

Neglecting legumes has compromised human health and sustainable food production

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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-used. 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.

Unlike other plants, legumes have mastered the art of symbiotic nitrogen fixation, leading to significant advantages for agricultural sustainability, both in developed and developing countries. Recent increases in grain legume yields are only between 0 and 2% per year (Fig. 1), and they contribute to just a small portion of staple food compared with cereals. The acreage and yield of corn is currently much higher than that of any of the grain legumes. A shift in land use towards grain legumes and away from livestock would substantially lower the carbon footprint for the production of protein 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 crops¹. 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 (for example, lupins) is currently used for animal feed, and

more than half of grain legume production worldwide is processed (for example, 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 that need to be addressed 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 documented². The past 50 years has seen a gradual increase in the area planted with grain legumes, but the area planted with cereals still outnumbers this fourfold (Fig. 1). Additionally, the increase in cereal production over the last half-century has predominantly been due to yield increase, brought about by changes in new varieties and agronomic practices. On the other hand, grain

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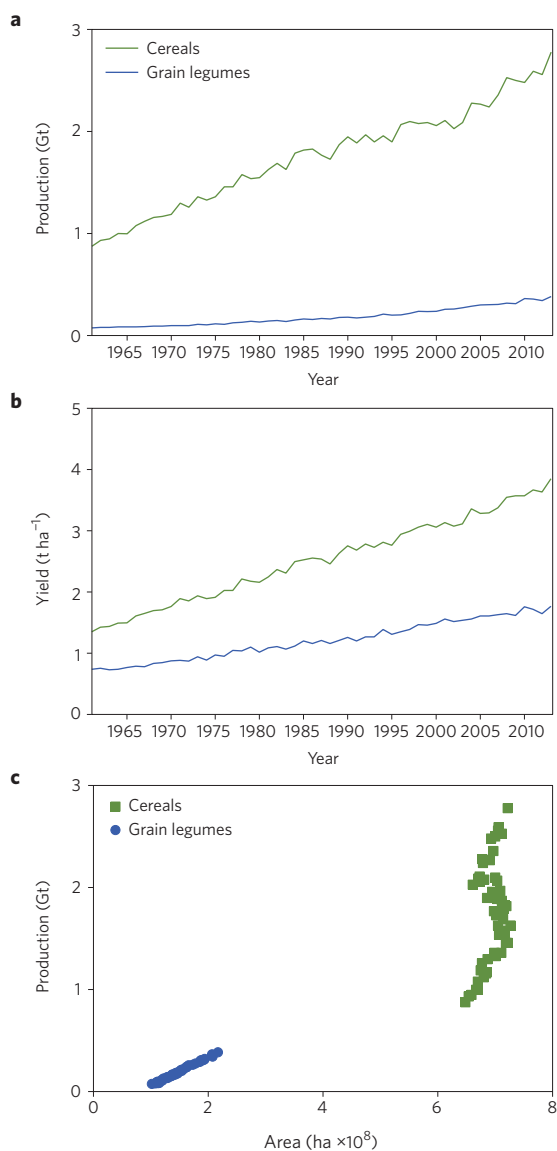


Figure 1 | World production of cereal and grain legumes over the past 50 years. **a,b**, Total world production (**a**) and yield (**b**) of dry grain legumes lags behind that of cereals. **c**, Increased production of grain legumes is associated with expansion of land area planted with the crops, compared with cereals whose increased production is due to yield improvements while land area has remained the same. Data from ref. 79. 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; miscellaneous grain legumes; pea; *Phaseolus* spp.; pigeon pea; and soybean. 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 assuming 70% of dry weight data in FAO was due to the grains. 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 aconitifolius* (moth bean) and *Phaseolus acutifolius* (teparty bean).

legume production increases have mostly been due to increases in the land area planted (Fig. 2). 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. By contrast, yields of faba bean and peas are increasing while the area harvested is decreasing (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, calculated by dividing mass grain dry yield by mass nitrogen fertilizer applied: G_w/N_s), reduced occurrence of disease and, in some cases, improved access to other essential elements such as phosphorus³. The nitrogen-fixing ability of legumes affords complementarity through natural soil fertilization. Grain legumes favour reduced greenhouse gas emissions in agricultural cropping systems — for example, emissions declined by 56% on a per-hectare basis when a lupin crop preceded wheat⁴. 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 fertilizer⁵.

About 21 Mt nitrogen is fixed annually by the crop legume–rhizobia symbioses⁶, returning 5–7 Mt of nitrogen to soils from about 190 million ha of grain legumes⁷, 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 minimizing future nitrogen fertilizer usage. The inclusion of grain legumes in cropping systems can enhance annual productivity⁸ 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 to the soil. However, the sustainable development of intensive agriculture is limited when grain legumes are intensively cultivated on the same farmland year after year⁹, for example through the build-up of autotoxins that influence soil microbe communities¹⁰. The cultivation of grain legumes is a very promising way for resource-poor farmers to increase income, especially when the comparatively low input cost compared to cereals is considered^{2,11}. For example, a formal survey of farmers in Bangladesh indicated awareness of the economic advantages of using integrated crop management practices for chickpea¹¹.

