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Farrer Review

The future of grain legumes in cropping systems

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Abstract. Grain legume production is increasing worldwide due to their use directly as human food, feed for animals, and industrial demands. Further, grain legumes have the ability to enhance the levels of nitrogen and phosphorus in cropping systems. Considering the increasing needs for human consumption of plant products and the economic constraints of applying fertiliser on cereal crops, we envision a greater role for grain legumes in cropping systems, especially in regions where accessibility and affordability of fertiliser is an issue. However, for several reasons the role of grain legumes in cropping systems has often received less emphasis than cereals. In this review, we discuss four major issues in increasing grain legume productivity and their role in overall crop production: (*i*) increased symbiotic nitrogen fixation capacity, (*ii*) increased phosphorus recovery from the soil, (*iii*) overcoming grain legume yield limitations, and (*iv*) cropping systems to take advantage of the multi-dimensional benefits of grain legumes.

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Introduction

Legumes have been cropped by humans for centuries. However, commonly legumes were included in cropping systems to provide fodder for animals and to enhance yields of subsequent grain crops. While the ancient Chinese included soybean and the Romans sometimes included pea in their crop rotations, seed harvest was usually not their prime motivation for growing these crops but rather it was the beneficial effect of improving the soil for growing cereal crops (Sinclair and Sinclair 2010). In the USA, soybean and to some extent peanut were introduced primarily as fodder crops. The potential for use of seeds of peanut, soybean, and cowpea for food and manufacturing feedstock was not recognised in the USA until the early 19th century. At that time, several uses of seeds of grain legumes in foods and industrial uses were identified. For example, George Washington Carver, who worked with comparatively primitive facilities at the Tuskegee Institute in Alabama, developed more than 100 products made from peanut seeds.

After World War II, the demand for the seeds of grain legumes, particularly soybean, began a large, steady increase (Fig. 1). There were several reasons for this increasing demand. One reason was the use of soybean seeds to supply protein for feed for animals, whose numbers increased in response to the demand for increasing consumption of meat associated with increasing affluence. A second reason was the use of the seed lipids in food products, e.g. as a cooking oil. Also, there was an increasing demand for soybean lipids in the manufacture of various products. This demand was met globally by increased production in the USA, Brazil, Argentina, and China. In addition to the increased production of soybean, in more recent times there has been a rapidly increasing demand for direct human consumption of grain legumes such as cowpea, peanut, and pigeon pea (Fig. 1). A possible further increase in demand may result from the recent suggestion that lipids from grain legumes could also be used directly as a source of biodiesel fuel.

Now, legumes are a major part of many people's diet worldwide. Direct consumption of grain legumes in many regions of the world will need to expand with human population to meet and improve their nutritional needs. The seed protein concentration of grain legumes is generally at least 25% (Table 1) and reaching as high as 50% in some genotypes of soybean. Cowpea is largely consumed across West Africa, while bean is widely consumed in the Americas and other areas worldwide. In India where much of the population is vegetarian, several legumes including pigeon pea, chickpea, mungbean, and lentils are cultivated on millions of hectares. Domestic production in India now falls short of demand and there is a net import of ~2.5–3.5 Mt pulses per year (Ali and Gupta 2012).

Continued increases in human population and affluence will sustain the increasing demand for grain legumes to feed animals and for direct human consumption (e.g. Ali and Gupta 2012). The expanding economies in Asia and elsewhere have already resulted in rapidly increasing demand for soybean protein to feed poultry and swine.

In addition to the increasing demand for grain legumes, these species bring to cropping systems the crucial capacity to decrease or eliminate the need for direct applications of some fertilisers. In many regions of the world, farmers simply do not have access to fertiliser. In regions of industrial agriculture where fertilisers are available, the skyrocketing costs of fertiliser (Fig. 2) are resulting in economic pressure on farmers

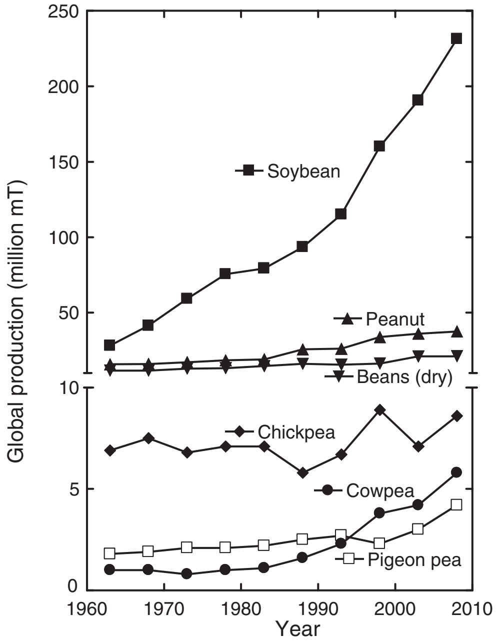

Fig. 1. Global production of various grain legumes since 1960.

Table 1. Approximate fraction of protein, lipid, and carbohydrate of seeds of several grain legumes

Legume	Protein (%)	Lipid (%)	Carbohydrate (%)
Soybean (*Glycine max*)	43	21	14
Peanut (*Arachis hypogea*)	30	50	14
Broad bean (*Vicia faba*)	32	1	55
Lentil (*Lens esculenta*)	30	3	62
Pea (*Pisum sativa*)	28	3	60
Pigeon pea (*Cajanus cajan*)	27	5	62
Cowpea (*Vigna unguiculata*)	27	5	62
Bean (*Phaseolus vulgaris*)	27	1	68

to minimise fertiliser inputs. The increasing cost of energy to manufacture nitrogen (N) fertiliser has forced prices to new, higher levels. Also, the costs of mining phosphorus (P) along with an apparent dwindling of P stocks have also stimulated P prices to higher levels. Increasing costs of fossil fuels will no doubt impact directly on the availability of N and P fertilisers in future cropping systems. In fact, in some regions fertiliser is now the largest single variable cost in growing grain crops (Purdue University 2012).

