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Neglecting legumes has compromised human health and sustainable food production

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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 greatly under-utilized. 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 has compromised human health, nutritional security and sustainable food production.

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 contribute to only a small portion of staple food compared with cereals. 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. They could make a larger contribution to sustainable cropping systems through symbiotic nitrogen fixation, providing nitrogen to the legume crop as well as for subsequent crops[1].Consumption of grain legumes offers human health and nutritional benefits. A significant portion of the grain legume crop in Europe and 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). 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. Here we discuss the benefits of legume crops to farming systems, identifying key issues to enable increased production, together with the importance of legume seeds and products to human health.

Sustainable agriculture

The importance of legumes in sustainable cropping systems has been extensively documented[2]. 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 (Fig. 2). Moreover, while increases in cereal production during the past 50 years have been predominantly due to increases in yield, driven by changes in agronomic practices and new varieties, increases in grain legume production are mostly due to increases in the land area planted (Fig. 3). For soybean and the major grain legumes such as chickpea, groundnut and lentil, yield has increased proportionately with land area planted. 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 (Fig. 3), 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: Gw/Ns, mass grain dry yield/ mass nitrogen fertilizer applied), reduced occurrence of disease and, in some cases improved access to other essential elements such as phosphorus[3]. 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 wheat[4]. 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 fertilizer[5].

About 21 Mt nitrogen is fixed annually by the crop legume–rhizobia symbioses[6], returning 5-7 Mt of nitrogen to soils from *ca.* 190 million ha of grain legumes[7], saving US $8–12 billion (Box 1). Moreover, the protein content of cereal grains produced following a legume crop is increased and the soil structure and health are improved after growing legumes. Accordingly, nitrogen fixing legumes provide unparalleled opportunities for minimising future nitrogen fertiliser usage. The inclusion of grain legumes in cropping systems can enhance annual productivity[8] as well as increase diversity in cropping systems, thereby reducing the reliance on a cereal monoculture. 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 year[9] for example, through the build-up of autotoxins that influence soil microbe communities[10]. Taken together with the relatively low input cost compared to cereal crops, grain legume cultivation is a particularly promising means for resource poor farmers to increase their income[2,11]. For example, a formal survey of farmers in Bangladesh indicated awareness of the economic advantages of using integrated crop management practices for chickpea[11].

Mitigating climate change

Future legume production will be influenced by climate change factors such as 1) increased atmospheric CO_2 levels favouring carbon gain because legumes use C_3

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 quality[12]. Regional yield changes will depend on the local manifestation of climate change (for example interactions between high CO_2, temperature and drought) as well as other factors. The negative impacts of climate change have already affected soybean production[13]. Soybean yields in the USA between 1994 and 2013 declined by 2–4% for every degree rise in temperature over the growing season resulting in losses of US$11 billion[13]. Rising global temperatures could therefore reduce the areas suitable for bean production[14]. Future climate conditions are predicted to be more favourable to common bean cultivation in the Northern Hemisphere than the Southern Hemisphere[15]; 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 Finland[16]. 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 Ethiopia[17].

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 for chickpea 610 to 1150 kg/ha. Such data indicate that substantial productivity improvements might be gained through improved crop management practices[18,19].

Symbiotic nitrogen fixation

The symbiotic relationship between legumes and nitrogen-fixing bacteria, which are housed in root nodules, benefits both partners[20]. The bacterial enzyme nitrogenase, which catalyses the fixation process, requires a highly reducing environment. A stable low oxygen environment is achieved within the nodules by the presence of an oxygen diffusion barrier[21]. 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, in return for dicarboxylic acids. While the residual nitrogen present in most agricultural soils can have a negative impact on nodule formation and lifespan[22], 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 cascades[23]. 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 as cover crops and as green manures[24] a molecular understanding of the nitrogen sensing components that lead to repression of nodulation is essential. The families of membrane transporters that can double up as nitrogen sensors identified in non-legumes, also occur in legumes[25,26].

Of the 400,000 plant species in existence today, only Actinorhizal plants and legumes have evolved nitrogen-fixing nodules. However, at least part of the genetic platform that facilitates the legume-rhizobia interaction is conserved with other symbioses[27]. Little is known about the drivers for nodulation, particularly amongst diverse soil rhizobial populations. The management of rhizobial populations under hostile soil conditions remains a challenge, particularly in new or expanded cropping areas[28]. Our current understanding of the factors that determine nodule lifespan is superficial. Nodule senescence is a complex, programmed process that is controlled by developmental factors and environmental triggers. Activation of the senescence program by environmental stress can lead to premature loss of nitrogen-fixing activity, increased proteolysis and ultimately the death of the infected cells[29].