Mitigating climate change

Future legume production will be influenced by climate change factors, such as: (1) increased atmospheric CO₂ levels favouring carbon gain because 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 quality¹². Regional yield changes will depend on the local manifestation of climate change (for example, interactions between high CO₂, temperature and drought) as well as other factors. Indeed, the negative impacts of climate change have already affected soybean production: 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 billion¹³. Rising global temperatures could

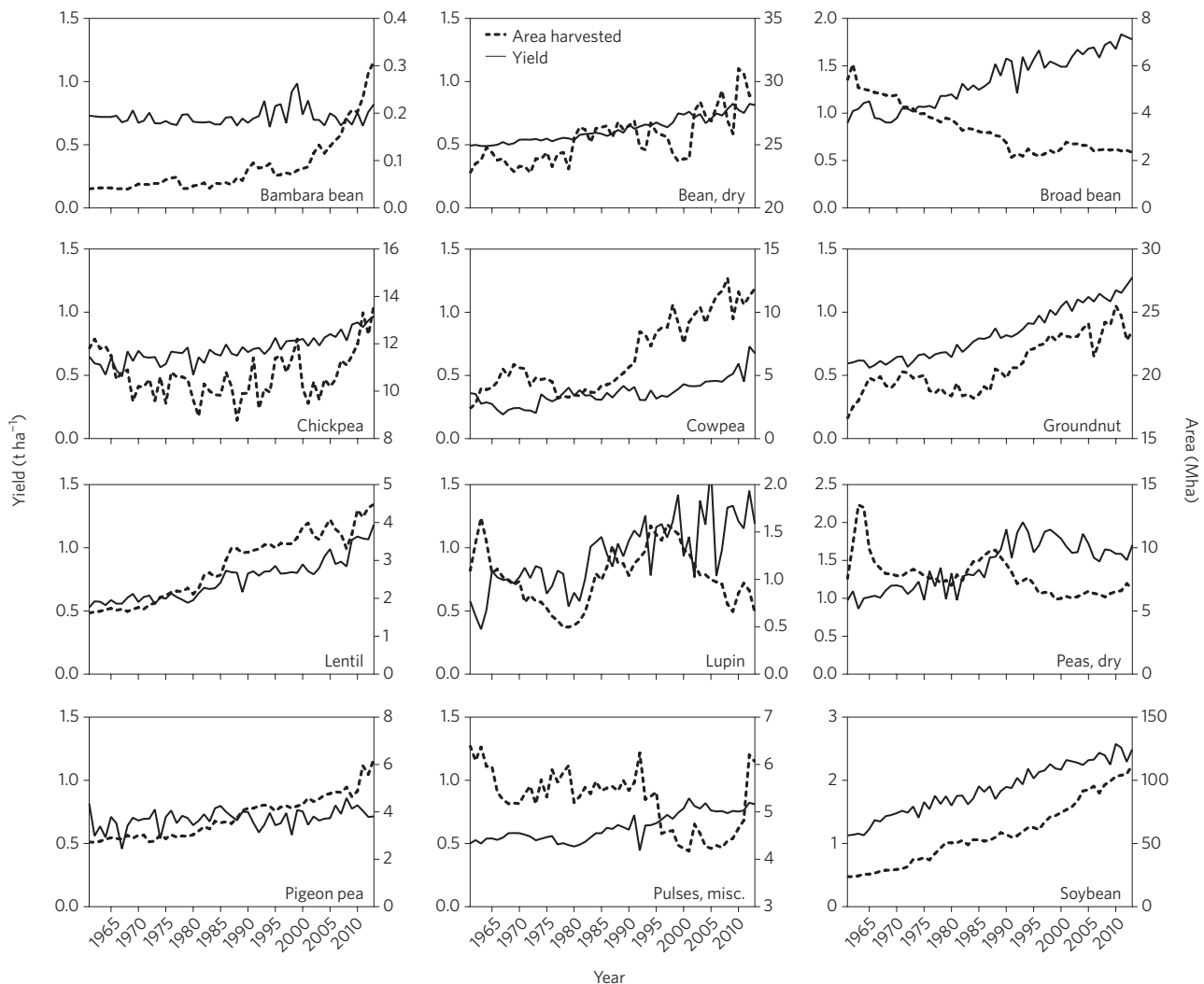


Figure 2 | The relationship between changes in yield and world area harvested for different grain legumes over the past 50 years. Most increases in yield are associated with expansion of land area planted with the crops. Data are for the legume species detailed in Fig. 1. Data from ref. 79.

therefore reduce the areas suitable for bean production¹⁴. Future climate conditions are predicted to be more favourable to common bean cultivation in the Northern Hemisphere than the Southern Hemisphere¹⁵; new grain legume growing areas should open up in Canada, northern Europe and Russia. Already, pea and faba bean are becoming increasingly important crops in Finland¹⁶. 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 Ethiopia¹⁷.

The yield gap for legume crops in Africa is more than 300%, with 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 1,320 kg ha⁻¹, for groundnut 1,180 to 2,010 kg ha⁻¹, for pigeon pea 550 to 770 kg ha⁻¹ and for chickpea 610 to 1,150 kg ha⁻¹. Such data indicate that substantial productivity improvements might be gained through improved crop management practices^{18,19}.

Symbiotic nitrogen fixation

The symbiotic relationship between nitrogen-fixing bacteria (which are housed in root nodules) and legumes benefits both partners²⁰. 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 barrier²¹. 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 lifespan¹, 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 cascades²². Consequently, one of the challenges facing scientists seeking to expand legume productivity is to maximize symbiotic nitrogen fixation while allowing nitrogen acquisition from the soil. To maximize beneficial nitrogen inputs from legumes as cover crops and as green manures²³, a molecular understanding of the nitrogen-sensing components that lead to repression of nodulation is essential. The families of membrane transporters that can double as nitrogen sensors identified in non-legumes also occur in legumes^{24,25}.

