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Critical Reviews in Plant Sciences

ISSN: 0735-2689 (Print) 1549-7836 (Online) Journal homepage: https://www.tandfonline.com/loi/bpts20

Legume Crops Phylogeny and Genetic Diversity for Science and Breeding

Petr Smýkal, Clarice J. Coyne, Mike J. Ambrose, Nigel Maxted, Hanno Schaefer, Matthew W. Blair, Jens Berger, Stephanie L. Greene, Matthew N. Nelson, Naghmeh Besharat, Tomáš Vymyslický, Cengiz Toker, Rachit K. Saxena, Manish Roorkiwal, Manish K. Pandey, Jinguo Hu, Ying H. Li, Li X. Wang, Yong Guo, Li J. Qiu, Robert J. Redden & Rajeev K. Varshney

To cite this article: Petr Smýkal, Clarice J. Coyne, Mike J. Ambrose, Nigel Maxted, Hanno Schaefer, Matthew W. Blair, Jens Berger, Stephanie L. Greene, Matthew N. Nelson, Naghmeh Besharat, Tomáš Vymyslický, Cengiz Toker, Rachit K. Saxena, Manish Roorkiwal, Manish K. Pandey, Jinguo Hu, Ying H. Li, Li X. Wang, Yong Guo, Li J. Qiu, Robert J. Redden & Rajeev K. Varshney (2015) Legume Crops Phylogeny and Genetic Diversity for Science and Breeding, Critical Reviews in Plant Sciences, 34:1-3, 43-104, DOI: 10.1080/07352689.2014.897904

To link to this article: https://doi.org/10.1080/07352689.2014.897904

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Published online: 24 Oct 2014.

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Critical Reviews in Plant Sciences, 34:43–104, 2015
Published with license by Taylor & Francis
ISSN: 0735-2689 print / 1549-7836 online
DOI: 10.1080/07352689.2014.897904

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Legume Crops Phylogeny and Genetic Diversity for Science and Breeding

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Economically, legumes (Fabaceae) represent the second most important family of crop plants after the grass family, Poaceae. Grain legumes account for 27% of world crop production and provide 33% of the dietary protein consumed by humans, while pasture and forage legumes provide vital part of animal feed. Fabaceae, the third largest family of flowering plants, has traditionally been divided into the following three subfamilies: Caesalpinioideae, Mimosoideae, and Papilionoideae, all together with 800 genera and 20,000 species. The latter subfamily contains most of the major cultivated food and feed crops. Among the grain legumes are some of mankind's earliest crop plants, whose domestication parallelled that of cereals: Soybean in China; faba bean, lentil, chickpea and pea in the Fertile Crescent of the Near East; cowpeas and bambara groundnut in Africa; soybean and mungbeans in East Asia; pigeonpea and the grams in South Asia; and common bean, lima bean, scarlet runner bean, tepary bean and lupin in Central and South America. The importance of legumes is evidenced by their high representation in *ex situ* germplasm collections, with more than 1,000,000 accessions worldwide. A detailed knowledge of the phylogenetic relationships of the Fabaceae is essential for understanding the origin and diversification of this economically and ecologically important family of angiosperms. This review aims to combine the phylogenetic and genetic diversity approaches to better illustrate the origin, domestication history and preserved germplasm of major legume crops from 13 genera of six tribes and to indicate further potential both for science and agriculture.

Keywords crop wild relatives, domestication, genetic diversity, introgression, legumes, phylogeny, Fabaceae

I. INTRODUCTION

Fabaceae (Leguminosae), with 800 genera and 20,000 species (Lewis *et al.*, 2005), is the third largest family of flowering plants, after the Orchidaceae and Asteraceae. It is an extremely diverse family with worldwide distribution, encompassing a broad range of life forms, from arctic alpine herbs and temperate or tropical perennial shrubs to annual xerophytes and equatorial giant trees. Some legumes are weeds of cereal agriculture, while others are major grain crops in their own right. These latter species are known as grain legumes, or pulses, and together with two pasture and forage legumes are the focus of this review. Members of the Fabaceae are characterized by the distinct fruit, termed a legume, which gives the family its original name. Flower structure is highly variable; however, the butterfly-like (papilionoid) flower is almost universal in the Papilionoideae subfamily (∼14,000 species). Fabaceae includes many economically important and versatile species, with the majority providing grains and pulses. Among the grain legumes are some of humanity's earliest crop plants, including soybean and mungbean in East Asia; faba bean, lentil, chickpea and pea in the Fertile Crescent of the Near East; and common bean or lupin in Central and South America. Legumes' symbiosis with nitrogen-fixing bacteria provides not only added value in agriculture, but also plays an important role in natural ecosystems. Moreover, the legume species *Pisum sativum* L., pea, was the key experimental organism for Mendel's pioneering work (1866) in establishing the underlying basis of heredity (Smýkal, 2014).

Reconstructing the phylogenetic relationship of the Fabaceae is essential to understanding the origin and diversification of this family. Phylogenetic analyses of Fabaceae began with the plastid *rbcL* gene (Doyle, 1995; Kass and Wink, 1997), followed by analyses including the more variable *matK* gene (Wojciechowski *et al.*, 2004; reviewed in Lewis *et al.*, 2005). Both are now accepted as barcoding regions for plants (CBOL, 2009). The picture is far from complete, however, as many species have not yet been sequenced or are represented by just one or two accessions. Nonetheless, for chickpea, common bean, cowpea and soybean, as well as for the model legumes *Medicago truncatula* Gaertn. and *Lotus japonica* (Regel) K. Larson, rapid progress has been made. The monophyly of the family has been repeatedly demonstrated through molecular systematics (Doyle *et al.*, 1995; Kass and Wink, 1997; Wojciechowski, 2003). Currently, based on morphological characters, the following three major groups are recognized and regarded as subfamilies: The mimosoid legumes, Mimosoideae (sometimes regarded as family Mimosaceae with four tribes and 3,270 species); the papilionoid legumes, Papilionoideae (or family Fabaceae/Papilionaceae with 28 tribes and 13,800 species); and the caesalpinioid legumes, Caesalpinoideae (or family Caesalpiniaceae with four tribes and 2,250 species) (Lewis *et al.*, 2005). Estimates for the date of origin and early evolution of the legumes vary, but a rich Eocene macrofossil record shows that some lineages of the family existed by around 50 million years ago (Mya). The earliest known legume pollen remains date back to about 60-75 Mya (Lavin *et al.*, 2005; Wojciechowski, 2003), predating the macrofossils.

Papilionoideae is a monophyletic group, according to all recent phylogenetic analyses, making it by far the largest subfamily, with 476 genera and about 14,000 species. It is estimated that all papilionoids shared a common ancestor, which experienced a 50 kb inversion in its chloroplast genome (Doyle *et al.*, 1995; Lavin *et al.*, 2005), around 50 Mya. The largest group of papilionoids is Hologalegina, with nearly 4,000 species in 75 genera, including the large galegoid tribes (Galegeae, Fabeae, Trifolieae, Genisteae, etc.), united by the loss of one copy of the chloroplast inverted repeat (IR), often referred as the IR-loss clade. Of great economic and scientific interest are the Fabeae and Trifolieae, which together comprise 11 genera and nearly 800 species. The tribe Genisteae belongs to the basal Genistoid clade, which diverged early in the evolution of the Papilionoid legumes (Lavin *et al.*, 2005). Like other Genistoid legumes, Genisteae species synthesize quinolizidine alkaloids, bitter compounds that provide a defense against pathogens and predators (Bunsupa *et al.*, 2013; Wink and Mohamed, 2003).

When cultivated grain legumes, or pulses, are considered, the Papilionoideae can be divided into the following four clades (Figure 1): (1) Phaseoloids (*Glycine* Willd., *Phaseolus* L., *Cajanus* L. and *Vigna* Savi), (2) Galegoids (*Pisum* L., *Lens* Mill.,

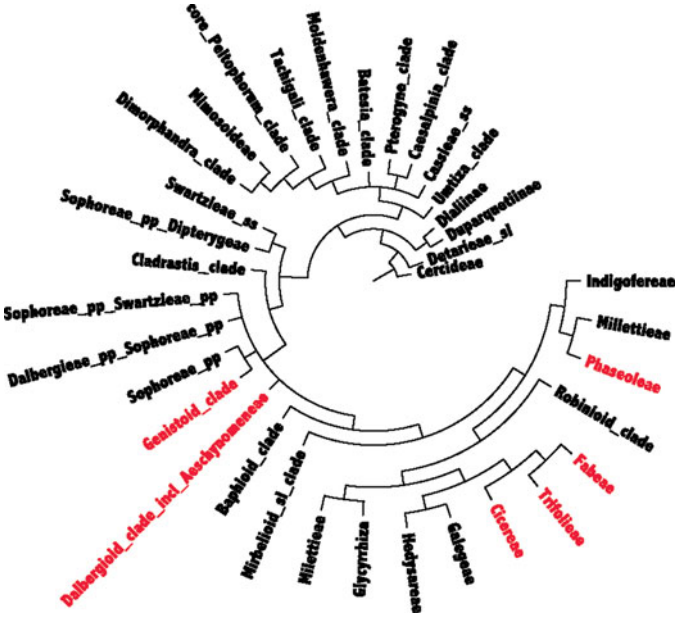


FIG. 1. Overview cladogram for the family Fabaceae based on tree of life (http://tolweb.org/tree/) information. Clades with major crops that are discussed in the review are highlighted in red. Abbreviations: pp - (partly), sl - *sensu lato* (broadly circumscribed), ss - *sensu stricto* (narrowly circumscribed).

Lathyrus L., *Vicia* L., *Medicago* L. and *Cicer* L.), (3) Genistoids (*Lupinus* L.) and (4) Dalbergoids (*Arachis* L. and *Stylosanthes* Sw.) (Lewis *et al.*, 2005). Phaseoloids are pan-tropical and often referred to as "warm season," "tropical" or "millettioid" clade. By contrast, Galegoids are often referred to as "cool-season," "temperate" or "Hologalegina" legume crops, since they are mainly distributed in temperate regions of the world, such as Europe and the Mediterranean.

The Mimosoideae and Caesalpinoideae are mostly woody trees and shrubs. Many are valuable for timber (*Acacia* spp. Mill., *Albizia* Benth., *Dalbergia* L.f.), dyes (*Indigofera tinctoria* L., *Haematoxylon campechianum* L., *Caesalpina brasiliensis* L.), tannins (*Acacia dealbata* Link., *A. decurrens* Desv.), resins (*Trachylobium verrucosum* (Gaertn.) Oliv), gums (*Senegalia senegal* Britton), insecticides (*Derris elliptica* (Wall.) Benth), medicines (*Cassia alata* (L.) Roxb., *Senna occidentalis* (L.) Link.), food (*Tamarindus indicus* L., *Ceratonia siliqua* L., *Leucaena esculenta* Sesse & Moc. Ex DC.) Benth.) and animal fodder (*Bauhinia* spp. L.).

This review aims to combine the phylogenetic and genetic diversity approaches to better illustrate the origin, domestication history and preserved germplasm of major legume crops from 13 genera of six tribes (Table 1) and to indicate further potential in both science and agriculture.

A. Genetic Diversity Conserved in *Ex Situ* Germplasm Collections and Its Characterization

Ex situ conservation was pioneered by N.I. Vavilov in 1926. Currently, 1,750 germplasm collections hold over 7 million crop plant accessions worldwide (FAO, 2010). Legumes (grain and forage) constitute the second largest group (1,041,345 accessions, 15% of all [FAO, 2010]) after cereals. The study of genetic diversity for both germplasm management and breeding has received much attention, especially following the introduction of the core collection concept by Frankel and Brown (1984). However, in practice, even the core collection approach did not help to fully characterize genetic diversity or use it in breeding.

The conserved germplasm is characterized for distinct morpho-agronomic traits, using sets of crop-specific descriptors. Approximately 78% of the 146,837 grain legume germplasm accessions held in CGIAR centers have been characterized for morphological traits, including for resistance to biotic and abiotic stresses. However, only a small percentage of these collections have been characterized for biochemical traits. More emphasis and funding are needed in order to generate data on biochemical characteristics associated with biotic and abiotic stresses (Upadhyaya *et al.*, 2011). The Global Crop Diversity Trust (GCDT) supports the development of global crops (including legumes) and regional strategies for *ex situ* conservation and utilization of crop diversity. These strategies represent a major investment in the field of plant genetic resources (PGR), mobilizing experts to collaboratively plan for the more efficient and effective conservation and the use of crop diversity. The themes viewed under these strategies include regeneration, crop wild relatives (CWR), collecting, crop descriptors, information systems, user priorities, new technologies and research, and challenges to building a strategy for rational conservation (Khoury *et al.*, 2010). There is an urgency to ensure that the diversity in landraces is sampled and conserved in *ex situ* genebanks, especially as farming evolves from subsistence to a market-orientated endeavor dominated by modern cultivars and resulting in the erosion of crop genetic diversity. A similar caution also applies to the *in situ* populations of wild relatives, as land use intensifies with urban expansion and climate change threatens ecology (Snook *et al.*, 2011). A further development in targeting germplasm for key traits is to use a GPS map of landrace collection sites, which can be overlaid with climate data corresponding to vegetative and reproductive growth stages, and to identify landraces corresponding to sites with severe abiotic stresses during the previous 25 years. The landraces encompass much of the original diversity, plus accumulated mutations and genetic recombinations since domestication. These landraces are now disappearing, replaced by improved, higher yielding modern cultivars from modern breeding programs, as exemplified on recent collecting missions in China (Bao *et al.*, 2008; He *at al.*, 2008). On the premise that such landraces may have had natural selection for tolerances to these stresses, Li Ling *et al.* (2013) identified pea landraces from China as priority candidates to evaluate for tolerance of reproductive frost stress, reproductive heat stress, and drought tolerance.

Adoption of the Germplasm Resource Information Network (GRIN-Global) database by international centers and national genebanks will allow for online queries across multiple

TABLE 1

List of taxonomical species, and current number of germplasm stored accessions of major legume crops and their gene pools

Genus	Number of taxonomic species	Number of domesti-cated/cultivated species	Species	Major crops	Number of species in genebanks	Number of accessions in germplasm	Primary genepool (GP1a, b) Based upon the Harlan and de Wet gene pool concept (1971)	Secondary genepool (GP2)	Tertiary genepool (GP3)	Crop wild relatives - priority species	References
Fabeae tribe											
Pisum	3	2	*P. sativum*, *P. sativum* subsp. *abysssinicum*	Pea	3	98,947	*Pisum sativum* subsp. *sativum*, subps. *elatius*	*P. fulvum, P. abyssinicum*	*Vavilovia formosa*	*Pisum sativum* subsp. *sativum*, *subps. elatius*, *P. fulvum*	Ambrose and Maxted, 2001; Smýkal *et al.*, 2011, 2013
Vicia	160–200	1 to 4 / 17 taxa cultivated	*V. faba* *V. narbonensis* *V. sativa*, *V. ervilia*	Faba Bean	95	38,000 (*V. faba*)	*V. faba*, *V. faba* subsp. *paucijuga*,*V. faba* subsp. *faba*, *V. faba* subsp. *faba* var. *minor*, *V. faba* subsp. *faba var. equina*, *V. faba* subsp. *faba* var. *faba* cultivars and landraces	no for *V. faba*	*V. kalakhensis* *V. johannis* *V. johannis* var. *ecirrhosa* *V. johannis* var. *procumbens* *V. johannis* var. *johannis*	*V. eristalioides*, *V. bithynica*, *V. eristalioides*, *V. galilaea*, *V. hyaeniscyamus*, *V. johannis*, *V. kalakhensis*, *V. narbonensis*, *V. serratifolia*	Duc *et al.*, 2010; http://gisweb.ciat.cgiar.org/GapAnalysis
Lens	5	1	*L. culinaris* subsp. *culinaris*	Lentil	6	58,407	*L. culinaris* subsp. *culinaris* cultivars and landraces, *L. culinaris* subsp. *tomentosus*, *L. culinaris* subsp. *odemensis*, *L. culinaris* subsp. *orientalis*	*L. ervoides, L. nigricans*	*L. lamottei*	*L. culinaris* subsp. *orientalis*, *L. odemensis*, *L. tomentosus*, *L. lamottei*, *L. nigricans*, *L.ervoides*	Tullu *et al.*, 2011; http://gisweb.ciat.cgiar.org/GapAnalysis
Lathyrus	160	4 / 4 taxa cultivated	*L. sativus*, *L. ochrus*, *L. clymenum*, *L. cicera,* cultivated (*L. tingitanus, L. latifolius*, *L. odoratus*, *L. sylvestris*)	Grasspea	46	3,043 *Lathyrus* sp. plus 12,133 of *L. sativus*	*L. sativus*, *L. ochrus*, *L. clymenum*, *L. cicera*	*L. chrysanthus, L. gorgoni, L.marmoratus, L. pseudocicera, L. amphicarpus, L. blepharicarpus, L. chloranthus, L. hierosolymitanus L. hirsutus*	*Lathyrus sp.*	*L. cicera, L. amphicarpos*, *L. belinensis*, *L. chrysanthus*, *L. hirticarpus*, *L. hirsutus*, *L. marmoratus*	Shehadeh *et al.*, 2013

(Continued on next page)

TABLE 1
List of taxonomical species, and current number of germplasm stored accessions of major legume crops and their gene pools *(Continued)*

Genus	Number of taxonomic species	Number of domesticated/cultivated species	Species	Major crops	Number of species in genebanks	Number of accessions in germplasm	Primary genepool (GP1a, b) Based upon the Harlan and de Wet gene pool concept (1971)	Secondary genepool (GP2)	Tertiary genepool (GP3)	crop wild relatives - priority species	References
Trifolieae tribe											
Trifolium	255	16	*T. pratense*, *T. repens*, *T. hybridum*, *T. resupinatum*, *T. subterraneum*, *T. incarnatum*, *T. alexandrinum*, *T. campestre*, *T. ambiguum*, *T. nigrescens*, *T. pannonicum*, *T. ochroleucon*, *T. fragiferum*, *T. medium*, *T. alpestre*, *T. arvense*	Clovers	188	74,000	*T. pratense*, *T. repens*	*T. hybridum*, *T. resupinatum*	*T. subterraneum*, *T. incarnatum*	*T. pannonicum*, *T. campestre*, *T. medium*, *T. fragifeum*, *T. glomeratum*, *T. alexandrinum*, *T. ambiguum*,	Abberton and Thomas, 2011
Medicago	87	12	*M. sativa*, *M. arabica*, *M. italica*, *M. littoralis*, *M. lupulina*, *M. minima*, *M. murex*, *M. orbicularis*, *M. scutellata*, *M. rigidula*, *M. rugosa*, *M. truncatula*	Alfalfa	80	91,000	*Medicago sativa* subsp. *falcata*, *M. sativa* subsp. *glomerata*, *M. sativa* subsp. *sativa*, *M. sativa* subsp. *tunetana*, *M. sativa* subsp. *varia*, *M. sativa* subsp. *falcata* var. *viscosa* [tetraploids]	*Medicago sativa* subsp. *caerulea*, *Medicago sativa* subsp. *falcata*, *M. sativa* subsp. *glomerata*, *M. sativa* nothosubsp. *tunetana*, *M. sativa* nothosubsp. *varia*, *M. sativa* subsp. *falcata* var. *viscosa* [diploid], *M. prostrata*	*Medicago arborea*, *M. cancellata*, *M. daghestanica*, *M. hybrida*, *M. marina*, *M. papillosa*, *M. pironae*, *M. rhodopea*, *M. rupestris*, *M. ruthenica*, *M. saxatilis*		Small 2011; Wiersema and León, 2013
Cicereae tribe											
Cicer	44	1	*C. arietinum*	Chickpea	32	98,313	*C. arientinum*, *C. reticulatum*	*C. echinospermum*	*C. bijugum*, *C. judaicum*, *C. chorassanicum*, *C. yamashitae*, *C. cuneatum*, *C. pinnatifidum*	*C. reticulatum* and further 15 out of 22 species	Mallikarjuna *et al.*, 2011; http://gisweb.ciat.cgiar.org/GapAnalysis
Phaseoleae tribe											
Phaseolus	76	4	*P. vulgaris*	Common Bean	54	261, 968	*P. vulgaris* cultivars, landraces and wild specimens	*P. polyanthus (syn. P. dumosus)* *P. costaricensis* *P. coccineus*	*P. parvifolius*, *P. acutifolius*	55 out of 83 taxa	Singh and Jauhar, 2005; Porch *et al.*, 2013; http://gisweb.ciat.cgiar.org/GapAnalysis
			P. acutifolius	Tepary Bean			*P. acutifolius*		*P. vulgaris*		
			P. coccineus	Scarlet Runner Bean			*P. coccineus*	*P. vulgaris*			
			P. lunatus	Lima Bean			*P. lunatus*		*P. vulgaris*		
Glycine	24	1	*G.max*	Soybean	24	156,849	*Subgenus Soja* = *G.soja*+*G. max*	*No*	*Subgenus Glycine*	*G.soja*	Carter *et al.*, 2004;

Vigna	150	8	*V. unguiculata*	Cowpea	102	65,323	*V. unguiculata* subsp. *unguiculata* var. *unguiculata*	*V. nervosa*	other Vigna species	103 out of 118 taxa	Maxted *et al.*, 2004; http://gisweb.ciat.cgiar.org/GapAnalysis
			V. subterranea	Bambara groundnut							
			V. radiata	Mung bean							
			V. mungo	Grams							
			V. angularis	Adzuki bean							
			V. aconitifolia	Moth bean							
			V. reflexopiloxa var. *glabra*	Creole bean							
			V. umbellata	Rice bean							
Cajanus	32	1	*C. cajan*	Pigeonpea	22	40,820	*Cajanus cajan*	*C. acutifolius, C. albicans, C. cajanifolius, C. confertifolius, C. lanceolatus, C. lineatus, C. reticulatum, C. scarabeoides, C. sericeus, C. trinervius, C. cajan subsp. pubescens*	*C. cinereus, C. confertiflorus, C. crassus, C. goensis, C. latisepalus, C. mollis, C. platycarpus, C. rugosus*, all other species in the genus	25 out of 30 species	Singh and Jauhar, 2005; Bohra *et al.*, 2010; http://gisweb.ciat.cgiar.org/GapAnalysis
Aeschynomeneae tribe											
Arachis	80	1	*A. hypogaea*	Groundnut (peanut)	80	128,435	*A. hypogaea* and *A. monticola*	All the diploid species of section *Arachis*	all the species of section *Procumbentes*	*A. cardenasii*, *A. diogoi*, *A. batizocoi*, *A. ipaënsis*, *A. duranensis*, *A. gregoryi*, *A. linearifolium*, *A. magna*, *A.valida*, *A. kempffmercadoi*, *A. stenosperma* and *A. hoehnei*	Upadhyaya *et al.*, 2011; Sharma *et al.*, 2013
Genisteae tribe											
Lupinus	267	4	*L. albus*	White lupin	90	38,000	*Lupinus albus, L. angustifolius, L. luteus, L. mutabilis*	*L. elegans, L. pubescens, L. nanus, L. polyphyllus, L. hartwegii, L. tomentosus, L. hispanicus*	*L. arizonicus, L. succulentus*		Wolko *et al.*, 2011; Drummond *et al.*, 2012
			L. angustifolius	Narrow-leafed lupin							
			L. luteus	Yellow lupin							
			L. mutabilis	Andean lupin							

genebanks for client-selected accessions, including multi-trait queries.