In addition to the economic pressures to minimise fertiliser use in cropping systems, there are environmental pressures to substantially decrease the negative impact of fertiliser application for cereal crops. Nitrogen fertilisers are major sources of greenhouse gases, particularly nitrous oxide, and result in contamination of water ways and human water supplies with nitrate. Similarly, loss of P from fields can contribute to algae blooms and eutrophication of streams and lakes. The 'dead zone' that exists at the mouth of the Mississippi River in the Gulf of Mexico is attributable to fertiliser from crop fields in the Midwest of the USA (Burkart and James 1999; Duan *et al.* 2010). Current and undoubtedly future environmental regulations in many regions of the world will restrict application of fertilisers on crops.

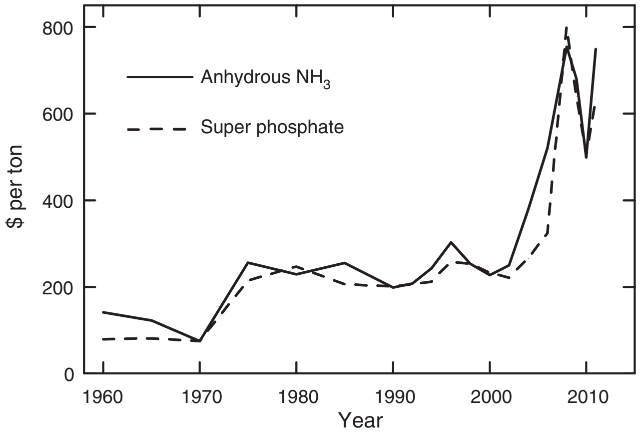

Fig. 2. World market price of anhydrous ammonia and super phosphate since 1960.

Grain legumes bring to cropping systems a much decreased demand for fertiliser. Legumes have the capacity to meet much of their own N requirements through symbiotic N fixation so that crop growth can be potentially fully sustained without N fertiliser. Also, the potential exists to return to the approach of the ancient Chinese and Romans to use grain legumes as an important means to increase the overall N input into cropping systems. As discussed later, some grain legumes have the unique capacity to recover P from the soil that is in forms unavailable to other crops. The need to decrease P application to cropping system could be a very important attribute grain legumes might bring to cropping systems. Nevertheless, grain legumes when grown on many soils will still likely require fertilisation to provide potassium since potassium plays a key role in electric charge balancing within the rhizosphere, especially for N_2-fixing legumes (Tang 1998).

In crop-livestock systems of developing countries, where cattle feed on cereal crop residues, N concentration of cereal residue is often much below the threshold needed in animal diets. Nitrogen concentrations of at least 1.0–1.2% are needed for microbial population in the rumen of livestock for an efficient feed digestion (Van Soest 1994), which are virtually never reached by cereal residues but legume residues are at or above this threshold (Sundstøl and Owen 1984). Therefore, it is possible that legume crop residues will be playing an increasing role as a source of inexpensive fodder or even key N-rich additive in cattle production.

Of course, inclusion of grain legumes in cropping systems is not without challenges. Since the plants and seeds are high in protein content, and in some species high oil content, they are attractive to diseases and insects. Also, maintaining high quality seeds stocks can be more difficult because of the comparatively low yield of parent plants and a comparatively short storage life of seeds. Farmers in developing areas in particular often cannot carry forward good quality seeds for optimum production.

Finally, certain grain legumes such as bean are often called the 'poor man's meat'. Consequently, outside regions where soybean and pea are major cash crops, grain legumes are still often viewed as secondary crops to facilitate the production of cereals. Grain legume production in developing countries is often ‘pushed’ to a more marginal area. For instance, the traditional chickpea production in Northern India has now almost fully shifted to the south (Gowda *et al.* 2009) despite the lower yield potential in these new niches. We argue in this paper, that grain legumes deserve a much more prominent role in future cropping systems in both developed and less-developed agriculture around the world.

We reviewed a decade ago key physiological traits that could be exploited for yield improvement of grain legumes (Sinclair and Vadez 2002). In view of recent research advances and expanded opportunities for legumes in cropping systems, we offer this updated review of the role of grain legumes in cropping systems. The objective of the current review is to discuss several key features of grain legumes that need to be exploited to meet the future demands for the enhanced role of grain legumes in cropping systems. These topics include (*i*) increased symbiotic N fixation capacity, (*ii*) increased P recovery from the soil, (*iii*) overcoming grain legume yield limitations, and (*iv*) the multi-dimensional benefit of legumes in cropping systems.

Symbiotic nitrogen fixation

All plants need large amounts of N because N is an essential component of all proteins and nucleic acids required for new, functioning cells. Therefore, it is not surprising that limited N availability in natural, non-legume plants systems results in restricted plant growth. Legumes ameliorated the N limitation by having evolved a capability to form a symbiosis with rhizobia and bradyrhizobia to fix atmospheric N. Symbiotic N fixation was a major evolutionary advantage because legume growth was not limited to N availability in the soil.

Nitrogen fixation symbiosis and an ability to sustain high rates of N fixation is a delicate activity for plants. Nitrogenase, which is the enzyme provided by the bacteria to fix atmospheric N, is extremely sensitive to exposure to even low concentrations of oxygen (Robson and Postgate 1980). Nitrogen fixation requires a low oxygen environment to sustain fixation so that achievement of high rates of N fixation activity requires a carefully regulated oxygen environment around nitrogenase. The regulation of oxygen concentration while maintaining high oxygen flux is a critical challenge in exploiting associative N fixation as an option to achieve high N input rates for cereal crops. The solution evolved by grain legumes is the development of specialised nodule structures that allow very controlled regulation of the oxygen atmosphere around nitrogenase to support high N fixation rates. In nodules, nitrogenase occupies the central volume of the nodule which is surrounded by a continuous cellular barrier in the inner nodule cortex that controls oxygen diffusion into the central volume (Tjepkema and Yocum 1974; Purcell and Sinclair 1993). The gas permeability of the cortex is under regulation by the plant so that oxygen concentration is maintained at a level that is not deleterious to nitrogenase, but allows high fixation rates (Minchin 1997).

