Legumes: Importance and Constraints to Greater Use

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Legumes, broadly defined by their unusual flower structure, podded fruit, and the ability of 88% of the species examined to date to form nodules with rhizobia (de Faria et al., 1989), are second only to the Graminiae in their importance to humans. The 670 to 750 genera and 18,000 to 19,000 species of legumes (Polhill et al., 1981) include important grain, pasture, and agroforestry species. Cohen (1977; cited by Bryan [2000]) reported domestication of lentils (*Lens esculenta*) at a site in Iran dating to 9,500 to 8,000 BP; Roosevelt et al. (1996) noted the use of Hymenaea as a food source in Amazonian prehistory. Bean (*Phaseolus vulgaris*) and soybean (*Glycine max*), staple crops in the Americas and Asia, respectively, were each domesticated more than 3,000 years ago (Hymowitz and Singh, 1987; Kaplan and Lynch, 1999). Use of legumes in pastures and for soil improvement dates back to the Romans, with Varro (37 BC; cited by Fred et al. [1932]) noting "Legumes should be planted in light soils, not so much for their own crops as for the good they do to subsequent crops." This paper briefly overviews the legumes and their importance in different agricultural and natural environments.

GRAIN AND PASTURE PRODUCTION

Grain and forage legumes are grown on some 180 million Ha, or 12% to 15% of the Earth's arable surface (Table I). They account for 27% of the world's primary crop production, with grain legumes alone contributing 33% of the dietary protein nitrogen (N) needs of humans (Vance et al., 2000). Under subsistence conditions, the percentage of legume protein N in the diet can reach twice this figure. In rank order, bean, pea (*Pisum sativum*), chickpea (*Cicer arietinum*), broad bean (*Vicia faba*), pigeon pea (*Cajanus cajan*), cowpea (*Vigna unguiculata*), and lentil constitute the primary dietary legumes (National Academy of Science, 1994). Legumes (predominantly soybean and peanut [*Arachis hypogeae*]) provide more than 35% of the world's processed vegetable oil (Table II), and soybean and peanut are also rich sources of dietary protein for the chicken and pork industries. The potential of legume crops is evident in the huge increase in soybean production in Brazil, with national mean yields increased from 1,166 kg ha^{-1} in 1968 to 1969 to 2,567 kg ha^{-1} in 2001 to 2002 (M. Hungria, personal communication). This followed selection for later maturity, aluminum tolerance, and calcium-use efficiency (Spehar, 1995). In the same crop, the controversy over molecular engineering, with some countries refusing to grow transgenic soybean illustrates the need for balance in future breeding activities.

Unfortunately, improvement in legume crop yields have not kept pace with those of cereals. Jeuffroy and Ney (1997) note that wheat (*Triticum aestivum*) yields in France increased 120 kg ha^{-1} year^{-1} between 1981 and 1996; those for pea increased only 75 kg ha^{-1} year^{-1} over the same period. The situation is worse in the developing countries where Oram and Agcaoili (1992) note that pea yields are only 45%, and faba bean and chickpea are only 75%, of those achieved in developed countries. In part, this difference is due to the unfavorable environmental conditions under which many legume species are grown. Legumes are often grown after corn or rice and are seeded toward the end of the growing season. They may have short growing seasons and may be subject to intermittent or terminal drought. Progressive soil chemical and physical degradation and acid soil conditions may also limit their productivity.

Drought problems for legumes are likely to worsen with the projected rapid expansion of water-stressed areas of the world from 28 to 30 countries today to 50 countries encompassing 3 billion people by 2030 (Postel, 2000). There is a crucial need to increase drought tolerance in legumes; increasing salinity tolerance is a parallel requirement in many areas. The more drought-tolerant legumes, such as cowpea, are deeply rooted and may have reduced leaf size with thickened cuticles to reduce water loss. Less tolerant legumes such as beans can be selected for early maturity, efficiency in the partitioning of nutrients toward reproductive structures, and phenotypic plasticity (Beaver et al., 2003). Pinto Villa, now grown over 90% of the pinto bean area in Mexico, has these characteristics.

Nutrient depletion of soil is a particular problem for small landholders in developing countries, where much grain-legume production occurs, and many farmers cannot afford to use fertilizers. Sanchez (2002) suggests average annual nutrient depletion rates across 37 African countries of 22 kg N ha^{-1}, 2.5 kg P ha^{-1}, and 15 kg K ha^{-1}. Soil acidity affects more

Table I. *Crop production and area harvested*

Source: Food and Agriculture Organization of the United Nations (FAO) database (http://apps.fao.org/page/collections).