With a wide range of approaches now available for genotyping, and with the declining cost of whole genome sequencing, the greatest limitation for gene banks is precise phenotyping, not only for descriptive traits, but also for agriculturally relevant quantitative traits relating to the expression of yield, crop growth and disease resistance. To increase precision, a single seed should be used for self-pollination to provide genetically uniform progeny for genotypic and phenotypic analysis. This level of precision is desirable if the key alleles of genes for important agronomic traits are to be identified, but broad characterization of diversity in germplasm can be based on a pooled DNA sample and phenotyping done on the bulked landrace mixture. Multi-environment analysis of quantitative variation involving multi-trait evaluation is far more informative than a single-environment trial and potentially provides some prediction for performance in other environments (Redden *et al.*, 2012). The challenge for gene bank curators is to strategically sample collections and maximize information from costly evaluation trials. One approach is to use core collections, geographically sub-sampled or sampled using molecular marker diversity to characterize species diversity, or to sample based on priority traits. This has led to the use of climatic site descriptors for characterization of natural selection, focusing on abiotic stress response, and has therefore provided lists of prospective germplasm with potential tolerances to heat, frost, and drought stresses (Li *et al.*, 2012, 2013). With current advances in genotyping and phenotyping methods, it is possible to effectively mine and explore the diversity stored in germplasm collections (McCouch, 2013).

B. Botanical Gardens and Herbariums as Sources of Information and Complementary Conservations

In addition to gene banks, botanical gardens offer an *ex situ* alternative to seed conservation. Botanical gardens face both challenges and opportunities in responding to global trends and, in particular, to climate change. The increased number of species at risk as a result of the changing climatic conditions will force many botanical gardens to refocus, to strengthen their conservation policies and to increase their participation in recovery programs for critically endangered species, including crop wild relatives (CWR). In addition, botanical gardens face an unprecedented opportunity to develop their role as introduction centers and play a major role in the assessment of new germplasm, both of ornamentals as well as other economically important plants (Heywood, 2011). Historically, botanical gardens have played a major role in plant introduction with far-reaching impacts and have been major drivers in human population growth and economic development of crops. Many botanical gardens manage seed banks of horticultural and wild species (such as the Millennium Seed Bank managed by Royal Botanic Garden at Kew, UK), have well-curated herbarium collections, are involved in re-introduction programs, and contain DNA storage facilities (DNA banks). Although herbarium and DNA banks are of relatively little practical use to conserve diversity, both provide valuable resources for studying CWR genetic diversity and information that can be used in gap analysis, as in the case of *Phaseolus* (Ramírez-Villegas *et al.*, 2010) and *Lathyrus* (Shehadeh *et al.*, 2013). Moreover, digitalization of and public access to herbarium vouchers allows for the remote study of morphological traits. These institutions often have the most direct knowledge and access to existing genetic diversity preserved *in situ*. Unfortunately, there is often an information gap between gene banks, botanical gardens and universities, which needs to be overcome in the near future by means of workshops, conferences and informal meetings.

C. *In Situ* Conservation of Crop Wild Relatives

In situ genetic reserve conservation may be defined as "the location, designation, management and monitoring of genetic diversity in natural wild populations within defined areas designated for active, long-term conservation" (Maxted *et al.*, 1997). A genetic reserve is actively managed, even if the management involves only regular monitoring of the target CWR taxa; as long as the target population levels are maintained above the minimum viable population of approximately 5,000 individuals no further conservation action may be required (Dulloo *et al.*, 2008). Importantly, *in situ* conservation action is a long-term commitment because significant resources have to be invested in order to establish a genetic reserve. Although the conservation goal is to always implement complementary conservation involving the parallel application of *in situ* and *ex situ* conservation techniques, there exists a preference for *in situ* conservation, primarily due to the overall need to maintain ecosystem health, but also because it has the advantage of maintaining the dynamic evolution of the CWR diversity itself in relation to parallel biotic and abiotic changes. Furthermore, due to the sheer number of CWR involved, the need to maintain effective genetic representation and the difficulty in precisely identifying which CWR or traits are required by plant breeders currently and in the future, *in situ* conservation is highly recommended, even if the main access route for breeders to diversity is via backup *in situ* samples deposited in *ex situ* genebanks.

All species in protected areas are passively conserved if the entire ecosystem or habitat is stable; however, without monitoring and active management, the genetic diversity within and between individual CWR populations could be eroded, and entire populations could even go extinct. Nonetheless, Stolten *et al.* (2006) emphasize that many protected areas already play an important role in the conservation of CWR species, even though many managers may be unaware that the land under their stewardship contains important crop genetic diversity. However, if our goal is to conserve the maximum genetic diversity within CWR taxa, then we need to study and monitor the genetic diversity and natural dynamics of CWR populations; otherwise, our efforts in establishing protected areas for these taxa may be wasted. It should also be noted that the *in situ*

management of CWR may differ significantly from that required for more traditional protected areas whose objective is to sustain climax communities. For example, CWR of major crop plants are often located in pre-climax communities (*Lathyrus ervoides* Grande, *Lens orientalis* Popow, *Cicer bijugum* Rech. f.) where the site management is comparatively intense, or the CWR may be closely associated with traditional farming practices (*Vicia johannis* Tamamschjan, *Lathyrus cicera* L., *Pisum sativum* subsp. *elatius* Asch. & Graebn.), in which case, genetic reserve management would need to be associated with maintenance of the traditional farming/ranching system (Lawn, 2014). Detailed guidelines on how to undertake *in situ* CWR conservation are provided by Iriondo *et al.* (2008); minimum standards for managing CWR genetic reserves are provided by Iriondo *et al.* (2012).

Specifically, there has been very limited effort to conserve legume CWR diversity *in situ*. This has in part been due to two related disconnects: (a) the disconnect between academic studies identifying where genetic reserves or less formal *in situ* management activities should be established and their actual implementation, and (b) lack of collaboration between the plant genetic resource and protected area communities (Meilleur and Hodgkin, 2004; Maxted and Kell, 2009). Consequently, native legume populations are susceptible to genetic erosion or even extinction (Maxted and Bennett, 2001). What was potentially the first recomendation for the establishment of *in situ* genetic reserves for legume CWR diversity was made by Maxted (1995), who proposed four locations to conserve Fabeae species in Syria and Turkey. Subsequently, three reserves were established within the Global Environment Facility project in Turkey, one of which, Ceylanpinar (Tan, 1998; Tan and Tan, 2002), emphasizes legume (and cereal) CWR *in situ* conservation as a priority. Within Syria, one of the sites recommended by Maxted (1995) has been established for *in situ* legume conservation in Suweida province (Amri *et al.*, 2008a, b). Further genetic reserves to conserve legume CWR have been established for *Lathyrus grimesii* Barneby in Nevada, USA (Hannan and Hellier, in Pavek and Garvey, 1999); for *Vavilovia formosa* (Stev.) Fed. at Akna Lich, on the Geghama mountain ridge, Yerevan province, Armenia and other legumes within the Erebuni Reserve near Yerevan, Armenia (Avagyan, 2008); and for wild bean populations (*Phaseolus* spp.) in Costa Rica (Baudoin *et al.*, 2008). However, admittedly none of these genetic reserves to date meets the minimum standards for managing CWR genetic reserves proposed by Iriondo *et al.* (2012), though the *in situ* conservation now in place is an important step forward.

Wild soybean (*Glycine soja* Willd.) is presumed to share a common ancestor with cultivated soybean (Hymowitz, 1970). Apart from *ex situ* conservation, *in situ* strategy is also used to conserve wild soybean, since populations of *G. soja* typically show high levels of genetic heterogeneity. In China, more than 40 *in situ* conservation sites located in 15 provinces and regions have been established (Zhao *et al.*, 2009). Their genetic diversity is identified by genotyping 40 individuals at 20 SSR marker loci for each population, and the results showed that at least 90% of the total genetic diversity was present (Guan *et al.*, 2006; Zhao *et al.*, 2006).

There have also been a number of gap analysis studies that have proposed where *in situ* genetic reserves might be sited. Gap analysis (Maxted *et al.*, 2008) involves four steps: (a) identify priority taxa; (b) identify genetic (or ecogeographic as a proxy for genetic) diversity and complementary hotspots using distribution and environmental data; (c) match current *in situ* and *ex situ* conservation actions with the identified genetic (or ecogeographic) diversity and complementary hotspots to identify the so-called 'gaps;' and (d) formulate revised *in situ* and *ex situ* conservation actions derived from identification of the gaps. This methodology has been applied for several legume CWR groups, including vetch *Vicia* subgenus *Vicia* (Maxted, 1995), lentils *Lens* (Ferguson *et al.*, 1998), Asiatic *Vigna* (Tomooka *et al.*, 2002), African *Vigna* species (Maxted *et al.*, 2004), perennial *Medicago* (Bennett*et al.*, 2006), 14 (including garden pea, faba bean and cowpea) globally important food crop gene pools (Maxted and Kell, 2009), *Medicago* of the Mediterranean Basin (Al-Atawneh *et al.*, 2009), *Phaseolus* species (Ramírez-Villegas *et al.*, 2010), *Medicago* species in the Former Soviet Union (Greene *et al.*, 2012), wild *Glycine* in Australia (Gonzalez-Orozco *et al.*, 2012) and *Lathyrus* species (Shehadeh *et al.*, 2013). However, in terms of establishing *in situ* conservation priorities, it is of greater practical value and is more cost efficient to establish multi-genepool conservation targets irrespective of individual genepool results. This multi-genepool approach has recently been used by Maxted *et al.* (2012) for the temperate legume genera *Cicer*, *Lathyrus*, *Lens*, *Medicago*, *Pisum* and *Vicia* species. This involved the collation of 200,281 unique geo-referenced records (*Cicer* - 452, *Lathyrus* - 61,081, *Lens* - 672, *Medicago* - 42,248, *Pisum* - 728 and *Vicia* - 95,100) collected between 1884 and 2008. The analysis identified the western Fertile Crescent (South-Central Turkey, western Syria and northeast Lebanon) as the area in which to focus *in situ* conservation efforts. The highest concentration of all priority species, and therefore the most species-rich hotspot, is in the north of the Bekaa valley in Lebanon and the adjoining Tel Kalakh region in Homs province, Syria, but there is currently no *in situ* conservation in this area, even though it has been shown to be suffering extensive genetic erosion (Keiša *et al.*, 2007). Undertaking similar multi-crop genepool analysis based perhaps on the legume species found in each of the Vavilov Centers should be a globally important priority. Once *in situ* locations are identified, they should be implemented to help improve global food security. New initiatives led by the Global Crop Diversity Trust (GCDT) (together with the Millenium Seed Bank, Royal Botanic Gardens, Kew) (Guarino and Lobell, 2011 and www.cwrdiversity.com) and the Food and Agriculture Organisation of the UN (FAO, 2013) are attempting to systematically plan and implement effective conservation of global CWR diversity, with the GCDT project focusing on *ex situ* conservation and the Food and Agriculture Organisation focusing on *in situ* conserva-

tion, with both projects promoting the use of conserved CWR diversity. The foundation of both projects is an annotated inventory of global priority CWR taxa for 173 priority crops, the Harlan and de Wet inventory (www.cwrdiversity.org/checklist/). Within the inventory, the family with the most CWR is the Fabaceae, with 253 global priority CWR from the genera *Arachis*, *Cajanus*, *Cicer*, *Glycine*, *Lablab* Adans., *Lathyrus*, *Lens*, *Lupinus*, *Medicago*, *Phaseolus*, *Pisum*, *Vicia* and *Vigna*. The GCDT *ex situ* project has collated over 8 million unique geo-referenced records for the *ex situ* gap analysis. There is a now an urgent priority to undertake the complementary *in situ* gap analysis for the legume taxa in order to identify globally where *in situ* conservation is required.

II. DOMESTICATION OF LEGUMES

Members of the Fabaceae family were domesticated as grain legumes in conjunction with the domestication of grasses for cereals (De Candolle, 1884; Vavilov, 1951; Smartt, 1990; Zohary and Hopf, 2000; Abbo *et al.*, 2012). However, more legumes were domesticated overall, resulting in Fabaceae becoming the family to contain the largest number of domesticates. Pea, faba bean, lentil, grass pea and chickpea are some of the world's oldest domesticated crops and arose in the Fertile Crescent of Mesopotamian agriculture. These legumes accompanied cereal production and formed important dietary components of early civilizations in the Middle East and the Mediterranean.

Archaeological evidence dates the existence of pea back to 10,000 BC in the Near East (Baldev, 1988; Zohary and Hopf, 2000) and Central Asia (Riehl *et al.*, 2013). In Europe, pea has been cultivated since the Stone and Bronze Ages and in India from 200 BC (De Candolle, 1884). Cultivation of pea spread from the Fertile Crescent into today's Russia, and westwards along the Danube valley into Europe and/or to ancient Greece and Rome, which further facilitated its spread to northern and western Europe. In parallel, pea cultivation moved eastward to Persia, India and China (Makesheva, 1979; Chimwamurombe and Khulbe, 2011).

Like pea, faba bean is an historically important crop. Faba bean remains have been found in archeological sites at Tell-el-Kerkh in northwest Syria, indicating that faba bean originated during the 10th millenium BC (Tanno and Wilcox, 2006). More recent, large-seeded, *major* type faba bean remains from the Mediterranean basin have been dated to the 2nd to 3rd millennia BC (Cubero, 1973) and likely represent a secondary center of domestication (Muratova, 1931), which was followed by their further spread into Europe. From their primary center in southwestern Asia, faba bean probably spread to Ethiopia. Introduction to South America in the 15th century has resulted in Peruvian and Bolivian faba bean landraces displaying a wide range of seed trait variability (Duc *et al.*, 2010).

Lentil is closely associated with wheat and barley cultivation in the Near East and is regarded as a founder crop of Old World Neolithic agriculture (Zohary and Hopf, 1973). Carbonized lentil seeds were retrieved from pre-farming (9,200-7,500 BC) Mureybit and Tell Abu Hureyra in Syria and from Netic Hagdud in Israel (cited in Zohary and Hopf, 2000). Charred lentil seeds dating to the 8th and 7th millennia BC were found in most of the Pre-Pottery Neolithic B early farming villages in the Near East. In later Neolithic settlements, lentil seeds were larger than 4 mm in diameter, indicating advanced domestication. In the 6th and 5th millennia, lentil spread into southeast Europe and later into Central Europe. Lentil accompanied wheat and barley in their spread southwards to Egypt and eastwards along the Caspian Sea to India. Charred lentil seeds were found in Afghanistan and dated to 2000 BC. However, archeological remains of lentils do not provide conclusive evidence of lentil's domestication, as the only indicative trait is the increase in seed size, which was slow and gradual (Zohary and Hopf, 2000).

The earliest archaeological evidence of grasspea (*Lathyrus sativus*) comes from Jarmo in Iraqi Kurdistan and is dated to 8000 BC. Remains of *Lathyrus* species have also been found at Ali Kosh (9500-7600 BC) and Tepe Sadz (7500-5700 BC) in Iran and are among the most common foods recorded at these sites (Jackson and Yunus, 1984). At Azmaska Moghila, in Bulgaria, remains dated at ca. 7000 BC have been tentatively identified as *L. cicera* L. (Renfrew, 1969). The species *L. sativus* is probably a derivative from the genetically closest species, *L. cicera* (Hopf, 1986). This somewhat smaller-seeded grasspea grows in countries from Greece to Iran and Transcaucasia. Remains of *L. sativus* have also been reported in India and have been dated back to 2000-1500 BC by Saraswat (1980) who indicated the possibility of diffusion of the crop from West Asia. *Vicia faba* L. and *V. ervilia* (L.) Willd. were already used by Neolithic and Bronze Age cultures in the eastern Mediterranean and in Asia Minor (Zohary and Hopf, 1973).

In contrast to the other crops domesticated during the Neolithic period, chickpea has followed a distinct evolutionary path, a series of bottlenecks from its narrow origin as a southeast Anatolian winter annual (*Cicer reticulatum* Ladiz.) to its current status as a South Asian and spring-sown Mediterranean crop (van Maesen, 1987; Abbo *et al.*, 2003). The earliest archeological remains of chickpea (10th millennium BP) were discovered within (Pasternak, 1998; van Zeist and de Roller, 1991, 1992) or close (Tanno and Willcox, 2006) to the current distribution of *C. reticulatum* in south-east Anatolia (Berger *et al.*, 2003). Thereafter, chickpea spread throughout the Eastern Mediterranean, presumably as a winter annual, like its wild progenitor, and was spread throughout the Mediterranean basin by the Greeks, Romans and Phoenicians. More recent chickpea remains are scarce, re-emerging only in Bronze Age sites in South Asia and in a much reduced, more southern Mediterranean distribution (Berger, 2013; Redden and Berger, 2007). Chickpea appeared in Ethiopia during the Iron Age (Dombrowski, 1970). The Spanish and Portuguese brought chickpea to the New World in the 16th century, while kabuli types were brought to India through Central Asia via the Silk Route in the 18th century (see references in Redden and Berger, 2007). Following the early Mediter-

ranean change from autumn- to spring-sowing, and concomitant movement to warmer climates to the south and southeast (Africa and South Asia), chickpea escaped low winter temperatures both in time and space (Berger, 2013). This evolutionary trajectory had important ramifications on chickpea lineage's capacity to deal with biotic and abiotic stresses.

The warm-season legumes of the Phaseolid group have been domesticated somewhat later than the cool-season legumes. Common bean in the Americas probably has the longest history as a domesticate, originating in parallel in two separate centers of domestication, one in the Andean mountains of South America, giving rise to the Andean genepool, and one in the Central American highlands and lowlands, giving rise to the Mesoamerican (Middle American) genepool (Blair *et al.*, 2009). Early archeological remains in caves of the Ayacucho and Guerrero regions of Peru and Mexico, respectively, suggest that domestication could have occurred as early as 10,000 years ago in the Andes and around 7,500 years ago in Central America. Four other related cultivated species in the genus *Phaseolus* were probably domesticated at a later date, as indicated by the lack of archeological records. Among these *Phaseolus* species, tepary bean (*P. acutifolius* A. Gray) was probably domesticated once or twice near the Mexico-USA border from wild populations of the same species, including *P. acutifolius* var. *tenuifolius* A. Gray, suffering a large bottleneck in the process (Blair *et al.*, 2012a). Some studies suggest that lima bean domestication may be similarly as old as common bean and occurred in parallel but over a broader region, including Central America and the Caribbean, all the way to the Amazon, Andes and Peruvian coast. This wide geographic span led to the creation of at least two genepools, again classified as Andean and Mesoamerican, but with four subgroups based on grain type. A closer relative to common bean and of more recent origin, the scarlet runner bean (*P. coccineus* L.) was domesticated exclusively in Central America and may have crossed naturally with common bean, resulting in the intermediate year-long bean (*P. dumosus* Macfad.).

The domestication of various *Vigna* species occurred over a wide range of Old World centers of domestication and additional regions not widely considered in crop history. The most important of these species is cowpea (*V. unguiculata* (L.) Walp., which was domesticated in the Sahel region of West Africa with influences from a large group of wild relatives found from West to East and Southern Africa, all the way to current Botswana. The oldest evidence that cowpea existed in West Africa was obtained from carbon dating specimens from the Kimtampo rock shelter in central Ghana (Flight, 1976). A minor relative of the cowpea was domesticated for its underground pods and is commonly known as Bambara groundnut (*Vigna subterranea* (L.) Verdc). This species was also domesticated in Africa, but its exact origin is unclear.

Meanwhile, in Asia, a range of important *Vigna* grain legumes was domesticated. These include mungbean (*V. radiata* (L.) R. Wilczek) and the grams (*V. mungo* (L.) Hepper), from South and East Asia, respectively. *Vigna* have been domesticated in an arc from the Indian subcontinent to the Far East (Smartt, 1990). Remains of Asian *Vigna* dating to 3500 to 3000 BC were found in archeological sites at Navdatoli in Central India (Jain and Mehra, 1980). However, the domestication dates of other *Vigna* crops, especially those from Africa, are largely unknown due to a lack of research and the tropical climates, which create poor conditions for preservation of archeological remains.

For pigeonpea (*Cajanus cajan* L.), historical evidence suggests a relatively short cultivation history, starting in 400 BC to 300 AD. Until recently, the origin of pigeonpea was unclear, with some researchers suggesting an African origin, others India. However, a number of archaeological, taxonomic and modern DNA-based studies now suggest India as single center of origin (Vavilov, 1928; van der Maesen, 1990; Kass *et al.*, 2012). From India, it traveled to East Africa and continued to the American continent with the misfortunes of the African slave trade.

The Phaseolid group contains a legume tree species domesticated for grain rather than fruit. This unique tree is *Erythrina edulis* Triana ex Micheli, which produces a large bean seed called Chachafruto, and which was domesticated along with a suite of Solanaceae shrubs and small trees for agroforestry systems in the Andes. Other legume trees produce edible pulp around their seeds, including species of *Inga* Mill., from South America and the Caribbean, and carob (*Ceratonia siliqua* L.), from the Mediterranean region. Other examples are the Mimosoid legume tree *Leucaena* Benth., which is used as a food crop throughout south-central Mexico, as well as tamarind (*Tamarindus indica* L.), a tree from India. Many sub-tropical and tropical legumes also produce valuable wood, resins, decorative beads, and medicinal products or toxins used for hunting and fishing. This shows the multi-functional nature of legumes, one of the reasons for their success and presence around the world.

The Dalbergoid clade contains the smallest number of domesticated legumes, with just one of worldwide importance, the cultivated peanut (groundnut) (*Arachis hypogaea* L.), and a few forage species of local importance, such as the genus *Stylosanthes* Sw., which has only recently been developed as a crop. The history of domestication of peanut dates back approximately 7,600 years in the Pantanal across the whole tropical world since the sixteenth century, mainly by Spanish and Portuguese traders (Krapovickas and Gregory, 1994; Valls and Simpson, 2005). The cultivated *A. hypogaea* is probably derived from the spontaneous inter-specific hybridization of two wild sympatric *Arachis* species; their genome combine as an allotetraploid, an event which makes all cultivars of peanuts highly monomorphic.