Another unique feature of the nodules is that they are elegantly ‘designed’ to be responsive to the supply and removal of water and organic materials into and out the nodule. Nodules are almost exclusively dependent on water flow from the phloem flow originating in the shoots since little water is exchanged by nodules with the surrounding soils (Walsh *et al.* 1989). Therefore, nodule activity is very sensitive to the balance of water input from the phloem and water output to the xylem. Not only is the water input critical in sustaining the activity of the nodules, delivery of photosynthate from the leaves provides the energy resource to support the high energy process of N fixation. Xylem flow is also essential to remove the accumulating N products (Walsh *et al.* 1989) in the nodule to prevent feedback inhibition of N fixation activity (Serraj *et al.* 1999*a*). Without the continuous circulation of water to and from the nodules, N fixation activity cannot be sustained.

The dependence of nodule activity on water flow makes the nodules potentially very sensitive to plant water status. When turgor pressure declines in the shoots, then there is a possibility of decreased phloem flow. Even though other processes may not yet be reacting to declining water status in the shoot, the sensitivity of nodules to turgor-driven flow in the phloem can hypothetically make nodule activity especially sensitive to changes in plant water status (Serraj *et al.* 1999*b*). Nitrogen fixation tends to be one of the most sensitive processes in some grain legume plants to developing water deficit with N fixation rates often decreasing in advance of leaf gas exchange (Fig. 3). The sensitivity of N fixation to soil drying is especially pronounced in soybean and cowpea, which have capacities for high N fixation rates (Sinclair and Serraj 1995).

Not only is nodule activity sensitive to the balance of water influx and efflux, the fixation process is very sensitive to feedback based on the levels of N products in the nodule (Serraj *et al.* 1999*b*). While the detailed biochemical sensitivity has not been fully resolved, experimental feeding of plants with amino acids can result in dramatic decreases in fixation rate (Vadez *et al.* 2000). Soybean nodules are also sensitive to feeding plants with ureides, which are the compounds used by soybean and cowpea to transfer much of the N from the nodules to the shoot.

On balance, nodule activity is under tight regulation by the host plant through water supply to the nodules and N feedback regulation in the nodules. Through these regulatory processes, N

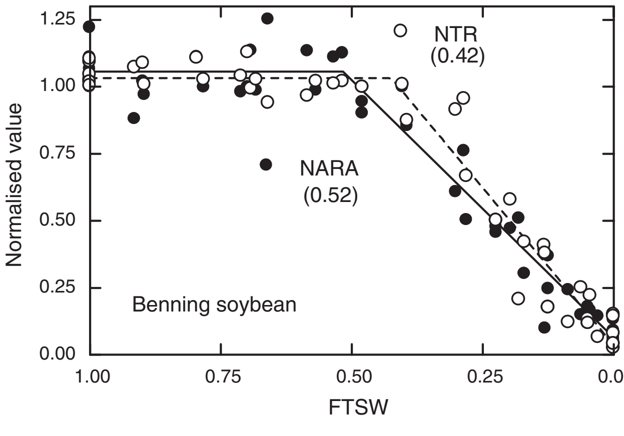

Fig. 3. Normalised nitrogen fixation rate measured by acetylene reduction assay (NARA) and normalised transpiration rate (NTR) with decreasing fraction of transpirable soil water (FTSW) in Benning soybean (J. M. Devi, pers. comm.).

fixation activity to a very large extent is under the control of the host plant. Only in extreme situation with a high preponderance of incompetent bacteria does it appear that bacteria play a major role in controlling fixation rates (Denison 2000). Unfortunately, research funds continue to be heavily focussed on 'improving' bacteria when the contribution of bacteria in influencing N fixation rate is likely to be very small compared with the regulation exerted by the plant. This is especially true in many cropping systems of the developing world where grain legumes are grown under abiotic limitations such as water and nutrients that would affect the whole plants to a much greater extent than the microsymbiont in the nodule.

An intriguing approach to ensure basal nodulation is the development of promiscuous host genotypes that form nodules with a range of 'natural' bacteria strains (Kueneman *et al.* 1984). The use of promiscuous soybean has led to significant N input in maize-soybean systems (Sanginga *et al.* 2002). It now appears in fact that promiscuous nodulation in legumes is likely more general than usually believed and host-strain specificity may be restricted to specific niches (Perret *et al.* 2000). In addition, even in areas where specific strains for a newly introduced legume species are lacking, as was the case when soybean cultivation began in France in the 1980s, it appears that a single inoculation is sufficient to establish the bacteria in the soil since inoculated strains remain in the soil even after long periods without cultivation of the host species (Obaton *et al.* 2002).

Consequently, a major shift in perspective to increase grain legume N fixation and its contribution to the N balance of the cropping system is needed. More research funds and effort need to be invested in research targeted to understanding and identifying superior host plants in their regulation of N fixation. There are large grain legume collections that have been virtually unexploited for this potential, except for soybean (Sinclair *et al.* 2000). One of the past difficulties for assessing genetic variability in large collections was their size and the lack of a sampling procedure to assess a representative set of germplasm. There now exists structured sets of representative germplasm from most major grain legume collections (e.g. chickpea, Upadhyaya and Ortiz 2001), which provide a gateway to explore diversity for the N fixation potential in legume germplasm collections.

Nitrogen feedback control of nitrogen fixation

To avoid the N feedback limitation on N fixation activity, it is critical that N products be expeditiously removed from nodules and sequestered in the shoot of the plant. Sequestration of the fixed N to a large extent in grain legumes is in leaf proteins. Not surprisingly, legume leaves tend to have very high N concentrations. Up to 50% of the N in soybean leaves is stored in ribulose 1,5-bisphosphate (Rubisco), which is the key photosynthetic enzyme for trapping carbon dioxide (Wittenbach *et al.* 1980). Rubisco is an especially effective means of storing N because this protein can be synthesised in abundance, it is innocuous in leaves, and it is stable until degraded by specific proteases (Hatayama *et al.* 2000). Levels of N concentrations in soybean leaves for example, can substantially exceed the concentration at which photosynthetic rates are maximised (Lugg and Sinclair 1981). A recent screening of the peanut reference collection also reveals that N levels in the field can be very large (from 1.9 to 2.8%) (Blümmel *et al.* 2012), which clearly opens a scope to target genotypes with high accumulation potential in the vegetative parts.