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 symbioses²⁶. Little is

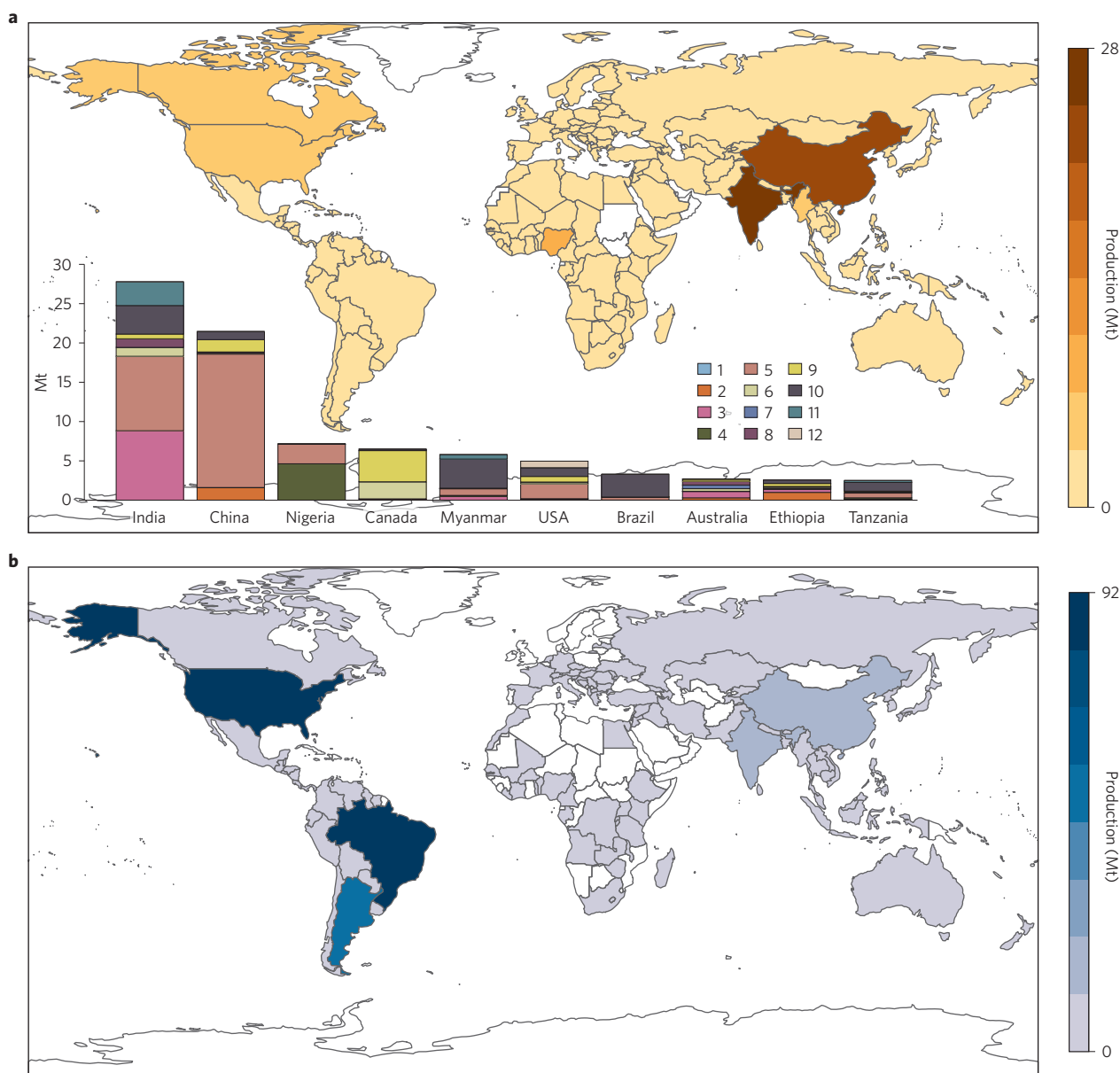


Figure 3 | World grain legume production in 2013. a, 121 million tonnes (Mt) of grain legumes (excluding soybean) were produced globally in 2013. Data comprises the grain legumes as cited in Fig. 1 plus string bean. Production of the 12 categories are presented as a stacked column graph by the ten net highest-producing countries (inset). 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; and 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. is a significant category of grain legumes by production (23.7 Mt). **b**, Global soybean production was 278 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 from FAO (www.fao.org, accessed 30/01/2016). The maps were generated using R ver. 3.1.3 (R Core Team 2015) with extension packages, rworldmap⁸⁰ and RColorBrewer⁸¹. Countries indicated in white are where data are unavailable.

known about the drivers for nodulation, particularly among diverse soil rhizobial populations. The management of rhizobial populations under hostile soil conditions remains a challenge, particularly in new or expanded cropping areas²⁷. Our current understanding of the factors that determine nodule lifespan is superficial. Nodule senescence is a programmed, complex 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 cells²⁸.

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. 3). However, legume crop yields tend to vary more than cereal crops²⁹, largely due to environmental constraints such as drought^{30,31}, which limits symbiotic nitrogen fixation^{32,33}. However, nitrogen fixation is extremely tolerant to soil drying in cowpea³⁴. 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.

Box 1 | The growing 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 growth⁸⁶. Global ammonia capacity is projected to grow by 16% between 2014 and 2019, with total industrial nitrogen demand set to grow by 28% over this time, compared with a 6% increase across the fertilizer sector⁸⁷.

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 approximately 5.0x10¹⁶ GJ)^{87,88}.

The environmental impact of nitrogen fertilizers is manifold, including:

- Loss of biodiversity through eutrophication. Recent studies show biodiversity recovering with more environmentally stringent practices since the 1980s⁸⁹. Eutrophication also increases production of bacterial nitrous oxide (N₂O), which is one of the most toxic greenhouse gases⁹⁰.
- 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 years⁹⁰. 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 around 80% to around 30% between 1961 and 2000^{86,91}. More than 50% applied nitrogen fertilizer was lost from cereal crops between 1961–2010^{5,92}, and in some cases >80% of applied nitrogen is lost through runoff⁹⁰.