Based on the distribution of *Glycine soja* Willd. in China, Japan, Korea, and the far eastern Russia in East Asia, it has been suggested that domestication occurred simultaneously at multiple sites (Xu *et al.*, 2002; Lee *et al.*, 2010). However, most recent studies indicate that cultivated soybean was domesticated only in China, which also has the earliest written historical records of soybean cultivation (Qiu *et al.*, 2010). Soybean

is mentioned in many Chinese books dating back 4,500 years. Based on ^{14}C radiocarbon dating, these soybean remains are more than 2,590 years old. However, the exact site of domestication has not been identified until now, although several candidate locations have been proposed, including the Huanghuai Region (Yellow River valley) (Li *et al.*, 2010a; Li *et al.*, 2013a; Guo *et al.*, 2010).

Finally, for the Genisteae, two lupin species, *Lupinus albus* L. and *L. mutabilis* Sweet, were introduced into agriculture 3,000–4,000 years ago in Egypt and the Andes, respectively. The timing of domestication of *L. mutabilis* in the New World closely mirrors that of *L. albus* in the Old World. As a cultigen with no known wild counterparts, it is cultivated from Venezuela to northern Argentina (Wolko *et al.*, 2011). Eastwood and Hughes (2008a) identified *L. piurensis* C.P. Sm. as the likely progenitor of *L. mutabilis*, which would place the origin of *L. mutabilis* in northern Peru and southern Ecuador. *Lupinus angustifolius* L. and *L. luteus* L. were introduced into agriculture more recently in Northern Europe in the nineteenth century. Three Old World lupin species (*L. angustifolius L. luteus* and *L. albus*) and one New World lupin species (*L. mutabilis*) have been domesticated and bred as grain crops. It is thought that cultivation of *L. albus* first occurred in Egypt around 2000–1000 BC and that its use spread around the Mediterranean as a fodder crop, a green manure crop, and a grain crop (Gladstone, 1970). Even in ancient times, soft-seeded and indehiscent types were available, but up until the twentieth century, all cultivated cultivars were bitter, and seeds had to be soaked and boiled to remove the alkaloids. In Germany, in the 1930s, von Sengbusch identified natural sweet-seeded mutants, which heralded the beginning of modern *L. albus* breeding (Gladstone, 1970). The first successful use of *L. angustifolius* in modern agriculture was as a fodder and green manure crop in France, Germany and the UK in the early nineteenth century (Wolko *et al.*, 2011). Domestication began in earnest at the start of the twentieth century with the development of sweet (low-alkaloid) cultivars in Germany, Poland and Russia (Wolko *et al.*, 2011). The process of domestication was completed in Australia through the incorporation of pod indehiscence, soft-seededness and early flowering (removal of vernalization responsiveness) genes (Berger *et al.*, 2012a). Australian sweet cultivars contain a recessive gene for white flower and seed color that distinguishes them from bitter, blue-flowered wild types. Since the final domestication of *L. angustifolius*, cultivars have been developed across Europe and in Australia in particular.

Unlike grain legumes, domesticated forage legumes retain many of the characteristics of their wild relatives, such as seed shattering and small seed size, since breeding emphasis has focused on fodder production and persistence under grazing and hay production. Also, unlike many domesticated crops, wild forms of forage legume species continue to occur naturally, and there are areas of the world where domesticated and wild forms hybridize readily. The wild nature of forage legumes makes it difficult to trace when domestication actually occurred (Small, 2011). However, there are records that early cultivation of clover (*Trifolium* L.) most likely started in southern Spain around 1000 AD. From there it spread to the Netherlands and Italy. Here the rotational cultivation of clover was recommended for the improvement of poor soils (Camillo Tarello in Ricordo d'agricultura, 1567). By the end of the seventeenth century, clover cultivation had spread over most of Europe, reaching the northern areas by the end of the eighteenth century (Kjaergaard, 2003). Cultivated clovers generally have larger leaves and flower earlier and more prolifically than their wild ancestors or relatives (Ravagnani *et al.*, 2012).

Fourteen annual *Medicago* species are cultivated (Wiersema and León, 2013), the most significant being *Medicago sativa* L. (alfalfa or lucerne) and annual medics (*Medicago* spp.), of which, *Medicago truncatula* Gaertn. (barrel medic), serves also as important model for legume genomics (Cook, 1999). Annual medics are even less domesticated than perennial alfalfa. In alfalfa (*Medicago* L.), the crop progenitor is thought to be *Medicago sativa* subsp. *caerulea* (Less. ex Ledeb.) Schmalh., which is a purple-flowered diploid that continues to have a sympatric range with the wild purple-flowered tetraploid, *Medicago sativa* subsp. *sativa*, whose domesticated form is alfalfa. The general consensus is that the crop originated in Vavilov's "Near Eastern Center" (Vavilov, 1951), which includes Asia Minor, Transcaucasia, Iran and Turkistan (Bolton *et al.*, 1962; Small, 2011). There is some suggestion that domestication may have occurred more than once and likely occurred in areas where horses were raised (Small, 2011). Lesins (1976) suggested the irrigated valleys of eastern Turkey and oases along the Central Iranian plateau may have been the first places alfalfa was cultivated between 5,500 and 4,000 BC. The earliest recorded use of alfalfa was found on brick tablets from central Turkey dated between 1,400 and 1,200 BC (Bolton *et al.*, 1962). Small (2011) suggests that alfalfa spread from north central Asia eastward into China and India and westward into the Middle East and northern Africa. By the fifth century BC, it had been spread to Europe by the Roman Empire, transported as the primary fodder for horses and other livestock. In the sixteenth century, alfalfa was introduced into South America, and by the eighteenth century, it had been introduced into New Zealand, Australia, South Africa and the Eastern United States. Alfalfa was introduced into the Western United States in the mid nineteenth century when South American cultivars were brought to California. Up until the sixteenth century, cultivated alfalfa was predominantly purple-flowered *M. sativa* subsp. *sativa*. Michaud *et al.* (1988) suggested that when purple-flowered alfalfa was introduced into Germany and Northern France around the sixteenth century, it hybridized with the yellow-flowered subspecies, M. *sativa* subsp. *falcata* (L.) Arcang., to form variegated alfalfa (*M. sativa* nothosubsp. *varia* (Martyn) Arcang.). Variegated alfalfa had greater winter hardiness, greater disease resistance, and was more tolerant to acidic soils; these hybrid forms were domesticated as well (Small, 2011). Although the yellow-flowered alfalfa contributed important agronomic characteristics

that expanded the production of alfalfa, it has been minimally domesticated and continues to be a poor seed producer. Relatively few yellow-flowered cultivars have been developed compared to purple-flowered and variegated alfalfa.

A. Genetic Aspects of Legume Domestication

Despite legumes' crucial role in providing much of the protein in the human diet and animal feed, comparably little is known about their domestication. The "domestication syndrome" for legumes includes changes in plant architecture, seed gigantism, transition from outcrossing to selfing, reduced seed dispersal and loss of seed dormancy (Hammer, 1984).

An increase in the seed size of domesticates compared to their wild relatives is suggested to be related to greater planting depth in agricultural systems, with larger seeds producing more vigorous seedlings (Abbo *et al.*, 2011). At the same time early farmers may have selected for a higher proportion of starch, oil and protein. Seed shattering was avoided during the selection process in order to reduce the occurrence of the natural explosive seed pod opening mechanism of wild legumes. Experiments growing wild peas and lentil have demonstrated that both seed dormancy and pod dehiscence cause poor crop establishment via reduced germination, as well as dramatic yield losses via seed shattering (Abbo *et al.*, 2011, 2013).

The loss of seed shattering has been a fundamental characteristic under selection in most legume grain crops in order to facilitate seed harvesting, while in wild plants, shattering is a fundamental trait for assuring seed dispersal. The evolution of the non-shattering trait would have occurred automatically as a result of harvesting that favored non-shattering mutants in harvested populations that were subsequebtly sown. Central to the ballistic mechanisms of seed dispersal in pea is the dehiscent pod (single carpel fused along its edges), where the central pod suture undergoes an explosive rupturing along a dehiscence zone (Ambrose and Ellis, 2008). In domesticated species, this is removed or delayed. Breeding experiments have shown single-locus control of pod dehiscence in lentil (Erskine, 1985), two in mungbean (Isemura *et al.*, 2012), yardlong bean (Kongjaimun *et al.*, 2012) and pea (Weeden, 2007). One locus controls the number of twists along the length of the shattered pod, while the second locus controls the percentage of shattered pods (Weeden and Wolko, 2001; Ambrose and Ellis, 2008).

Probably the second most important domestication trait in grain legumes relates to seed dormancy, often called hard-seededness due to the physical barrier of testa water permeability. As greater seed size was selected and seeds were stored from one season to another, the potential for absorption of water and germination during storage made it necessary to select for seed dormancy. Moreover, seed imbibition plays a crucial role in reducing the cooking time of most grain legumes. Hence, reducing seed coat thickness led to a concurrent reduction of seed coat impermeability during domestication. This was largely overcome in all domesticated grain legumes (Werker *et al.*, 1979; Smartt, 1990; Weeden, 2007). A single recessive locus has been reported in lentil (Ladizinsky, 1985), while Weeden (2007) has identified two to three loci involved in pea seed dormancy, mediated by testa thickness and the structure of the testa surface. Among the legumes, unlike most cereal families (except for the millets), related species within a single genus have been domesticated at different stages, periods and places but with similar results in terms of cultivated crop characteristics. As well as suggesting that the domestication of plant crops was a directed, intentional and transmitable process, this makes several genera of legumes valuable and interesting for further study. For example, *Lupinus* provides a useful system for exploring plant domestication, as there are four related species whose domestication spans ancient (*L. albus* and *L. mutabilis*) and recent (*L. angustifolius* and *L. luteus*) times. All four species share the same domestication traits (reduced alkaloids, seed indehiscence, soft-seededness, and removal of the vernalisation requirement). Identification of the causal genes would allow for the development of diagnostic markers to improve the efficiency of introgression of genetic and phenological diversity from wild into domesticated germplasm. Similarly, in the genera *Phaseolus* and *Vigna*, there are clusters of cultivated species that allow for comparisons of the domestication traits, genes and mechanisms. This is in contrast to *Arachis*, *Cicer*, *Cajanus*, *Erythrina* and *Glycine*, which have only single domesticates. However, the last three of these genera can be compared to the other tropical legumes, which is why common bean and cowpeas have been suggested as models for soybean and pigeonpea.

In order to identify genetic basis of domestication traits, genetic analysis has been performed in wild to cultivated mungbean and pigeonpea crosses (Isemura *et al.*, 2012; Kongjaimun *et al.*, 2012; Kassa *et al.*, 2012), resulting in the identification of quantitative trait loci (QTLs) for 38 domestication-related traits or single-nucleotide polymorphisms derived from 670 genes. Comparably smaller numbers and mostly anonymous markers were used for mapping pea domestication traits, resulting in the identification of around 20 loci (Weeden, 2007). In common bean, seed size appears to be under multi-genic control, with 10 QTL found in wild x cultivated advanced backcross population analysis (Blair *et al.*, 2006; Blair and Izquierdo, 2012). Seed coat color genes are divided into those that control pattern and those that control tone of color (Caldas and Blair, 2009). These genes are underlayed by pro-anthocyanidin pathway genes, resulting in the accumulation of tannins and anthocyanins (Díaz *et al.*, 2010). Determinacy is also believed to be an important trait in the domestication of common bean from a viny wild phenotype to a short, rapidly maturing phenotype in some regions of early agriculture in the Americas.

III. TRIBE FABEAE RCHB.

The tribe Fabeae contains the following five accepted genera: *Lathyrus* L. (grasspea/vetchling; about 160 species); *Lens* Mill. (lentil; 4 species); *Pisum* L. (pea; 2-3 species); *Vicia* L. (vetch; about 160-200 species) and the monotypic genus *Vavilovia* Fed.

(Smýkal *et al.*, 2011; Schaefer *et al.*, 2012). The tribe Fabeae is sister to the Trifolieae tribe (Steele and Wojciechowski, 2003; Schaefer *et al.*, 2012). The tribe is morphologically characterized by mostly paripinnate, often tendrillous leaves and a pubescent style or a pollen brush (Lavin and Delgado, 1990). Stylar shapes and hair patterns are one of the principal diagnostic characteristics within the genera of Fabeae (Gunn and Kluve, 1976; Kupicha, 1981; Schaefer *et al.*, 2012). The clade is considered one of the youngest tribes among legumes (Kupicha, 1981; Steele and Wojciechowski, 2003; Wojciechowski *et al.*, 2004; Lock and Maxted, 2005), and estimates based on rates of evolution in the *maturase K* chloroplast gene place the age of the crown node at 17.5 Mya, in the mid-Miocene (Lavin *et al.*, 2005). A recent Bayesian molecular clock analysis of combined plastid and nuclear sequences also suggests a crown age of 23 – 16 Mya (Schaefer *et al.*, 2012).

Ancestral range reconstructions (Kenicer *et al.*, 2005; Schaefer *et al.*, 2012) place the area of origin in the Eastern Mediterranean, which is also the current center of diversity of the tribe (Kupicha, 1981). From there, a minimum of three dispersal events to the middle-Atlantic islands and seven to the Americas are required to explain the current distribution pattern (Schaefer *et al.*, 2012). South America was probably colonized twice from the Mediterranean and once via range expansion into North America. In Africa, Fabeae species, all descendants of Mediterranean lineages, occur only in the northern regions with extension into tropical mountains (D. R. Congo, Tanzania, Uganda) and into Ethiopia (Schaefer *et al.*, 2012).

A. Genus *Lathyrus* L.

The greatest diversity of *Lathyrus* species is found in Europe, Asia and North America (Kupicha, 1981; Kupicha, 1983; Kenicer *et al.*, 2005; Schaefer *et al.*, 2012), but its distribution extends to South America and East Africa. Most species are adapted to temperate regions, but some can be found at high altitudes in tropical Africa. The genus contains many restricted endemic species. *Lathyrus* underwent several long-distance dispersal events, from Asia via Beringia to North America and into South America (Schaefer *et al.*, 2012). Most species of *Lathyrus* are mesophytes of open woodlands, forest margins, and roadsides, with several-drought tolerant and halophytic species.

The generic boundaries between *Lathyrus* and the other Fabeae genera have been much debated (Kupicha, 1981; Schaefer *et al.*, 2012). This taxonomic confusion has led to an abundant and complex synonymy. Molecular study of *Lathyrus* phylogeny, based on nuclear (ITS) and chloroplast (*trnL-F, trnS-G*) markers using a large set of geographical and taxonomic samples, was done by Kenicer *et al.* (2005). Based on a very limited sampling, Steele and Wojciechowski (2003) suggested that *Lathyrus*, *Lens* and *Pisum* might all be nested in *Vicia*. This was recently confirmed in a comprehensive analysis by Schaefer *et al.* (2012), who demonstrated that nuclear ITS and chloroplast DNA regions lead to phylogeny estimates with *Pisum* and *Vavilovia* nested in *Lathyrus*, *Lens* nested in *Vicia* s. str. and all four genera (*Pisum*, *Vavilovia*, *Lathyrus*, *Lens*) nested in *Vicia* s. l. Consequently, a monophyletic *Lathyrus* will have to include both *Pisum* and *Vavilovia*. To maintain most of the species names in *Lathyrus*, a recircumscription of *Vicia* has been proposed, which would mean that the clade containing *Vicia tetrasperma* (L.) Schreb. and another clade containing *Vicia hirsuta* (L.) Gray and *Vicia sylvatica* L., among others, will be split from *Vicia* s. str. and become two additional genera (Schaefer *et al.*, 2012).

Several methods have been used to study the phylogenic relationships among different *Lathyrus* species, including morphological traits, crossability, karyotype analysis, chromosome banding and *in situ* hybridization and molecular markers (reviewed in Kumar *et al.*, 2013). *Lathyrus* is predominantly a true diploid with a chromosome number of $2n = 2x = 14$ (also reconstructed as the ancestral number), with a few exceptions having $2n = 28$ or 42 (Schaefer *et al.*, 2012 and references therein). There are a few polyploid species among the perennials, including hexaploid (*L. palustris* L., $2n = 6x = 42$) and tetraploid (*L. venosus* Muhl ex Willd., $2n = 4x = 28$). Natural and induced autopolyploids have also been reported in *L. sativus*, *L. odoratus* L., *L. pratensis* L. and *L. venosus*. Genome size of 52 measured species ranges from $1C = 3.43$ pg (*L. miniatus*) to 18.2 pg (*L. sativus*) (RBG Kew DNA C-values database).

*1. Crop grasspea (*Lathyrus sativus *L.)*

The most widely cultivated *Lathyrus* species for human consumption is the grasspea (*L. sativus*) which serves as a key famine food for rural populations in countries like Kenya, Ethiopia, India, and Bangladesh. Other species, which are grown for forage and/or grain purposes, are *L. cicera*, *L. ochrus* (L.) DC., *L. clymenum* L., *L. tingitanus* L., *L. latifolius* L. and *L. sylvestris* L. (IPGRI, 2000, Table 1), which are important animal fodders. *Lathyrus cicera* is cultivated in Greece, Cyprus, Iran, Iraq, Jordan, Spain and Syria, and *L. ochrus* in Cyprus, Greece, Syria and Turkey (Saxena *et al.*, 1993). Other species, like *L. hirsutus* and *L. clymenum*, are cultivated as minor forage or fodder crops in the southern United States and Greece (Sarker *et al.*, 2001). The primary gene pool of cultivated *Lathyrus sativus* and *L. cicera* is limited to cultivars, landraces and escapes from cultivation, while the secondary gene pool includes *L. chrysanthus* Boiss., *L. gorgonii* Parl., *L. marmoratus* Boiss. & Blanche, *L. pseudocicera* Pamp., *L. amphicarpos* L., *L. blepharicarpos* Boiss., *L. chloranthus* Boiss. & Balansa, *L. cicera*, *L. hierosolymitanus* Boiss. and *L. hirsutus* L. The remaining species are included in the tertiary gene pool (Table 1). Although the progenitor of *L. sativus* remains unknown, *L. cicera* is the most probable candidate, as it is morphologically and cytogenetically closest to the cultivated species (Jackson and Yunus, 1984; Hopf, 1986).

Ex situ Lathyrus sativus germplasm collections total 38,360 accessions, with the largest number held at the International Center for Agriculture in Dry Areas (ICARDA) (9,000), followed by China (5,200) and Australia (2,445) (Cambel, 1997; Kumar *et al.*, 2013, Table 1). Besides cultivated *L. sativus*, there

are smaller collections of the remaining *Lathyrus* species, which may be better represented in botanical gardens; however, such displays often offer only a single accesion per species. Australian Grain Genebank holds 553 acc. of 37 *Lathyrus* species, EURISCO lists 1,645 acc. of 66 species, USDA holds 445 acc. of 49 species and VIR has 5,500 acc. of 58 species. Breeding efforts focused on three species–*L. sativus*, *L. cicera* and *L. ochrus*, and, to a lesser extent, *L. clymenum*–with an aim at improving grain yield, biomass, resistance to biotic and abiotic stresses, and, most importantly, to reduce the neurotoxin in its seeds. Unfortunately *Lathyrus* seeds, apart of being protein rich, contain the water soluble non-protein amino acid β-diaminopropionic acid (ODAP), which has been found to be a neurotoxin linked to an irreversible neurological disorder called lathyrism (Barrow *et al.*, 1974). Several low β-diaminopropionic acid (with $< 0.1\%$ ODAP) cultivares were developed through intraspecific hybridization in Bangladesh, ICARDA, Ethiopia, Canada and Australia.

Evaluation of *Lathyrus* germplasm has been undertaken for different traits in order to identify useful donors for important parameters, including low ODAP content, phenology and yield-related traits. For example, Chowdhury and Slinkard (2000) studied genetic diversity in 348 accessions of *L. sativus* from 10 geographical regions using polymorphism for 20 isozymes. They observed the closest genetic distance between populations from the Near East and North Africa. The most extensive study of 1,082 accessions belonging to 30 species evaluated for 21 descriptors and agronomic traits was performed at ICARDA (Cambell, 1997). A detailed cataloguing of grasspea germplasm comprising characterization and evaluation information on 63 traits for 1,963 accessions was perfromed in India (Kumar *et al.*, 2013). ODAP content in seeds was found to vary from 0.02% to 2.59%. Interestingly, ODAP concentration in *L. cicera* is lower compared to that of *L. sativus* (reviewed in Kumar *et al.*, 2013).

Genetic diversity of *Lathyrus* has experienced serious genetic erosion, largely as a result of intensification of agriculture, overgrazing, and the decline of permanent pastures (Maxted and Bisby, 1986, 1987). Despite *L. sativus* being among the hardiest crop species, able to withstand conditions from flooding to severe drought, the genetic diversity of grasspea has suffered a great deal from a ban on its sale, causing serious erosion of landraces. Development of less toxic cultivars that retain palatability remains a holy grail in arid land crop research. Grasspea is one of the hardiest but most underutilized crops for adaptation to fragile agro-ecosystems due to its ability to survive under extreme climatic conditions, such as drought, water stagnation and heat stress (Vaz Patto *et al.*, 2006; Kumar *et al.*, 2013). It is an annual, cool-season legume crop of economic and ecological significance in South Asia, sub-Saharan Africa, and, to a lesser extent, in Central and West Asia, North Africa, southern Europe and South America. It is grown mainly for food in India, Bangladesh, Nepal, Pakistan, Ethiopia and for feed and fodder purposes in other countries (Kumar *et al.*, 2013). Grasspea grains provide a good protein supplement (24–31%) to the cereal-based diet of poor people in areas of its major production. Globally, the area under grass pea cultivation is estimated at 1.50 million ha, with annual production of 1.20 million tonnes (Kumar *et al.*, 2011).

B. Genus *Vicia* L.

The genus *Vicia*, with 160-200 species, is rich in diversity. The uncertain number of species reflects the abundant use of synonymous names and similar species descriptions. The distribution and species numbers of *Vicia* parallel that of *Lathyrus*, although it might be argued that *Vicia* shows less morphological diversity. The best known species of the genus are the faba bean, *V. faba*, and *V. sativa*.