Crop	Production	Area Harvested
	$Mt \times 10^6$	$ha \times 10^6$
Grain legumes	275	160
Forage legumes	605	20
Wheat	583	214
Rice (*Oryza sativa*)	590	152
Maize (*Zea mays*)	609	138
Barley (*Hordeum vulgare*)	141	54
Potatoes (*Solanum tuberosum*)	308	19
Cassava (*Manihot esculenta* Crantz.)	179	20
Total	3,320	777

than 1.5 billion ha worldwide, with acid soil constraints to legume production likely to increase as the result of acid rain, long-term N fertilization, and natural weathering (Graham and Vance, 2000). H ion concentration per se, Al and Mn toxicity, and P, Mo, or Ca deficiency all contribute to the problem (Graham, 1992). Nodulation and N fixation and survival of rhizobia in soil are particularly affected under low P, acid soil conditions and will be considered in more detail later in this paper.

Diseases and pests are also major constraints to legume production, especially in the tropics and subtropics. In common bean, for example, important pathogens include several viruses, fungi-causing root rots, anthracnose, angular leaf spot, bean rust, white mold and web blight, and the bacteria responsible for common bacterial blight and halo blight (Coyne et al., 2003). In Minnesota alone, losses due to root rot are estimated at $4 million annually. A number of these pathogens are seed transmitted; others can be carried by insects. Limiting crop losses requires an integrated approach that may include certified seed programs, fallow periods to reduce vector populations, plowing to bury infected plant tissue, biological control of root disease, chemical application, and resistance breeding (Beaver et al., 2003; Coyne et al., 2003). Molecular markers have permitted rapid progress in disease resistance breeding in beans (Kelly et al., 2003), but many of the measures suggested above are beyond the resources of the subsistence farmer, which is another reason why legume yields in third-world countries are low.

Use of legumes in the human diet can also be problematic. Legume seeds generally contain 20% to 30% protein and are Lys rich, complementing the nutritional profiles of cereals and tubers in the diet (Duranti and Gius, 1997). However, legumes are limited in sulfur amino acids, contain antinutritional factors including lectins and flatulence factors, and are commonly hard to cook. Preference for particular grain types or seed color also affects marketability.

Forage legumes have been the foundation for dairy and meat production for centuries (Russelle, 2001). When properly managed, they are rich sources of

protein, fiber, and energy. Even in intensive animal and milk production, where grain crops are major feed sources, forage legumes are required to maintain animal health (Wattiaux and Howard, 2001). Meat and dairy production in developing countries is almost solely dependent upon forage legumes and grasses. Alfalfa (*Medicago sativa*) is the prevalent forage legume in temperate climates (Russelle, 2001), with more than 72 million Mg of alfalfa worth $7 billion produced annually in the U.S. alone. Alfalfa is the third or fourth most valuable crop in the U.S. (U.S. Department of Agriculture, National Agricultural Statistics Service, http://www.nass.usda.gov:81/ipedb/hay.htm). Other important temperate pasture species include clovers (*Trifolium* spp.), trefoil (*Lotus corniculatus*), sweetclovers (*Melilotus* spp.), and vetches (*Vicia* spp.).

Inclusion of legumes is critical for sustainable meat and dairy production on the infertile savannah soils of the tropics and subtropics (Consultative Group on International Agricultural Research, http://www.cgiar.org/research/res_cattle.html). Incorporation of improved legumes into these ecosystems has lagged due to lack of information, seed costs, and poor infrastructure. Species from the genera *Aeschynomene*, *Arachis*, *Centrosema*, *Desmodium*, *Macroptilium*, and *Stylosanthes* offer promise for improved tropical pasture systems (Thomas and Sumberg, 1995; Giller, 2001). Of these, *Stylosanthes* spp. with some 30 species distributed throughout the tropics (de Leeuw et al., 1994), has been most widely adopted, with *Stylosanthes guyanensis* and *Stylosanthes hamata* now grown as improved pasture in Australia, China, Latin America, and West Africa.