Global grain legume production in 2013 was 399 Mt, with soybean (278 Mt) contributing a significant portion to the agricultural exports of the Americas (Fig. 4). However, legume crop yields tend to vary more than cereal crops[30] largely due to environmental constraints such as drought[31,32], which limits symbiotic nitrogen fixation[33,34]. However, nitrogen fixation is extremely tolerant to soil drying in cowpea[35]. The incorporation of improved drought tolerance and nitrogen fixation traits into elite lines of grain legumes is anticipated to generate better yielding cultivars that can be grown on marginal land.

Technologies for legume Improvement

Gregor Mendel used a legume, the common garden pea, to demonstrate the 'particulate nature of inheritance' in 1865[36]. Nevertheless, many grain legume breeding programs suffer from low genetic diversity and low rates of genetic progress. For example, several bottlenecks during and after domestication in chickpea have limited genetic diversity in the crop gene pool[37]. For soybean, five introductions accounted for 55% of the pedigree in public soybean cultivars in the USA in the 1990s[38]. Innovative methods of crop breeding, based on the animal model[39], may conserve genetic diversity while accelerating grain legume genetic improvement, and help to bridge the genetic gap between grain legumes and their wild and landrace relatives (Fig. 5). When combined with genomics-assisted breeding[40], it should be possible to unlock valuable genes such as drought and heat stress tolerance in wild legumes, and move them efficiently into cultivated varieties[41]. Rapid introgression of important genes is a major challenge facing grain legume breeders. Grain legumes are a vital part of the response to the 2009 Declaration of the World Summit on Food Security, which requires a 70% increase in agricultural output 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 is widely recognized with much attention paid to rice and other cereal crops[42]. Large genetic and phenotypic variation exists in the world collections (Table 1, Fig. 6). It is therefore important to have a systematic inventory of legume 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 collections 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, with some restrictions. 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. Moreover, several accessions are duplicated across genetic resource centres. The format of the data should be standardized to facilitate easy access.

Whole genome sequencing is an affordable and powerful tool to delineate genomic information of core germplasm[43], and generate high resolution genetic maps for important agronomic traits, develop molecular markers for breeding and identify important genes for crop improvement[40]. 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. These resources will accelerate the development of genomics-assisted breeding strategies for legume crop improvement (Fig. 7).

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 programs[44]. 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 inbreeding[45]. Selection for complex traits was shown to be more efficient when based on genomic relationship information in animals[46]. For grain legumes, many of which are self-pollinating crops, genomic selection offers the prospect of accelerating genetic progress for yield[47]. Advanced phenotyping technologies are available to measure morphological and physiological traits[48]. High-throughput image-based phenotyping platforms will make significant impact in plant phenomics[49]. Accurate physiological phenotyping of specific and well defined traits will also contribute to improved breeding outcomes[50].

Bringing in orphans

Orphan crops 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 tropics[51]. 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 south-western 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 conductance[52]. The oil-rich marama bean, a perennial legume of Southern Africa growing in the Kalahari Desert, can be more nutritious than soybean[53]. 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.

Nutrition and health

Legumes are a crucial source of a variety of phytochemicals that are important for human health. These include protein, low glycaemic index carbohydrate, fibre, minerals, vitamins carotenoids and polyphenols[54]. Consequently, legumes hold a near-unique position among foodstuffs because of their health determinant properties[55]. Studies in China revealed that all-cause mortality was increased in individuals on a legume-free diet[56]. Moreover, the mortality hazard ratio declined by 8% in older people globally for every 20 g increase in daily grain legume intake[55]. 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 mortality[57].