In addition to N storage in proteins of photosynthesis, some legumes have a layer of cells in leaves between the palisade and spongy mesophyll that stores glycoproteins (Klauer *et al.* 1996). Lansing and Franceschi (2000) examined leaves of 39 legume species and found a protein-rich, paraveinal layer in many species. No information was presented on the possibility of genetic variability within a species in the presence/absence of the paraveinal layer or in the extent of the N storage capacity of the paraveinal layer may vary among genotypes. Since the paraveinal layer is potentially an important storage structure of protein, more attention appears to be needed on the possibility of exploiting this tissue for greater N storage.

The importance of N storage in leaves in regulating N fixation rates is consistent in the high correlation ($r^2 = 0.83$) observed in well-watered soybean between N fixation rate and leaf area (Denison *et al.* 1985). Greater rates of leaf area development provide more sites for the sequestration of N in enzymes of photosynthesis and higher N fixation rates. Unfortunately, many grain legumes currently tend to have slow initial development of leaf area, and flowering may occur early in the growth cycle. These development traits result in a limited capacity to store N, and N fixation rate is necessarily decreased by feedback restrictions. More rapid leaf area development and delayed flowering are options for increasing N storage and hence, N fixation activity and crop yield. In common bean, for example, climbing-type cultivars with delayed flowering and continued production of leaves after flowering commonly out-yield bush-type cultivars with early flowering (Clark and Francis 1985; Kornegay *et al.* 1992). Of course, delayed maturity and large leaf area can be counterproductive in environments with late-season drought or adverse temperature (Berger *et al.* 2012). For example, larger leaf area development can result in rapid water use under terminal drought conditions where water savings may be necessary in chickpea (Zaman-Allah *et al.* 2011*a*) and cowpea (Belko *et al.* 2012).

A corollary in overcoming the loss of N fixation with early flowering is to expand the period of active N fixation beyond flowering. Often grain legumes such as common bean seem to have very limited N fixation after flowering (e.g. Hungria and Neves 1987; Piha and Munns 1987) and it seems to be related to a shortage of carbohydrate supply to the nodules (Lawn and Brun 1974), but this decrease does not seem to be obligatory, at least in soybean (Denison and Sinclair 1985).

In addition to expanded N storage in leaves, another possibility is to increase N storage in stems. Stem N storage could be beneficial for eventual release of N to support growing seeds, for retention in the crop residue to enrich the soil, or for enhanced quality if used as fodder. While no screens of genotypes for storage of stem N concentrations appear to have been done in grain legumes, it may be useful to identify those genotypes that have large N stem storage capacity. Another approach for N storage is to fully exploit the capacity of some tropical legumes to produce tubers on their roots (Tropical Legumes 1979). For example, yam bean (*Pachyrhizus erosus* and *Pachyrhizus ahipa*) has been found to accumulate substantial amounts of N in their tubers (Castellanos-Ramos *et al.* 2009; Rodríguez-Navarro *et al.* 2009). A speculative research topic would be investigation of the ability of these tubers to store N either for use in seed growth by the legume crop or for providing an N source for a succeeding cereal crop.

Water-deficit impact on nitrogen fixation

As discussed previously, symbiotic N fixation of grain legumes is often quite sensitive to developing water deficits. In comparing the decrease in transpiration and N fixation rates with soil drying, it is not uncommon to have N fixation decrease in advance of leaf gas exchange as indexed by transpiration (Fig. 3). Consequently, the large need for N by the growing plant and seeds makes grain legumes especially vulnerable to water deficits. In a simulation study, Sinclair *et al*. (2010) found that decreasing the sensitivity of N fixation to soil drying in soybean would increase yields substantially in most soybean production areas in the USA.

Soybean has been given the most research attention of the grain legumes for genetic variation in the tolerance of N fixation to soil drying. In screens beginning with 3500 soybean plant introduction lines, Sinclair *et al*. (2000) identified several genotypes in which N fixation was actually more tolerant of soil drying than leaf gas exchange. Using the cultivar Jackson in which tolerance to soil drying of N fixation was equal to that of leaf gas exchange, a breeding effort resulted in the release of high-yielding germplasm with drought-resistant N fixation (Chen *et al.* 2007).

While Sinclair and Serraj (1995) compared the sensitivity of N fixation of nine grain legume species to soil drying and found substantial variations, their study was generally based on only a single cultivar for each species. They identified peanut as being a tolerant species, yet recently Devi *et al*. (2010) reported a large range in sensitivity among 17 Indian cultivars and breeding lines. The threshold fraction of transpirable soil water (FTSW) at the initiation of the decline in N fixation activity ranged from a very sensitive value of 0.59 to a tolerant value of 0.28. Genetic variation for N fixation sensitivity to water deficit in grain legumes other than soybean is largely unexplored. Breeding programs may need to be initiated to ensure high tolerance of N fixation to soil drying in genotypes released for commercial production.

Phosphorus accumulation

Like N, P is an essential element in plants and is required particularly to support energy transfer within cells. Much of the P in the plant is in inorganic form and readily reacts in the sequence of events resulting in energy transfer. Commonly the leaf cytoplasm of P-sufficient plants has concentrations in the range of 5–10 mM (Bieleski 1973). Abundant inorganic P can be stored in the vacuoles of cells in substantial excess to provide a P reserve for late-season plant growth when P in the soil solution may no longer be available. Phosphorus concentration in the cell vacuole can be as high as 25 mM (Lauer *et al.* 1989; Lee *et al.* 1990). The lack of vacuoles in young leaf cells to supply stored P causes the development of meristems to be especially inhibited by deficient P uptake (Fredeen *et al*. 1989; Rao *et al.* 1993).

