (39%), C (26%), D (11%)	720	11	2	ib	Not available
Lima bean	<i>Phaseolus lunatus</i>	6420	C (47%), P (35%)	672	11	2	ib-ob	Not available
Grass pea	<i>Lathyrus sativus</i>	6698	M (38%), K (12%), O (12%)	8064	7	2	ib-ob	Not available
Hyacinth bean Lablab bean	<i>Dolichos lablab</i> <i>Lablab purpureus</i>	1292	N (33%), D (29%), P (13%), C (12%)	365	11	2	ib	Not available
Lentil	<i>Lens culinaris</i>	29434	M (42%), A (16%), P (11%)	4032	7	2	ib	R
Narrow-leafed lupin	<i>Lupinus angustifolius</i>	2957	K (28%), L (21%), E (10%), J (10%), P (10%)	893	20	2	ib	X
White lupin	<i>Lupinus albus</i>	4155	L (18%), K (12%), P (11%)	576	25	2	ib	Not available
Pea	<i>Pisum sativum</i>	54019	P (13%), A (11%), M (11%)	4685	7	2	ib	Not available
Peanut (groundnut)	<i>Arachis hypogaea</i>	47591	F (31%), G (29%), P (20%), B (17%)	2755	10	4	ib	U
Pigeonpea	<i>Cajanus cajan</i>	25510	F (52%), G (44%)	845	11	2	ib-ob	S
Soybean	<i>Glycine max</i>	93676	B (31%), P (23%), N (15%)	1085	20	2	ib	W, Y

Footnotes:

a	<p>Total number of accessions is the sum of data from GENESYS-PGR, China, India (NBPGR), Japan and Australia. Data accessed 17 February 2016 through:</p> <ul style="list-style-type: none"> (i) GENESYS Global Portal on Plant Genetic Resources, http://www.genesys-pgr.org (ii) http://www.most.gov.cn/ztl/kjzykfgx/kjzygjctjpt/kjzyptml/201407/t20140716_114275.htm (iii) http://www.nbpgr.ernet.in/Research_Projects/Base_Collection_in_NGB.aspx (iv) https://www.gene.affrc.go.jp/databases_en.php (v) Stoutjesdijk, P. Plant genetic resources for food and agriculture: second national report-Australia, Technical Report 13.11. Canberra, December. CC BY 3.0. (ABARES, 2013) <p>More information associated to Table 1 can be accessed via http://legumecrops.wildsoydb.org/. It is expected that there are several duplicated accessions across collections, and several accessions are located in non-listed institutions and not accounted for.</p>																																																																
b	<p>% in brackets is the percentage of the total number of accessions held by the institute/system. Only institutes holding 10% or more of the total number of accessions were listed. Letters represent holding institutes are listed below. For institution “A” the number of <i>Vicia</i> accessions included both broad bean and vetch.</p> <table border="0"> <tr> <td>A</td> <td>Australia</td> <td>Australian Temperate Field Crops Collection (Horsham, Vic.)</td> <td>http://agriculture.vic.gov.au</td> </tr> <tr> <td>B</td> <td>China</td> <td>Institute of Crop Sciences, Chinese Academy of Agricultural Sciences</td> <td>http://www.cgris.net/cgris_english.html</td> </tr> <tr> <td>C</td> <td>Colombia</td> <td>Centro Internacional de Agricultura Tropical</td> <td>http://www.ciat.cgiar.org</td> </tr> <tr> <td>D</td> <td>Ethiopia</td> <td>International Livestock Research Institute</td> <td>http://www.ilri.cgiar.org</td> </tr> <tr> <td>E</td> <td>Germany</td> <td>Genebank, Leibniz Institute of Plant Genetics and Crop Plant Research</td> <td>http://www.ipk-gatersleben.de</td> </tr> <tr> <td>F</td> <td>India</td> <td>International Crop Research Institute for the Semi-Arid Tropics</td> <td>http://www.icrisat.org</td> </tr> <tr> <td>G</td> <td>India</td> <td>National Bureau of Plant Genetic Resources</td> <td>http://www.nbpgr.ernet.in</td> </tr> <tr> <td>H</td> <td>Japan</td> <td>NIAS Genebank</td> <td>https://www.gene.affrc.go.jp/databases_en.php</td> </tr> <tr> <td>I</td> <td>Nigeria</td> <td>International Institute of Tropical Agriculture</td> <td>http://www.iita.org</td> </tr> <tr> <td>J</td> <td>Portugal</td> <td>Banco de Germoplasma – Departamento de Recursos Genéticos e Melhoramento, Estação Agronómica Nacional, Instituto Nacional de Investigação Agrária</td> <td>https://www.genesys-pgr.org/wiews/PRT005</td> </tr> <tr> <td>K</td> <td>Russia</td> <td>N.I. Vavilov Research Institute of Plant Industry</td> <td>http://www.vir.nw.ru</td> </tr> <tr> <td>L</td> <td>Spain</td> <td>Junta de Extremadura. Dirección General de Ciencia y Tecnología. Centro de Investigación Agraria Finca La Orden – Valdesequera</td> <td>http://centrodeinvestigacionlaorden.es https://www.genesys-pgr.org/wiews/ESP010</td> </tr> <tr> <td>M</td> <td>Syria</td> <td>International Centre for Agricultural Research in Dry Areas</td> <td>http://www.icarda.cgiar.org</td> </tr> <tr> <td>N</td> <td>Taiwan</td> <td>Asian Vegetable Research and Development Center</td> <td>http://www.avrdc.org</td> </tr> <tr> <td>O</td> <td>Ukraine</td> <td>Ustymivka Experimental Station of Plant Production</td> <td>https://www.genesys-pgr.org/wiews/UKR008</td> </tr> <tr> <td>P</td> <td>US</td> <td>National Plant Germplasm System</td> <td>http://www.ars-grin.gov/npgs/index.html</td> </tr> </table>	A	Australia	Australian Temperate Field Crops Collection (Horsham, Vic.)	http://agriculture.vic.gov.au	B	China	Institute of Crop Sciences, Chinese Academy of Agricultural Sciences	http://www.cgris.net/cgris_english.html	C	Colombia	Centro Internacional de Agricultura Tropical	http://www.ciat.cgiar.org	D	Ethiopia	International Livestock Research Institute	http://www.ilri.cgiar.org	E	Germany	Genebank, Leibniz Institute of Plant Genetics and Crop Plant Research	http://www.ipk-gatersleben.de	F	India	International Crop Research Institute for the Semi-Arid Tropics	http://www.icrisat.org	G	India	National Bureau of Plant Genetic Resources	http://www.nbpgr.ernet.in	H	Japan	NIAS Genebank	https://www.gene.affrc.go.jp/databases_en.php	I	Nigeria	International Institute of Tropical Agriculture	http://www.iita.org	J	Portugal	Banco de Germoplasma – Departamento de Recursos Genéticos e Melhoramento, Estação Agronómica Nacional, Instituto Nacional de Investigação Agrária	https://www.genesys-pgr.org/wiews/PRT005	K	Russia	N.I. Vavilov Research Institute of Plant Industry	http://www.vir.nw.ru	L	Spain	Junta de Extremadura. Dirección General de Ciencia y Tecnología. Centro de Investigación Agraria Finca La Orden – Valdesequera	http://centrodeinvestigacionlaorden.es https://www.genesys-pgr.org/wiews/ESP010	M	Syria	International Centre for Agricultural Research in Dry Areas	http://www.icarda.cgiar.org	N	Taiwan	Asian Vegetable Research and Development Center	http://www.avrdc.org	O	Ukraine	Ustymivka Experimental Station of Plant Production	https://www.genesys-pgr.org/wiews/UKR008	P	US	National Plant Germplasm System	http://www.ars-grin.gov/npgs/index.html
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c	<p>Genome size is estimated from C-value [Bennett MD, Leitch IJ. Plant DNA C-values database (release 6.0, Dec. 2012) http://www.kew.org/cvalues/]</p>																																																																
d	<p>“Breeding system” is defined following Simmonds, N.W. and J. Smartt. 1999. Principles of Crop Improvement. 2nd Ed. Blackwell Science, Oxford.</p> <p>ib inbred, usually selfed, tolerant of inbreeding ob outbred, suffers inbreeding depression ib-ob-out-bred, usually nearer ib than ob</p> <p>Additional reference: Singh R.J. et al. (2007) Landmark research in legumes. Genome 50:525-537</p>																																																																
e	<p>Major websites for <i>de novo</i> genome information (in alphabetical order):</p>																																																																