Legumes also contribute to reduced risk of mortality via benefits on major chronic diseases and their risk factors. These include cardiovascular disease, diabetes, cancer, obesity and gut health[58]. Observational studies have shown that legumes can reduce cardiovascular disease risk, and intervention studies suggest that this is mediated via improvements in blood pressure, lipid profile, inflammation, blood sugar metabolism and body weight[54,59]. Legumes also offer a food-based solution to decreasing risk of pre-diabetes[60] and diabetes management as well as diabetes-associated complications, especially cardiovascular disease[61]. A meta-analysis of 11 studies showed that daily consumption of legumes for more than 4 weeks resulted in a significant reduction in fasting blood glucose and insulin[62]. The effects are more pronounced when legumes are consumed as part of a low glycaemic index diet. 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. A number of meta-analyses of observational studies have associated eating legumes with lower risk of several cancers including bowel cancer[54]. There is growing evidence that the human microbiome plays an important role in health outcomes including cardiovascular disease, obesity and colorectal cancer. Increasing evidence suggests that legumes can act as prebiotics that potentially alter bowel flora affecting production of gut hormones and consequently appetite[54].

Human studies using lupin-enriched foods provide insights into possible mechanisms by which legumes contribute to cardio-metabolic health. Flour made from lupin seeds contains about 45% protein and 30% fibre. Lupin-enriched foods, such as bread, pasta and biscuits, are palatable and acceptable to consumers. In clinical trials, lupin flour-enriched bread reduced appetite and energy intake, suppressed plasma ghrelin, an orexigenic hormone that stimulates appetite, and reduced post-meal glucose and insulin responses[63]. Thus, bread with lupin-kernel flour has the potential to influence appetite, reduce energy intake and improve glucose control. Regular consumption of lupin-enriched bread by overweight men and women did not alter body weight or body composition, but did reduce blood pressure and improve measures of insulin resistance[64,65].

The positive findings on insulin resistance in normoglycaemic overweight individuals suggest that lupin foods could benefit people 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 glucose (control), or glucose plus lupin flour, or glucose plus fibre and protein from soya isolates[66]. 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 on lupin-enriched foods provide evidence that legumes have cardiovascular benefits, particularly in patients with diabetes who are at a significantly increased risk of cardiovascular disease. The legume intake needed for health benefits is not clear, but observational and intervention studies indicate that intakes averaging 15 to 30 g/day are likely to be beneficial[54].

Grain legumes such as cowpea have potential uses in the cosmetic, food, textile and pharmaceutical sectors because of their therapeutic properties[67]. 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 elements[68]. Cowpea proteins have high lysine contents and are potentially an excellent supplement for cereal-based diets[69]. The marama bean serine protease inhibitor that prevents elastase activity provides a safe and natural tryptase 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 diseases[70].

Conclusions and perspectives

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. Recent increasing nitrogen fertilizer costs have focused attention on improving efficiency in cropping systems and also created a notional “legume-envy”, culture. However, while attempts to create nitrogen-fixing cereals are underway, grain legumes currently receive less research and development attention. Addition of legumes to existing cropping systems also increases the diversity of such systems. The legume/rhizobia symbiosis 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 soils[71]

Grain 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 often exist for cereals, particularly in developing countries, as well as inputs have been insufficient into grain legume breeding and agronomic technologies required to improve yields. Our current overreliance on a handful of major staple cereal crops has inherent agronomic, ecological, nutritional and economic risks and restricts the contributions made by under-utilized future crops such as grain legumes. The static or declining production trends especially in developing countries, despite increasing global demand, threatens current and future food security. The UN FAO 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. Legume crops will however only achieve a competitive advantage if their profitability to the farmer exceeds that of the dominant cereals. To hasten the adoption of grain legume production technology by resource-poor farmers in developing countries, on-farm, farmer-participatory adaptive research and developmental approaches are required, to a much greater extent than currently being implemented. The potential socio-economic gains through a boost in grain legume production and consumption are enormous. Hence, the increased public perception of the health and well-being advantages of a grain legume-rich diet may be an important driver of culture change with regard to the key role that grain legumes play in food security.

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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-ML 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 Figs and Table 1. KHMS co-created the network, discussed the idea, contributed to various sections, Figs 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 Figs. WAC wrote parts of the text, contributed citations and edited Table 1 and Figs. HB discussed the content, prepared Fig. 1 and Supplementary Figs, 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. AJM 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 Fig. MC co-created the network, prepared Box 1, discussed the idea and edited the Figs 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 (including soybean) in FAO data: bambara bean; broad bean and faba bean; chickpea; cowpea; groundnut; lentil; lupin; string beans and miscellaneous grain legumes; pea; *Phaseolus* spp.; pigeon pea. 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 *Pachyrrhizus 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 aconitifolius* (moth bean) and *Phaseolus acutifolius* (tepary bean). Data source: FAO, http://faostat3.fao.org/compare/E, accessed 05/01/2016.