Presently underutilized crop and pasture legumes could still emerge. Ladizinsky and Smartt (2000) address opportunities for improved adaptation via further domestication. More exotic examples include marama bean (*Tylosema esculentum*; Dakora et al., 1999), sword beans (*Canavalia gladiata*; Ekanayake et al., 2000), and *Desmanthus illinoensis* among grain crops, and annual medics and *Biserrula pelecinus* among pasture species (Howieson et al., 1995, 2000).

Table II. *Major crops oil production*

Source: FAO Database (http://apps.fao.org/page/collections).

Crop	Oil Production
	$Mt \times 10^6$
Soybean	26.8
Peanut	5.3
Palm	23.9
Canola (*Brassica napus*)	12.6
Sunflower (*Helianthus annuus*)	9.1
Cotton (*Gossypium hirsutum*)	4.1
Olive	2.7
Coconut (*Cocos nucifera*)	3.6
Maize	2.0
Total	90.1

Again, germplasm collection and evaluation must continue to be a research emphasis.

AGROFORESTRY

Sprent and Parsons (2000) discuss the importance of woody tree legumes in forestry. Important genera include *Acacia*, *Anadenathera*, *Calliandra*, *Dalbergia*, *Erythrina*, *Gliricidia*, *Melanoxylon*, *Parkea*, *Prosopis*, *Pterocarpus*, and *Samanea*. Values for the percentage of plant N derived from fixation in such species listed by Giller (2001) range from 2% to 100% but need to be treated with caution. J. Grossman (personal communication) suggests that *Inga oerstediana*, widely used in southern Mexico as a shade tree with coffee, may not even be capable of establishing an effective symbiosis.

Food security issues, pressure on the land, and increasing soil degradation (Franzluebbers et al., 1998; Cassman, 1999; Sanchez, 2002) have led to increasing research interest in tree-fallow and alley-cropping systems for subsistence farmers in Africa and Asia. These are reviewed by Buresh et al. (1997) and by Buresh and Cooper (1999). In tree fallows, *Sesbania* spp., *Leucaena* spp., *Tephrosia* spp., *Crotalaria* spp., *Glyricidia* spp., or *Cajanus* spp. are interplanted into corn, and allowed to grow as dry-season or longer-term fallows. The wood is harvested, and the N-rich leaves, pods, and green stem material are hoed into the soil just before the rainy season (Sanchez, 1999). Gathumbi et al. (2002) reported aboveground biomass production in a 6-month period of 8 to 15 Mg ha^{-1}, with total N accumulation of 100 to 178 kg ha^{-1}. Significant crop yield increases in the season after tree fallow have been reported. Legume tree fodder with high levels of crude protein and minerals, and in some cases, good digestibility is readily accepted by livestock. Fertilization with rock phosphate is often needed to improve the N benefits from tree fallows.

Alley cropping, with crops grown between hedgerows, and tree prunings used as mulch or green manure can also provide significant N to the interspersed crop. In Costa Rica, *Phaseolus* spp. beans grown between *Erythrina poeppigiana* rows and supplied prunings from these trees yielded 15% to 50% more than beans grown in monoculture (Henriksen et al., 2002). *Sesbania* sp. has been used similarly for alley cropping in rice. Nevertheless, Giller (2001) points to problems with this system, including competition for moisture between trees and crop plants, and declining yield benefits over time on infertile or acid soils.

The increased role for N-fixing legumes under subsistence conditions has recently been recognized with the award of the 2002 World Food Prize to Dr. Pedro Sanchez, former director-general of the International Center for Research in Agroforestry.

NATURAL ECOSYSTEMS

N is the primary nutrient limiting plant production in most natural ecosystems (Seastedt and Knapp, 1993; Vitousek et al., 1997). Legumes, through their symbiotic abilities, can play an important role in colonizing disturbed ecosystems, including those that are fire prone (Arianoutsou and Thanos, 1996). Rates of N$_2$ fixation in such environments are often low, but can still satisfy much of the legume's N needs. B. Tlusty and P.H. Graham (personal communication) found the percentage of plant N derived from fixation values for five legumes in a seeded and inoculated long-grass prairie to range from 36% to almost 100%. Spehn et al. (2002) examined plant species and functional groupings among grassland communities in seven countries in Europe. Two years after sowing, the presence of legumes affected N pool size in five of the seven sites. Such a build-up in soil N is probably not open ended, because Pearson and Vitousek (2001) noted a 10- to 20-fold decline in nodule mass and N fixation between 6- and 20-year-old regenerating stands of *Acacia koa*. A model developed by Vitousek and Field (1999) associated reduction in N$_2$ fixation with shade, P limitation, and grazing.