Q	http://cowpeagenomics.med.virginia.edu/CGKB
R	http://knowpulse.usask.ca/portal/lentil-genome
S	http://legumeinfo.org/genomes
T	http://nipgr.res.in/CGAP/home.php
U	http://peanutbase.org/home
V	http://plantgenomics.snu.ac.kr/mediawiki-1.21.3/index.php/Main_Page
W	http://soybase.org
X	http://www.ncbi.nlm.nih.gov
Y	https://phytozome.jgi.doe.gov/pz/portal.html

Box 1. The growing economic and environmental cost of nitrogen fertilization.

The relationship between the use of synthetic nitrogen fertilizers and global population growth belies the untapped potential of biological nitrogen fixation by grain legume crops. Some headline facts in this debate:

- Synthetic nitrogen fertilizers sustain 30-50% of present crop yields and will need to increase with further population growth⁷¹. Global ammonia capacity is projected to grow by 16% between 2014 and 2019, with total industrial nitrogen demand grow by 28% over this time, compared with a 6% increase across the fertilizer sector.
- Synthetic ammonia by the Haber-Bosch process presently consumes 1.5% of the global total primary energy consumption (at >200 Mt.yr⁻¹, 41 GJ.t⁻¹ ammonia, global energy consumption *ca.* 5.0x10¹¹ GJ^{71,72}).
- The environmental impact of nitrogen fertilizers is manifold, including:
 - Loss of biodiversity through eutrophication. Remarkably, recent studies show biodiversity recovering with more environmentally stringent practices since the 1980s⁷³.
 - Eutrophication also increases production of bacterial nitrous oxide (N₂O), which is one of the most toxic greenhouse gases (UNEP and WHRC, 2007).
 - Production of N₂O and other reactive nitrogen by-products of fossil fuel combustion, including from ammonia synthesis. The average lifetime N₂O in the atmosphere is >100 years (UNEP and WHRC, 2007). The global atmospheric N₂O concentration is now 18% higher than in pre-industrial times, and it is estimated that >30% of all atmospheric N₂O results from agriculture.
- The nitrogen-use efficiency of cereals decreased from *ca.* 80% to *ca.* 30% between 1961-2000^{74,75}. More than 50% applied nitrogen fertilizer was lost from cereal crops between 1961-2010^{3,76}, and in some cases >80% of applied nitrogen is lost through runoff (UNEP and WHRC, 2007).