Figure 2. 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.

Figure 3. 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 05/01/2016.

Figure 4. 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[72] and RColorBrewer[73]. Countries indicated in white are where data are unavailable.

Figure 5. 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)[74]. 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)[75]. The tree was constructed in MAFFT[76] using maturase K protein sequence similarity. Tree visualization was performed in FigTree[77].

Figure 6. **Phenotypic variability in chickpea germplasm conserved at ICRISAT, India**. **a.** Variation in canopy development and leaf colour in chickpea germplasm in the field. **b.** Variation in pod size and pod colour. **c.** Variation in pod development and pod numbers on chickpea branches. **d.** Variation in seed size and colour in chickpea germplasm collection. (Photo credit, Hari Upadhyaya).

Figure 7. 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.

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	*Vigna angularis*	9978	B (54%), N (24%), H (16%)	528	11	2	ib	V
Bambara beans	*Vigna subterranea*	2183	I (94%)	864	11	2	ib	Not available
Black gram	*Vigna mungo*	1668	N (51%), P (18%), K (13%)	528	11	2	ib	Not available
Mung bean	*Vigna radiata*	23658	B (28%), N (28%), G (18%), P (17%)	509	11	2	ib	S, V
Cowpea	*Vigna unguiculata*	42301	I (38%), P (20%)	576	11	2	ib	Q
Broad bean Faba bean	*Vicia faba*	30073	M (33%), B (16%), A (12%)	12797	6	2	ob	Not available
Chickpea	*Cicer arietinum*	76221	F (27%), G (19%), M (19 %), P (10%)	912	8	2	ib	S, T
Common bean	*Phaseolus vulgaris*	102732	C (30%), P (13%)	576	11	2	ib	S, Y
Tepary bean	*Phaseolus acutifolius*	1257	P (39%), C (26%), D (11%)	720	11	2	ib	Not available
Lima bean	*Phaseolus lunatus*	6420	C (47%), P (35%)	672	11	2	ib-ob	Not available
Grass pea	*Lathyrus sativus*	6728	M (38%), K (12%), O (12%)	8064	7	2	ib-ob	Not available
Hyacinth bean Lablab bean	*Dolichos lablab* *Lablab purpureus*	1292	N (33%), D (29%), P (13%), C (12%)	365	11	2	ib	Not available
Lentil	*Lens culinaris*	29430	M (42%), A (16%), P (11%)	4032	7	2	ib	R
Narrow-leafed lupin	*Lupinus angustifolius*	2956	K (28%), L (21%), E (10%), J (10%), P (10%)	893	20	2	ib	X
White lupin	*Lupinus albus*	4155	L (18%), K (12%), P (11%)	576	25	2	ib	Not available
Pea	*Pisum sativum*	54062	P (13%), A (11%), M (11%)	4685	7	2	ib	Not available

Peanut (groundnut)	*Arachis hypogaea*	47650	F (31%), G (29%), P (20%), B (17%)	2755	10	4	ib	U
Pigeonpea	*Cajanus cajan*	25514	F (52%), G (44%)	845	11	2	ib-ob	S
Soybean	*Glycine max*	93706	B (31%), P (23%), N (15%)	1085	20	2	ib	W, Y

Footnotes:

[a] Total number of accessions is the sum of data from GENESYS-PGR, China, India (NBPGR), Japanand Australia. Data accessed 21 April 2016 through:

(i) GENESYS Global Portal on Plant Genetic Resources, http://www.genesys-pgr.org
(ii) http://www.most.gov.cn/ztzl/kjzykfgx/kjzygjjctjpt/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)

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.

[b] % 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 *Vicia* accessions included both broad bean and vetch.