Kupicha (1976) undertook a comprehensive revision of the genus, dividing the species into two subgenera, Vicilla and Vicia, based on flower arrangement and the presence/absence of nectariferous spots on the stipules. Kupicha's subgenus Vicilla is further divided into 17 sections, while the subgenus Vicia is divided into five sections with 38 species. Section Faba of Kupicha (1976) includes *V. faba*, *V. galilaea* Plitmann & Zohary, *V. johannis* Tamamschjan, *V. narbonensis* L., *V. hyaeniscyamus* Mouterde and *V. bithynica. Vicia faba* stands out due to its karyological ($2n = 12$) crossing barrier (Maxted, 1995), and this different characteristic is also supported by a recent phylogenetic study based on chloroplast and ITS sequences (Schaefer *et al.*, 2012). A biosystematic study of the genus was conducted by Hanelt and Mettin (1989) using morphological characteristics and classical karyology, which largely agreed with Kupicha's results. The presence of pubescence on the adaxial side of the style is typical for the groups *Lathyrus* and *Pisum* (Kupicha, 1981). However, several *Vicia* species, including *V. ervilia* and *V. koeieana* Rech. f., also show this type of pubescence and in fact do not appear in the core *Vicia* clade (Schaefer *et al.*, 2012). Species in the genus *Lens* also have this pubescence pattern, rendering it of little use for morphology-based classification. Problems over the taxonomic distinction within species can be attributed to large variation in morphology and karyotypes (Maxted *et al.*, 1991). Maxted (1993, 1995) revised *Vicia* subgenus Vicia and proposed nine sections and nine series. Chromosome numbers in *Vicia* vary between $2n = 10$, 12, 14, 28, and 42, with an ancestral number of $2n = 14$ (Schaefer *et al.*, 2012 and references cited therein). Notably, cultivated *V. faba* with a chromosome number of 12 and genome size of $1C = 13.3$ pg is reproductively isolated from its closest relatives. Faba bean is partially allogamous, with the rate of out-crossing differing between environments and genotypes and ranging from 4 to 84% (Bond and Poulsen, 1983; Suso *et al.*, 2001; Hu *et al.*, 2011). The genome size of 88 analyzed *Vicia* species varies from $1C = 1.83$ pg (*V. lunata* (Boiss. & Balansa) Boiss. & Balansa) to 27.4 pg in *V. faba* (RBG Kew DNA C-values database).

Faba bean stands as an exception among the cultivated legumes, as there is no known wild progenitor. *Vicia faba* subsp. *paucijuga* (Alef.) Murat. from Pakistan and Afghanistan has been suggested as the progenitor, because it showed

primitive characteristics. Another proposed, close wild relative, *V. pliniana* (Trabut) Murat. from Algeria (Muratova, 1931), is currently considered to be only a morphological variety of *V. faba* subsp. *faba* var. *minor.* Morphological similarity led Hopf (1973) to propose *V. narbonensis* as the faba bean ancestor; however, its crossing barriers and phylogenetic results (Schaefer *et al.*, 2012) do not support this hypothesis. In summary, we do not know the faba bean progenitor and cannot be sure it is not extinct. Once more genomic information has been gathered, more light may be shed on this question. No chloroplast DNA variation has been detected among *V. faba* genotypes (Shiran and Mashayek, 2004), whereas mitochondrial DNA displays variation in sequence and size (Flamand *et al.*, 1993). The extreme genome size of *V. faba* (13,000 Mb) can be explained by a high number of retrotransposons (Pearce *et al.*, 1996).

Except for *V. faba* and *V. sativa,* the species of the large *Vicia* genus are poorly systematically conserved *ex situ*. The VIR collection has the largest set of 5,500 acc. of 58 *Vicia* species; the USDA holds 942 acc. of 51 species; the Australian Grain Genebank has 1,924 acc. of 60 species, plus 1,013 acc. of *V. sativa*; and EURISCO lists 7,303 acc. of 117 species and 6,968 acc. of *V. sativa*, the majority of which are at the Gatersleben genebank in Germany.

1. *Forage vetches (*Vicia *sp.)*

Numerous species of the vetch genus (*Vicia* L.) represent a frequent component of local floras and bring an essential contribution to the quality of pasture and meadow communities and soil fertility. Among such are narrow-leafed vetch (*V. sativa* subsp. *nigra* (L.) Ehrh.), large-flowered vetch (*V. grandiflora* Scop.), hairy vetch (*V. villosa* Roth), Hungarian vetch (*V. pannonica* Crantz) and tiny vetch (*V. hirsuta* (L.) Gray). Of these, common vetch (*V. sativa*) is the most commonly used, providing palatable forage (fresh, hay and silage) and grain to livestock. *V. sativa* originated from southern Europe and is now widespread in the Mediterranean basin, in west and central Asia, China, eastern Asia, India and in the USA. It is moderately tolerant of cold and can grow in areas with mild winters. *V. sativa* is found in areas with annual rainfall ranging from 310 mm to 1630 mm and on a large variety of soils with a preference for well-drained, moderately fertile soils with soil pH ranging from 6.0 to 7.0. It is not tolerant of drought during the early stages of establishment and it is advisable to plant it in autumn (FAO, 2010). It can withstand short waterlogging periods but no extended flooding periods. Like other *Vicia* species, the seeds of *V. sativa* contain numerous antinutritional factors, notably cyanogenic amino acids and cyanogenic glycosides that are toxic to monogastric animals. The nutritive value of common vetch hay is higher than that of alfalfa and sainfoin at similar vegetation stage (Heuzé *et al*., 2013). These species have not been bred and cultivars are result of selection from wild populations. These species are of interest for drought prone regions in order to provide good quality animal feedstock with minimal input.

2. *Crop faba bean (*Vicia faba *L.)*

In the case of faba bean, there are 37 collections, holding approximately 38,000 accessions (Duc *et al.*, 2010, Table 1), which comprise around 17% of total grain legume accessions worldwide (Suso *et al.*, 2006). Most of the accessions from European collections are listed in the EURISCO database with available passport data (Duc *et al.*, 2010). Of these, 30% have cultivar names, and 52% are of European origin. Since faba bean is an open-pollinated species, it is important to prevent cross-pollination during regeneration in order to preserve the unique genetic identity of the landraces (Suso *et al.*, 2006; Hu *et al.*, 2011). In addition, a large proportion of the germplasm is not stored under long-term storage conditions and is subject to a wide variety of regeneration cycles ranging from 5 to 35 years. Interestingly, winter faba beans from China were found to be distinct from the winter gene pool in the rest of the world (Bao *et al.*, 2006; Zong *et al.*, 2009).

A global composite collection of 1,000 accessions was collaboratively developed under the Generation Challenge Program (GCP) using genomic microsatellites (Sadiki *et al.*, 2006). Repetitive sequences and other DNA-based markers have been used to assess genetic diversity (Zeid *et al.*, 2003; Gutierrez *et al.*, 2006; Torres *et al.*, 2006; Sanz *et al.*, 2007; Terzopolous and Bebeli, 2008; Zong *et al.*, 2009; Kwon *et al.*, 2010) among cultivated faba genotypes. Phenotypic traits of agronomic interest were used to evaluate *ex situ* faba bean germplasm collections in Europe, at ICARDA and in China (reviewed in Duc *et al.*, 2010). Particularly, flowering response and stem architecture (internode length and strength, branching, determinate growth) were investigated in relation to crop adaptation to diverse agronomic practices and climatic zones. Drought tolerance was detected in accessions from the Mediterranean region, while frost tolerance was found in German landraces (Arbaoui *et al.*, 2008). Sources of resistance/tolerance to various fungal, viral and pest biotic stresses were identified and used in breeding (Sillero *et al.*, 2010). Genetic variation was used to develop zero-tannin-content and low-vicine, convicine faba bean cultivars (reviewed in Duc *et al.*, 2010). The low-vicine, convicine "Fevita" types remove the danger of favism, which has been linked to a genetic variant of glucose-6-phosphate dehydrogenase deficiency in humans (Arese and De Flora, 1990). Significant genetic variation for all these traits of interest exists within faba bean germplasm, providing an excellent resource for plant breeders (Duc *et al*., 2010). Fast and reliable screening methods have been adjusted to fulfil the needs of breeding programmes both for fungal diseases (Sillero *et al*., 2006), parasitic weeds (Rubiales *et al*., 2006) and abiotic stresses (Stoddard *et al*., 2006). Many of these traits of interest have already been incorporated into modern cultivars but several others, many of which are controlled quantitatively by multiple genes, have been more difficult to manipulate.

Faba bean is now cultivated over a latitudinal range from the equator to approximately 50 °N and 40 °S and an altitude range from sea level to above 3,000 m. The long period of cultivation across such diverse environments has resulted in the

differentiation of germplasm into distinct groups based on seed size (*paucijuga*, *minor*, *equina* and *major*) and region of adaptation (winter, spring types) (Flores *et al*., 2013). Despite the complicated, large genome, significant efforts have been made to understand the genetics and genomics of faba bean. Linkage maps of faba bean have been constructed based on various marker types, and various QTLs (Quantitative Trait Loci) have been identified (reviewed in Gnanasambandam *et al.*, 2012; Ma *et al.*, 2013).

The long history of cultivation, wide distribution across various climate environments and the response to human selection have caused faba bean to become a most versatile crop for use as food, feed, forage, vegetable and as a cover crop. According to FAO, the annual harvested faba bean acreage averaged 2.5 million hectares from 2005 to 2010, with an annual production of approximately 4.2 million tonnes and mean yield of 1,666 kg/ha (FAOSTAT, 2012). The high-protein seeds of faba bean are a staple in the diets of many societies in the Middle East and North Africa. Snacks made from faba bean have been marketed in China and elsewhere. In China, substantial amounts of faba bean are used to produce pastes or doubangjiang, an indispensible condiment in Chinese cuisine. Although global faba bean acreage and production has experienced a steady reduction over the past four decades, demand for faba bean in the world market has driven the production upwards in Australia and France in recent years (FAOSTAT, 2012). Immature faba bean seeds (fresh or frozen) are a favored vegetable in many countries. Like other food legumes, faba bean contains numerous phytonutrients, such as vitamins, minerals and phenolics, which contribute to the overall antioxident activities of plant foods (Oomah *et al.*, 2011; Baginsky *et al.*, 2013). Faba bean provides an alternative to soybean meal for animal feed in temperate regions where soybean cannot be grown. Faba bean is one of the a few plant species capable of producing the medicinally important molecule, L-3,4-dihydroxyphenylalanine (L-DOPA), the major ingredient of several prescription drugs used to treat Parkinson's disease (Apaydin *et al*., 2000).

Faba bean is an ideal cover crop or for green manure, particularly for organic growers, since it has been documented as having the highest capacity for fixing atmospheric nitrogen among the major cool-season food legumes (Herridge *et al.*, 1994). Faba bean has undergone significant improvement in yield and other agronomic traits during the past half century. However, similar to other temperate-region legume crops, faba bean faces major challenges from more profitable crops, such as wheat, corn and soybean, for a place in growers' crop rotation plan. Despite the fact that the global acreage dedicated to faba bean production dropped significantly, from six million ha in the 1960s to 2.5 million ha in recent years (FAOSTAT, 2012), there remains potential for increased faba bean cultivation world-wide remains good because of the steady growth of the consumer population. New advances in genomics are expected to have enormous impact on the genetic improvement of the faba bean crop. As in the case of other grain legumes, yield stability is a major challenge for faba bean breeding. Many efforts have been made recently to improve abiotic tolerance and climate adaptation, though progress has been slow, since the partially allogamous nature of faba bean slows the process of developing pure lines. Nevertheless, useful genetic resources with good drought tolerance have been identified (Khan *et al.*, 2007). Enhancing winter-hardiness of faba bean will mitigate the cold damage and ensure crop productivity (Arbaoui *et al.*, 2008; Link *et al.*, 2010; Hu *et al.*, 2011; Flores *et al.*, 2012). Other abiotic stresses, like heat tolerance and water logging, also require attention. Identifying and incorporating host resistance to biotic stresses is needed (Infantino *et al*., 2006; Tivoli *et al*., 2006; Pérez-de-Luque *et al.*, 2010; Sillero *et al*., 2010).

Tannins and vicine-convicine are the two major antinutritional elements of concern for faba bean. Tannins impart a bitter flavor to the seed and reduce the digestibility of protein, while vicine-convicine aglycone derivatives may induce favism (Arese and De Flora, 1990). Useful natural mutants have been identified in faba bean germplasm. Tannins can be removed by incorporating one of the two independent, recessive genes named *zt*1 and *zt*2 (Picard, 1976), which also determine the white-flower phenotype. Vicine and convicine can be lowered by incorporating the spontaneous recessive mutant (Duc *et al.*, 1989). Molecular markers linked to these genes have been developed (Gutierrez *et al.*, 2006; 2007 and 2008), and these genes have been incorporated into a few European cultivars (Duc, personal communication).

In recent years, crosses were made using very diverse germplasm, and elite breeding lines adapted to various production regions were developed. The success of this breeding effort demonstrates the benefit of including diverse germplasm from different origins (Gnanasambandam *et al.*, 2012).

C. Genus *Pisum* L.

The *Pisum* genus is distinguished morphologically from the related genera *Lathyrus* and *Vavilovia* by the presence of large, leafy stipules, which are semi-amplexicaul. The genus *Pisum* contains the flavonoid phytoalexin pisatin, which is shared with genus *Lathyrus* but not found in *Vicia* species (Bisby *et al.*, 1994), which have wyerone instead. The *P. sativum* L. complex (*P. sativum* subsp. *sativum* and subsp. *elatius* Asch. & Graebn.) is native to the Europe-Mediterranean region and Middle and northwest Asia, whereas *P. fulvum* Sibht -Sm. is restricted to the Middle East. *Pisum sativum* subsp. *abyssinicum* A. Braun is found in cultivation (together with *P. sativum* subsp. *sativum*) in Eastern Africa. This taxon is native to Ethiopia and Yemen, has very low genetic diversity (see later section) and possesses a distinct set of phenotypic characteristics (early flowering, an adaptation useful for avoiding drought periods; unipinnate and strongly serrate leaflets), as well as unique alleles at particular loci. The classification of *Pisum* L. has changed over time from a genus with five species, to a monotypic genus, to a genus with two species (reviewed in Smýkal *et al.*, 2011, 2013). In Yarnell's review (1962), *P. humile* Mill. (*P. syriacum* (A. Berger) C. O.

Lehm., *P. sativum* var. *pumilio* Meikle), *P. elatius* M. Bieb., *P. abyssinicum,* and *P. sativum* were considered conspecific, even though they often differ by inversions and translocations. The most appropriate status for *P. sativum* subsp. *abyssinicum* is still under debate, as it has been resurrected as a third species by some authors (Maxted and Ambrose, 2001; Vershinin *et al.*, 2003; Jing *et al.*, 2007). The most recent studies place it between *P. fulvum* Sibth. & Sm. and a subset of *P. elatius* (Vershinin *et al.*, 2003; Jing *et al.*, 2010). While most authors agreed with the original suggestion of Linné, who described the genus *Pisum* as distinct from *Lathyrus* (Linné, 1753), the recent molecular phylogenetic analysis (Schaefer *et al.*, 2012) finds it deeply nested in *Lathyrus*. Interestingly, Lamarck (1778) described the garden pea as *Lathyrus oleraceus* Lam., disagreeing openly with Linné's suggestion. Depending on how that complex is treated, the genus *Pisum* may be incorporated into a larger genus *Lathyrus* to represent a natural (monophyletic) group.

The primary gene pool consists of the *Pisum sativus/elatius* complex, although it is difficult to specify concisely because of the fertility barriers, caused by nucleo-cytoplasmic conflict, which exist within the species *P. sativum* (Bogdanova *et al.*, 2009). A secondary gene pool generally extends to the other species in the genus, *P. fulvum* and *P. sativum* subsp. *abyssinicum* (Table 1), but with new knowledge regarding relationships with sections of *Lathyrus,* especially the closely related *L. ochrus*, *L. clymenum*, *L. articulatus* L. and *L. neurolobus* Boiss. & Heldr. (Schaefer *et al.*, 2012), it may be useful to examine these sections more thoroughly. The tertiary gene pool currently consists of *Vavilovia formosa* (Stev.) Fed. (= *Pisum formosum* (Steven) Alef., *Pisum aucheri* Jaub. & Spach.), which might be reconsidered to be within the secondary pool, as shown by Golubev (1990), and after the tribe circumscription, it would consist of numerous *Lathyrus* and *Vicia* species (Table 1).

The beautiful Vavilovia (*Vavilovia formosa*) was first described in 1813 by Steven and assigned to the genus *Orobus* L. It was later associated with both *Lathyrus* and *Pisum*. Fedorov (1939) revised the taxonomy based on morphological characteristics, such as flower and stipule shape, absence of tendrils, presence of creeping, and thread-like rhizomes, as well as characteristics of disjunctive distribution range, ecology and perennial habit. Fedorov (1939) ultimately separated *Orobus* L. into the monotypic genus *Vavilovia*. *Vavilovia* combines several of the morphological traits of the genera *Lathyrus* and *Pisum,* and Makasheva (1979) proposed that *Vavilovia* be considered the ancestor of both genera. Recent molecular phylogenetic analyses have shown its sister group relationship to *Pisum* (Oskoueiyan *et al.*, 2010; Schaefer *et al.*, 2012; Mikič *et al.*, 2013).

Pea genetic diversity spreads in the area of the Fertile Crescent through Turkey, Syria, Iraq, Israel and Lebanon, to Central Asia and the Mediterranean region (Smýkal *et al.*, 2011). There are two wild *P. sativum* populations, which are morphologically, ecologically and genetically distinct, variously described as subspecies of *P. sativum* or as species, *P. sativum* subsp. *elatius* M. Bieb. and *P. sativum* subsp. *sativum* (formerly *P. humile* (syn. *P. syriacum*) (Ben-Ze'ev and Zohary, 1973; Smýkal *et al.*, 2011). Recent phylogenetic studies based on retrotransposon insertion markers support the model of *P. sativum* subsp. *elatius* as a paraphyletic group, within which all *P. sativum* are nested (Vershinin *et al.*, 2003; Jing *et al.*, 2005, 2010; Nasiri *et al.*, 2010). The phylogenetic relationships of pea have been reconstructed by Ellis *et al.* (1998) and by Pearce *et al.* (2000) using molecular, multiloci approaches, finding that *P. fulvum* and *P. sativum* subsp. *abyssinicum* formed sister clades. *Pisum sativum* subsp. *elatius* is positioned between *P. fulvum* - *P. sativum* subsp. *abyssinicum* and cultivated *P. sativum*. On the same set of pea accessions, Vershinin *et al.* (2003) separated *P. fulvum* as an ancient lineage, while *P. sativum* subsp. *elatius* accessions formed a polytomy with *P. humile* and *P. sativum* subsp. *abyssinicum* accessions. Extremely low diversity of *P. sativum* subsp. *abyssinicum* was detected in several studies (Pearce *et al.*, 2000; Weeden and Wolko, 2001; Vershinin *et al.*, 2003; Jing *et al.*, 2005, 2010), which could be explained by its passage through a bottleneck caused by a putative hybridization event between *P. fulvum* and *P. sativum*, as suggested by Kloz (1971). A phylogenetic analysis based on the combination of mitochondrial, chloroplast and nuclear genome markers placed the *P. sativum* accessions in a distinct clade separated from all *P. fulvum* and *P. sativum* subsp. *abyssinicum* accessions (Kosterin and Bogdanova, 2008; Kosterin *et al.*, 2010) and suggested that all wild forms of *Pisum sativum* should be included in a paraphyletic *P. sativum* subsp. *elatius*.

All *Pisum* species are diploid with 2n = 14. For cultivated pea, nuclear genome size estimates have been produced for several accessions using different methods and are estimated to be 1C = 4.4 to 4.8 pg DNA corresponding to the haploid genome size (1C) of 4.45 Gb, with a large part (75 to 97%) comprised of repetitive sequences (reviewed in Smýkal *et al.*, 2012).

*1. Crop pea (*Pisum sativum *L.)*

There is no international genetic resource center for pea, following the relinquishing of this role by the International Center for Agricultural Research in Dry Areas (ICARDA) in the early 2000s. However, the ICARDA pea collection is still conserved, though not actively curated. There are substantial national pea collections: 98,947 accessions are distributed over 28 genebanks, comprised of landraces (38%), commercial cultivars (34%), mutant/genetic stocks (5%), wild relatives (2.6%) and breeding lines (13%) (Smýkal *et al.*, 2013, Table 1). The actual number of unique lines is substantially less due to duplication of stocks among genebanks. Of these, only 1,876 (2%) are wild pea relatives; approximately one quarter (24,000) are commercial cultivars and landraces; and 8,500, 600 and 6,000 represent breeding and recombinant inbred lines or mutant stocks, respectively. Moreover, there is a large bias (17%) towards Western and Central European accessions. Less represented are the Mediterranean (2.5%) and the Balkan (2%) regions, as well as the Caucasus (0.8%) and Central Asia (2%), the centers of pea

crop domestication and diversity (Smýkal *et al.*, 2013). The largest pea germplasm collections are held by INRA France (8,839 accessions with 4,818 acc. of TILLING mutants); the Australian Grains Genebank (AGG; formerly Australian Temperate Field Crops Collection, 7,432 acc.); the Vavilov Institute, Russia (6,790 acc.); the USDA (6,827 acc.); ICARDA (6,105 acc.); the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany (5,343 acc.); Instituto Di Genetica Vegetale Italy (4,558 acc.); the Institute of Crop Sciences, China (3,837 acc.); the National Bureau of Plant Genetic Resources, India (3,609 acc.); and the John Innes Center, UK (3,567 acc.) (Smýkal *et al.*, 2013). Some of these genebanks have also identified a core collection comprising around 5–10% of the collection size to represent a cross section of the diversity, usually based on geographic diversity of collection sites for landraces, to facilitate a search of the germplasm for alleles of key traits (Redden *et al.*, 2005).

In addition to wild and cultivated accessions, there are also pea mutant stocks held at John Innes Collection, Norwich, UK (575 accessions); the Institute of Plant Genetics Resources collection, Plovdiv, Bulgaria (122 accessions); and a targeted-induced local lesions in genomes (TILLING) population of 4,818 lines (1,840 described by phenotype and 93 symbiotic mutants for 26 genes) held at INRA, Dijon, France. In addition, fast neutron generated deletion mutant resources (around 3,000 lines) are available for pea, which have been useful in identifying several developmental genes. These genetic stocks have well-identified phenotypic markers of high penetrance, ranging across seed and pod types to stem fasciation and internode length (Redden *et al.*, 2005).