References

- 1 Siddique, K. H. M. Johansen, C. & Turner, N.C. Innovations in agronomy for food legumes. *Agr. for Sus Dev* **32**, 45-64 (2012).
- 2 Barton, L., Thamo, T., Engelbrecht, D. & Biswas, W. K. Does growing grain legumes or applying lime cost effectively lower greenhouse gas emissions from wheat production in a semi-arid climate? *J Clean Prod* **83**, 194-203, (2014).
- 3 Lassaletta, L., Billen, G., Grizzetti, B., Anglade, J. & Garnier, J. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. *Environ Res Lett* **9**, (2014).
- 4 Malik, A. I. A., M. O.; Zaman, M. S.; Flower, K.; Rahman, M. M. & Erskine, W. Relay sowing of lentil (*Lens culinaris* subsp. *culinaris*) to intensify rice-based cropping. *Journal of Agricultural Science* doi: 10.1017/S0021859614001324 (2015).
- 5 Huang, L.-F., Song L., Mao, W., Shi, K., Zhou, Y. & Yu, J. Plant-Soil Feedbacks and Soil Sickness: From Mechanisms to Application in Agriculture. *J Chem Ecol* **39**, 232-242, (2013).
- 6 Nayyar, A., Hamel, C., Lafond, G., Gossen, B.D. & Hanson, K. Soil microbial quality associated with yield reduction in continuous-pea. *Appl Soil Ecol* **43**, 115-121, (2009).
- 7 Myers, S. S *et al.* Increasing CO₂ threatens human nutrition. *Nature* **510**, 139-142, (2014).
- 8 Mourtzinis, S. *et al.* Climate-induced reduction in US-wide soybean yields underpinned by region- and in-season-specific responses. *Nat Plants* **1**, 1-4, (2015).
- 9 Beebe, S. *et al.* Genetic Improvement of Common Beans and the Challenges of Climate Change. *Crop Adaptation to Climate Change*, 356-369, (2011).
- 10 Ramirez-Cabral, N. Y. Z., Kumar, L. & Taylor, S. Crop niche modeling projects major shifts in common bean growing areas. *Agr Forest Meteorol* **218-219**, 102-113 (2016).
- 11 Peltonen-Sainio, P., Jauhiainen, L., Hakala, K. & Ojanen, H. Climate change and prolongation of

- growing season: changes in regional potential for field crop production in Finland. *Agr Food Sci* **18**, 171 (2009).
- 12 Andrews, M. & Hodge, S. Climate Change, a Challenge for Cool Season Grain Legume Crop Production. *Cli.Change Manag. Cool Season Grain Leg. Cr*, 1-9 (2010).
 - 13 Bhatia, V. S., Singh, P., Wani, S. P., Kesava Rao, A. V. R. & Srinivas, K. Yield Gap Analysis of Soybean, Groundnut, Pigeonpea and Chickpea in India Using Simulation Modeling. Report No. 31, 156 International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). Patancheru 502 324, Andhra Pradesh, India (2006).
 - 14 Oldroyd, G. E. D. Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nat Rev Microbiol* **11**, 252-263 (2013).
 - 15 Li, Y. Z., Green, L. S., Holtzapffel, R., Day, D. A. & Bergersen, F. J. Supply of O₂ regulates demand for O₂ and uptake of malate by N₂-fixing bacteroids from soybean nodules. *Microbiol-Uk* **147**, 663-670 (2001).
 - 16 Peoples, M. B., Herridge, D. F. & Ladha, J. K. Biological Nitrogen-Fixation - an Efficient Source of Nitrogen for Sustainable Agricultural Production. *Plant Soil* **174**, 3-28 (1995).
 - 17 Reid, D. E., Ferguson, B. J. & Gresshoff, P. M. Inoculation- and Nitrate-Induced CLE Peptides of Soybean Control NARK-Dependent Nodule Formation. *Mol Plant Microbe In* **24**, 606-618 (2011).
 - 18 Li, X. X., Sorensen, P., Li, F. C., Petersen, S. O. & Olesen, J. E. Quantifying biological nitrogen fixation of different catch crops, and residual effects of roots and tops on nitrogen uptake in barley using in-situ N-15 labelling. *Plant Soil* **395**, 273-287, (2015).
 - 19 Bouguyon, E. *et al.* Multiple mechanisms of nitrate sensing by Arabidopsis nitrate transceptor NRT1.1. *Nat Plants* **1**, 15 (2015).
 - 20 Leran, S. *et al.* Nitrate sensing and uptake in Arabidopsis are enhanced by ABI2, a phosphatase inactivated by the stress hormone abscisic acid. *Sci Signal* **8** (2015).
 - 21 Parniske, M. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nat Rev Microbiol* **6**, 763-775 (2008).

- 22 Howieson, J. & Ballard, R. Optimising the legume symbiosis in stressful and competitive environments within southern Australia - some contemporary thoughts. *Soil Biol Biochem* **36**, 1261-1273 (2004).
- 23 Puppo, A. *et al.* Legume nodule senescence: roles for redox and hormone signalling in the orchestration of the natural aging process. *New Phytol* **165**, 683-701 (2005).
- 24 Cernay, C., Ben-Ari, T., Pelzer, E., Meynard, J. M. & Makowski, D. Estimating variability in grain legume yields across Europe and the Americas. *Sci Rep* **5**, 10.1038/srep11171 (2015).
- 25 Farooq, M. *et al.* Drought Stress in Grain Legumes during Reproduction and Grain Filling. *Journal of Agronomy and Crop Science* (in press) (2016).
- 26 Daryanto, S., Wang, L. & Jacinthe, P. A. Global Synthesis of Drought Effects on Food Legume Production. *PloS one* **10**, e0127401 (2015).
- 27 Sinclair, T. R., Messina, C. D., Beatty, A. & Samples, M. Assessment across the United States of the Benefits of Altered Soybean Drought Traits. *Agron J* **102**, 475-482 (2010).
- 28 Devi, M. J., Sinclair, T. R., Beebe, S. E. & Rao, I. M. Comparison of common bean (*Phaseolus vulgaris* L.) genotypes for nitrogen fixation tolerance to soil drying. *Plant Soil* **364**, 29-37 (2013).
- 29 Sinclair, T. R. *et al.* Variation among Cowpea Genotypes in Sensitivity of Transpiration Rate and Symbiotic Nitrogen Fixation to Soil Drying. *Crop Sci* **55**, 2270-2275 (2015).
- 30 Fairbanks, D. J. & Rytting, B. Mendelian controversies: A botanical and historical review. *Am J Bot* **88**, 737-752 (2001).
- 31 Abbo, S., Berger, J. & Turner, N. C. Evolution of cultivated chickpea: four bottlenecks limit diversity and constrain adaptation. *Funct Plant Biol* **30**, 1081-1087 (2003).
- 32 Gizlice, Z., Carter, T. E. & Burton, J. W. Genetic Base for North-American Public Soybean Cultivars Released between 1947 and 1988. *Crop Sci* **34**, 1143-1151 (1994).
- 33 Cowling, W. A. The challenge of breeding for increased grain production in an era of global climate change and genomics. *World Agriculture* **5**, 50-55 (2015).
- 34 Varshney, R. K. *et al.* Analytical and Decision Support Tools for Genomics-Assisted Breeding. *Trends in*

plant science, (2015).