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.	http://centrodeinvestigacionlaorden.es
		Centro de Investigación Agraria Finca La Orden – Valdesequera	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

c	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/]
d	"Breeding system" is defined following Simmonds, N.W. and J. Smartt. 1999. Principles of Crop Improvement. 2nd Ed. Blackwell Science, Oxford. ib inbred, usually selfed, tolerant of inbreeding ob outbred, suffers inbreeding depression ib-ob-out-bred, usually nearer ib than ob Additional reference: Singh R.J. et al. (2007) Landmark research in legumes. Genome 50:525-537
e	Major websites for *de novo* genome information (in alphabetical order): 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/bioproject/PRJNA179231 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 growth[79]. 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*. 5.0×10^{16} GJ[78,80].
- 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 1980s[81].
    - Eutrophication also increases production of bacterial nitrous oxide (N_2O), which is one of the most toxic greenhouse gases[82].
    - Production of N_2O and other reactive nitrogen by-products of fossil fuel combustion, including from ammonia synthesis. The average lifetime N_2O in the atmosphere is >100 years[82,84]. The global atmospheric N_2O concentration is now 18% higher than in pre-industrial times, and it is estimated that >30% of all atmospheric N_2O results from agriculture.
- The nitrogen-use efficiency of cereals decreased from *ca*. 80% to *ca*. 30% between 1961-2000[82,83]. More than 50% applied nitrogen fertilizer was lost from cereal crops between 1961-2010[5,85], and in some cases >80% of applied nitrogen is lost through runoff.