Atmospheric CO$_2$ enrichment and N deposition, each a major ecological concern, are likely to have opposing effects in natural ecosystems. Hardy and Havelka (1976) showed N$_2$ fixation enhanced under CO$_2$ enrichment, and both legume biomass and frequency were enhanced in free-air CO$_2$ enrichment studies (Reich et al., 2001; Teyssonneyre et al., 2002). Total N in *Lespedeza capitata* and *Lupinus perrenis* increased 58.3% and 32.0%, respectively at 560 μmol mol^{-1} CO$_2$ (Reich et al., 2001). In contrast, C$_3$ and C$_4$ grasses were responsive to N deposition, whereas legumes showing little response. Influence of N on legume/grass balance in pastures is well documented. In a model developed by Thornley et al. (1995), the legume fraction in pasture declined from 18% to 1% as N supply was increased.

INDUSTRIAL AND MEDICINAL USE OF LEGUMES

In addition to traditional food and forage uses, legumes can be milled into flour, used to make bread, doughnuts, tortillas, chips, spreads, and extruded snacks (R. Phillips personal communication) or used in liquid form to produce milks, yogurt, and infant formula (Garcia et al., 1998). Pop beans (Popenoe et al., 1989), licorice (*Glycyrrhiza glabra*; Kindscher, 1992), and soybean candy (Genta et al., 2002) provide novel uses for specific legumes.

Legumes have been used industrially to prepare biodegradable plastics (Paetau et al., 1994), oils, gums, dyes, and inks (Morris, 1997). Galactomannan gums derived from *Cyamopsis* spp. and *Sesbania* spp. are used in sizing textiles and paper, as a thickener, and in pill formulation.

Many legumes have been used in folk medicine (Duke, 1992; Kindscher, 1992). Isoflavones from soybeans and other legumes have more recently been suggested both to reduce the risks of cancer and to lower serum cholesterol (Kennedy, 1995; Molteni et al., 1995). Soybean and soyfood phytoestrogens have been suggested as possible alternatives to hormone replacement therapy for postmenopausal women.

Several U.S. cities and states now require that fleet vehicles be powered in part by biodiesel fuel from soybean. Some states require that biodiesel be included at a fixed percentage in all diesel fuels (http://www.biodiesel.org).

BIOLOGICAL N FIXATION

A hallmark trait of legumes is their ability to develop root nodules and to fix N_2 in symbiosis with compatible rhizobia. This is often a critical factor in their suitability for the uses outlined above.

Formation of symbiotically effective root nodules involves signaling between host and microsymbiont. Flavonoids and/or isoflavonoids released from the root of the legume host induce transcription of nodulation genes in compatible rhizobia, leading to the formation of lipochitooligosaccharide molecules that, in turn, signal the host plant to begin nodule formation (Long, 1996). Numerous changes occur in host and bacterial gene expression during infection, nodule development, and function (Vance, 2002), with approximately 100 host legume and rhizobial genes involved.

Some 40 to 60 million metric tons (Mt) of N_2 are fixed by agriculturally important legumes annually, with another 3 to 5 million Mt fixed by legumes in natural ecosystems (Smil, 1999). This is amazing efficiency given the miniscule quantities of nitrogenase involved (Delwiche, 1970).

Why is symbiotic N fixation in legumes so important? In addition to its role as a source of protein N in the diet, N from legume fixation is essentially "free" N for use by the host plant or by associated or subsequent crops. Replacing it with fertilizer N would cost $7 to 10 billion annually, whereas even modest use of alfalfa in rotation with corn could save farmers in the U.S. $200 to 300 million (Peterson and Russelle, 1991). Furthermore, fertilizer N is frequently unavailable to subsistence farmers, leaving them dependent on N_2 fixation by legumes or other N_2-fixing organisms.

One of the driving forces behind agricultural sustainability is effective management of N in the environment (Graham and Vance, 2000). Application of fertilizer N increased approximately 10-fold to 90 million Mt between 1950 and 1995 (Frink et al., 1999) with significant energy consumption for N fertilizer synthesis and application. Further increases in N needs for agriculture are projected for the period to 2030 (Tilman, 1999), and these needs will contribute to environmental pollution. To the extent that farming practices can make use of the more economically viable and environmentally prudent N_2 fixation (Peoples et al., 1995; Vance, 2001), agriculture and the environment will benefit. The ability of legumes to sequester C has also been seen as a means to offset increases in atmospheric CO_2 levels while enhancing soil quality and tilth. Resh et al. (2002) found that soils under N_2-fixing trees sequestered 0.11 ± 0.07 kg m^2 $year^{-1}$ of soil organic carbon, whereas there was no change under *Eucalyptus* spp. Carbon sequestration under *Prosopis* spp. has also been reported.