- 35 Varshney, R. K. Exciting journey of 10 years from genomes to fields and markets: Some success stories of genomics-assisted breeding in chickpea, pigeonpea and groundnut. *Plant Sci* **242**, 98-107, doi:10.1016/j.plantsci.2015.09.009 (2016).
- 36 McCouch, S. *et al.* Feeding the future. *Nature* **499**, 23-24 (2013).
- 37 Yang, H. *et al.* Sequencing consolidates molecular markers with plant breeding practice. *Theor Appl Genet* **128**, 779-795 (2015).
- 38 Cowling, W. A. Sustainable plant breeding. *Plant Breed* **132**, 1-9 (2013).
- 39 Goddard, M. E. & Hayes, B. J. Mapping genes for complex traits in domestic animals and their use in breeding programmes. *Nat Rev Genet* **10**, 381-391 (2009).
- 40 Hayes, B. J., Visscher, P. M. & Goddard, M. E. Increased accuracy of artificial selection by using the realized relationship matrix. *Genet Res* **91**, 47-60 (2009).
- 41 Cowling, W. A. *et al.* Using the Animal Model to Accelerate Response to Selection in a Self-Pollinating Crop. *G3-Genes Genom Genet* **5**, 1419-1428 (2015).
- 42 Granier, C. & Vile, D. Phenotyping and beyond: modelling the relationships between traits. *Curr Opin Plant Biol* **18**, 96-102 (2014).
- 43 Fahlgren, N., Gehan, M. A. & Baxter, I. Lights, camera, action: high-throughput plant phenotyping is ready for a close-up. *Curr Opin Plant Biol* **24**, 93-99 (2015).
- 44 Ghanem, M. E., Marrou, H. & Sinclair, T. R. Physiological phenotyping of plants for crop improvement. *Trends in plant science* **20**, 139-144 (2015).
- 45 Steele, W. M., Allen, D. J. & Summerfield, R. J. in *Grain legume crops* (eds R. J. Summerfield & E. H. Roberts) 520-583 (Collins, 1985).
- 46 Beebe, S. E., Rao, I. M., Blair, M. W. & Acosta-Gallegos, J. A. Phenotyping common beans for adaptation to drought. *Front Physiol* **4**, doi:10.3389/Fphys.2013.00035 (2013).
- 47 Nepolo, E., Takundwa, M., Chimwamurombe, P. M., Cullis, C. A. & Kunert, K. A review of

- geographical distribution of marama bean [*Tylosema esculentum* (Burchell) Schreiber] and genetic diversity in the Namibian germplasm. *Afr J Biotechnol* **8**, 2088-2093 (2009).
- 48 Singh, J. & Basu, P. S. Non-Nutritive Bioactive Compounds in Pulses and Their Impact on Human Health: An Overview *Food and Nutrition Sciences* **3**, 1664-1672 (2012).
- 49 Singh, B. B., Ajeigbe, H. A., Tarawali, S. A., Fernandez-Rivera, S. & Abubakar, M. Improving the production and utilization of cowpea as food and fodder. *Field Crop Res* **84**, 169-177 (2003).
- 50 Lambot, C. in *Challenges and opportunities for enhancing sustainable cowpea production*. (eds C. A. Fatokun, S. A. Singh Tarawali, B. B., P. M. Kormawa, & M. Tamo) 367-375 International Institute of Tropical Agriculture, Ibadan, Nigeria, (2002).
- 51 Nadaraja, D., Weintraub, S. T., Hakala, K. W., Sherman, N. E. & Starcher, B. Isolation and partial sequence of a Kunitz-type elastase specific inhibitor from marama bean (*Tylosema esculentum*). *J Enzym Inhib Med Ch* **25**, 377-382 (2010).
- 52 Darmadi-Blackberry, I. *et al.* Legumes: the most important dietary predictor of survival in older people of different ethnicities. *Asia Pacific J. Clin. Nut* **13**, 217-220 (2004).
- 53 Chang, W. C. *et al.* A bean-free diet increases the risk of all-cause mortality among Taiwanese women: the role of the metabolic syndrome. *Pub Health Nut* **15**, 663-672, (2012).
- 54 Trichopoulou, A. *et al.* Diet and overall survival in elderly people. *BMJ* **311**, 1457-1460 (1995).
- 55 Hashemi, Z. *et al.* Cooking enhances beneficial effects of pea seed coat consumption on glucose tolerance, incretin, and pancreatic hormones in high-fat-diet-fed rats. *Appl Physiol Nutr Me* **40**, (2015).
- 56 Nothlings, U. *et al.* Intake of vegetables, legumes, and fruit, and risk for all-cause, cardiovascular, and cancer mortality in a European diabetic population. *J Nutr* **138**, 775-781 (2008).
- 57 Lee, Y. P. *et al.* Lupin-enriched bread increases satiety and reduces energy intake acutely. *Am J Clin Nutr* **84**, 975-980 (2006).
- 58 Hodgson, J. M. *et al.* Effects of increasing dietary protein and fibre intake with lupin on body weight and composition and blood lipids in overweight men and women. *Int J Obesity* **34**, 1086-1094 (2010).