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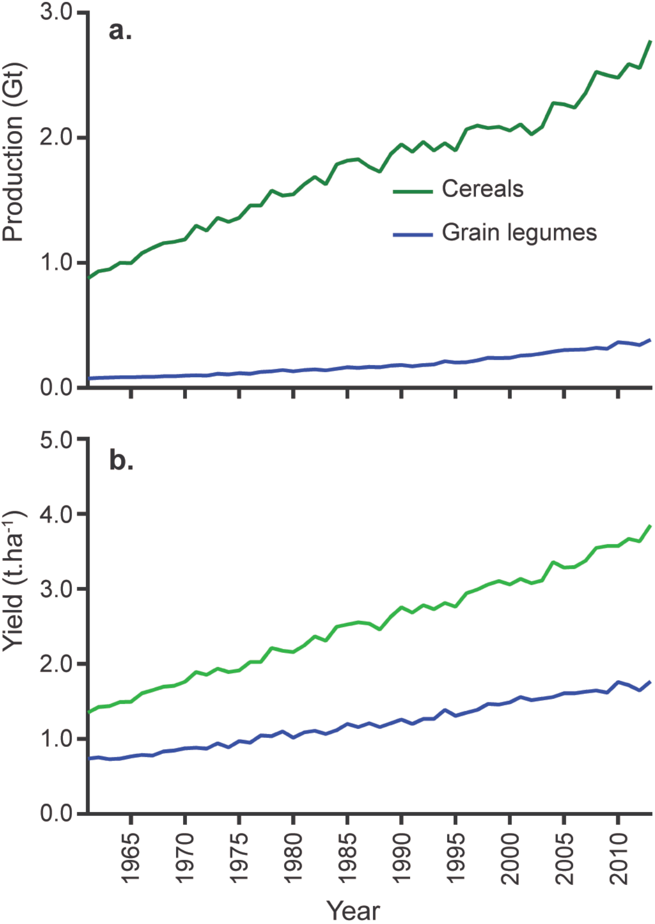
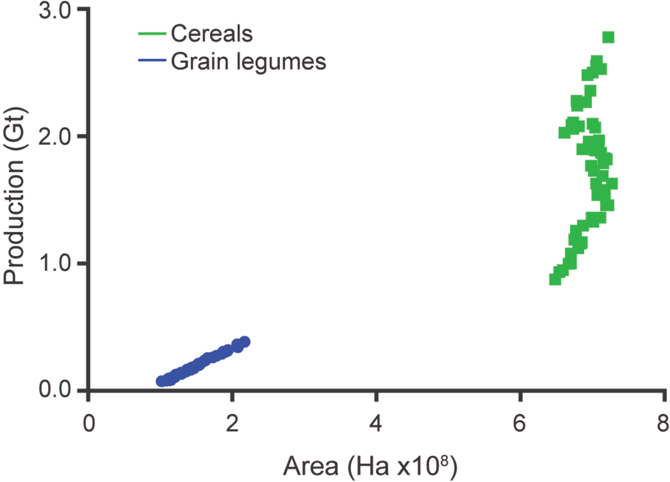
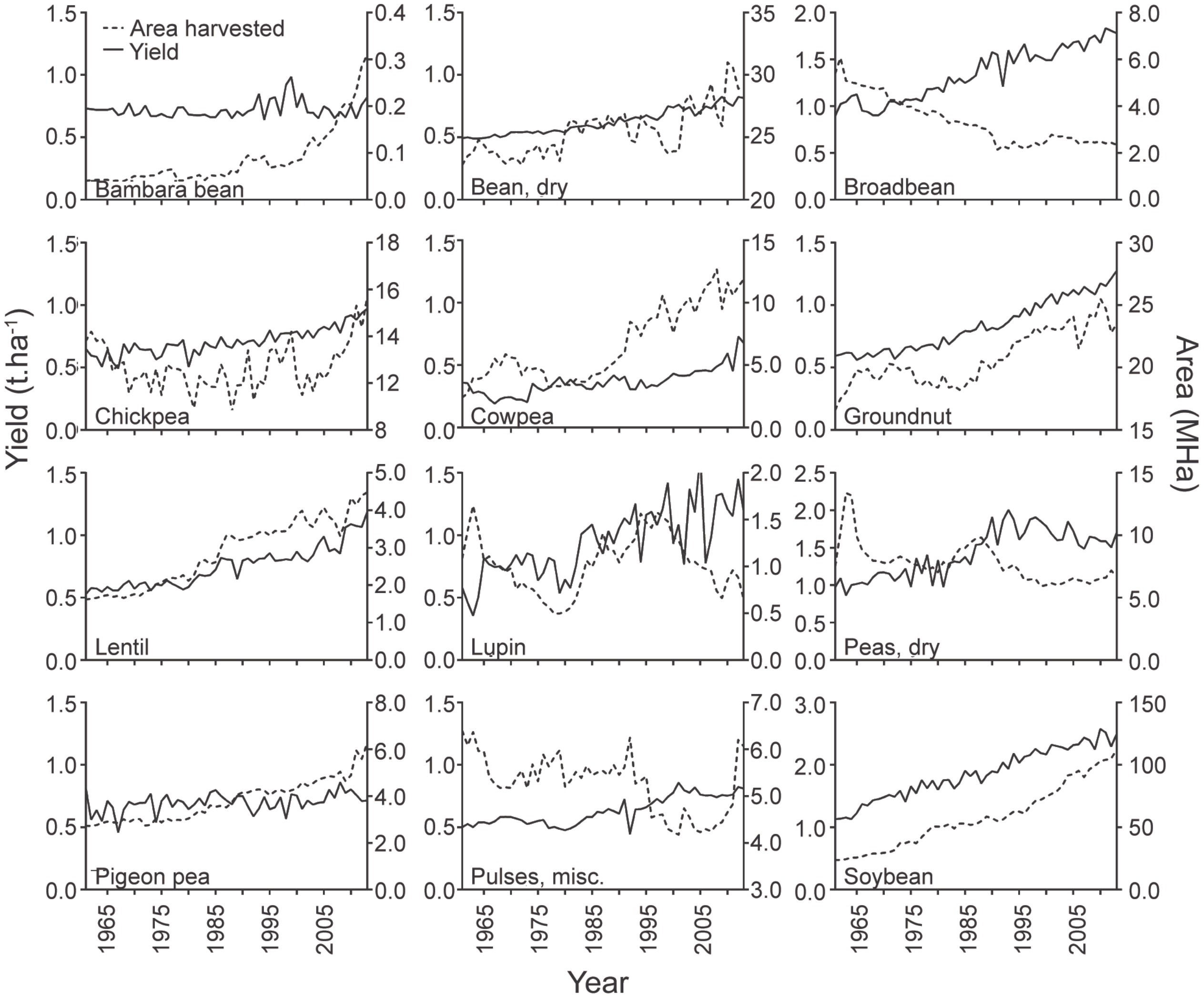
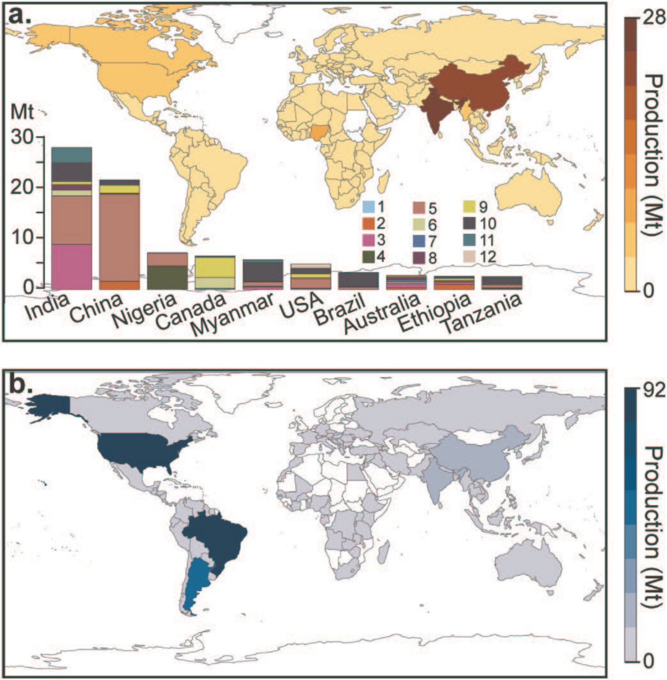