Plants are well equipped to uptake P from the soil solution. There are at least two uptake pathways. The Michaelis-Menten coefficient (Km) for the high affinity P-uptake system is as low as 3 μM (Furihata *et al.* 1992; Schachtman *et al.* 1998). Bhadoria *et al*. (2004) found the Km for P uptake by intact peanut plants to be 10 μM. A common difficulty in recovering P from the soil is that it is not readily available to plants because P complexes in the soil with aluminum, iron and calcium. These complexes are essentially insoluble resulting in very little movement of P in the soil solution, and none of the complexes can be taken up directly by roots (Sinclair and Vadez 2002). While large amounts of P may exist in the soil, there is little evidence that the complexed P in the soil is available to cereal crops.

Grain legume species, however, have evolved mechanisms to allow recovery of P from unavailable forms. For example, when grown on soils with no available P, Ae *et al*. (1990) found that pigeon pea thrived for 1 month after sowing while four other crop species died from P deficiency. A similar experiment with peanut showed it survived for 2 months after sowing while three other species died (Ae and Shen 2002).

There appear to be at least three mechanisms that can be employed by grain legumes to release unavailable P in the soil for recovery by the plants. One mechanism is the exudation of organic acids from legume roots which decreases the pH in the soil surrounding the roots and releases P. Several organic acids are exuded with citrate being predominant among common bean (Shen *et al.* 2002), soybean and cowpea (Nwoke *et al.* 2008). Malate is exuded predominately by lupin, field pea, and faba bean (Nuruzzaman *et al.* 2005*a*). Chickpea was found to exude large amounts of citrate and malate (Ohwaki and Hirata 1992). Other organic acids exuded by grain legumes include oxalate, tartrate and acetate. However, the effectiveness of these organic acids in mobilising P is highly dependent on the soil and the soil environment (Hinsinger 2001; Jones *et al.* 2003). For example, organic acid mediated solubilisation of P by addition of citrate or oxalate varied widely among 20 contrasting soils (Jones *et al.* 2003). Release of organic acids may not be functional in acid soils of the Sahelian zone. It seems likely that soil characterisation will be required to select the appropriate grain legume genotype for high return of P on a particular soil.

Like many crop species, grain legumes can also release phosphatase enzymes into the soil to breakdown organic material that contains P. Lupin appears to be the most studied of the grain legumes and has been shown to employ a dual attack of exudation of organic acid and acid phosphatase (Gilbert *et al.* 1999). Also, genetic variation in root phosphatase activity has been demonstrated for common bean (Helal 1990).

There appears to be a third mechanism expressed by some grain legumes for recovering P from unavailable forms. Ae and Shen (2002) reported an ability of peanut and pigeon pea to recover P from unavailable forms by a contact reaction between the root surface and the insoluble P adjacent to the root. The mechanism was not resolved but they showed that a substance resides in cell walls acting directly on unavailable soil P, and it is not a pectic substance. Unfortunately, this apparently unique mechanism expressed by grain legumes has not been the subject of recent study.

A corollary with the solubilisation of P in the soil is distribution of roots through the soil volume to access insoluble P. Length and density of root hairs appear to be particularly important in contacting soil P. Root hairs disperse organic acids in the soil (Lynch 2007) and account for much of P uptake (Gahoonia and Nielsen 1998). Genetic variation has been found in root hair characteristics and have been identified in cowpea (Krasilnikoff *et al.* 2003), common bean (Yan *et al.* 2004) and soybean (Wang *et al.* 2004).

Since most P is in the top soil layers, a focus of improved rooting has been an increase in rooting surface in these top layers (Lynch and Brown 2001) with one approach being the identification of genotypes with root angles that encourage high rooting in the top soil layers. However, these top soil layers are also the first to dry so that there may be limited soil water in which soluble P can reside. Therefore, one of the future challenges to resolve will be to increase access to P where legumes are cultivated in low available P soil and under conditions of water limitation.

Another root alternative for scavenging soil P is the development of cluster roots, like in lupins (Neumann *et al.* 2000; Shane *et al.* 2003; Lambers *et al.* 2006). Cluster roots develop in response to pockets of soil P in situations of extremely low soil P availability (Lambers *et al.* 2006). Legumes seem to have a high potential for formation of cluster roots and their development seems to be regulated by P nutritional status (Neumann *et al.* 2000).

From a system perspective, the capabilities described above for legumes to acquire P from non-available pools are generally very beneficial for rotation crops such as canola, wheat or maize (e.g. Hens and Hocking 2004; Nuruzzaman *et al.* 2005*b*, Jemo *et al*. 2006). Faba bean appears to be one of the most promising of several legumes to express an advantage in P recovery (Nuruzzaman *et al.* 2005*b*). However, the extent of the benefit of legume P acquisition to the cropping system may be limited in some cases such as in acidic soil (Li *et al.* 2010).

Increasing grain legume yields

Commonly, the yields of grain legumes are substantially lower than cereals. Obviously, grain legume crops would be more attractive to farmers if yield could be increased. There are, however, several very important reasons why yields are lower than cereals and these are difficult to overcome. First, grain legumes are often assigned niches in the cropping season where duration of growth is limited due to temperature or rainfall patterns. As a consequence, these short-season crops do not have the time to acquire the resources necessary to achieve higher yields.

A second limit on grain legume yields is that their seeds are more energy dense than cereals. The higher protein content of grain legume seeds requires greater amounts of photosynthate to be used in synthesising the large amounts of protein (Sinclair and deWit 1975). Soybean and peanut are especially high in protein and lipid content, together constituting from 60 to 80% of the seed (Table 1). This fact alone limits the yields of soybean and peanut to substantially lower levels as compared with the cereals.

Maximising nitrogen fixation

Nitrogen fixation rate is highest during the vegetative growth stage when photosynthate tends to be freely available to nodules. With the initiation of grain growth, there is a shift in the supply of photosynthate away from the nodules to developing seeds (Herridge and Pate 1977). As a result, early-to-flower genotypes can have low, even negligible, N accumulation as a result of fixation (Graham and Temple 1984). Therefore, during seed growth N is retrieved from leaves and stems for transfer to the developing seeds. The loss in N from the vegetative tissues results in their senescence as a result of the 'self-destruct' process proposed by Sinclair and deWit (1975).