- 59 Lee, Y. P. *et al.* Effects of lupin kernel flour-enriched bread on blood pressure: a controlled intervention study. *Am J Clin Nutr* **89**, 766-772 (2009).
- 60 Belski, R. *et al.* Effects of lupin-enriched foods on body composition and cardiovascular disease risk factors: a 12-month randomized controlled weight loss trial. *Int J Obesity* **35**, 810-819 (2011).
- 61 Dove, E. R. *et al.* Lupin and soya reduce glycaemia acutely in type 2 diabetes. *Brit J Nutr* **106**, 1045-1051 (2011).
- 62 Kouris-Blazos, A. B., R. Health benefits of legumes and pulses with a focus on Australian sweet lupins. *Asia Pacific Journal of Clinical Nutrition* (2016).
- 63 Sulieman, S. & Tran, L. S. P. Phosphorus homeostasis in legume nodules as an adaptive strategy to phosphorus deficiency. *Plant Sci* **239**, 36-43, (2015).
- 64 South, A. rworldmap: A new R package for mapping global data. . *R J.* **3/1**, 35-43 (2011).
- 65 Neuwirth, E. *RColorBrewer: ColorBrewer Palettes. R package version 1.1-2.*, <http://CRAN.R-project.org/package=RColorBrewer> (2014).
- 66 Lavin, M., Herendeen, P. S. & Wojciechowski, M. F. Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the tertiary. *Syst Biol* **54**, 575-594 (2005).
- 67 Gepts, P. *et al.* Legumes as a model plant family. Genomics for food and feed report of the cross-legume advances through genomics conference. *Plant Physiol* **137**, 1228-1235 (2005).
- 68 Katoh, K. & Standley, D. M. MAFFT Multiple sequence alignment software Version 7: Improvements in performance and usability. *Mol Biol Evol* **30**, 772-780 (2013).
- 69 Lemey, P., Rambaut, A., Drummond, A. J. & Suchard, M. A. Bayesian phylogeography finds its roots. *Plos Comput Biol* **5**, doi:10.1371/journal.pcbi.1000520 (2009).
- 70 Longnecker, N. *Passion for Pulses.* Australian National University Press, Crawley, (1999).
- 71 Heffer, P. & Prud'homme, M. *Fertilizer Outlook 2015-2019*, www.fertilizer.org (2015).
- 72 Administration, U. S. E. I. *Total Primary Energy Consumption*, www.eia.gov (2015).

- 73 Storkey, J. *et al.* Grassland biodiversity bounces back from long-term nitrogen addition. *Nature* **528**, 401-404 (2015).
- 74 Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R. & Polasky, S. Agricultural sustainability and intensive production practices. *Nature* **418**, 671-677 (2002).
- 75 Erisman, J. W., Sutton, M. A., Galloway, J., Klimont, Z. & Winiwarter, W. How a century of ammonia synthesis changed the world. *Nat Geosci* **1**, (2008).
- 76 Ladha, J. K. *et al.* Global nitrogen budgets in cereals: A 50-year assessment for maize, rice, and wheat production systems. *Sci Rep-Uk* **6** (2016).

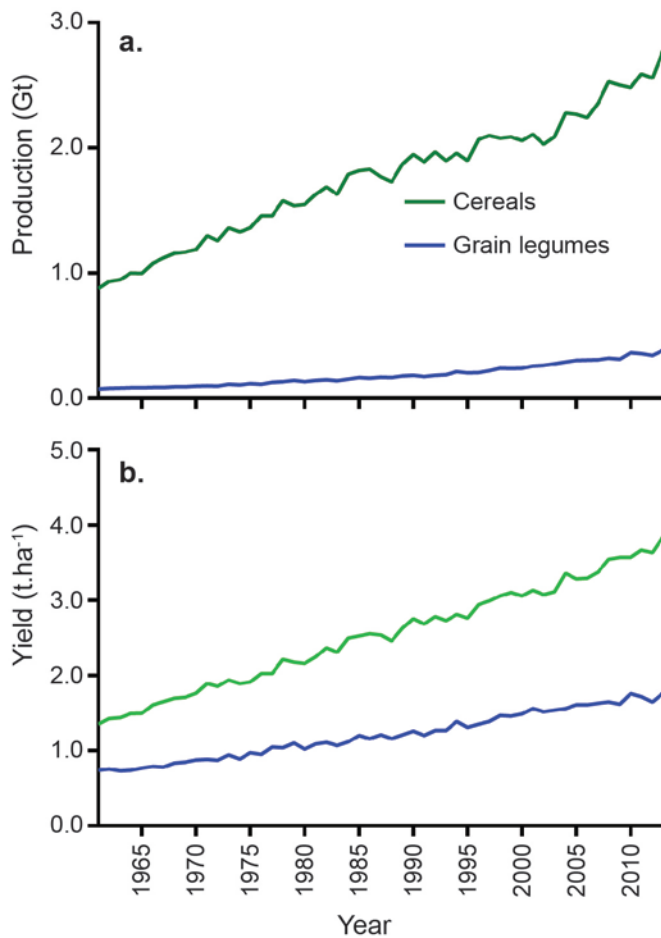


Figure 1. Increase in total world production (a) and yield (b) of dry grain legumes compared to cereals.

Cereals include wheat, rice, barley, maize, rye, oats and millet, and grain legumes includes 11 of the 12 major categories of grain legume in FAO data: bambara bean; broad bean and faba bean; chickpea; cowpea; groundnut; lentil; lupin; string beans and miscellaneous grain legumes; pea; *Phaseolus*spp.; pigeonpea. All production values are dry clean weights, excluding pod weights. Production of string beans were neither dried nor shelled so data were excluded. Data for groundnuts in shells were converted using 70% in FAO data. Miscellaneous grain legumes include *Dolichos*spp. (lablab or hyacinth bean), *Canavalia*spp. (jack or sword bean), *Psophocarpustetragonolobus* (winged bean), *Cyamopsistetragonoloba*(guar bean), *Stizolobium*spp. (velvet bean) and *Pachyrrhizuserosus* (yam bean). *Phaseolus* spp.includes *Phaseolus vulgaris* (kidney, haricot, common bean), *Phaseoluslunatus* (lima, butter bean), *Phaseolusangularis*(adzuki bean), *Phaseolus aureus* (mungo bean, golden, green gram), *Phaseolusmungo* (black gram, urd), *Phaseoluscoccineus* (scarlet runner bean), *Phaseoluscalcaratus* (rice bean), *Phaseolusaconitifolius* (moth bean) and *Phaseolusacutifolius*(tepary bean). Data source: FAO, <http://faostat3.fao.org/compare/E>, accessed 05/01/2016.