Technologies for legume improvement

Gregor Mendel used a legume, the common garden pea, to demonstrate the ‘particulate nature of inheritance’ in 1865³⁵. Nevertheless, many grain legume breeding programs suffer from low genetic diversity and low rates of genetic progress. For example, several bottlenecks both during and after domestication in chickpea have resulted in limited genetic diversity in the crop gene pool³⁶. For soybean, 55% of the pedigree in public soybean cultivars in the USA in the 1990s was accounted for by five introductions³⁷. Innovative methods of crop breeding, based on the animal model³⁸, may conserve genetic diversity while accelerating grain legume genetic improvement, and may help to bridge the genetic gap between grain legumes and their wild and landrace relatives (Fig. 4). When combined with genomics-assisted breeding³⁹, it should be possible to unlock valuable genes such as drought and heat stress tolerance in wild legumes, and move them efficiently into cultivated varieties⁴⁰. 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 crops⁴¹. Large genetic and phenotypic variation exists in the world collections (Table 1 and Fig. 5). 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

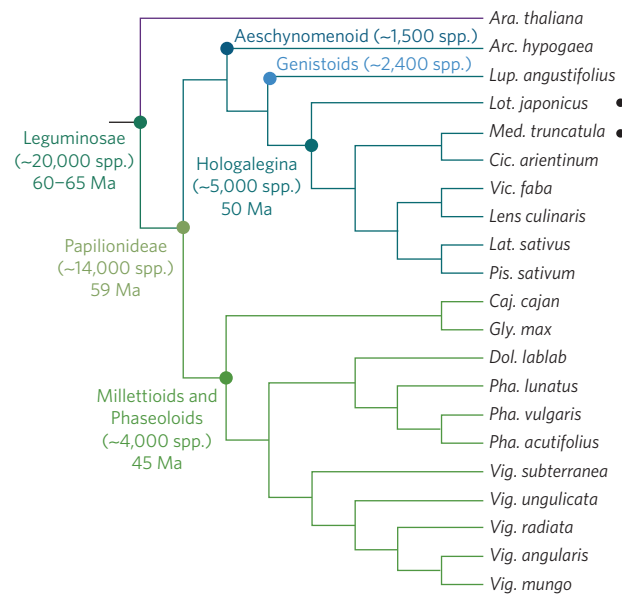


Figure 4 | Taxonomic relationships within the Papilionideae family showing the two major clades of cultivated legume, the cool season Hologalegina (blue) and the warm season Phaseoloids (light green).

Methodology adapted from ref. 82. 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*. The black dots denote forage species, included because of their value as model legumes (that is, not pulse crops). Ma, millions of years; the evolutionary ages are from ref. 83. The tree was constructed in MAFFT⁸⁴ using maturase K protein sequence similarity. Tree visualization was performed using FigTree⁸⁵.

GENESYS (Global Gateway to Genetic Resources)⁴². In addition to major CGIAR (Consultative Group for International Agricultural Research) 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, China, with some restrictions. The National Institute of Agrobiological Sciences (NIAS) Genebank⁴³ holds the largest germplasm database in Japan. The germplasm from India can be accessed through the National Bureau of Plant Genetic Resources (NBPGR) database⁴⁴. 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 germplasm⁴⁵, and to generate high-resolution genetic maps for important agronomic traits, develop molecular markers for breeding and identify important genes for crop improvement³⁹. 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. 6).

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

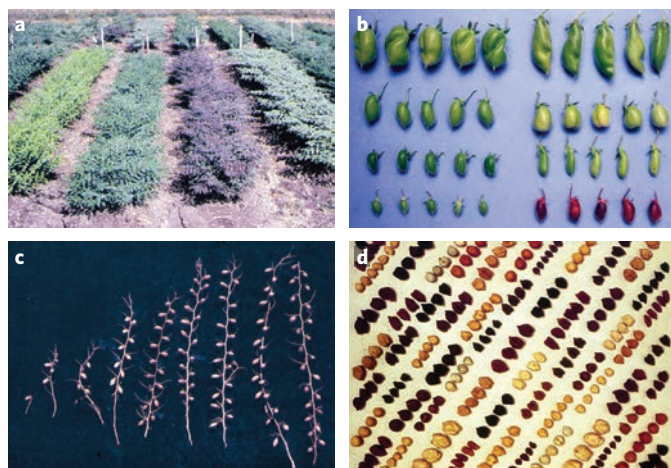


Figure 5 | Phenotypic variability in chickpea germplasm conserved at ICRIASAT, India. **a**, Variation in canopy development and leaf colour in chickpea germplasm in the field. **b**, Variation in pod size and pod colour. **c**, Variation in pod development and pod numbers on chickpea branches. **d**, Variation in seed size and colour in chickpea germplasm collection. Images courtesy of Hari Upadhyaya.

versus cereals is at least partly explained by low genetic diversity in grain legume breeding programs⁴⁶. 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 inbreeding⁴⁷. In animals, selection for complex traits was shown to be more efficient when based on genomic relationship information⁴⁸. For grain legumes, many of which are self-pollinating crops, genomic selection offers the prospect of accelerating genetic progress for yield, when analysis is based on the animal model⁴⁹. Advanced phenotyping technologies are available to measure morphological and physiological traits⁵⁰, and high-throughput image-based phenotyping platforms will make a significant impact in plant phenomics⁵¹. Accurate physiological phenotyping of specific and well-defined traits will also contribute to improved breeding outcomes⁵².