The amount of N a plant can store in vegetative tissue before seed growth is therefore crucial in determining total amounts of fixed N. As discussed previously, storage of fixed N during vegetative growth becomes a major issue. Nitrogen can be stored during vegetative development only to the extent that tissues are available to receive the fixed N. Not surprising, there is a close correlation between N storage in the vegetative tissue and crop mass. This is illustrated in Fig. 4 showing the amount of N storage in pea, wheat, and maize across a range of crop masses. These relationships are based on the empirical relationships found by Lemaire *et al*. (2008). While pea has the greatest storage capacity among these three species due mainly to high leaf N concentration, large plant masses still must be developed to attain high nitrogen storage levels. Often legumes are initially slow growing and do not obtain large plant masses before anthesis. Genotypes with more rapid vegetative development, particularly rapid leaf area development, are strong candidates for increasing plant N storage capacity.

Minimising water-deficit limitation

In many areas, grain legumes are grown under water-limited conditions. Crops such as cowpea, pigeon pea, and chickpea are grown where soil water may be substantially limiting. Peanut is commonly grown on sandy soil with low water holding capacity. Yields are necessarily limited by the amount of water available to support growth. To quantify this relationship, the mechanistic expression of water-use efficiency derived by Tanner and Sinclair (1983) can be used. Rearranging their equation, the

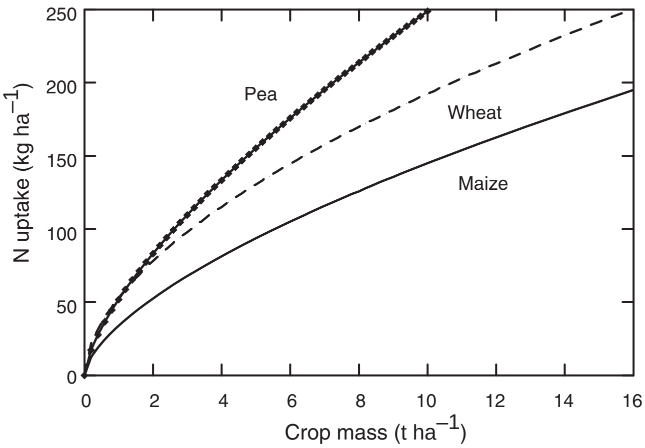

Fig. 4. Nitrogen uptake capacity as a result of nitrogen storage capability in the vegetative mass of pea, wheat, and maize based on relationships presented by Lemaire *et al.* (2008).

following expression of maximum grain yield (Y_{max}) is obtained.

$$Y_{max} \leq W * HI * k/VPD \tag{1}$$

where: W = total amount of water available for transpiration ($t\,ha^{-1}$), HI = harvest index, k = mechanistically defined transpiration coefficient (5–6 Pa for grain legumes), VPD = mean vapour pressure deficit weighted for daily transpiration rate distribution (VPD, Pa). The weighted daily VPD is ~75% of the difference between the maximum and minimum vapour pressure (Tanner and Sinclair 1983).

In water-limited environments, a grain legume crop may not have any more than 150 mm (1500 $t\,ha^{-1}$) of water available to it. Also, the season of growth is arid and the value of VPD may be 2.5 kPa (2500 Pa), or more. Assuming a grain legume crops with HI equal to 0.35 and a k value of 6 Pa, Y_{max} can be calculated as follows.

$$Y_{max} \leq 1500 * 0.35 * 6/2500 = 1.26\,t\,ha^{-1} \tag{2}$$

Clearly, high grain legume yields cannot be expected in such water-limited conditions. Doubling the available water to 300 mm will double yield to 3.52 $t\,ha^{-1}$.

Aside from irrigation, a possible plant trait that could be selected for genetic modification is plant behaviour to decrease the 'effective' VPD. While VPD is seemingly an environmental variable, the crop could have suppressed leaf gas exchange under high VPD conditions, usually midday, so that the effective daily VPD for transpiration is shifted to a lower value. If genotypes were selected that restricted transpiration during midday, the effective VPD appropriate for Eqn 2 might be only 2.0 kPa. In this case, the maximum yield for these genotypes is increased to 1.58 $t\,ha^{-1}$.

In fact, genotypes of several grain legumes have been identified that express a maximum transpiration rate. The soybean genotype PI 461937 was identified in soybean as having limiting leaf hydraulic conductance in the leaves resulting in a maximum transpiration rate (Sinclair *et al.* 2008). Devi *et al.* (2010) identified nine genotypes of peanut with approximately constant transpiration rates above a VPD ranging from 2.0 to 2.6 kPa. Zaman-Allah *et al.* (2011*b*) identified two peanut genotypes with reduced transpiration rates above 2.5 kPa. Figure 5 illustrates the differences in response in transpiration to increasing VPD among four peanut genotype. A search for this trait within the germplasm of all grain legumes selected for limited watered conditions is needed. In environments of intermittent drought, not only would this trait result in a lower effective VPD, but it would conserve soil water to extend the period that a crop can remain productive between rain events and avoid the consequences of severe drought.