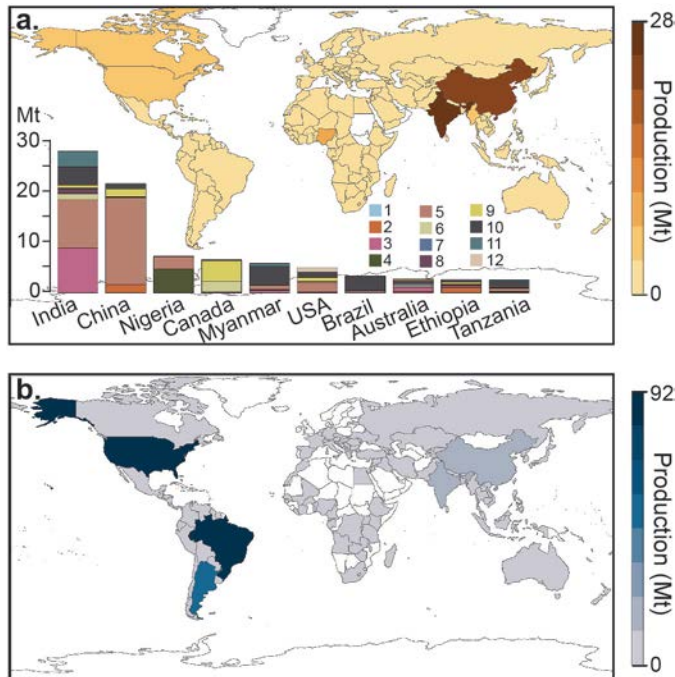


Figure 2: World grain legumes production in 2013.

a. 121 Mt of grain legumes (excluding soybean) were produced globally in 2013. Data comprises the grain legumes as cited in Fig 1 plus string bean. Production of the 12 categories are presented in the inset of Fig 2a as a stacked column graph by the ten net highest-producing countries: 1. bambara bean, 2. broad bean and faba bean, 3. chickpea, 4. cowpea, 5. groundnut, 6. lentil, 7. lupin, 8. miscellaneous grain legumes, 9. pea, 10. *Phaseolus*spp., 11. pigeonpea, 12. string bean. Of these, the top three grain legumes (excluding soybean) were groundnut (42.8 Mt), chickpea (13.3 Mt) and pea (11.5 Mt). *Phaseolus*spp. are a significant category of grain legumes by production (23.7 Mt).

b. Global soybean production. Global production was 278 million tons (Mt) in 2013, accounting for 70% of global grain legumes produced. The top five soybean producing countries were the USA (91.4 Mt), Brazil (81.7 Mt), Argentina (49.3 Mt), China (12.0 Mt) and India (11.9 Mt). Data source: FAO, www.faostat.fao.org, accessed 30/01/2016. The maps were generated using R ver. 3.1.3 (R Core Team 2015) with extension packages, rworldmap⁶⁴ and RColorBrewer⁶⁵. Countries indicated in white are where data are unavailable.

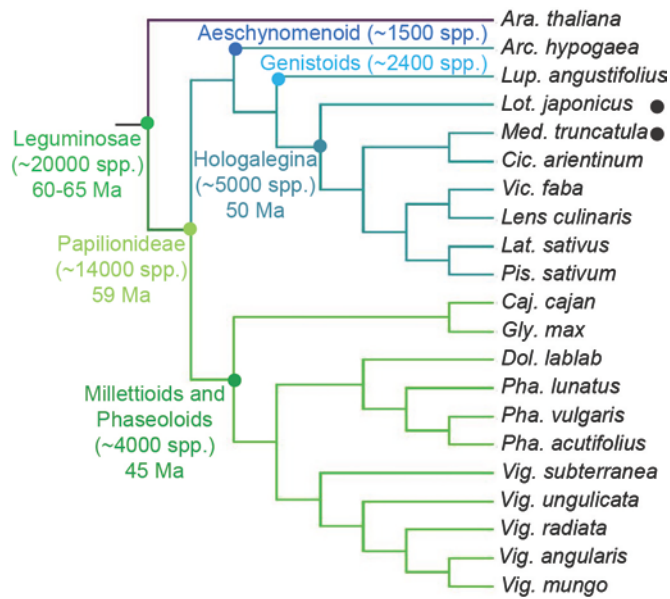


Figure 3: Taxonomic relationships within the Papilionideae family showing the two major clades of cultivated legume; the cool season Hologalegina (blue) and the warm season Phaseoloids (light green) using methodology (adapted from Lavin et al., 2005⁶⁶).

Clades are denoted by coloured circles and corresponding labels at nodal points. *Arabidopsis thaliana* has been included as an out-group from which the phylogeny was rooted. Genus abbreviations: *Ara.*, *Arabidopsis*; *Arc.*, *Archis*; *Lup.*, *Lupinus*; *Lot.*, *Lotus*; *Med.*, *Medicago*; *Cic.*, *Cicer*; *Vic.*, *Vicia*; *Lat.*, *Lathyrus*; *Pis.*, *Pisum*; *Caj.*, *Cajanus*; *Gly.*, *Glycine*; *Dol.*, *Dolichos*; *Pha.*, *Phaseolus*; *Vig.*, *Vigna*. ● denotes forage species, included due to their value as model legumes (i.e. not pulse crops). Ma denotes evolutionary age in millions of years, according to Gepts et al. (2005)⁶⁷. The tree was constructed in MAFFT⁶⁸ using maturase K protein sequence similarity. Tree visualization was performed in FigTree⁶⁹.