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 people who have limited access to animal protein. The seeds have a high protein content (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 tropics⁵³. 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 US. 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 conductance⁵⁴. The oil-rich marama bean, a perennial legume growing in the Kalahari Desert of southern Africa, can be more nutritious than soybean⁵⁵. A major drawback of all these legume crops (or potential crops such as marama bean) is inefficient harvesting techniques due to the shape and density of branches — 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 GI (glycaemic index) carbohydrate, fibre, minerals, vitamins, carotenoids and polyphenols⁵⁶. Consequently, legumes hold a near-unique position among foodstuffs because of their health-determinant properties⁵⁷. Studies in Taiwan involving people of Chinese origin revealed that all-cause mortality was increased in individuals on a legume-free diet⁵⁸. Moreover, the mortality hazard ratio declined by 8% in older people globally for every 20 g increase in daily grain legume intake⁵⁷. The first study to assess the link between health and a Mediterranean diet, which included a 20 g intake of legumes per day, found a 10% reduction in all-cause mortality⁵⁹.

Legumes contribute to reduced risk of mortality because of their benefits against major chronic diseases and their risk factors — including cardiovascular disease, diabetes, cancer, obesity and gut health⁶⁰. 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^{56,61}. Legumes also offer a food-based solution to decreasing risk of pre-diabetes⁶² and diabetes management as well as diabetes-associated complications, especially cardiovascular disease⁶³. 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 insulin⁶⁴. The effects are more pronounced when legumes are consumed as part of a low-GI 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 cancer⁵⁶. There is growing evidence that the human microbiome plays an important role in health outcomes with several conditions, such as 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 appetite⁵⁶.

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 responses⁶⁵. Thus, bread made from lupin flour may influence appetite, improve glucose control, and reduce energy intake. And although regular consumption of lupin-enriched bread by overweight men and women did not alter body weight or body composition, it did reduce blood pressure and improve measures of insulin resistance^{66,67}.

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

Common name	Scientific name	No. of accessions*	Main holding institutes [†]	Genome size (Mb) [‡]	No. of chromosomes (haploid)	Ploidy	Breeding system [§]	De novo genome sequencing
Adzuki bean	<i>Vigna angularis</i>	9,978	B (54%), N (24%), H (16%)	528	11	2	ib	V
Bambara beans	<i>Vigna subterranea</i>	2,183	I (94%)	864	11	2	ib	Not available
Black gram	<i>Vigna mungo</i>	1,668	N (51%), P (18%), K (13%)	528	11	2	ib	Not available
Mung bean	<i>Vigna radiata</i>	23,658	B (28%), N (28%), G (18%), P (17%)	509	11	2	ib	S, V
Cowpea	<i>Vigna unguiculata</i>	42,301	I (38%), P (20%)	576	11	2	ib	Q
Broad bean/faba bean	<i>Vicia faba</i>	30,073	M (33%), B (16%), A (12%)	12,797	6	2	ob	Not available
Chickpea	<i>Cicer arietinum</i>	76,221	F (27%), G (19%), M (19%), P (10%)	912	8	2	ib	S, T
Common bean	<i>Phaseolus vulgaris</i>	102,732	C (30%), P (13%)	576	11	2	ib	S, Y
Tepary bean	<i>Phaseolus acutifolius</i>	1,257	P (39%), C (26%), D (11%)	720	11	2	ib	Not available
Lima bean	<i>Phaseolus lunatus</i>	6,420	C (47%), P (35%)	672	11	2	ib-ob	Not available
Grass pea	<i>Lathyrus sativus</i>	6,728	M (38%), K (12%), O (12%)	8,064	7	2	ib-ob	Not available
Hyacinth/lablab bean	<i>Dolichos lablab</i> <i>Lablab purpureus</i>	1,292	N (33%), D (29%), P (13%), C (12%)	365	11	2	ib	Not available
Lentil	<i>Lens culinaris</i>	29,430	M (42%), A (16%), P (11%)	4,032	7	2	ib	R
Narrow-leafed lupin	<i>Lupinus angustifolius</i>	2,956	K (28%), L (21%), E (10%), J (10%), P (10%)	893	20	2	ib	X
White lupin	<i>Lupinus albus</i>	4,155	L (18%), K (12%), P (11%)	576	25	2	ib	Not available
Pea	<i>Pisum sativum</i>	54,062	P (13%), A (11%), M (11%)	4,685	7	2	ib	Not available
Peanut (groundnut)	<i>Arachis hypogaea</i>	47,650	F (31%), G (29%), P (20%), B (17%)	2,755	10	4	ib	U
Pigeonpea	<i>Cajanus cajan</i>	25,514	F (52%), G (44%)	845	11	2	ib-ob	S
Soybean	<i>Glycine max</i>	93,706	B (31%), P (23%), N (15%)	1,085	20	2	ib	W, Y

*Total number of accessions is the sum of data from GENESYS-PGR, China, India (NBPG), Japan and Australia. Data from refs 42–44,74,75 (accessed 21 April 2016). More information associated with 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.

[†]The % 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 and 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 Science; 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.nbpg.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/views/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 - Valdequera; https://www.genesys-pgr.org/views/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/views/UKR008
P	USA	National Plant Germplasm System; http://www.ars-grin.gov/npgs/index.html

[‡]Genome size is estimated from C-value²⁶.

[§]'Breeding system' is defined following refs 77,78. ib, inbred, usually selfed, tolerant of inbreeding; ob, outbred, suffers inbreeding depression; ib-ob, outbred but usually nearer ib than ob.