On drying soil, another approach to shift the effective VPD to a lower value is to initiate midday decreases in stomatal conductance earlier in the soil drying cycle. Commonly, such restrictions on transpiration begin when the fraction of FTSW is in the range of 0.25–0.40. However, there are a few reports of genetic variation within a species for the threshold value of soil water where transpiration decreases. Hufstetler *et al.* (2007) compared the threshold among 21 soybean genotypes grown on a sandy soil and found significant genetic differences. Devi *et al.* (2009) compared the threshold for the decrease in transpiration of 17 peanut genotypes grown on a silty loam soil and found a wide range of 0.22–0.71 in the FTSW threshold for

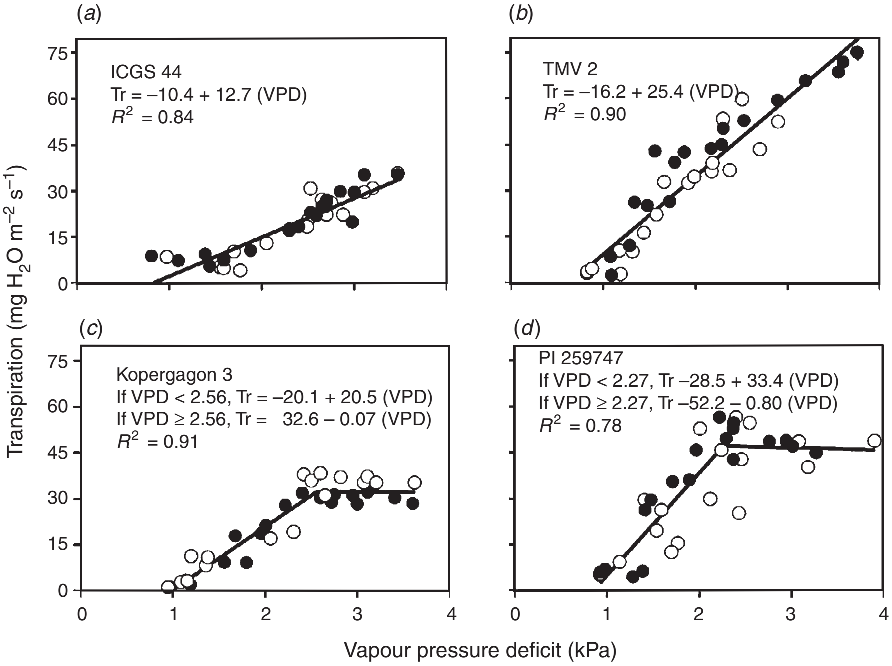

Fig. 5. Transpiration rate of four peanut genotypes when subjected to a range of vapour pressure deficits. The two symbols represent results from two experiments (Devi *et al.* 2010).

the initiation of restricted water loss. Zaman-Allah *et al*. (2011*b*) also found differences in the FTSW threshold for the transpiration decline in chickpea from 0.35 to 0.63. A variation in the FTSW threshold from 0.44 to 0.68 has been found in cowpea by Belko *et al*. (2012). Those genotypes with a high FTSW threshold would have a lower effective VPD when soil dries, and also confer the benefit of water conservation in environments of intermittent drought.

Grain legumes in future cropping systems

Despite the many benefits that grain legumes bring to the cropping system, they are often viewed as less important than cereals and the proportion of crop land area devoted to grain legume remains relatively low in many cropping systems. Below we review some of the challenges that seem to limit more widespread adoption of grain legume production, and possible solutions to promote legumes in cropping systems.

Improving legume disease resistance

As discussed above, the tissues of grain legumes are rich in N and P, which makes them attractive for herbivory and diseases. Peanut, for example, can be devastated by foliar and viral diseases. Aschochyta blight has destroyed the entire chickpea industry in Western Australia in the late nineties (Gan *et al.* 2006). In other areas, this disease has forced the chickpea crop to spring sowing to avoid the spread of the disease (Abbo *et al.* 2003). Flower thrips or root rot diseases are primary constraints to cowpea production in the Sahel (Jackai and Daoust 1986). While cereal crops also suffer pests and diseases, chemical solutions are often employed because cereals in contrast to grain legumes in many regions of the world are grown as cash crops resulting in immediate income. Small-holder farmers cannot afford the price of fungicide or insecticide to apply to grain legumes.

An opportunity to improve pest resistance of grain legumes is to use the most recent advances of molecular techniques to exploit resistant germplasm in breeding programs by introgressing resistance genes into popular cultivars. Disease resistance is often related to the action of one or few genes that are frequently easy to move in modern breeding programs. There are also an increasing number of disease resistance genes being identified. Model legume crops and syntenic relationships between legumes may allow identification of disease resistance clusters across species, thereby accelerating the rate of disease resistance improvement (Choi *et al.* 2004).

The assembly of structured and representative sets of germplasm from the entire legume collection would facilitate a more thorough exploration of existing disease resistance. In addition, the molecular genetic tools now allow the exploitation of disease resistance characteristics expressed in wild relatives of cultigens. For instance, in tetraploid cultivated peanut there exists no absolute resistance to early and late leaf spot and to rust, but absolute resistance is available in the diploid wild relative of peanuts (Pande and Rao 2001). In the case of peanut, the cultivated tetraploid was isolated from its wild diploid ancestor. However, recent work has re-created a tetraploid peanut from the 'forced' hybridisation of diploid ancestors and duplication of chromosomes (Simpson and Starr 2001), and these synthetic tetraploids are now used to harness these resistances for the benefit of the cultigens. An example of success using this approach has been reported in breeding peanut for root nematode resistance (Chu *et al.* 2007). There is also similar on-going work against aschochyta blight in chickpea in Western Australia. Several breeding lines have been developed from the aschochyta-sensitive 'Genesis' cultivar (Khan *et al.* 2009). Wild chickpea germplasm has also been used to introduce disease tolerance (Singh *et al.* 1998; Knights *et al.* 2008). Increasing disease resistance is a concrete possibility that would significantly decrease the risk of cultivating legumes and would enhance their attractiveness.

Availability of good quality seeds

Poor quality seeds lead to poor crop stands and low productivity. This is especially the case for the legume production of small-holder farmers that have no access to good quality seeds. In that context, an opportunity for improvement would be the creation and promotion of farmer-based seed production units, in close relation with breeding institutions. This would allow good quality seed production and enhance farmer access, and at the same time create a new livelihood from the price premium received from seed production (Shiferaw *et al.* 2008).

The reasons for poor quality seeds are numerous. As discussed previously, grain legumes are often grown under marginal conditions (e.g. Gowda *et al.* 2009) resulting in abiotic stress causing both low yield and low seed quality. That is, low rainfall or extreme temperatures during seed growth cause losses in seed germination potential. Also, the high N and P content of grain legume seeds makes them very attractive targets for diseases and insects (Rachie and Roberts 1974). Pod-sucking insects can directly attack seeds during seed development. Post-harvest pests can be a serious problem during seed storage, for instance bruchids in cowpea seeds (Fujii *et al.* 1989). Another post-harvest problem for legumes with seeds high in oil content is that the lipids may not be stable and they degrade in storage resulting in loss of seed quality.