Genomics-assisted Crop Improvement

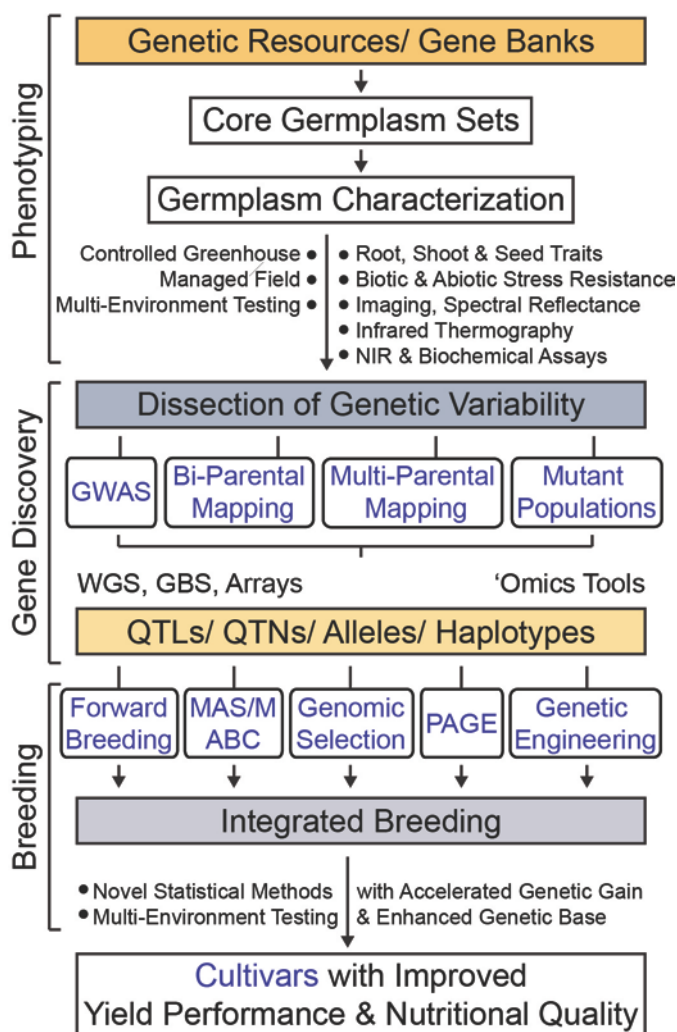


Figure 4: Major strategies and pipelines in genomics-assisted crop improvement for grain legumes. Large-scale germplasm stored in different genebanks can be characterised into smaller sets such as a core/mini-core germplasm set. Such small sets of germplasm can be characterised extensively for traits of interest. Subsequently, specialised genetic stocks such as a mini-core collection (diverse set), bi-parental and multi-parent mapping populations and mutant populations can be developed. Subjecting the populations to Whole Genome Sequencing (WGS)/Genotyping-By-Sequencing (GBS)/ -array-based genotyping together with phenotyping for traits of interest can provide Quantitative Trait Loci (QTLs), Quantitative Trait Nucleotides (QTNs), superior alleles and haplotypes. In the end, modern breeding approaches such as Marker Assisted Selection (MAS), Marker-Assisted Backcrossing (MABC) and Genomic Selection (GS) can be deployed for integrating/accumulating superior alleles. QTNs can be edited through genome editing approach called Promotion of Alleles through Genome Editing (PAGE). Candidate genes identified by using -omics approaches can be deployed in genetic engineering approach. By using one or more of the approaches mentioned above, cultivars with improved yield and nutritional quality can be developed.

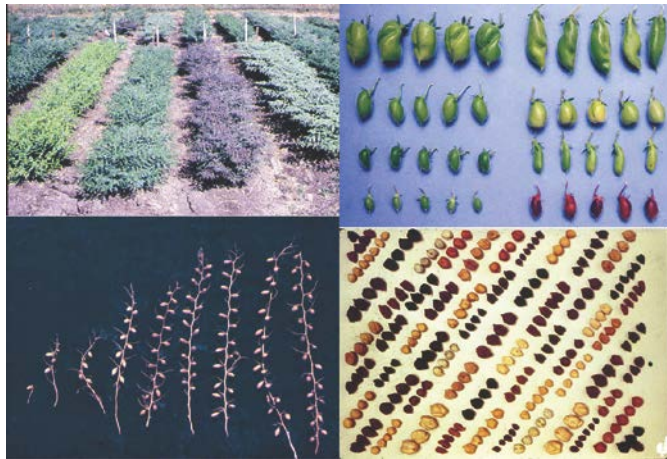


Figure 5. Phenotypic variability in chickpea germplasm conserved at ICRISAT, India.