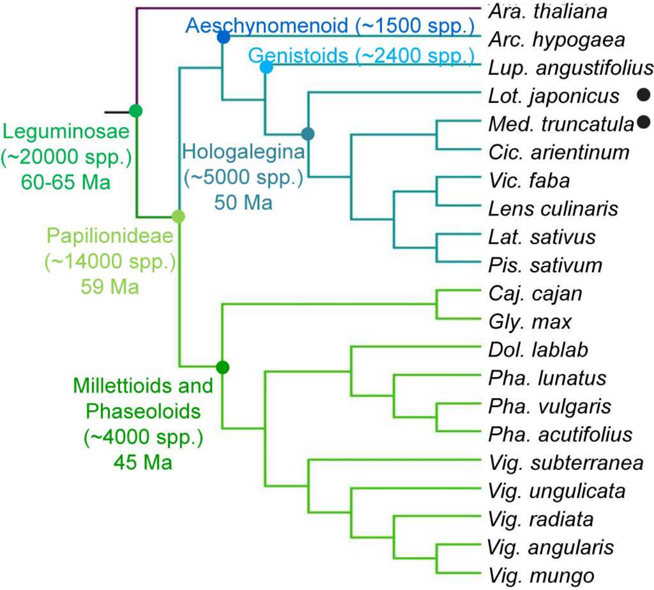
a.
Production (Gt)
3.0
2.0
1.0
0.0
Cereals
Grain legumes
b.
Yield (t.ha^{-1})
5.0
4.0
3.0
2.0
1.0
0.0
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year

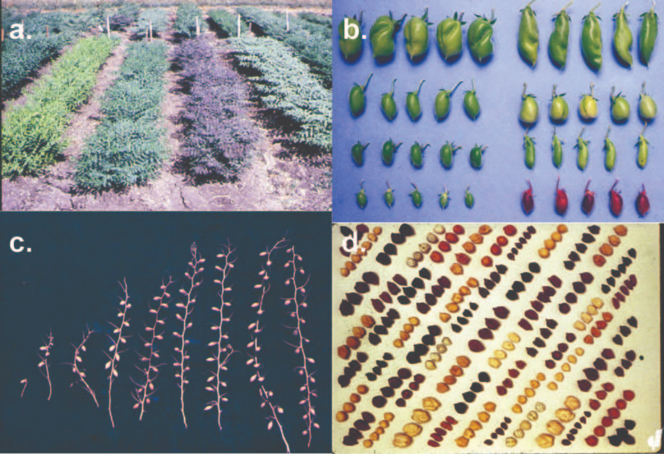

Cereals
Grain legumes
Production (Gt)
3.0
2.0
1.0
0.0
0
2
4
6
8
Area (Ha x10^8)