Several studies of pea germplasm using morphological descriptors and agronomical traits have been published (Ali *et al.*, 2007; Sardana *et al.*, 2007; Smýkal *et al.*, 2008a; Sarikamis *et al.*, 2010; Azmat *et al.*, 2012). Different molecular techniques were applied over the last two decades to study pea genetic diversity. Using these markers, several major world pea germplasm collections have been analyzed and representative core collections formed (Baranger *et al.*, 2004; Loridon *et al.*, 2005; Jing *et al.*, 2005, 2007, 2010, 2012; Smýkal *et al.*, 2008a, 2011, 2013; Zong *et al.*, 2009; Nasiri *et al.*, 2010; Kwon *et al.*, 2012; Majeed *et al.*, 2012). All these studies give a consistent view: the *Pisum* genus is very diverse, and the diversity is structured, showing a range of degrees of relatedness that reflect taxonomic identifiers, eco-geography and breeding gene pools (Ellis, 2011; Jing *et al.*, 2012; Smýkal *et al.*, 2011, 2013).

Pea is an important food legume in the temperate and elevated sub-tropical cropping zones, grown as dry grain, as green unripe fresh grain for vegetable use and for canning, and as green leaves (Muelbauer and Tullu, 1998). The crop is also used for fodder. The total world grain production fluctuates 10 – 12 million tonnes, with Canada as the leading producer, followed by USA, India, Russia, France and China (see Smýkal *et al.*, 2012 for review). However mean yield is relatively low 1,558 kg/ha, while European records are around 6,000 kg/ha, indicating a gap in yield stability and biological potential of the crop. Up to half of the area in which pea is sown may be used for the production of vegetables, green snap bean pods, green seed for vegetables (fresh, frozen or canned), green leaves and for direct livestock grazing. China, with 1.3 million ha sown, is a major producer of peas for green pods/seed (FAOSTAT 2012). Although pea is currently recognized as a protein crop (20-25%), its potential is also as a source of high-quality starch (up to 50%) and even putatively as an oil (1-5%) source (Khodapanahi *et al.*, 2012). The key breeding objectives involve increasing yield potential by improving biotic and abiotic stress resistances and enhancing quality for diverse food markets. Quality includes improved appearance of the seeds, as well as improved nutritional value, cooking quality and flavor.

The energy and health benefits of peas derive mainly from the concentration and properties of starch, protein, fiber, vitamins, minerals and phytochemicals. Fiber from the seed coat and the cell walls of the cotyledon contributes to gastrointestinal function and health and reduces the digestibility of starch in peas. The intermediate amylose content of pea starch also contributes to its lower glycaemic index and reduced starch digestibility. Pea protein, when hydrolyzed, may yield peptides with bioactivities, including angiotensin I-converting enzyme inhibitor activity and antioxidant activity. The vitamin and mineral contents of peas may play important roles in the prevention of deficiency-related diseases, specifically those related to deficiencies of Se or folate (Dahl *et al.*, 2012). Peas contain a variety of phytochemicals once thought to be only anti-nutritive factors. These include polyphenolics, in colored seed coat types in particular, which may have antioxidant and anticarcinogenic activity, saponins, which may exhibit hypocholesterolaemic and anticarcinogenic activity, and galactose oligosaccharides, which may exert beneficial prebiotic effects in the large intestine (Dahl *et al.*, 2012). Development of low-phytate cultivars has become an important objective in several crops, including pea. This is because a major part of the total phosphorus in pea seeds is stored as phytate, an organic molecule that binds with some mineral cations and is excreted due to the lack of phytase enzymes in humans and non-ruminant animals. This causes nutrient deficiency as well as environmental pollution. Chemical mutagenesis led to identification of low-phytate pea lines (Rehman *et al*., 2012).

Genetic diversity available in wild *Pisum* species has been so far poorly exploited. Several large studies were published primarily for quantitative disease reactions (Infantino *et al*., 2006; Tivoli *et al*., 2006; Sillero *et al*., 2006). Many pea germplasm screens have been conducted for biotic and abiotic stresses, agronomic traits and seed quality (e.g., nutrition) but the studies are small (less than 20 accessions), the data is unavailable, published in difficult-to-access sources or unpublished. The most attention has been given to *P. fulvum*, as a donor of bruchid resistance and source of novel powdery mildew resistance (Clement *et al*., 2002, 2009; Fondevilla *et al*., 2007, 2008; Byrne *et al*., 2008). Incomplete levels of resistance to powdery mildew, rust (*Uromyces pisi* (Pers.) Wint.), crenate broomrape (*Orobanche*

crenata) and *Mycosphaerella pinodes* are available in accessions of *P. sativum* subsp. *sativum*, subsp. *abyssinicum*, subsp. *elatius* and *P. fulvum* (Fondevilla *et al*., 2005, 2007, 2011; Rubiales *et al*., 2005, 2009; Barilli *et al.*, 2009). Wild *Pisum* in its native range displays a typical winter habit in which plants germinate in autumn, overwinter in the vegetative state, and flower in response to increasing day-length in spring (Abbo *et al.*, 2003; Weller *et al*., 2009, 2012). Wild *Pisum* was identified as a source of alleles of flowering locus *Hr* implicated to influence winter frost tolerance (Lejeune-Hénaut *et al*., 2008). Moreover, the flowering allele *Hr* enhances the capacity of pea photoperiodic lines to produce basal laterals, which is often found in primitive accessions of *Pisum sativum* subsp. *sativum; P. sativum* subsp. *elatius* and *P. fulvum* (Weller *et al.*, 2009, 2012). The majority of cultivated pea accessions from higher latitudes have a quantitative long-day response and are grown as a spring crop, while the obligate or near-obligate requirement for long-days suits pea to a winter cropping cycle and has been retained in some forage cultivars (Weller *et al*., 2009, 2012). There is some interest to develop pea as winter crop in order to escape drought and heat stress during flowering and seed set periods.

D. Genus *Lens* Miller

The lentils (*Lens* Miller), a small genus of Mediterranean origin, are nested in the core clade of the genus *Vicia* (Schaefer *et al.*, 2012). Different taxonomists have recognized different numbers of species within the genus. There were considered to be five lentil species: *Lens culinaris* Medik., *L. orientalis* Popow, *L. ervoides* Grande, *L. nigricans* (M. Bieb.) Godr. and *L. montbretii* (Fisch. & C. A. Mey.) P. H. Davis & Plitm. (Cubero, 1981).

Lens montbretii has been transferred from the genus *Lens* to the genus *Vicia* on the basis of its different morphology and cytology, with 2n = 12 chromosomes (Ladizinsky and Sakar, 1982). *Lens lamottei* was distinguished on the basis of an herbarium specimen of *L. nigricans* (Czefranova, 1971). An additional species *L. odemensis* was recognized by Ladizinsky *et al.* (1984) as a new species due to the difference in stipules from *L. nigricans* (Ladizinsky, 1986). As the last discovered taxon, *L. tomentosus* was described as distinct from *L. orientalis* by tomentose pods, a minute satellite and one large, metacentric chromosome (Ladizinsky, 1997). Current classification recognizes one cultivated lentil (*L. culinaris* subsp. *culinaris*) and six related taxa: *L. culinaris* subsp. *orientalis*, *L. culinaris* subsp. *tomentosus*, *L. culinaris* subsp. *odemensis*, *L. ervoides*, *L. nigricans* and *L. lamottei* (Ferguson *et al.*, 2000). The wild relatives of the cultivated lentil have a wide distribution. *L. culinaris* subsp. *orientalis* (Boiss.) Ponert, naturally distributed from Turkey to Uzbekistan, is considered the putative progenitor of the cultivated lentils (Ladizinsky, 1979a). *Lens culinaris* subsp. *tomentosus* is restricted to northern Syria, Iraq and eastern Turkey; *L. ervoides* occurs along the eastern Mediterranean coast to former Yugoslavia, often in shady habitats, such as pine plantations; *L. lamottei* is found in Morocco, Spain and Southern France; and *L. nigricans* occurs from southwest Turkey to the southwestern Mediterannean (Ferguson and Erskine, 2001).

The cultivated lentils were divided into two subspecies by Barulina (1930) and two races by Cubero (1981), the large-seeded macrosperma and small-seeded microsperma race. The small-seeded varietal group is traditionally grown in the Middle East, South Asia, North Africa, and mainly in Turkey, whereas the large-seeded varietal group is usually grown in Canada (FAOSTAT, 2013) and large seeded varietal group is grown in the Americas and Southern Europe (Sekhon *et al.*, 2007).

Lentil is a self-pollinated species with cleistogamous flowers and consequently usually has <0.8% natural cross pollination (Wilson and Law, 1972). All species of *Lens* have a chromosome number of 2n = 2x = 14, which is also inferred as the ancestral number for the clade (Schaefer *et al.*, 2012). The genome size is estimated to be 1C = 4.20 pg, corresponding to 4,063 Mb/C (Arumuganathan and Earle, 1991).

Phylogeny and genetic diversity of the genus *Lens* has been studied first by seed protein electrophoresis (Ladizinsky, 1979b; Sultana *et al.*, 2006) and isozyme markers (Zamir and Ladizinsky, 1984; Pinkas *et al.*, 1985; Hoffman *et al.*, 1986; Muehlbauer *et al.*, 1989; Erskine and Muehlbauer, 1991; Mayer and Soltis, 1994; Ferguson and Robertson, 1996). The DNA-based markers, such as RFLP (Havey and Muehlbauer, 1989; Muench *et al.*, 1991; Rajora and Mahon, 1994), RAPD (Sharma *et al.*, 1995; Ferguson *et al.*, 2000; Sonnante and Pignone, 2001; Toklu *et al.*, 2009; Tewari *et al.*, 2012), AFLP (Sharma *et al.*, 1996; Zavodna *et al.*, 2000; Duran and Perez de le Vega, 2004; Kahraman *et al.*, 2004; Rubeena *et al.*, 2006; Fiocchetti *et al.*, 2009; Toklu *et al.*, 2009), microsatellite markers (Duran and Perez de le Vega, 2004; Hamwieh *et al.*, 2009; Liu *et al.*, 2008; Babayeva *et al.*, 2009; Reddy *et al.*, 2010; Gupta *et al.*, 2012, Tewari *et al.*, 2012; Zaccardelli *et al.*, 2012), inter simple sequence repeat (ISSR) (Zavodna *et al.*, 2000; Sonnante and Pignone, 2001; Toklu *et al.*, 2009), internal transcribed spacers (ITS) (Fernandez *et al.*, 2000; Mayer and Bagga, 2002; Sonnante *et al.*, 2003), non-transcribed spacer (NTS) (Fernandez *et al.*, 2005), sequenced tagged microsatellite site (STMS) (Inder *et al.*, 2008; Datta *et al.*, 2011), single-nucleotide polymorphisms (SNPs) (Alo *et al.*, 2011), and resistance gene analogue (RGA) (Yaish *et al.*, 2004; Sari *et al.*, 2013) were used to analyze phylogenetic relationships among taxa in the genus *Lens,* as well as the genetic diversity of cultivated lentil.

1. *Crop Lentil (*Lens culinaris *Medik.)*

Ex situ collections of lentil number over 58,407 and are held in 12+ collections (Tullu *et al.*, 2011, Table 1). This world collection is shared among 40 genebanks, which have a large amount of cross-duplication. The world lentil collection is held by ICARDA and holds 10,000+ accessions, followed by India (7,712 acc.), Australia (5,254 acc.), USA (3,187 acc.) and the Vavilov Institute, Russia (2,556 acc.). Most other national collections hold some portion of the subsets of this collection (Coyne and McGee, 2013). The ICARDA has globally

mandated research for lentil improvements; it holds roughly 600 wild accessions (Redden *et al.*, 2007) and the largest collection of wild *Lens* accessions from 12 countries (Furman, 2006). The wild relative collections total 852 accessions (GENESYS 2013, Redden pers comm, for ATFCC) of 6 wild *Lens* taxa (*L. culinaris* subsp. *orientalis*, *L. odemensis*, *L. tomentosus*, *L. ervoides*, *L. montbretii*, and *L. nigricans*) (Ferguson *et al.*, 2000; Sarker and Erskine, 2006) representing 24 countries. *Ex situ* collections give priority to the conservation of lentil landraces in order to maximize domestic diversity, as well as to conserve cultivars and landraces that have valuable combinations of traits and assembled linkage groups of valuable genes (Furman *et al.*, 2009). Documentation of agronomic and descriptor traits in the lentil genepool exists across more than half of the world lentil collection at International Lentil Information System (ILIS). ILIS enabled the lentil germplasm to be explored for multiple traits a with search/query program, to target the preferred germplasm for breeders to assess, or for targeted acquisition of germplasm from other genebanks (Balachandra *et al.*, 2006; Redden *et al.*, 2007). With the integration of the ATFCC collections into the Australian Grains Genebank (AGG) in 2013, the ILIS database will be transferred into GRIN-Global.

Large-scale genotypic characterization of lentil genetic resources is lacking. The largest published study used sequences of 22 genes from 308 lentil accessions (133 cultivated and 175 wild) to determine the population structure (K = 8) and to propose theories on taxonomy and domestication origins (Alo *et al.*, 2011). The next largest study was conducted on an ICARDA core collection of 57 cultivated and 52 wild lentil accessions (Hamwieh *et al.*, 2009). Cluster analysis based on SSRs defined the two groups into two unsurprising clusters, cultivated and wild. A comparison of 30 landraces from South Asia to 130 from 13 other countries using RAPDs and isozymes was performed by Ferguson *et al.* (1998). Numerous small-scale (less than 45 lentil lines) studies have been published using various DNA marker classes: RAPDs (Fikiru *et al.*, 2010; Hoque and Hasan, 2012), ISSRs (Fikiru *et al.*, 2011), AFLPs and SSRs (Sultana and Ghafoor 2008; Babayeva *et al.*, 2009; Reddy *et al.*, 2010; Datta *et al.*, 2011; Zaccardelli *et al.*, 2012). Seed proteins of 13 polymorphic peptides were investigated in 144 lentil landraces collected in Pakistan (Sultana *et al.*, 2006). Several lentil core collections have been assembled (Erskine and Muehlbauer, 1991; Simon and Hannan, 1995; Furman, 2006; Hamwieh *et al.*, 2009). 4,036 ICARDA accessions were evaluated for quantitative characteristics of time to flower, time to maturity, plant height, and lowest pod height (Erskine *et al.*, 1989). Another study examined the relationship between the yield of seed and straw of 3,586 ICARDA accessions (Erskine, 1983). Response to temperature and photoperiod effect on time to flowering was investigated in 231 and 369 ICARDA accessions (Erskine *et al.*, 1990, 1994, respectively). A study of 3,512 ICARDA accessions noted the presence of iron deficiency in a calcareous soil linked to geographical origin (Erskine *et al.*, 1993). Similarly, within 495 ICARDA accessions grown in boron-deficient soil, yields revealed striking genetic differences associated with geographic origin (Srivastava *et al.*, 2000). Next, a study screened 310 lines for growth in soil with a high concentration of boron and identified tolerance in accessions from Afghanistan and Ethiopia (Hobson *et al.*, 2006). Characterization of the USDA lentil core collection of 287 lines identified useful trait variation for phenology, morphology, seed and straw yields for use in breeding (Tullu *et al.*, 2001). Lentil is confounded by a number of important production constraints, particularly biotic stresses (Chen *et al.*, 2009, 2011; Podder *et al.*, 2012). The most important of these diseases on a global scale are ascochyta blight (*Ascochyta lentis* Bond. & Vassil.), rust (*Uromyces viciae-fabae* (Pers.) Schroet), botrytis grey mold (*Botrytis cinera* Pers. Ex Fr. and *Botrytis fabae* Sard), anthracnose (*Colletotrichum truncatum* (Schw.) Andrus & Moore), stemphylium blight (*Stemphylium botryosum* Wallr.), powdery mildew (*Erysiphe pisi* DC.), fusarium wilt (*Fusarium oxysporum* Schlecht. :Fr. f.sp. *lentis* Vasudeva and Srinivasan), sclerotinia stem rot (*Sclerotinia sclerotiorum* (Lib.) de Bary) and broomrape (*Orobanche crenata* Forssk) with several wild lentil species and accession found to be source of resistances (Buchwaldt *et al.*, 2004; Fernández-Aparicio *et al.*, 2008, 2009; Chen *et al.*, 2009; Tullu *et al.*, 2006; 2010; Vail *et al.*, 2012; Rubiales *et al.*, 2013; Shaikh *et al.*, 2013).

Lentil is a highly nutritious food, high in protein, minerals and vitamins (Bhatty, 1988). It is consumed as a soup and forms the protein staple for a large portion of Asia. Consumption is particularly high in Sri Lanka and Nepal, followed by Syria and Turkey (Erskine, 2009). Lentils are combined with the carbohydrate staples rice and wheat, forming a complete protein diet (Erskine, 2009). Lentil has the potential to reduce micronutrient (iron and zinc) deficiency though the consumption of 100 g daily (Thavarajah *et al.*, 2009). Additionally, lentil is a promising source of antioxidant phenolics and could serve as a dietary supplement (Zou *et al.*, 2011). Lentil is typically grown in dryland cropping systems in rotation with grains, such as wheat and rice (Materne and Siddique, 2009). World production was 4.55 M tons in 2012 with mean yield of 1,070 kg/ha. Leading producers include Canada, with 1.49 M tons, followed by India (0.95 M tons), Australia (0.46 M tons), Turkey (0.44 M tons), USA (0.24 M tons) and Nepal (0.21 M tons) (FAOSTAT, 2012). While India has increased production over the last five years, Canada's production more than doubled in the same time period (Erskine, 2009; FAOSTAT 2012). Regionally, Asia produces close to half of the world's lentils (2.07 M tons).

IV. TRIBE TRIFOLIEAE (BRONN) ENDL.

A. Genus *Medicago* L.

The tribe Trifolieae, subtribe Trigonellinae, includes *Medicago* L. (alfalfa) and *Trifolium* L. (clover), along with *Melilotus* (L.) Mill. (sweet clover) and *Trigonella* L. (Maureira-Butler *et al.*, 2008), with a total of c. 87 species in *Medicago*. Phylogenetic relationships within the genus have proved difficult to

resolve (Maureira-Butler *et al.*, 2008; Steel *et al.*, 2010). Using morphological traits, Small and Jomphe (1989) proposed 12 sections and 8 subsections. However, incongruence has been reported between morphological and molecular inferences (Bena, 1998). Incongruence has also been reported in an analysis using two nuclear-encoded genes and a mitochondrial gene (Maureira-Butler *et al.*, 2008). Results of a phylogenetic analysis of plastid *trnK/matK* and nuclear *GA3ox1* sequences supported the previously recognized groups, sect. Medicago and sect. Buceras, but suggested that *M. arborea* L., *M. citrina* (Font Quer) Greuter and *M. strasseri* Greuter, Matthäs & Risse, currently in sect. Dendrotelis, be moved to sect. Medicago. There was also little support for sect. Lupularia and sect. Platycarpa (Steele *et al.*, 2010). Difficulty in resolving the *Medicago* phylogeny may be due to historic and ongoing hybridization within the genus (Maureira-Butler *et al.*, 2008; Steele, *et al.*, 2010). More recently, Yoder *et al.* (2013) used whole-genome sequence data from 29 *Medicago* taxa to examine phylogenetic relationships. Using 87,596 polymorphic single-nucleotide sites, Yoder *et al.* (2013) found that the consensus topography was consistent with previous classifications of major sections and subsections and was also able to resolve ambiguities among several species.

Alfalfa is part of the *Medicago sativa* complex that includes diploid (2n = 16) and tetraploid (2n = 32) forms that have either blue flowers and coiled pods or yellow-flowers and sickle-shaped pods. Some forms are characterized by the presence of glandular trichomes on pods. Small (2011) proposed the most recent taxonomic classification based on ploidy level, hybridization, flower color, fruit coiling and the presence of glandular hairs on fruits. Using the classification of Small (2011), taxa within the *M. sativa* complex fall into either the primary or secondary gene pool of alfalfa, depending on ploidy level. Crop wild relatives (CWR) in the primary alfalfa gene pool include the tetraploid forms of *M. sativa* subsp. *falcata*, *M. sativa* L. subsp. *glomerata* (Balb.) Rouy, *M. sativa* subsp. *sativa*, *M. sativa* L. nothosubsp. *tunetana* Murb., *M. sativa* L. nothosubsp. *varia*, and *M. sativa* subsp. *falcata* var. *viscosa* (Rchb.) Posp. (USDA GRIN 2013, Table 1). References outlining the intraspecific and interspecific crossing studies used to designate the alfalfa gene pool can be found in Small (2011).

Alfalfa is a highly diverse crop. It is a perennial, autotetraploid (2n = 4x = 32) (McCoy and Bingham, 1988), and is cross-pollinated by insects, predominately bees. The facts that taxa within the *Medicago sativa* complex occur sympatrically, that taxa at the same ploidy level freely intercross, and that the ploidy barrier is relatively weak due to the frequency of gamete reduction contribute substantially to the diversity seen in alfalfa (Kaljund and Leht, 2013). Taxa within the *Medicago sativa* complex extend across Eurasia, from the British Isles into Eastern Siberia, southward around the northern rim of the Mediterranean and the Black Sea, and south into Eastern Turkey, Northern Iraq and Iran, and East into Kazakhstan. M. *sativa* subsp. *glomerata* extends into Northern Algeria. Phylogeographic analysis provides ample evidence that germplasm within the *Medicago sativa* complex exhibits extensive adaptation to a broad array of environments (Sakiroglu *et al.*, 2010; Sakiroglu and Brummer, 2013). *Medicago sativa* subsp. *sativa* is found growing in the steppe, in fertile meadows, and even on sand dunes. The species grows best in fertile, moist soil at a pH of 6.0-6.5. The diploid version of subsp. *sativa*, *M. sativa* subsp. *caerulea* is more drought tolerant, and some ecotypes are adapted to saline soils (Lubenets, 1953). *Medicago sativa* subsp. *falcata* is adapted to the dry cold steppe area and may be more broadly adapted than subsp. *sativa* (Oakley, 1917; Lesins and Lesins, 1979). *M. sativa* subsp. *glomerata* occurs in moist, montane areas (Small, 2011). *Medicago sativa* subsp. *falcata* var. *viscosa* and *M. sativa* subsp. *varia* possess the same broad adaptation as *M. sativa* subsp. *falcata*. Although these infraspecific taxa can be distinguished by flower color and pod shape, numerous ecotypes reflect extensive variation within taxa with regard to leaf size and shape, growth habit (upright to prostrate), leaf and pod pubescence, and degree of pod curl. This tremendous diversity is reflected in the numerous synonyms associated with the species. Small (2011) provides a list of synonyms in his recent monograph.