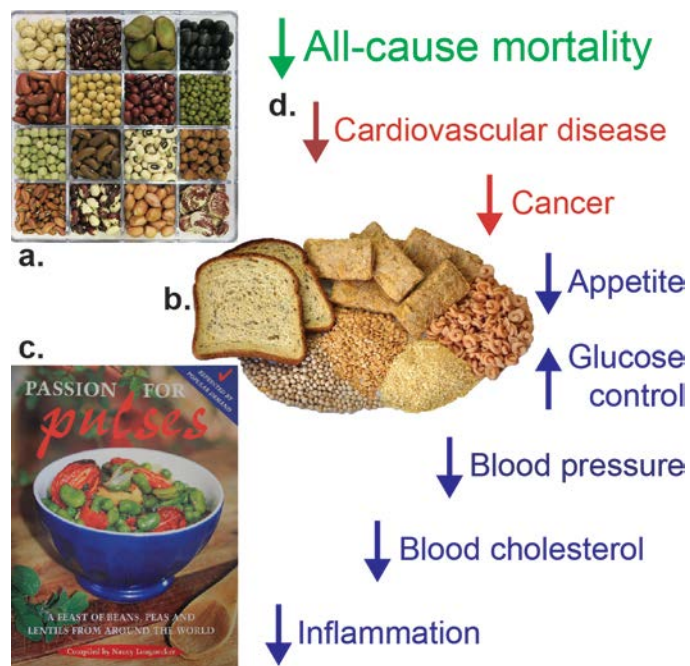
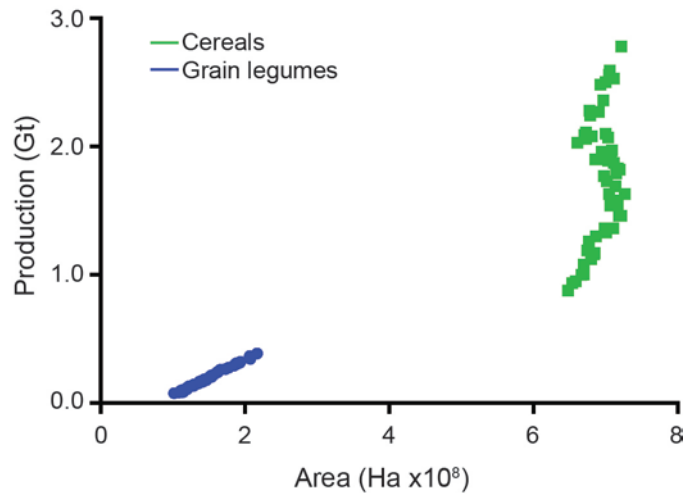


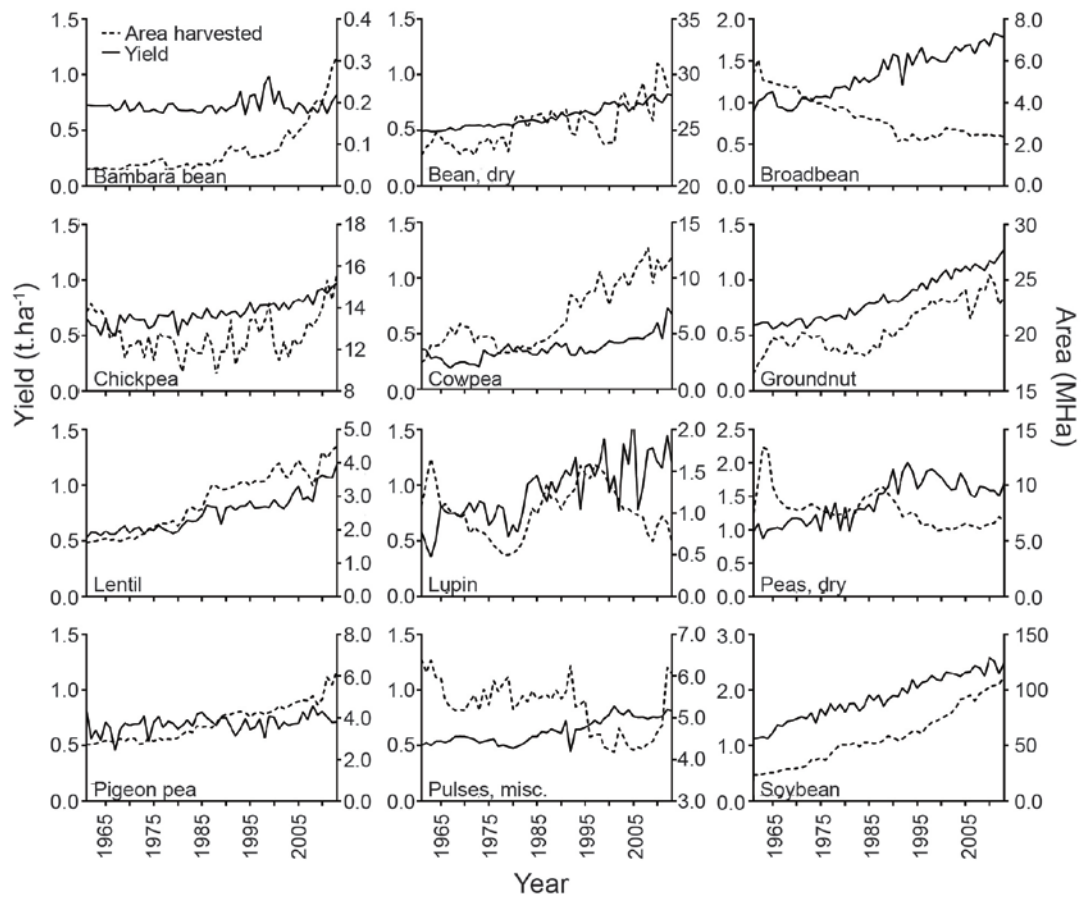
Figure 6: The human health benefits of food legumes.

- a. Common grain legumes in the human diet.
- b. Lupin as an example of processed staple foods.
- c. Passion for Pulses⁷⁰.
- d. Key benefits of dietary grain legumes on human health.



Supplementary Figure 1. Relationship between changes in production and world area harvested for different grain legumes over the past 50 years.

Increased production of grain legumes is associated with expansion of land area planted to the crops compared with cereals whose increased production is due to yield improvements while land area has remained the same. Data are for the legume and cereal species detailed in Fig. 1. Data source: FAO <http://faostat3.fao.org/compare/E>, accessed 05/01/2016.



Supplementary Figure 2. Relationship between changes in yield and world area harvested for different grain legumes over the past 50 years.

Most increases in yield are associated with expansion of land area planted to the crops. Data are for the legume and cereal species detailed in Fig. 1. Data source: <http://faostat3.fao.org/compare/E>, accessed 5/1/2016.