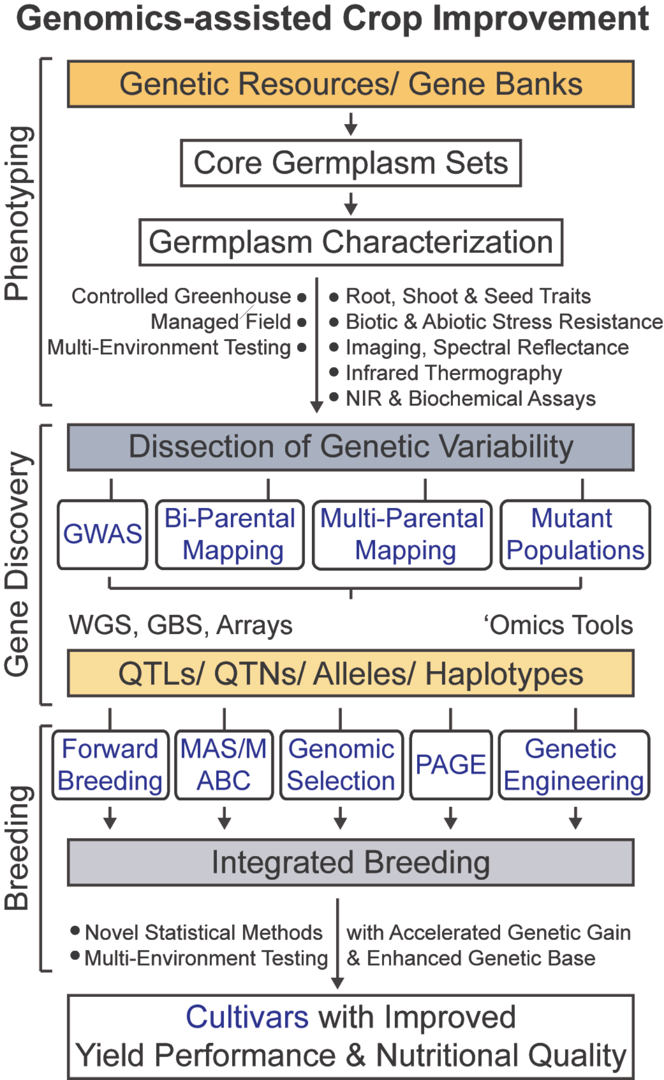


Area harvested
Yield
Bambara bean
Bean, dry
Broadbean
Chickpea
Cowpea
Groundnut
Lentil
Lupin
Peas, dry
Pigeon pea
Pulses, misc.
Soybean
Yield (t.ha^{-1})
Area (MHa)
Year
1965
1975
1985
1995
2005
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0.1
0.2
0.3
0.4
20
25
30
35
4.0
6.0
8.0
8
10
12
14
16
18
5.0
15
3.0
1.0
50
100
150


a.
Mt
30
20
10
0
India
China
Nigeria
Canada
Myanmar
USA
Brazil
Australia
Ethiopia
Tanzania
1
2
3
4
5
6
7
8
9
10
11
12
28
Production (Mt)
0
b.
92
Production (Mt)
0


Ara. thaliana
Aeschynomenoid (~1500 spp.)
Arc. hypogaea
Genistoids (~2400 spp.)
Lup. angustifolius
Lot. japonicus ●
Med. truncatula ●
Cic. arientinum
Vic. faba
Lens culinaris
Lat. sativus
Pis. sativum
Caj. cajan
Gly. max
Dol. lablab
Pha. lunatus
Pha. vulgaris
Pha. acutifolius
Vig. subterranea
Vig. ungulicata
Vig. radiata
Vig. angularis
Vig. mungo
Leguminosae (~20000 spp.) 60-65 Ma
Hologalegina (~5000 spp.) 50 Ma
Papilionideae (~14000 spp.) 59 Ma
Millettioids and Phaseoloids (~4000 spp.) 45 Ma


a.
b.
c.
d.


Genomics-assisted Crop Improvement
Phenotyping
Genetic Resources/ Gene Banks
Core Germplasm Sets
Germplasm Characterization
Controlled Greenhouse •
Managed Field •
Multi-Environment Testing •
• Root, Shoot & Seed Traits
• Biotic & Abiotic Stress Resistance
• Imaging, Spectral Reflectance
• Infrared Thermography
• NIR & Biochemical Assays
Gene Discovery
Dissection of Genetic Variability
GWAS
Bi-Parental Mapping
Multi-Parental Mapping
Mutant Populations
WGS, GBS, Arrays
'Omics Tools
QTLs/ QTNs/ Alleles/ Haplotypes
Breeding
Forward Breeding
MAS/MABC
Genomic Selection
PAGE
Genetic Engineering
Integrated Breeding
• Novel Statistical Methods
• Multi-Environment Testing
with Accelerated Genetic Gain
& Enhanced Genetic Base
Cultivars with Improved
Yield Performance & Nutritional Quality