^{||}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://nigpr.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

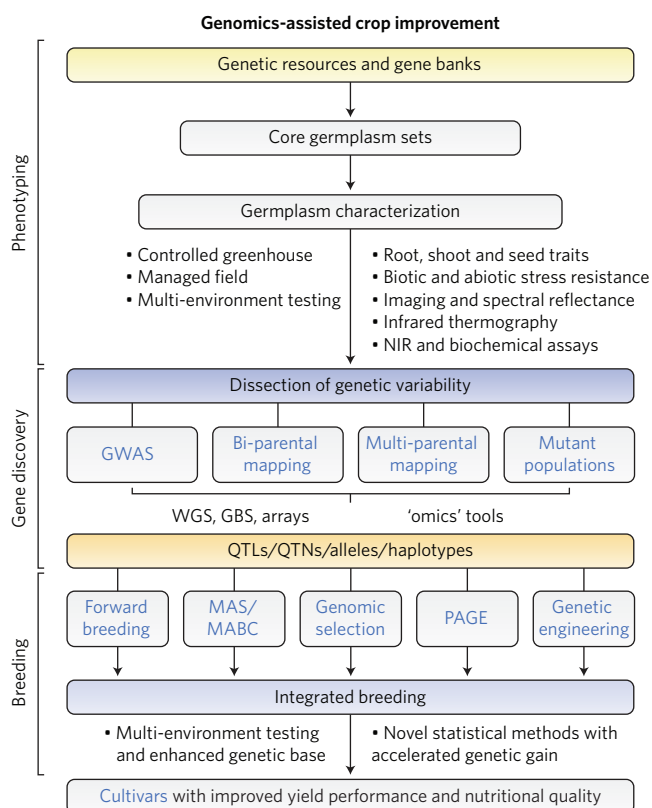


Figure 6 | Major strategies in genomics-assisted crop improvement for grain legumes. Large-scale germplasm stored in different gene banks can be characterized into smaller sets such as a core/mini-core germplasm set. Such small sets of germplasm can be characterized extensively for traits of interest. Subsequently, specialized 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) and/or 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 can be deployed for integrating/accumulating superior alleles. QTNs can be edited through a genome-editing approach called PAGE (promotion of alleles through genome editing). Candidate genes identified using 'omics' approaches can be deployed in genetic engineering approaches. By using one or more of the approaches mentioned above, cultivars with improved yield and nutritional quality can be developed.

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 controlled, randomized, crossover trial, in which participants consumed a beverage containing glucose (control), or glucose plus lupin flour, or glucose plus fibre and protein from soya isolates⁶⁸. Post-beverage glycaemic responses were significantly lower in participants following intake of the lupin beverage than the control beverage over a 4 h period after 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 per day are likely to be beneficial⁵⁶.

Grain legumes such as cowpea also have potential uses in the cosmetic, food, textile and pharmaceutical sectors because of their therapeutic properties⁶⁹. 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 elements⁷⁰. Cowpea proteins have high lysine contents and are potentially an excellent supplement for cereal-based diets⁷¹. And 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 human elastase has been suggested to have an important role in various inflammatory disorders, including pulmonary emphysema, sepsis, arthritis, nephritis and certain skin diseases⁷².

Conclusions and perspectives

The current use of nitrogen fertilizers in agriculture is ~110 Mt per annum, with the majority directed to cereal production. However, only 30–50% of applied nitrogen is used by the 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. But, 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 but largely untapped potential for sustainable agriculture, plant diversity and enhancement of primary production with reduced fertilizer use — benefits that may also extend to phosphorus-poor soils⁷³.

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 because of high variability in their yields and competition from high-yielding cereal crops. In addition, government price support policies often exist for cereals, particularly in developing countries, but inputs into grain legume breeding and agronomic technologies have been insufficient 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-used 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. 2016 as the UN FAO international year of pulses (grain legumes) 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 wellbeing advantages of a grain-legume-rich diet may be an important driver of culture change in considering grain legumes as key to food security.

References

- 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).
- Siddique, K. H. M., Johansen, C. & Turner, N. C. Innovations in agronomy for food legumes. *Agron. Sustain. Dev.* **32**, 45–64 (2012).

3. Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R. & Polasky, S. Agricultural sustainability and intensive production practices. *Nature* **418**, 671–677 (2002).
4. 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).
5. 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**, 105011 (2014).
6. Herridge, D. F., Peoples, M. B. & Boddey, R. M. Global inputs of biological nitrogen fixation in agricultural systems. *Plant Soil* **311**, 1–18 (2008).
7. Reeves, T. G., Thomas, G. & Ramsay, G. *Save and Grow in Practice: Maize, Rice, Wheat. A Guide to Sustainable Cereal Production* (FAO UN, 2016).
8. Malik, A. I. *et al.* Relay sowing of lentil (*Lens culinaris* subsp. *culinaris*) to intensify rice-based cropping. *J. Agr. Sci.* **154**, 850–857 (2015).
9. Huang, L.-F. *et al.* Plant–soil feedbacks and soil sickness: from mechanisms to application in agriculture. *J. Chem. Ecol.* **39**, 232–242 (2013).
10. 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).
11. Johansen, C. *et al.* Integrated crop management of chickpea in environments of Bangladesh prone to botrytis grey mould. *Field Crops Res.* **108**, 238–249 (2008).
12. Myers, S. S. *et al.* Increasing CO₂ threatens human nutrition. *Nature* **510**, 139–142 (2014).
13. Mourtzinis, S. *et al.* Climate-induced reduction in US-wide soybean yields underpinned by region- and in-season-specific responses. *Nature Plants* **1**, 14026 (2015).
14. Beebe, S. *et al.* in *Crop Adaptation to Climate Change* (eds Yadav, S. S., Redden, R. J., Hatfield, J. L., Lotze-Campen, H. & Hall, A. E.) Ch. 16 (Wiley-Blackwell, 2011).
15. 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).
16. 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**, 171–190 (2009).
17. Andrews, M. & Hodge, S. in *Climate Change and Management of Cool Season Grain Legume Crops* (eds Yadav, S. S., McNeil, D. L., Redden, R. & Patil, S. A.) Ch. 1 (2010).
18. 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 (International Crops Research Institute for the Semi-Arid Tropics, 2006).
19. Anderson, W., Johansen, C. & Siddique, K. H. M. Addressing the yield gap in rainfed crops: a review. *Agron. Sustain. Dev.* **36**, 18 (2016).
20. Oldroyd, G. E. D. Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nature Rev. Microbiol.* **11**, 252–263 (2013).
21. 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. *Microbiology* **147**, 663–670 (2001).
22. 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).
23. 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).
24. Bouguyon, E. *et al.* Multiple mechanisms of nitrate sensing by *Arabidopsis* nitrate transceptor NRT1.1. *Nature Plants* **1**, 15015 (2015).
25. 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**, ra43 (2015).
26. Parniske, M. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nature Rev. Microbiol.* **6**, 763–775 (2008).
27. 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).
28. 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).
29. 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**, 11171 (2015).
30. Farooq, M. *et al.* Drought stress in grain legumes during reproduction and grain filling. *J. Agron. Crop Sci.* <http://dx.doi.org/10.1111/jac.12169> (2016).
31. Daryanto, S., Wang, L. & Jacinthe, P. A. Global synthesis of drought effects on food legume production. *PLoS ONE* **10**, e0127401 (2015).
32. 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).
33. 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).
34. 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).
35. Fairbanks, D. J. & Rytting, B. Mendelian controversies: a botanical and historical review. *Am. J. Bot.* **88**, 737–752 (2001).
36. 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).
37. 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).
38. Cowling, W. A. The challenge of breeding for increased grain production in an era of global climate change and genomics. *World Agri.* **5**, 50–55 (2015).
39. Varshney, R. K. *et al.* Analytical and decision support tools for genomics-assisted breeding. *Trends Plant Sci.* <http://dx.doi.org/10.1016/j.tplants.2015.10.018> (2015).
40. 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 (2016).
41. McCouch, S. *et al.* Feeding the future. *Nature* **499**, 23–24 (2013).
42. GENESYS (accessed 21 April 2016); <http://www.genesys-pgr.org>
43. https://www.gene.affrc.go.jp/databases_en.php (accessed 21 April 2016).
44. http://www.nbpg.ernet.in/Research_Projects/Base_Collection_in_NGB.aspx (accessed 21 April 2016).
45. Yang, H. *et al.* Sequencing consolidates molecular markers with plant breeding practice. *Theor. Appl. Genet.* **128**, 779–795 (2015).
46. Cowling, W. A. Sustainable plant breeding. *Plant Breed.* **132**, 1–9 (2013).
47. Goddard, M. E. & Hayes, B. J. Mapping genes for complex traits in domestic animals and their use in breeding programmes. *Nature Rev. Genet.* **10**, 381–391 (2009).
48. 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).
49. Cowling, W. A. *et al.* Using the animal model to accelerate response to selection in a self-pollinating crop. *Genes Genom. Genet.* **5**, 1419–1428 (2015).
50. Granier, C. & Vile, D. Phenotyping and beyond: modelling the relationships between traits. *Curr. Opin. Plant Biol.* **18**, 96–102 (2014).
51. 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).
52. Ghanem, M. E., Marrou, H. & Sinclair, T. R. Physiological phenotyping of plants for crop improvement. *Trends Plant Sci.* **20**, 139–144 (2015).
53. Steele, W. M., Allen, D. J. & Summerfield, R. J. in *Grain Legume Crops* (eds Summerfield, R. J. & Roberts, E. H.) 520–583 (Collins, 1985).
54. Beebe, S. E., Rao, I. M., Blair, M. W. & Acosta-Gallegos, J. A. Phenotyping common beans for adaptation to drought. *Front. Physiol.* **4**, 35 (2013).
55. Nepolo, E., Takundwa, M., Chimwamurombe, P. M., Cullis, C. A. & Kunert, K. A review of geographical distribution of maramba bean (*Tylosema esculentum* (Burchell) Schreiber) and genetic diversity in the Namibian germplasm. *Afr. J. Biotechnol.* **8**, 2088–2093 (2009).
56. Kouris-Blazos, A. & Belski, R. Health benefits of legumes and pulses with a focus on Australian sweet lupins. *Asia Pac. J. Clin. Nutr.* **25**, 1–17 (2016).
57. Darmadi-Blackberry, I. *et al.* Legumes: the most important dietary predictor of survival in older people of different ethnicities. *Asia Pac. J. Clin. Nutr.* **13**, 217–220 (2004).
58. 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. *Public Health Nutr.* **15**, 663–672 (2012).
59. Trichopoulos, A. *et al.* Diet and overall survival in elderly people. *Brit. Med. J.* **311**, 1457–1460 (1995).
60. Kushi, L. H., Meyer, K. A. & Jacobs, D. R. Jr Cereals, legumes, and chronic disease risk reduction: evidence from epidemiologic studies. *Am. J. Clin. Nutr.* **70**, 451–458 (1999).
61. Flight, I. & Clifton, P. Cereal grains and legumes in the prevention of coronary heart disease and stroke: a review of the literature. *Eur. J. Clin. Nutr.* **60**, 1145–1159 (2006).
62. 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. Metab.* **40**, 323–333 (2015).