*1. Crop alfalfa (*Medicago sativa *L.)*

There are over 91,000 accessions of *Medicago* held at major gene banks globally (FAO 2010, Table 1). Almost half of the global collection is represented by wild species (47%), while landraces, breeding lines and advanced cultivars make up 6%, 7%, and 6% of the global collection, respectively. Thirty-four percent of the collection is made up of unknown accession types (FAO, 2010). Greene *et al.* (2012) examined the representation of global *ex situ* collections for alfalfa CWR species native to the Russian Federation and neighboring countries. They found that representation of the Crimea, Mountain Central Asia (with the exception of subsp. *sativa*) and Eastern Siberia was weak, despite the fact that these are important areas of diversity and adaptation to extreme environments. Taxa with limited representation included *M. sativa* subsp. *falcata* var *viscosa* and *M. sativa* subsp. *glomerata*, whose tetraploid versions are in the primary gene pool and whose diploid versions are in the secondary gene pools (Table 1). Underrepresented CWR in the tertiary genepool included *M. saxatilis*, *M. papillosa*, *M. rupestris*, *M. daghestanica*, and *M. marina* (Greene *et al.*, 2012). Parts of the world where valuable alfalfa germplasm occurs but has not been extensively sampled include Iran, Iraq, Afghanistan and Northern Pakistan (Bauchan and Greene, 2002). In a recent global gap analysis of 13 alfalfa CWR species, 70% of the species were ranked as high-priority species to collect, 15% were medium priority and 15% were low priority (CWR and Climate Change 2013a). Examining the online interactive map, collecting gaps for high-priority alfalfa CWR taxa include the southeastern part of the Crimea peninsula, southern Georgia, Armenia and parts of Turkey (CWR and Climate Change, 2013b). Although there are collection gaps, utilization of alfalfa germplasm is not hampered by a lack of diversity in *ex situ* collections, but rather by the challenges of evaluation and prebreeding. Substantial effort

was made from the early 1980s to the mid 1990s to evaluate the USDA alfalfa collection. Recent efforts have provided chromosome counts on taxa within the *Medicago sativa* complex that have diploid and tetraploid forms (Brummer *et al.*, 1999; Sakiroglu and Brummer, 2011; Sakiroglu and Kaya, 2012). Currently, about a third of the collection has been evaluated for resistance to 13 diseases, seven insects, seven feed quality traits, and five abiotic stress tolerance traits. These data are publically available in GRIN (Bauchan and Greene, 2002).

Alfalfa, also known as lucerne, is the most widely grown forage legume in the world. It is difficult to overstate the importance of alfalfa in the world economy. In the United States, alfalfa routinely places among the top five crops in the nation in terms of both farmgate value and total acreage. In terms of protein production, alfalfa placed third, behind soybeans and corn, in 2009. From a global perspective, alfalfa is among the top 10 crops for protein production (Sumner and Rosen-Molina, 2011). In 2009, the FAO estimated that alfalfa was grown on approximately 30 million hectares worldwide; 66% was produced in North America and Europe, 23% in South America, and the remainder in Asia, Africa and Oceania (FAO, 2013). Valuable characteristics of alfalfa include adaptation to a wide range of climates, ability to fix up to 560 kg/ha atmospheric nitrogen per year, production of large amounts of biomass that is highly nutritious and between 15 and 22% crude protein, production of sweet nectar that attracts bees, deep tap roots that improve soil tilth and a perennial growth habit that reduces soil erosion. Alfalfa is used primarily as animal feed in the form of forage and fodder. It is especially important for dairy cows but is also an important feed for horses, beef cattle, sheep, chickens, turkeys and other farm animals. Alfalfa is also used as a green manure, as a rotation crop and as ground cover (Small, 2011). Its characteristics make it a valuable crop for supporting biodiversity and agroecosystem services (Putnam, 2001). In Australia, alfalfa has been used to reduce soil salinization (Robertson, 2006), and in the United States, cultivars have been developed to support bioremediation of high-nitrogen soils (Russelle, 2007). Alfalfa is also consumed directly by humans as alfalfa sprouts, juice and powder. Potential new uses include biofuel and the production of industrial enzymes, such as peroxidase, alpha-amylase, cellulase, and phytase (Small, 2011).

Conventional alfalfa breeding programs generally identify useful germplasm in nurseries or pest and disease screening trials. Selections are then incorporated into elite populations using phenotypic or genotypic recurrent selection. Synthetic cultivars are then developed by intercrossing individual plants and harvesting equal quantities of seed from each parent, which is bulked to form the Synthetic 1 generation. However, MAS and genetic engineering are being adopted, especially in private industry. Reich (2012) describes efforts to develop cultivars resistant to saline soils using conventional breeding techniques along with marker-assisted selection and genetic engineering to reach their goals. Genetic engineering efforts are also focused on developing alfalfa that is more nutritious by decreasing lignin production and increasing tannin production (McCaslin and Reisen, 2012).

B. Genus *Trifolium* L.

Trifolium is one of the largest genera in the tribe, with about 255 species (Zohary and Heller, 1984; Gillett and Taylor, 2001). The genus is cosmopolitan, with species that occur mostly in the northern hemisphere. Primary centers of diversity are Eurasia (150-160 species), North America (60-65 species) and Africa (25-30 species). Over half of its species originated in the Mediterranean region. While most species occupy temperate and subtropical regions, some occur in the Tropics of West Africa and South America, where they are generally restricted to montane and alpine zones (Raven and Polhill, 1981; Zohary and Heller, 1984; Small, 1989). The genus includes annuals and perennials (Watson *et al.*, 2000). *Trifolium* species occur in a wide range of habitats, including meadows and prairies, open woodlands, semi-deserts, mountains, and alpine peaks. A common feature of these diverse habitats is high solar radiation; few clover species tolerate shade.

In some studies (Roskov, 1989), the genus is divided into three separate genera: *Chrysaspis* Desv. (pavis free, wings and keel knitted only in the basal part), *Amoria* C. Presl. (pavis free, wings and keel knitted into a tube) and *Trifolium* s. str. (all petals knitted into a tube). The genus *Chrysaspis* is very close to the genus *Melilotus* (Roskov, 1989). The genus name refers to the distinctive leaves, which are usually composed of three leaflets (trifoliolate). *Trifolium* is a member of a large, monophyletic clade of 45 genera – mostly the temperate and herbaceous (Polhill, 1981; Doyle, 1995). *Trifolium* belongs to the vicioid subclade and is closely related to *Medicago*, *Melilotus*, and *Trigonella*. Altogether they comprise *Trifolieae* s. str. or subtribe *Trigonellinae* of *Trifolieae* s. l. (Zohary, 1972). *Trifolium* is the only one of these four genera with some species restricted to the New World. *Trifolium* differs from these allied genera by ovule morphology and by the position of seeds in the pod (Heyn, 1981). Wings are clawed, and keels are adnate to the staminate fascicle (Hossain, 1961).

There are some species that appear to be intermediate between all four closely allied genera (Heyn, 1981). Nuclear and chloroplast sequences from a variety of genes and genic regions support the monophyly of *Trifolium* (Steele *et al.*, 1998, 1999). Within *Trifolieae* tribe s. str., *Trifolium* is more derived because of a trend towards reduction of pod size, reduction of the number of seeds per pod, and loss of the pod septum, resulting in indehiscence and unique fruit dispersal accessories (Zohary and Heller, 1984; Small, 1989). Most contemporary classifications recognize *Trifolium* as one large genus of eight sections: Lotoidea, Paramesus, Mistyllus, Vesicaria, Chronosemium, Trifolium, Trichocephalum and Involucrarium (Hossain, 1961; Zohary and Heller, 1984; Ellison *et al.*, 1996). Bobrov (1967) recognized nine to eleven smaller, segregated genera. Biogeography, morphological evolution, and the existing classification for *Trifolium* were examined by Watson *et al.* (2000). *Trifolium* was

found to be monophyletic. The two largest sections of the genus, sections Lotoidea and Trifolium, are not monophyletic; only one small section (Chronosemium) is. Sect. Lotoidea is the largest section and is considered ancestral to all other sections on the basis of a worldwide distribution, large size (over 90 species), and morphological heterogeneity among species (Zohary, 1972; Zohary and Heller, 1984). Six sections occur in the Old World, primarily in Eurasia, with some species extending into Africa. One section (Involucrarium) is restricted to the New World and occurs in both North and South America. The monophyly of a clade with New World species of sections Involucrarium and Lotoidea is confirmed by molecular data, even if no section is considered to be monophyletic (Steiner *et al.*, 1997).

Some contrasting views have been proposed on the origin and radiation of *Trifolium*. Most frequently mentioned is the Mediterranean origin of the genus, probably in the Early Miocene. A single origin of all North and South American species is hypothesized, while the species of sub-Saharan Africa may originate from three separate dispersal events (Ellison *et al.*, 2006). Gillett (1952) and Taylor (1985) suggested a Mediterranean origin on the basis of species diversity, morphological heterogeneity, and chromosome number. Raven and Polhill (198l) agreed that *Trifolium* is of Eurasian origin and suggested that repeated migrations to North America occurred. These migrations were followed by multiple radiations and dispersal events. Old World origin for *Trifolium* is in contrast to the hypothesis of Zohary (1972) that the genus originated in North America and that migration and colonization led the species via the Bering Strait to Asia, followed by a series of secondary radiations in the Mediterranean region and dispersal into Africa. The molecular data support a Mediterranean origin of *Trifolium*, with the New World clade deeply nested among the Old World species. Zohary and Heller (1984) indicated two regions of interest for genus evolution: the Mediterranean region, with 110 species belonging to seven sections, and the Californian region, which includes a smaller number of species.

A hypothetical ancestral form for *Trifolium* was described as a perennial with large flowers on bracteate pedicels, with a simple calyx, choripetalous corolla, and numerous ovules (Celakovsky, 1874; Bobrov, 1967). Some species of section Lotoidea are similar to this proposed archetype (Zohary and Heller, 1984). The annual habit evolved from a perennial repeatedly. Most species of *Trifolium* are diploid, with approximately 20% polyploidy occurrence. Most of the polyploid species are Old World perennials, with 65% in section Lotoidea (Zohary and Heller, 1984). Hybridization among *Trifolium* species is rare or non-existant (Wexelsen, 1928; Zohary, 1972). Chromosome numbers are known for at least 184 species of *Trifolium* (Zohary and Heller, 1984). Over 80% of the examined species are $2n = 16$, and $x = 8$ is the basal number of the genus (Goldblatt, 1981). Aneuploidy ($2n = 10$, 12, or 14) has been identified in 31 species, eleven of which have both aneuploid and diploid ($2n = 16$) or polyploid counts. Polyploidy has been identified in 24 species, of which six are exclusively tetraploid, two are hexaploid, and one is dodecaploid. Eleven species have both diploid and polyploid counts, while three have multiple polyploid counts at the tetraploid level and above. Nitrogen-fixing root nodules have been reported in over 125 species of clover (Sprent, 2001).

*1. Crop clover (*Trifolium*)*

The genus *Trifolium* includes about ten species of agricultural significance. The most important are white clover (*Trifolium repens* L.) and red clover (*T. pratense* L). Clovers are of global agricultural significance as forage species, particularly important in temperate areas, both for direct grazing and for conserved forage (Zohary and Heller, 1984). At least 16 species of *Trifolium* are actively cultivated (Gillett and Taylor, 2001, Table 1), a fairly large number for a single genus. Many native species are also used for animal grazing (Crampton, 1985). Overall, approximately 74,000 accessions of *Trifolium* are held in global *ex situ* collections, 53% of which are wild, 14% of which are cultivated and 33% are of unknown improvement status (FAO, 2010, Table 1). The largest collections are held by Australia, New Zealand, and ICARDA (FAO, 2010). The Australian Temperate Forage Legume Center (*Trifolium*), Perth, Western Australia, has 119 species and 11,000 accessions. The Genebank of the VIR, Saint Petersburg, Russian Federation, has 4,605 accessions of the clover genus. ICARDA conserves 4,536 accessions. USDA conserves 6,229 accessions of the genus: 815 accessions of *T. repens*, 1,367 accessions of *T. pratense*, and 4,047 accessions of other *Trifolium* species. The Leibniz Institute of Plant Genetics and Crop Plant Research has collectively 1,657 accessions, of which 136 acc. are of *T. repens*, 572 acc. are of *T. pratense* and 949 acc. are of other *Trifolium* species. Thanks to the efforts of Dr. Norman Taylor, the U.S. collection houses samples of almost all species in the genus and has accessions from 74 countries (GRIN, 2013). The International Livestock Research Institute genebank, in Addis Ababa, Ethiopia, holds an important collection of wild clovers native to Ethiopia and other African countries. Significant collections of breeding lines and cultivars are also held by AgResearch, New Zealand (Margot Forde Forage Germplasm Center). Like most germplasm collections of crop species, agriculturally important clover species are well represented in genebanks, while wild species frequently are represented by only a few accessions. In reviewing the U.S. clover collection, Morris and Greene (2001) concluded that it contained gaps for (i) cultivars and landraces of red and white clover originating from China, Japan, South America, and South Africa; (ii) obsolete cultivars developed in the USA; (iii) minor-use species; (iv) related wild species; and (v) germplasm distinguished by traits that may be of value to the nutritional supplement or bioremediation industries and that may convey adaptation to abiotic stress or be supportive of sustainable agriculture. Other important questions that need to be examined in order to determine the global *ex situ* coverage of *Trifolium* include the extent to which current collections represent an appropriate level of geographical coverage around

the globe and to what degree the major collections are sampling independent geographical regions (Abberton and Thomas, 2011). The study of variation in clover germplasm collections based on morphological, phenological, and agronomical characters and molecular markers has resulted in the development of core collections (Kouame and Quesenberry, 1993; Vymyslický *et al.*, 2010, 2012). No concordance between morphologic and RAPD marker classification of wild red clover populations was also reported by Greene *et al.* (2004). White clover wild relatives often display contrasting phenotypes for agriculturally important traits, such as drought tolerance (*T. occidentale* D. E. Coombe), cold tolerance (*T. pallescens* Schreb.), high inflorescence and seed set (*T. nigrescens* Viv.), presence/absence of stolons (*T. occidentale* vs. *T. pallescens* and *T. nigrescens*), and annual/perennial growth habit (*T. nigrescens* vs. *T. occidentale*). Generation of segregating progenies from these crosses would enable mapping of these traits and the discovery of the hidden genes. This could have dramatic consequences on clover breeding programs (Ravagnani *et al.*, 2012).

White clover (*T. repens* L.) is a perennial legume and the primary legume found in grazed pastures in most parts of the world. It could be also used for silage. Most often, it is used in mixed swards with grasses – mostly perennial ryegrass (*Lolium perenne* L.). A very important attribute of white clover is its nitrogen fixation, contributing about 250 kg N/ha per year in mixed grassland. White clover develops a dense network of stolons, which enhances grazing tolerance, winter hardiness and persistence. Resistance to pests and diseases, efficient use of water and nutrients, and compatibility with grass are important targets of white clover breeding (Abberton and Thomas, 2011). Breeding programs for white clover are carried out throughout the world: New Zealand (Williams *et al.*, 2007), Australia (Lane *et al.*, 1997; Jahufer *et al.*, 2002), the United States (Taylor, 2008) and the UK (Abberton and Marshall, 2010). They are focused on particular environments and management systems but share the objectives of more fully realizing the potential of white clover to contribute to livestock nutrition and soil fertility (Abberton and Thomas, 2011).

Red clover (*T. pratense*) is an important perennial legume in many parts of the world with oceanic climate: Western and Northern Europe, parts of Russia, Japan and the USA (Taylor and Smith, 1995). It has erect stems emerging from a meristematic 'crown.' Red clover is a high-yielding forage crop under optimal climates, is typically used for silage and is not tolerant to intensive grazing. Red clover cultivars are classified by ploidy level and by maturity. Tetraploid cultivars are artificially produced by chromosome doubling of diploid lines. Early flowering or 'double cut' cultivars are widely grown and give two more or less equal conservation cuts and subsequent lower yielding cuts. Late flowering or 'single cut' types give a greater proportion of their yield at the first cut. Red clover is traditionally important in organic farming systems, where it is used as a source of nitrogen in crop rotation and for its high protein content in modern silage technologies. Red clover is an important feed resource for pollinating insects (Abberton and Thomas, 2011).

Important breeding objectives include yield, persistence and pest and disease resistance (Boller *et al.*, 2010). Programs of interspecific hybridization between red clover and related species were reviewed by Abberton (2007). The main emphasis has been increasing longevity through crosses with more persistent species, particularly *T. medium* L. (Jakesova *et al.*, 2011). Many other clover species are used in agriculture as minor crops with different purposes. Clovers are very popular for pollinators, especially *T. hybridum* L., *T. resupinatum* L., *T. pannonicum* Jacq., *T. alexandrinum* L., and *T. incarnatum* L. (Ishii, 2013). A number of minor clover species may also be important with respect to future breeding efforts. Among these are the species most closely related to the putative diploid ancestors of white clover, namely *T. pallescens* and *T. occidentale*. Other species, such as *T. elegans* Savi, are of local agricultural importance, and consideration with respect to conservation and use needs to be given to all of them. *T. diffusum* Ehrh. has been used in programs of interspecific hybridization with red clover (Strzyzewska, 1995).

V. TRIBE CICEREAE

A. Genus *Cicer* L.

The genus *Cicer* was transferred from the tribe *Vicieae* Alefeld to its own tribe, *Cicereae* Alef., due to some morphological differences (Kupicha, 1977). Currently, *Cicer* includes 44 taxa, 9 annuals and 35 perennials (van der Maesen *et al.*, 2007; Davies *et al.*, 2007). The following taxa, *C. uludereensis* Dönmez (Dönmez, 2011), *C. floribundum* Fenzl. var. *amanicola* M. Öztürk & A. Duran (Öztürk *et al.*, 2011), *C. heterophyllum* Contandr., Pamukc. & Quezel var. *kassianum* M.Öztürk & A.Duran (Öztürk, 2011) and *C. incisum* (Willd.) K. Maly subsp. *serpentinica* M. Öztürk & A. Duran (Öztürk *et al.*, 2013) have recently been discovered in Turkey. The most widely known species in the genus *Cicer* is the cultivated chickpea (*Cicer arietinum* L.), with $2n = 2x = 16$ chromosomes and a genome size of ~738 Mb (Varshney *et al.*, 2013a). The 'macrosperma' or 'kabuli' and 'microsperma' or 'desi' chickpeas are distinguished on the basis of size and coloration of seeds and flowers and pigmentation on plants (Muehlbauer and Singh, 1987). Both of the cultivated chickpeas are thought to be derived from *C. reticulatum* (Ladizinsky and Adler, 1976; Toker, 2009), which is native to southeastern Turkey and northern Syria (Ladizinsky and Adler, 1976; Zohary and Hopf, 2000, Toker, 2009). According to the classical definition of Harlan and deWet (1971), there is a primary (*C. arietinum* and *C. reticulatum*), secondary (*C. echinospermum* P. H. Davis), and tertiary gene pool (*C. pinnatifidum* Jaub. & Spach., *C. bijugum* Rech. f., *C. judaicum* Boiss, *C. yamashitae* Kitam., *C. chorassanicum* Popow, and *C. cuneatum* Hochst. ex A. Rich. and perennial wild Cicer species) (Ahmad *et al.*, 1988; Table 1).

*1. Crop chickpea (*Cicer arietinum *L.)*

The *ex-situ* collections of chickpea landraces and wild relatives are stored in 44 genebanks worldwide. These collections hold a combined 98,313 accessions, with largest collections at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) in India (20,140 accessions) and ICARDA in Syria (13,818 accessions) (Genesys 2013, Table 1). Other genebanks with over 1,000 accessions include: the USDA in Pullman, Washington, USA (6,789 acc.); Aegean Agricultural Research Institute in Izmir Turkey (2,075 acc.); the Australian Temperate Field Crops Collection (ATFCC) in Horsham, Australia (8,655 acc.); the National Plant Gene Bank of Iran (5,700 acc.); the Vavilov Institute in Russia (2,091 acc.); and the Institute for Agrobotany Tápiószele, Hungary (1,170 acc.). Significant source countries for chickpea landrace accessions are India (10,526), Iran (8,912), Turkey (4,927), Syria (2,517), Afghanistan (1,949), Spain (1,494), Pakistan (1,272), and Ethiopia (1,175), plus over 60 additional countries that are also sources of additional cultivars and landraces (Redden *et al.*, 2007; Genesys, 2013). Over 75% of the ICRISAT collection consists of desi-type accessions, 21% are kabuli type and 4% are intermediate, while the ICARDA collection consists mainly of kabuli types (Redden *et al.*, 2007). There may be over 15% overlap between the ICRISAT and ICARDA collections; much higher levels of duplication occur between these two collections and national collections around the world, as well as among various national collections. The ATFCC has 4,001 landraces, cultivars and wild relatives, the latter numbering 241 accessions, all of which are duplicated in the ICRISAT, ICARDA and USDA collections. The total *ex-situ* holdings of the 27 species of wild *Cicer* are 1,105 accessions, which included 147 accessions of uncertain identification. There are 166 accessions of the progenitor *C. reticulatum* and 64 of *C. echinospernum* (Genesys, 2013, plus the ATFCC collection), although the number of unique accessions is reduced due to repeated subsampling of the original accessions (Berger *et al.*, 2003). For example, 43 subsequent accessions have been subsampled from *C. reticulatum* ILWC 21, originally collected from a single site along the Savur-Midyat road in southeastern Anatolia (Berger *et al.*, 2003). Fortunately, the numbers of unique *C. reticulatum* and *C. echinospernum* accessions will more than double as a result of a 2013 joint Turkish-USA-Australian collecting expedition in Turkey that specifically targets *Cicer* wild relatives (Berger, personal communication).

Chickpea ranks second among food grain legumes in the world after common bean with production of 11,308 Kt and mean yield of 931 kg/ha (FAOSTAT, 2012). Chickpea is grown in over 50 countries, ranging from subtropical and temperate regions of the world, for its protein-rich seeds. Chickpea seeds are a rich source of minerals, fiber, unsaturated fatty acids, β-carotene and do not contain any antinutritional factors (Jukanti *et al.*, 2012). Due to its high nutritional value, chickpea is considered one of the most nutritious food grain legumes and serves as an important protein source for humans who consume vegetarian diets. Because chickpea plants are efficient symbiotic nitrogen fixers, chickpea fits well in crop rotation, improving soil fertility and playing an important role in the sustainability of farming systems.