Giller (2001) suggests that rates of N_2 fixation of 1 to 2 kg N ha^{-1} growing season day^{-1} should be possible in all legumes. Rates reported by Unkovich and Pate (2000) and van Kessel and Hartley (2000) are clearly less than this, with the latter authors reporting a decline in average N_2 fixation rate for both soybean and beans over the period since 1985. Constraints to N_2 fixation include drought (Sinclair et al., 1987), soil acidity, N fertilization, and nutrient limitations. Many cultivars also show only limited ability to fix N_2 in symbiosis.

Management of soil acidity for temperate and tropical regions has often differed but increasingly depends on acid-tolerant legume cultivars and rhizobia (Howieson et al., 2000), with soil liming only to a pH at which Al and Mn are no longer toxic. Acid soil management was of critical importance in opening the Brasilian Cerrado to agriculture, but it was serendipitous that the acid-tolerant *Rhizobium tropici* could replace other less tolerant bean rhizobia (Hungria et al., 1997). Identification of additional acid-tolerant host and rhizobial germplasm and the deployment of acid tolerance genes such as occur in *R. tropici* CIAT899 (Graham et al., 1982) are priority areas.

Maximum benefits from N_2 fixation depend on soil P availability (Kennedy and Cocking, 1997), with 33% of the world's arable land limited in P (Sanchez and Euhara, 1980). Acid-weathered soils of the tropics and subtropics are particularly prone to P deficiency. Even where P fertilization is adequate, <15% of that P may be taken up by plants in the first year (Holford, 1998). Perhaps of greater concern, reserves of rock phosphate could be depleted in only 60 to 90 years (Abelson, 1999).

Plants dependent on symbiotic N_2 fixation have ATP requirements for nodule development and function (Ribet and Drevon, 1996) and need additional P for signal transduction and membrane biosynthesis. Phosphorus concentrations in the nodule are often significantly higher than those in shoot or root tissue (Israel, 1987). Al-Niemi et al. (1997) suggest that bacteroids can be P limited even when plants have received otherwise adequate P levels. Given this requirement for symbiosis, approaches leading to improved P acquisition and use in legumes (rhizosphere acidification, acid phosphatase secretion, root

architectural changes at low P, enhanced P transport and use-efficiency, and functional differences in mycorrhizal symbioses) all need further study. White lupine (*Lupinus albus*) and common bean are excellent model legumes for such studies. Each undergoes change in root architecture and rhizosphere chemistry at low P (Johnson et al., 1996; Nielsen et al., 1998; Miller et al., 2001), improving soil exploration and phosphate scavenging. Transgenic alfalfa has proved extremely useful in understanding the genetic and molecular basis of low soil P, acid, and aluminum stress responses (Tesfaye et al., 2001). Results in this study highlight the need for more effective transformation and regeneration protocols in the more recalcitrant legumes, including bean and cowpea. Progress in the study of nodulation and N_2 fixation under drought or salinity stress has been minimal, largely because the legume and the process of nodulation are more susceptible to these constraints than is the microorganism.

SYNOPSIS

Legumes play a critical role in natural ecosystems, agriculture, and agroforestry, where their ability to fix N in symbiosis makes them excellent colonizers of low-N environments, and economic and environmentally friendly crop, pasture, and tree species. Legume yields unfortunately continue to lag behind those of cereals. A research orientation that better balances the needs of third-world or sustainability-oriented agriculture with the breakthrough technologies of genomics and bioinformatics is needed. It requires stronger and more adventurous breeding programs, better use of marker-assisted technologies, and emphasis on disease resistance, enhanced N fixation, and tolerance to edaphic soil constraints. It also requires extension of existing low-cost technologies, such as rhizobial inoculation, to the small farmer. To paraphrase a comment by Catroux et al. (2001) "we enter the era of biotechnology knowing more and more about the growth of legumes at the gene level, but except for some producers in developed countries, unable to effectively translate these into major gains in productivity."

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