63. 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).
64. Sievenpiper, J. L. *et al.* Effect of non-oil-seed pulses on glycaemic control: a systematic review and meta-analysis of randomised controlled experimental trials in people with and without diabetes. *Diabetologia* **52**, 1479–1495 (2009).
65. Lee, Y. P. *et al.* Lupin-enriched bread increases satiety and reduces energy intake acutely. *Am. J. Clin. Nutr.* **84**, 975–980 (2006).
66. 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).
67. 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).
68. Dove, E. R. *et al.* Lupin and soya reduce glycaemia acutely in type 2 diabetes. *Brit. J. Nutr.* **106**, 1045–1051 (2011).
69. Singh, J. & Basu, P. S. Non-nutritive bioactive compounds in pulses and their impact on human health: an overview. *Food Nutr. Sci.* **3**, 1664–1672 (2012).
70. 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).
71. Lambot, C. in *Challenges and Opportunities for Enhancing Sustainable Cowpea Production* (eds Fatokun, C. A., Tarawali, S. A., Singh, B. B., Kormawa, P. M. & Tamò, M.) 367–375 (International Institute of Tropical Agriculture, 2002).
72. 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. Chem.* **25**, 377–382 (2010).
73. Sulieman, S. & Tran, L. S. P. Phosphorus homeostasis in legume nodules as an adaptive strategy to phosphorus deficiency. *Plant Sci.* **239**, 36–43 (2015).
74. http://www.most.gov.cn/ztlz/kjzykfgx/kjzygjctjpt/kjzyptml/201407/t20140716_114275.htm (accessed 21 April 2016).
75. Stoutjesdijk, P. *Plant genetic resources for food and agriculture: second national report* Technical Report 13.11 (ABARES, 2013)
76. Bennett, M. D. & Leitch I. J. Plant DNA C-values database (v.6.0, December 2012; accessed 21 April 2016); <http://www.kew.org/cvalues/>
77. Simmonds, N. W. & Smartt, J. *Principles of Crop Improvement* 2nd edn (Blackwell Science, 1999).
78. Singh, R. J. *et al.* Landmark research in legumes. *Genome* **50**, 525–537 (2007).
79. FAOSTAT (accessed 5 January 2016); <http://faostat3.fao.org/compare/E>
80. South, A. rworldmap: a new R package for mapping global data. *The R Journal* **3/1**, 35–43 (2011).
81. Neuwirth, E. *RColorBrewer: ColorBrewer Palettes. R package version 1.1–2* (2014); <http://CRAN.R-project.org/package=RColorBrewer>
82. 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).
83. 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).
84. Katoh, K. & Standley, D. M. MAFFT Multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780 (2013).
85. Lemey, P., Rambaut, A., Drummond, A. J. & Suchard, M. A. Bayesian phylogeography finds its roots. *PLoS Comput. Biol.* **5**, e1000520 (2009).
86. Erismann, J. W., Sutton, M. A., Galloway, J., Klimont, Z. & Winiwarter, W. How a century of ammonia synthesis changed the world. *Nature Geosci.* **1**, 636–639 (2008).
87. Heffer, P. & Prud'homme, M. *Fertilizer Outlook 2015–2019* (2015); www.fertilizer.org
88. US Energy Information Administration *Total Primary Energy Consumption* (2015); www.eia.gov
89. Storkey, J. *et al.* Grassland biodiversity bounces back from long-term nitrogen addition. *Nature* **528**, 401–404 (2015).
90. UNEP and WHRC *Reactive Nitrogen in the Environment: Too Much or Too Little of a Good Thing?* (The United Nations Environment Program, 2007); www.unep.org/pdf/dtie/Reactive_Nitrogen.pdf
91. Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R. & Polasky, S. Agricultural sustainability and intensive production practices. *Nature* **418**, 671–677 (2002).
92. Ladha, J. K. *et al.* Global nitrogen budgets in cereals: a 50-year assessment for maize, rice, and wheat production systems. *Sci. Rep.* **6**, 19355 (2016).

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Author contributions

C.H.F. co-created the network, discussed the idea, organized the content, wrote the abstract, introduction and 'Conclusions and perspectives' sections, and edited the final article before submission. H.-M.L. discussed and contributed to the content, prepared Fig. 3, Table 1 and the associated webpage (<http://legumecrops.wildsoydb.org/>). R.V. provided information concerning genetics and breeding. H.T.N. discussed and contributed to the content and coordinated the genetic and breeding topics including the figures and Table 1. K.H.M.S. co-created the network, discussed the idea, contributed to various sections and figures, and edited the final version. T.D.C. discussed the content, contributed to the section on sustainable agriculture, contributed edits to several sections, and gave suggestions on figures. W.A.C. wrote parts of the text, contributed citations and edited Table 1 and figures. H.B. discussed the content, prepared Fig. 1 and Fig. 2, and contributed to the section 'Sustainable agriculture'. T.A.M. discussed the idea and contributed to the section 'Nutrition and health'. J.M.H. contributed to the section 'Nutrition and health'. J.W.C. produced Fig. 4 and finalized the references. A.J.M. contributed to the section 'Symbiotic nitrogen fixation'. K.K. and J.V. contributed to the section 'Bringing in orphans'. C.C. organized the section 'Bringing in orphans' and reviewed the final version of the section. J.A.O. discussed the idea and provided information for the section 'Nutrition and health'. M.L.W. contributed to the section 'Nutrition and health'. Y.L. discussed the idea and contributed to the section 'Sustainable agriculture'. H.S., K.S. and J.Y. discussed the idea and helped to edit the content before submission. N.F. contributed to the section 'Mitigating climate change'. B.N.K. contributed to sections focussed on legume nitrogen fixation and helped to edit the content before submission. F.-L.W. produced Table 1 and the associated webpage (<http://legumecrops.wildsoydb.org/>). B.V. contributed to the section and citations on abiotic stress, and Fig. 6. M.C. co-created the network, prepared Box 1, discussed the idea and edited the figures before submission.

Additional information

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Competing interests

The authors declare no competing financial interests.