While loss of genetic diversity is a universal phenomenon among crops (Tanksley and McCouch, 1997), in chickpea there has been a particularly drastic narrowing of genetic diversity due to a series of bottlenecks unique to this crop (Abbo *et al.*, 2003a). Consequently, chickpea displays a lack of adaptive diversity for a range of biotic and abiotic stresses. Unlike cultivated chickpea, wild *Cicer* species possess useful variation for morphological traits (Robertson *et al.*, 1995), protein content (Ocampo *et al.*, 1998), and genetic sources for resistance to both biotic (Di Vito *et al.*, 1996; Collard *et al.*, 2001; Ansari *et al.*, 2004; Rubiales *et al.*, 2004) and abiotic stresses (Singh *et al.*, 1990, 1998; Croser *et al.*, 2003; Toker, 2005; Toker *et al.*, 2007ab; Canci *et al.*, 2009). Wild *Cicer* species were identified as sources of resistance to a number of diseases and pests such as ascochyta blight [*Ascochyta rabiei* (Pass.) Labr.], fusarium wilt [*Fusarium oxysporum* Schlechtend. Fr. f. sp. *ciceris* (Padwick) Matua & K. Sato], botrytis gray mold (*Botrytis cinera* Pers. ex. Fr.), rust (*Uromyces ciceris-arietini* (Grognot) Jacz. & Boyd), pod borer (*Helicoverpa armigera* Hubner), leaf miner (*Liriomyza cicerina* Rond.), seed-beetles (*Callosobruchus* Pic. sp.) and nematodes (Di Vito *et al.*, 1996; Collard *et al.*, 2001; Croser *et al*., 2003; Ansari *et al.*, 2004; Sharma *et al*., 2005; Sillero *et al.*, 2012). By far the most pressing issue relating to chickpea genetic resources is the urgent need to collect and characterize annual wild relatives, particularly those that are readily crossable with domestic chickpea (Ben-David *et al.*, 2010). Numbers of independent accessions in the primary genepool are <20 per species, as indicated more than a decade ago (Berger *et al.*, 2003). Even with such an extremely limited collection, the utility of annual wild *Cicer* genetic resources for providing useful adaptive variation and genetic diversity is unparalleled, as outlined in previous sections.

VI. TRIBE PHASEOLEAE (BRONN) DC.

A. Genus *Phaseolus* L.

According to the most recent monograph of the genus (Freytag and Debouck, 2002), there are 76 species of *Phaseolus*, all distributed in the New World with a center of diversity in Mexico. Recent phylogenetic analyses of chloroplast and nuclear ribosomal DNA regions (Delgado-Salinas *et al.*, 1993, 1996, 2006) revealed that the genus in its current circumscription is monophyletic and that all species can be grouped in two clades. Clade A comprises the three well-supported groups Pauciflorus, Pedicellatus, and Tuerckheimii, plus a few species of unclear affinity (P. *glabellus* Piper, *P. macrolepis* Piper, and *P. oaxacanus* Rose), and is mainly Mexican. Clade B comprises five groups (Filiformis, Vulgaris, Lunatus, Leptostachyus, and

Polystachios) and has a much broader distribution range, including the Andes and several islands, such as the Galapagos-endemic *P. mollis* Hook. f. (Delgado-Salinas *et al.*, 2006; Porch *et al.*, 2013). Freytag and Debouck (2002) prefer to group not by molecular phylogeny but by taxonomic characteristics and describe 16 sections of the genus. The five most important crop species of the genus, *P. acutifolius* (tepary bean), *P. coccineus* (scarlet runner bean), *P. lunatus* L. (lima bean), *P. polyanthus* Greenm. (year bean), and *P. vulgaris* L. (common bean) belong in two clades only, the Vulgaris and the Lunatus groups (Delgado-Salinas *et al.*, 1999), which also agree in the sections defined by Freytag and Debouck (2002). Molecular clock analyses revealed a stem age estimate for the *Phaseolus* clade of c. 8 million years and a crown age of max. 6 million years (Delgado-Salinas *et al.*, 2006).

The basic chromosomal number for *Phaseolus* species is n = 11. Despite all the cultivated species in the genus *Phaseolus* having the same number of chromosomes, many of the species are difficult to cross and are organized into primary, secondary, tertiary and quaternary genepools relative to the *P. vulgaris* (Table 1). In this regard, *P. coccineus* (scarlet runner bean) and *P. dumosus* (year-long bean) are in the secondary genepool, with simple crosses possible but with some difficulties for F_1 recovery as well as for introgression of genomic segments when backcrossing or deriving inter-specific lines. Cytoplasmic effects are important, and introgressions tend to be small, partial segments of the genome. *P. acutifolius* (tepary bean) and its close wild relatives from *P. parvifolius* Freytag (Blair *et al.*, 2012a) are in the tertiary genepool of common bean, principally crossable only with embryo rescue and with congruent backcrossing to avoid cytoplasmic effects and to increase the rate of introgression (Muñoz *et al.*, 2006). Meanwhile, *P. lunatus* (Lima bean) and the related species of *P. augusti* Harms and *P. bolivianus* Piperare in the quaternary genepool of common bean, and no confirmed crosses among these species have been possible (Porch *et al.*, 2013). The primary centers of origin for the *Phaseolus* cultigens are in the New World; however, for each crop there has been a different spread outside the original range, with greater spread for common bean than for any of the other species. Common bean has secondary centers of diversity in Africa, Brazil, the Caribbean, China, Europe and India (Zhang *et al.*, 2008; Asfaw *et al.*, 2009; Blair *et al.*, 2010; Sharma *et al.*, 2013), while tepary bean has spread very little outside its original range in northern Mexico, spreading only to parts of Central America (Blair *et al.*, 2012a). Similarly, scarlet runner beans have spread ancestrally from Central America only to northern South America, while year-long beans for the most part remain in the Guatemalan highlands. Overall, this reflects the original diversity of the wild species in the genus, which are more diverse in the Mesoamerican center than in the South American centers. The genome sizes of the *Phaseolus* cultigens are small, ranging between 450 and 650 Mb (Pedrosa Harand *et al.*, 2006, 2013).

B. Crop Common bean (*Phaseolus vulgaris* L.)

Several large germplasm collections for *Phaseolus* exist around the world, holding 261,968 accessions (FAO, 2010, Table 1). The largest, with 36,000 accessions, is at the International Center for Tropical Agriculture (CIAT) based in Cali, Colombia. This collection includes a duplicate of the USDA collection, which consists of almost 18,000 accessions when considering all the species of *Phaseolus*, including wild and cultivated. Common beans make up the majority of the collection, and the representation of other species is limited in all of the collections. Other important *in situ* collections are found in Bolivia, Brazil and Mexico. Core collections have been made in both the CIAT and the USDA collections, while working collections are found in many other countries. A reference collection with representative sampling of the core collection was described by Blair *et al.* (2013). Apart from this, collections of common bean and, many times, scarlet runner beans are found in many European countries. A recent EU-funded project, PHASEOLEU, compiled data on the common beans in Europe. The state of collections in African countries are often precarious, although collections exist in Burundi, Democratic Republic of Congo, Ethiopia, Kenya, Republic of South Africa, Rwanda, Tanzania, Uganda and Zimbabwe. These countries should place a greater emphasis on protecting the genetic wealth of beans in Africa, since many of the African countries are large *per capita* consumers of beans. Additional collections of common bean are found in Asia at the Indian Council for Agricultural Research (ICAR) and at the Chinese Academy of Agricultural Sciences (CAAS). Collections of beans in Bhutan, Laos, Myanmar, Nepal, Pakistan, Thailand and Vietnam would be of interest, as these are not represented in the international collections at USDA based in Fort Collins, Colorado or at CIAT. The recent improvements to genebanks in many provinces of China as well as in Beijing have created good conditions for the storage of landraces and cultivars, especially of snap bean types. Worldwide, there may be over 100,000 landraces of *Phaseolus* preserved in genebanks, but the documentation of these needs to be improved and shared among countries that are part of the FAO treaty on genetic diversity, under which beans is a species with prioritized access as a food crop. Increased collections of wild relatives are needed, as shown by the low representation of wild *P. vulgaris* in the CIAT collection (1,300 accessions with gaps in the regions sampled). The loss of scarlet runner bean and tepary bean genotypes due to changes in local agriculture in producing countries also argues for greater preservations efforts. An interesting model used for common bean and some lima beans has been the *ex situ* collection system found in such organizations as the Seed Savers Exchange in the United States or the seed fairs for farmer-to-farmer exchange of seed found in Colombia and other countries with a wealth of landraces.

A core collection of 1,400 genotypes has been created from the FAO-protected germplasm and has been characterized at the phenotypic level for basic traits (flower color, growth habit,

maturity date, etc.). About half of this collection (the reference collection referred to above) has been genotyped with multi-copy AFLP and RAPD markers and more recently with single-copy SSR and SNP markers (Blair *et al.*, 2009, 2013). Apart from this, there are core collections for the CAAS, EMBRAPA and USDA genebanks, with the latter one holding 700 genotypes out of a total of 16,000 accessions of common bean. The FAO collection was prepared with the intent to cover all geographical regions where common beans are grown and does represent the current races of common bean well (Blair *et al.*, 2009). It is also important for national collections to be represented by a core set of germplasm that has been well characterized and genotyped, such as in the CFP collection center in Bolivia (Avila *et al.*, 2012). Core collections for the other species of cultivated *Phaseolus* have not been made, perhaps because there are so few actually collected that it is impossible to sample randomly from within the genebanks. Genotyping has proved useful for identifying duplicates in the tepary bean collection, where monomorphism is high in the cultivars but low in the wild accessions (Blair *et al.*, 2012a). Genetic mapping in common bean is quite advanced (Galeano *et al.*, 2011), however, the other species of *Phaseolus* still have no genetic maps. In some cases, such as for tepary beans, inter-specific crosses may be necessary for polymorphism mapping, but in common bean, crosses between races or between Andean and Mesoamerican genepools often suffice. Therefore, in *P. vulgaris*, many traits have been tagged, and several reviews describe the genes or QTL involved in controlling certain insect-, disease- and stress-resistance mechanisms.

The most important of all the *Phaseolus* cultigens, the common bean, spread from its origins in the New World throughout Africa, Asia and Europe to become a leading food crop as a dry grain of a multitude of shapes, sizes and color and as a vegetable favored for its lightly flavored pods. Although far less important than cereals, common bean is a cheap source of vegetable proteins, calories and micronutrients. Like other legumes, the major limitations are the low content of sulphur-amino acids and the presence of antinutritional compounds. Common beans are primarily grown for home or local consumption in the developing world, while in the developed world they are primarily grown for processing uses and for exports. Brazil and Mexico are the largest producers of dry grain, while China is the largest producer of common beans as a vegetable. Argentina and Canada are considered among the largest exporters, along with China and the United States (FAOSTAT, 2012). Vegetable production of common beans is common in Kenya as well as around the Mediterranean for the winter diet of Europeans. Even parts of West Africa produce snap or dry beans. Dry bean production then continues on into many countries in Southern Africa. In Asia, common beans are found in India, along the western Bhat range and in the Himalayas. Neighboring Nepal also produces many different landraces of common bean. In China, red dry beans are used for pastries, but northern production of the crop for the export market has become significant and competes with soybean in rotation with maize.

Lima bean improvement programs are independent of common bean improvement. Scarlet runner bean and tepary bean accessions have been used to obtain resistance genes and other traits for common bean. Wild relatives of common bean from the same species are an important source of diversity for the crop as well (Blair *et al.*, 2012b; Blair and Izquierdo, 2012). Tepary beans are by far the least consumed of the five cultivars, although tepary beans are still grown in northern Mexico and among native peoples in the Southwestern US. Scarlet runner bean and year-long bean are grown locally in parts of Central and South America, Asia and Africa, and some fetch a high price as an export crop for European markets. Lima beans are mainly a food security crop in dryland areas of the Caribbean, Mexico and Peru but are also an important fresh vegetable.

Early maturity, adaptation to higher altitude, upright plant type, high pod quality and seed yield, and some resistances to diseases such as viruses and rust, insect pests, and drought and abiotic constraints such as deficiency of nitrogen, phosphorus and zinc or tolerance to aluminium and manganese toxicity have been bred into common bean cultivars (reviewed in Singh and Schwartz, 2010, 2011).

Common bean is by far the most widely grown of the *Phaseolus*, as it is the most important legume for direct human consumption, grown on over 20 M ha worldwide and having both a dry grain (seed) and vegetable (snap pod) market. However average yield is low, 804 kg/ha, compare to other legumes (FAOSTAT, 2012). It is cultivated extensively in the five continents and spans from 52°N to 32°S latitude, and from near sea level in the continental USA and Europe to elevations of more than 3000 m above sea level in Andean South America. In summary, common beans are one of the most widespread crops of the world and deserve their position as the most commonly grown legume for direct human consumption as food.

C. Genus *Vigna* Savi

The genus *Vigna* contains c. 150 species distributed throughout both the Old and New Worlds, species that can be grouped into the six subgenera Vigna, Ceratotropis, Plectotropis, Sigmoidotropis, Lasiosporon, and Haydonia (Vaillancourt *et al.*, 1993; Vijaykumar *et al.*, 2010). The genus is polyphyletic, with one clade comprised of New World species and the genera *Ramirezella* and *Oxyrhynchus* (Delgado-Salinas *et al.*, 1993). The Old World species, however, seem to form a monophyletic group, with the possible exception of *V. frutescens* A. Rich. (Vaillancourt *et al.*, 1993). The *Vigna* species grow in warm temperate and tropical regions globally. It is most closely related to *Phaseolus*, and Asian *Vigna* (subgenus Ceratotropis) was categorized as *Phaseolus* until 1970 (Verdcourt, 1970). *Vigna* differs from *Phaseolus* in biochemistry and pollen structure and in the details of its style and stipules (Verdcourt, 1970). The subgenus Vigna or African *Vigna* comprises c. 40 species, among them the agriculturally important species *V. unguiculata* (cowpea or

black-eyed pea), *V. mungo* (black gram) *V. radiata* (mungbean), and *V. subterranea* (Bambara groundnut), along with related wild species and accessions (Tomooka *et al.*, 2002, 2005, 2006; Vijaykumar *et al.*, 2010). The subgenus Ceratotropis currently consists of 16 (Verdcourt, 1970) to 17 (Maréchal *et al.*, 1978) recognized species, which are naturally distributed across Asia and thus are often called Asiatic or Asian Vigna (Singh *et al.*, 2006). Tomooka *et al.* (2002) describes 21 species of Asian *Vigna*, 8 of which are used for human food or animal feed. This is in contrast to the African *Vigna* (the subgenus Vigna), out of whose 36 species only two have been domesticated (Maréchal *et al.*, 1978, Table 1). *V. lancoelata* is endemic to Australia, and four others are also distributed in Africa or Asia (Lawn, 2014). Chromosome complements in Vigna species are $2n = 2x = 22$, with the exception of *V. glabrescens* ($2n = 4x = 44$). Chromosome rearrangements play a significant role in the genetic differentiation of Asian Vigna species. Even the two close relatives *V. radiata* and *V. mungo* have some structural differentiation of their genomes (Bisht and Singh, 2013). The progenitor of cowpea is *V. unguiculata* var. *spontane*a (formerly var. *dekindtiana*), whose habitat has been found in all lowland areas of Subsaharan Africa, outside the high rain forests and deserts. However, southern Africa has been suggested as the center of origin for wild cowpea (Padulosi and Ng, 1997). The restricted distribution of these primitive forms of wild cross-compatible cowpea relatives in this part of southern Africa provides strong evidence that the region is probably the centre of origin of wild cowpea. The existence of substantial variation among traditional cowpea cultivars grown by farmers in western and central Africa confirms that the region is the possible center of diversity for cowpea. The revision of subgenus Ceratotropis by Tateishi (1985) is the most comprehensive one to date. The eight cultivated species of the subgenus Ceratotropis as described by Tomooka *et al.* (2002) are *Vigna radiata* (green gram or mungbean*), V. mungo* (black gram or urd bean), *V. angularis* (small red bean or azuki/adzuki bean), *V. umbellata* (rice bean or red bean), *V. aconitifolia* (moth bean), *V. reflexopiloxa* var. *glabr*a (Creole bean), *V. trilobata* (wild bean) and *V. trinervia* (Tooapée).

*1. Crop cowpea (*Vigna unguiculata *(L.) Walp.)*

Cultivated cowpea is divided into four cultivar groups: Biflora, Sesquipedalis, Textilis and Unguiculata. Cowpea belongs to culti-group unguiculata, while the yard-long bean or asparagus bean belongs to sesquipedalis. While cowpea is grown mainly for its dry grains in sub-Saharan Africa, South and Central America, the southern United States and Europe, the yard-long bean is commonly grown in Southeast Asia for the long, green, fleshy pods consumed as a vegetable. Because of its drought tolerance, cowpea is well adapted to the dry savanna; consequently, it is probably the most commonly grown and consumed legume in the dry savanna regions of sub-Saharan Africa. Most wild species of *Vigna* have adapted to various environments through the evolutionary process of diversification or specialization. They can provide an important gene pool for cultivated crops of *Vigna*. For example, some wild *Vigna* species can grow in extreme or marginal environments and are therefore believed to harbor interesting genetic information. However, wild *Vigna* species are rarely collected, with the exception of some efforts undertaken in the past decade by the the National Institute of Agrobiological Sciences genebank in Japan and Kasetsart University, Thailand to collect Asian species. The most comprehensive collection of *V. vexillata* (L.) A. Rich. is in the seed bank of the Royal Botanic Gardens of Belgium. According to the study of Maxted *et al.* (2004), more than 20 species of African *Vigna* species are not conserved in any *ex-situ* collection. However, there are many collections of *Vigna* subgenus Cerototropis germplasm. Most of these collections consist primarily of accessions of the cultigens in this subgenus, and most of the accessions conserved were evaluated on basic agronomic traits. The main collections are at the International Institute for Tropical Agriculture (IITA) in Nigeria mainly for *Vigna unguicalata*, and for predominantly *Vigna spp. mungo & radiata* Asian Vegetables Research and Development Center (AVRDC), Taiwan and the National Board for Plant Genetic Resources, India for *Vigna spp. angularis & umbellata* at the Institute of Crops Sciences (ICS), Beijing, China; and for a range of *Vigna spp.* in the Plant Genetic Resources Conservation Unit, Georgia, USA. Wild *Vigna* species of subgenus Cerototropis are poorly represented in world genebanks. Some countries have comprehensive collections of their own indigenous *Vigna* genetic resources, such as *V. radiata* var. *sublobata* (Roxb.) Verdc. in the CSIRO collections (Lawn and Cottrell, 1988; Tomooka *et al.*, 2002).

Several studies have focused on the genetic diversity of *Vigna* (Kaga *et al.*, 1993; Wang *et al.*, 2008; Undal *et al.*, 2011; Kumar *et al.*, 2012; Kaewwongwal *et al.*, 2013) and QTL analysis (Young et al, 1993; Tomooka *et al.*, 2002, 2005, 2006; Sholihin and Hautea, 2002; Humphry *et al.*, 2005; Kasettranan et al., 2010; Kongjaimun *et al.*, 2012; Chankaew *et al.*, 2014; Kajonphol *et al.*, 2012). To better characterize the cowpea germplasm, a core collection of 2,062 accessions was defined based on geographical, agronomical and botanical descriptors (Mahalakshmi *et al.*, 2007). A mini-core set of 374 accessions was further defined and are being used intensively in several cowpea breeding programs. The main objectives are to evaluate the entire cowpea germplasm for priority traits and to complete the agromorphological description of wild *Vigna* accessions. Primary production constraints, include drought and heat stresses, insects (flower thrips, pod-sucking bugs, cowpea aphid), diseases (viral, fungal, bacterial and nematode) and *Alectra* and *Striga* parasitic weeds. Research has been intensified in recent times to develop cowpea cultivars with enhanced levels of drought tolerance (Adegbite and Amusa, 2008). A few accessions of the wild *Vigna* species have also been screened for resistance to insect pests of cowpea. Many accessions of *V. vexillata* were found to show high levels of resistance to pod-sucking bugs and storage weevils and moderate resistance to maruca pod borers (Singh *et al.*, 1992). However, the basic need for

exploiting the wild relatives is its cross compatibility with cultivated cowpea. It is possible that some of the available wild cowpea lines belong to the same or different gene pools. The subspecies or cultivars that constitute the primary and secondary gene pools for cowpea are not yet well defined. Cross compatibility studies have shown that lines that can hybridize successfully with cultivated species are found only among members of the subspecies *unguiculata*, i.e. those belonging to section Catiang in the genus Vigna (Tomooka *et al.*, 2002).

Cowpea is among the top five food legumes or pulses grown worldwide and has a presence on every continent except Oceania and Australia. The West African subregion contributes to about 95% of global cowpea production, with Nigeria being the largest producer of cowpeas in the world (FAOSTAT, 2012). The crop's reputation as very adapted to drought conditions makes it ideal for rotations and inter-cropping with sorghum and millets in these regions, but it is also grown in wetter areas, along with maize. Cowpeas are intermediate in nitrogen fixation, fixing more than common bean and less than soybean. It is the most important legume for cereal legume rotations in the world. Of growing importance to food security in many parts of Eastern Africa, South Asia and especially Southern Africa, the cowpea deserves more investment in agronomic and breeding activities. Bambara groundnuts, which set seed under ground, are of limited importance but are interesting for their high level of disease resistance compared to *Arachis* groundnut. They are found mostly in Southern, Eastern and Western Africa in a range extending from Malawi to Senegal, but they are not consumed outside of the Sub-Saharan region.

*2. Crop mungbean (*Vigna radiata *(L.) R. Wilczek)*

Mungbean is a photo- and thermosensitive crop. The best temperature for its cultivation is 30–35°C with good atmospheric humidity. It is cultivated throughout South and Southeast Asia, including India, Pakistan, Bangladesh, Sri Lanka, Myanmar, Thailand, Philippines, Laos, Cambodia, Vietnam, Indonesia, Malaysia, South China and Taiwan. It is also grown to a lesser extent in many parts of Africa, the United States (especially in Oklahoma), and has been recently introduced in parts of Australia. Black gram (*Vigna mungo*) is also an important pulse crop of India. Black gram is widely adapted both to semi-arid and subtropical areas. Black gram is a protein- rich food (about 26% protein) that consequently legume by India's vegetarian population. In addition to being an important source of human food and animal feed, black gram also plays an important role in sustaining soil fertility by improving soil physical properties and fixing atmospheric nitrogen. Also, as a drought-resistant crop, it is suitable for dryland farming and is predominantly used as an intercrop with other crops.