Limited adoption of grain legumes

Despite the benefits of legumes, to provide a healthy and rich source of protein and minerals while also contributing to soil fertility, the adoption of grain legumes and the intensification of legume production in cereal-legumes systems remain low. This is the case even in areas with high human populations (Kerr *et al.* 2007). Therefore, breeding for more productive and resilient cultivars will be of no benefit if these efforts do not include bottom-up efforts to expand adoption of grain legumes by farmers. Therefore, one of the challenges that increasing grain legume production will face in the small-holder setting of developing countries will be to understand better the socioeconomic and cultural determinants of legume production and consumption. Of course, the lack of good seed as described above is a major limit to increasing yields and expanding grain legume production. In addition, grain legumes may have a greater labour requirement (weeding, harvesting) (Snapp *et al.* 2002) than cereals. Since grain legumes are often cultivated by women, and become a mainstay of the diet when populations cannot afford meat, there can be a negative stigma about the value of grain legumes. To expand the cultivation of grain legumes in less developed areas, all of these socioeconomic and cultural factors need to be well understood to fully unlock the potential of legumes to improve cropping systems and the livelihoods of these farmers (Sperling *et al.* 1993; Snapp and Silim 2002).

Legume residue for cattle feed

In small-holder settings, which are often mixed farming systems combining crop and livestock, the main component of cattle feed is often crop residues. In India, 40% of the cattle feed is crop residue and it is predicted that this share will increase to 70% by 2020 (Roy and Singh 2008). Most of those residues come from cereals, and legumes contribute only 10% of the total. To improve rumen digestion and animal growth, it will be necessary to have crop residue that has substantially greater N concentration than the 0.6–0.8% provided by cereal residue. A recent evaluation of fodder quality in the peanut germplasm clearly showed a range of variation for fodder N concentration that could be exploited in breeding programs (Blümmel *et al.* 2012). More importantly, there appears to be limited or no trade-off between fodder quality traits and grain productivity. So, there is clearly an opportunity to breed both for fodder quality and pod productivity in peanut. Important topics of investigation are to fully document the quality of grain legume residue as animal fodder, and the extent of the trade-off between fodder production and seed yield. In any case, in highly populated crop-livestock systems, higher quality feed residues from grain legumes have clearly an additive role to play in the economics of the legume value chain.

Legumes in the context of cropping systems

We envision that grain legumes will have an increasing place in cropping systems in the future in both less developed and developed regions of the world. A major reason for this prediction is that grain legumes can fulfil several roles: an immediate seed crop for consumption or marketing, a means to increase soil fertility as result of its nutrient rich residues, and a key component of livestock feed. In many cropping systems, grain legumes are likely to be needed to fulfill all three roles of increased seed yield, enhanced soil fertility, and cattle feed provider. The balance between these roles will be resolved by the relative economic return from marginal increases in seed yield as compared to retention of N and P in vegetative tissue for incorporation into soils and/or for animal fodder. For situations where the price of applying fertilisers severely limits the amount of fertiliser that can be economically applied to cereal crops, it could be necessary to rely on the preceding grain legume crop to leave plant residue that will supply N and P for the succeeding crop. In view of the increasing price of fertilisers, it seems likely the role of provider of nutrients will be increasing in most cropping systems. Clearly, grain legumes will remain the backbone of farming systems in poorly endowed areas, especially for their capacity to fix N.

Consequently, a major task in the future will be the selection of species and cultivars that can be used across various cropping systems, as previously shown (Snapp *et al.* 1998). A major consideration will be balancing legume grain production, which offers an immediate economic return, with the accumulation of N and P in the vegetation of the grain legume crop for the benefit of subsequent cereal crops in a cropping system. The trade-off between these two roles will be dictated by the perception of risk by farmers (Lawn 1989) and the local economic conditions of fertiliser price and grain price.

Genotypes will need to be developed that offer a range of return in the use of accumulated N and P for seed growth and for retention of nutrients in the vegetative mass to be retained in the field. One important consideration in growing legumes for improving soil fertility will be the temporal dynamics of N release from legume residues. It will be useful to have legumes that release nutrients from their organic residue that coincides with the period of highest demand by the subsequent crop. For example, pigeon pea has been shown to have a relatively slow release of N from its organic matter in comparison to other legume crops (Cadisch and Giller 1997).

Conclusions for research opportunities

Major research opportunities to enhance the roles of grain legumes exist in each of the topics discussed above. Several priority areas seem apparent. Nitrogen fixation activity of grain legumes needs to be enhanced. Instead of the common focus on the bacteria component of the N fixation symbiosis, the regulation of activity by the host plant needs to be fully appreciated. A major thrust is needed to identify plant characteristics and germplasm that allow greater N fixation capacity. The ability of the host plant to store fixed N appears to be a major component of increasing N fixation input. Also, limitations of abiotic stresses, particularly water deficit, require extensive investigation.

The unique ability of some legumes to accumulate P from forms normally unavailable in many soils needs to be fully investigated. Phosphorus is expensive, and is often a limiting resource in many cropping systems. Legumes that can recover normally unavailable forms of soil P could be major assets in future cropping systems. The retention of some P, and N, in the vegetative tissue to be returned to the soil after seed harvest could be a major advance in future cropping systems.

Finally, the range of potential roles of grain legumes in cropping systems needs to be appreciated in focusing future research. There is a need for expanded research on grain legumes to maximise their productivity in terms of N and P accumulation, and increased productivity both in terms of seed production and vegetative residue returned to the cropping system. Such investigations will include assessments of the grain legume species that might be most appropriate to fit the needs of each cropping system. In a world of increasing demands for plant products, including protein and oils, at the same time of greater economic and environmental pressures on cropping systems, it is apparent that grain legumes need to become a major component of future cropping systems.

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