Meanwhile, mungbeans and black gram are found mainly in Asia and retain importance at their centers of origin (China and India). Southeast Asia, from Myanmar to the Philippines, also produces a large number of mungbeans where they can be double-cropped after rice. They are fast-growing, early maturing and drought-tolerant and can therefore be grown on residual moisture after a crop of vegetables and cereals or at the end of the rainy season. Other Asian species of legumes little known in the West are urd beans and moth beans, but these are adaptable outside their current range and fit into additional agro-ecological niches.

The nitrogen fixation potential of the Asian *Vigna* species has been poorly studied. The mining of elite genes in wild *Vigna* species will be a great genetic resource for Vigna crops. At present, the production of mungbean, adzuki bean and cowpea is being seriously damaged by different diseases or pests, especially bruchid, a pest that occurs frequently among stored *Vigna* seeds. However, the wild types of *Vigna* have resistant genes, which have proved to be transferable into cultivated crops by direct crosses or by using bridge plants (Tomooka *et al.*, 2008; Pandiyan *et al.*, 2008). Disease and insect resistance breeding has been a priority at IITA (Smithson *et al.*, 1980). Curiously, disease resistance breeding has not been a priority in cowpea, perhaps because of its origin in the drier parts of West Africa, while insects, nematodes and viruses are important constraints which so far have had few resistance sources.

A total of 10,551 accessions of various Vigna species comprised of mungbean (3,704), urd bean (3,131), moth bean (1,486), rice bean (2,045) and azuki bean (185) have been stored at −18°C in the long-term repository of the national gene bank at NBPGR, New Delhi. Green gram germplasm accessions are maintained by more than 35 institutions globally, which hold a total of more than 25,000 accessions. IITA maintains over 15,000 accessions of cowpea, the Asian Vegetable Crops Research Centre, AVRDC at Taiwan, maintains 5,616 accessions of mungbean, and over 12,000 various *Vigna* are held in the Conservation Unit in Georgia. Limited germplasm accessions of moth bean are also available in several countries, including Bangladesh, Belgium and Kenya.

D. Genus *Glycine* Willd.

The genus *Glycine* contains c. 22 species, which can be grouped in two subgenera. The first, subgenus Soja, includes two Asian annuals: *G. max* (the cultivated soybean) and the similar wild species *G. soja* Siebold & Zucc. (Doyle *et al.*, 1990). *Glycine max* is thought to be derived from a common ancestor with the wild *G. soja* lineage (Kim *et al.*, 2010; Li *et al.*, 2013b). Domestication of soybean was initiated c. 6,000-9,000 years ago in Asia and has resulted in considerable genetic differences between *G. max* and *G. soja*, as revealed by a comparison of whole-genome sequences (Kim *et al.*, 2010). The second clade, subgenus Glycine, comprises c. 20 wild species. They are all perennials and restricted in their distribution to the Australian continent (Doyle *et al.*, 1990). *G. soja* and *G. max* both have 20 chromosomes (2n = 40) and can easily interbreed. The split between *G. max* and *G. soja* was estimated to have occurred c. 3,000-5,000 years ago (Carter Jr. *et al.*, 2004; Lee *et al.*, 2010) based on molecular phylogenetic analyses and historical documents and 270,000 years ago based on comparative analysis of re-sequenced wild soybean genome (Kim *et al.*, 2010) using cultivated soybean (Glyma1.0, var. Williams 82) as the

reference genome. This suggests that the domestication time of soybean remains to be ascertained.

*1. Crop soybean (*Glycine max *L.)*

As the center of cultivated soybean (*G. max*), China has the most abundant genetic resources for soybean, with >23,000 cultivated soybean accessions and >7,000 wild soybean (*Glycine soja*) accessions conserved at the Chinese National Soybean GeneBank (CNSGB) (Qiu *et al.*, 2013) and replicated at the National Germplasm Storage Facility in Qinhai (Qiu *et al.*, 2011).

In order to efficiently analyze and utilize this large *ex-situ* collection, a series of the core collections, including primary core, core, mini-core and integrated applied core collections– has been constructed based on the study of phenotypic and genotypic (SSR markers) datasets (Qiu *et al.*, 2013). In the past decades, these soybean core collections were widely used in the genomic study, molecular evolution clarification, elite genetic resources discovery, gene identification, elite lines development, and so on. For example, the analysis of the mini-core collection using SSR markers and allelic variation of the soybean determinate growth habit regulated gene *GmTfl1* revealed that human selection for determinacy took place at early stages of landrace radiation (Tian *et al.*, 2010). Twenty-one SSR markers were identified in the soybean applied core collection as associated with important agronomy traits, including high oil content, high protein content, drought tolerance, soybean cyst nematode resistance. Guo *et al.* (2013) identified three new low-frequency alleles of *GmF3′H* and *GmF3′5′H* in the mini-core collection. This indicated that this series of core collections with concentrated genetic diversity will play an important role in soybean molecular breeding (Qiu *et al.*, 2013). The second largest collection of soybean accessions is conserved by the USDA: 19,557 cultivated soybean accessions, derived from 87 countries, 1,181 wild soybean accessions and 1,038 representatives of the 20 perennial species. In recent years, Brazil has conserved 2,000 special accessions, with the exception of the USDA soybean accessions introduced. Most of the cultivated soybean accessions are from China, Japan or Korea; therefore, redundancy in the global collections may be as high as 70% (Nelson, 2009). In Japan, approximately 11,300 soybean accessions are conserved at the National Institute of Agrobiological Sciences (NIAS) Genebank. These accessions include local landraces collected in Japan and overseas, as well as cultivars and breeding lines developed by regional Japanese agricultural research institutes (Kaga *et al.*, 2012).

A large-scale evaluation of 17 traits was conducted for >20,000 soybean accessions conserved in CNSGB, but none of the 17 traits were completely identified in all the accessions. The accession evaluation rate was different for various traits, but the average was 35% (Qiu *et al.*, 2011). In order to characterize phenotype and genotype of soybean accessions efficiently, additional core collections have been developed from the whole collection of soybean accessions (Brown *et al.*, 1987; Yaklich *et al.*, 1999; Zhao *et al.*, 2005; Wang *et al.*, 2006; Cho *et al.*, 2008; Oliveira *et al.*, 2010; Kaga *et al.*, 2012). Due to their reduced size, these core collections could be studied extensively, and the information derived can be used to guide more efficient utilization of the much larger reserved collection (Qiu *et al.*, 2013).

The soybean is classified as an oilseed rather than as a pulse by the FAO, due to the 20-25% oil content of the seeds. Soybean seed is also rich in protein content (40%), higher than that of all the pulses. Its cultivation and production is 2.5x that of all other grain legumes taken together, with a world production of 253,137 Kt with an average yield of 2,374 Kg/ha. Due to its amino acid composition, soybean is considered a source of complete protein. The remaining proportions are soluble or starch-converted sugars (35%) and minerals. The seeds also contain important isoflavones, such as genistein, daidzein and glycitein, which act as phytoestrogens. Traditional nonfermented food uses of soybean include soy milk, tofu and tofu skin. Fermented foods include soy sauce, fermented bean paste, natto, and tempeh, among others. The oil is used in many industrial applications. Only a very small proportion of the crop is consumed directly by humans; however, it is used in a large variety of processed foods. The grain is also used as animal feed. Interestingly, soybean did not become an important crop outside of Asia until about 1910. The main world producers of soy are the United States (35%), Brazil (27%), Argentina (19%), China (6%) and India (4%), with world total production at 249 million metric tons (FAOSTAT, 2012). The breeding effort is largely at private companies that focus on yield stability, resistances to pests and diseases (Wilcox, 1983) and altered oil composition. Breeding of low-phytate soybeans are desirable from both a nutritional and environmental standpoint and also provide an economic advantage to producers (Maroof *et al.*, 2009). It is notable that a large proportion (up to 81% in 2011) of globally cultivated soybeans is transgenic, mainly for herbicide (Roundup Ready®, Liberty Link®) and pest (*Bt*) resistances, but also for altered oil composition (gene silencing to suppress the GmFAD3 gene family in *Plenish*® soybean) (www.gmo-compass.org).

E. Genus *Cajanus* L.

The pigeonpea (*Cajanus cajan* L.) belongs to the legume subtribe Cajaninae. This subtribe contains a total of 13 genera. Until recently, the genera *Atylosia* Wight & Arn. and *Cajanus* were considered closely related genera, but van der Maesen (1990) merged the genus *Atylosia* with *Cajanus*. In total, the combined genus *Cajanus* now has 32 species. These species are endemic to Asia (18), Australia (13) and western Africa (1) (van der Maesen, 1990). The primary gene pool consists of the cultivated species and its landraces, whereas the secondary gene pool consists of ten wild relative species. There are 20 wild species in the tertiary gene pool (Table 1). Wild species placed in the quaternary gene pool of *Cajanus* belong to different genera, such as *Flemingia* Roxb. ex W. T. Aiton, *Rhynchosia*

Lour., *Dunbaria* Wight & Arn., and *Eriosema* (DC.) Desv. The genus *Cajanus* has the same chromosome number (2n = 22) in all its species (Deodikar and Thakar, 1956; Dundas, 1990). The genome size of cultivated pigeonpea has been estimated as 833 Mb (Varshney *et al.*, 2012). India is the primary center of pigeonpea diversity, while East Africa is considered the secondary center of diversity (Songok *et al.*, 2010).

*1. Crop pigeonpea (*Cajanus cajan *L.)*

A total of 40,820 *Cajanus* accessions, comprising landraces, modern cultivars and CWR, have been conserved in *ex-situ* genebanks. The ICRISAT genebank holds 13,771 accessions, including 8,315 landraces, 4,830 breeding lines, 71 improved cultivars, and 555 accessions of wild relatives from 74 countries (Table 1). Other genebanks conserving pigeonpea germplasm are the National Bureau of Plant Genetic Resources (11,427 accessions), New Delhi, India; All India Coordinated Research Project on Pigeonpea (5,195 accessions); Indian Agricultural Research Institute (IARI), New Delhi (1,500 accessions); and the Crop Plant Genetic Resources Center, Muguga (1,380 accessions), Kenya. Based on available passport and morpho-agronomic data of the entire pigeonpea collection at ICRISAT, a "core collection" of 1,290 accessions was developed. This core collection was designed to represent the genetic variability of the entire collection and was further evaluated for various morphological, agronomic, and quality traits (Reddy *et al.*, 2005). In addition to field evaluation, the diversity in the core collection was estimated using SSR markers. Furthermore, a subset of about 10% of the accessions from the core collection was selected. This subset contained 146 accessions and represented more than 80% of the diversity of the entire pigeonpea collection (Upadhyaya *et al.*, 2010). A number of marker systems have been used in *Cajanus* to detect polymorphism. Initially, biochemical markers were used to analyze the relationships of wild relatives with the cultivated pigeonpea and identified *C. cajanifolius* (Haines) Maesen as the closest relative to pigeonpea (Krishna and Reddy, 1982). RFLP markers were also used to determine phylogenetic relationships among 12 *Cajanus* species (Nadimpalli *et al.*, 1994). Two species, *C. cajanifolius* and *C. scarabaeoides* (L.) Thouars, showed a close relationship with each other; however, *C. cajanifolius* was closest to *C. cajan*. Other marker systems used to estimate the polymorphism in *Cajanus* were RAPD (Ratnaparkhe *et al.*, 1995), AFLP (Punguluri *et al.*, 2006), DArT (Yang *et al.*, 2006), SSR (Saxena *et al.*, 2010a, b; Bohra *et al.*, 2011a), and, recently, single-nucleotide polymorphism (Saxena *et al.*, 2012; Roorkiwal *et al.*, 2013). All marker-based studies have revealed that a very low level of diversity is present in cultivated pigeonpea, whereas the wild relatives of pigeonpea showed enormous diversity (Ratnaparkhe *et al.*, 1995; Punguluri *et al.*, 2006; Saxena *et al.*, 2010a, b; Bohra *et al.*, 2011a). These studies also revealed that two of the wild relatives, *C. cajanifolius* and *C. scarabaeoides*, are closely related to pigeonpea. Cytological studies have also proved that *C. cajanifolius* is the progenitor species of *C. cajan*, as both species have similar karyotypes, and the hybrids produced from crossing the two species have normal meiosis with high pollen fertility (Pundir and Singh, 1985; Mallikarjuna *et al.*, 2006).

Pigeonpea (*Cajanus cajan*) is a short-lived perennial shrub that is cultivated as an annual grain legume crop in tropical and subtropical regions. Its cultivation area is 4.64 M ha, with an annual production of 3.43 million tonnes and a mean productivity of 780 kg/ha, making it the sixth most important legume food crop in the world (FAOSTAT, 2012). It is primarily grown for dry, dehulled, split seeds, green seeds and pods as vegetables. It can also be used as forage, fodder, fuel and medicine (Saxena *et al.*, 2010). The deep roots of pigeonpea help recycle minerals from deep soil and make them available to other intercropping plants. Pigeonpea has several unique characteristics that render it an ideal crop for sustainable agricultural systems. Its partial out-crossing nature affects its breeding and selection efficiency and makes research activities more difficult in comparison to other food legumes. However, the presence of both additive and non-additive genetic variations allows for the development of both high-yielding, pure-line cultivars and hybrids (Saxena, 2008). Pigeonpea improvement programs have evolved around long-duration, photo-sensitive types and earliness, whereas dwarfness, disease resistance (mainly fusarium wilt, sterility mosaic disease and phytophthora blight), insect resistance (pod borers, *Helicoverpa armigera* and *Maruca vitrata*, and pod fly, *Melanagromyza obtusa*), abiotic stress tolerance (soil salinity and water logging), fodder, yield, and yield-related traits are the prime targets for pigeonpea improvement (Saxena, 2008).

VII. TRIBE AESCHYNOMENEAE

A. Genus *Arachis* L.

The genus *Arachis* is divided into nine sections (Arachis, Trierectoides, Erectoides, Extranervosae, Triseminatae, Heteranthae, Caulorrhizae, Procumbentes, and Rhizomatosae) based on morphological, cross-compatibility and geographic origin/distribution and has a total of 80 species. All of the species are diploid in nature, except two tetraploids, *A. hypogaea* L. and *A. monticola* Krapov. & Rigoni. Of the nine sections, *Arachis* is the largest section, comprised of 32 species, including the cultivated groundnut (*A. hypogaea*) (Krapovickas and Gregory, 1994; Valls and Simpson, 2005). All species within the *Arachis* sections are found mostly in Brazil, followed by Paraguay, Argentina and Uruguay (Upadhyaya *et al.*, 2011). *Arachis* species can be grouped into nine sections comprised of 80 species with both annual and perennial life cycles (Krapovickas and Gregory, 1994; Valls and Simpson, 2005). Of these nine sections, the most important section is *Arachis*, which includes the cultivated and domesticated groundnut (*Arachis hypogaea*). The cultivated groundnut is amphidiploid (tetraploid) and originated through a single hybridization event between two diploid wild species, *A. duranensis* Krapov. & W. C. Greg. (A-genome) and *A. ipaënsis* Krapov. & W. C. Greg. (B-genome), followed by a

spontaneous chromosome duplication (Halward *et al.*, 1991). Because of its uncommon origin, the resulting cultivated tetraploid (*A. hypogaea*, AABB genome) was reproductively isolated from its wild relatives.

Along with cultivated groundnut, *A. monticola* is another tetraploid species and seems to have been the intermediate species in the domestication of cultivated groundnut from diploid species. Cultivated groundnut species (*A. hypogaea*) were classified into two subspecies (*A. hypogaea* subsp. *hypogaea* and *A. hypogaea* subsp. *fastigiata* Waldron) based on differences in growth habit, reproductive modes, flowering on mainstem, seed size, and maturity duration, with a total of six botanical cultivars (Krapovickas and Gregory, 1994). The subspecies *hypogaea* shows a spreading growth habit, alternating vegetative and reproductive nodes, absence of flowers on the mainstem, medium-to-large seeds and medium-to-late maturity. The botanical variety *A. hypogaea* var. *hypogaea* (Virginia and Runner market types) is the most cultivated group. Subspecies *fastigiata* shows an erect growth habit, sequential reproductive nodes, the presence of flowers on the mainstem, small seeds, and early maturity. It can be divided into the botanical cultivars *fastigiata* (Valencia), *vulgaris* Krapov. & W. C. Greg. (Spanish), *peruviana* Krapov. & W. C. Greg., and *aequatoriana* Krapov. & W. C. Greg. (Krapovickas and Gregory, 1994; Burrow *et al.*, 2013).

Based on compatibility features and genetic variability, Singh and Simpson (1994) have classified the genus *Arachis* into four gene pools (Table 1). The first gene pool includes two tetraploid species (*A. hypogaea* and *A. monticola*) from section Arachis. The secondary gene pool includes the remaining diploid species of section Arachis that show strong cross-compatibility with *A. hypogaea*. The tertiary gene pool includes species from section Procumbentes, which show weak cross-compatibility with *A. hypogaea*. The quaternary gene pool prescribes the most distantly related wild relatives to *A. hypogaea* and includes all species from the remaining seven sections of the genus *Arachis*. Despite the availability of broad genetic variations among species of the tertiary and quaternary (fourth) gene pools, the breeding community has been unable to exploit them because of incompatibility problems; thus, efforts need to be undertaken in finding efficient allele sharing methodologies for further improvement of cultivated groundnut. The hybrid origin of cultivated groundnut, followed by reproductive isolation and further sections during domestication, left groundnut's primary gene pool with very limited genetic diversity. Earlier, genetic diversity studies using a range of molecular markers reported a very low level of diversity in the primary gene pool (Kochert *et al.*, 1996; Subramaninan *et al.*, 2000; Herselman, 2003). Nevertheless, in the few other studies in which large germplasm sets were used reported low levels of diversity in primary gene pools, while better genetic diversity still exists within the wild relatives (Varshney *et al.*, 2009a; Koppolu *et al.*, 2010; Khera *et al.*, 2013). Similarly, diversity array technology (DArT) and kompetitive allele specific PCR (KASP) markers showed very low polymorphism in cultivated genotypes and moderate polymorphism in diploid wild relatives (see Varshney *et al.*, 2013b).

*1. Crop groundnut (*Arachis hypogaea *L.)*

Ex situ germplasm collections for groundnut are maintained in India, China, United States, Argentina and Brazil, holding all together 128,435 accessions (FAO, 2010, Table 1). The largest collection for groundnut is held at ICRISAT in India, where a total of 15,445 accessions representing 93 countries have been conserved. The other main institutes that conserve groundnut germplasm include the National Bureau of Plant Genetic Resources (14,585 accessions) and the Directorate of Groundnut Research of the Indian Council of Agricultural Research (9,024 accessions), both in India; the Oil Crops Research Institute of the Chinese Academy of Agricultural Sciences (8,083 accessions) and the Crops Research Institute of the Guangdong Academy of Agricultural Sciences (4,210 accessions) in China; the United States Department of Agriculture (9,917 accessions), Empresa Brasiliera de Pesquisa Agropecuaris (EMBRAPA)-CENARGEN (2,420 accessions) and the Instituto Agronomico de Campinas (2,140 accessions) in Brazil; and Instituto Nacional de Technologia Agropecuaria (3,640 accessions) and Instituto de Botánica del Nordeste (472 accessions) in Argentina. As far as wild relatives are concerned, Texas A & M University (1,200 accessions) holds the largest collection, followed by *USDA (*607 accessions), North Carolina State University (406 accessions) in the United States; EMBRAPA-CENARGEN in Brazil (1,220 accessions), ICRISAT in India (477 accessions) and the Instituto de Botánica del Nordeste (472 accessions) in Argentina. To facilitate maintenance and especially phenotyping, core collections (i.e. 10% of the entire germplasm collection) were developed for USDA germplasm (831 accessions) (Holbrook *et al.*, 1993) and ICRISAT (1,704 accessions) (Upadhyaya *et al.*, 2003). In addition, a composite collection of 1,000 accessions was developed by ICRISAT based on phenotypic data, geographic origin and taxonomic data. To assist breeders in handling small sets of their working collection, a further, smaller germplasm set (reference set) comprising 300 genotypes was developed after screening 20 SSR markers in the composite set (Upadhyaya *et al.*, 2002, 2003). An even smaller germplasm set called the 'mini-core collection' (i.e. 10% of the core collections and 1% of the entire germplasm collection) was constituted by ICRISAT (184 accessions) (Upadhyaya *et al.*, 2002), USDA/ARS (112 accessions) (Holbrook and Dong, 2005) and China (298 accessions) (Jiang *et al.*, 2008).All three mini-core collections have been well phenotyped over the years for several agronomic traits, and next-generation genotyping has been planned for the three above-mentioned germplasm sets for conducting genome-wide association analysis (GWAS).

Groundnut or peanut is a crop of global importance that supports the livelihood of millions of resource-poor farmers in the semi-arid tropics (SAT). Besides being an important crop for cooking oil, food, and feed, it also enriches soil by fixing nitrogen. Currently, this crop is grown in more than 100 countries

in an area of 24 million ha with a total production of 38 million tonnes and mean yield of 1,675 kg/ha (FAOSTAT, 2012). The range of usage is increasing by the processing industry is continuously increasing the range of usage; thus the projected demand for groundnut is very high. This crop is highly regarded among all economic classes, especially among the poor, it serves as a good source of nutrition for people and their livestock. Groundnut kernels contain 48–50% oil and 25–28% protein, providing 564 kcal of energy for every 100 g (Jambunathan, 1991). In addition, groundnut contains several micronutrients and health-enhancing components, including minerals, antioxidants and vitamins, along with some biologically active polyphenols, flavonoids and isoflavones (see Janila *et al.*, 2013). The breeding objectives for groundnut are based on consumer and local industry preferences. Nevertheless, the majority of the improvement programs across the world have similar objectives and are continuously working on yield enhancement, early maturity, biotic resistance, abiotic stress tolerance, preharvest dormancy, high oil or protein contents and high oleate trait. Among these, significant achievements have been made in improving biotic resistance and high oleate trait by developing and releasing improved cultivars. Breeders are still working to develop improved cultivars with increased pod yield and abiotic stress tolerance. The main biotic stresses include foliar fungal diseases (late leaf spot, early leaf spot and rust), soil-borne fungi, bacterial wilt, groundnut rosette virus (GRV), peanut bud necrosis (PBND), peanut stunt virus (PSV), peanut strip virus (PStV), tomato spotted wilt virus (TSWV), and nematodes. Terminal drought is the major abiotic stress, followed by acidic soil, low soil fertility, and low temperature. The breeding approaches used in genetic enhancement of groundnut are the same as those used with all other self-pollinated crops, including selection, pedigree, inter-mating, mutation and backcross breeding (Holbrook and Stalker, 2003).

VIII. TRIBE GENISTEAE

A. Genus *Lupinus* L.

The taxonomy of the Genisteae tribe and other Genistoid legumes has been an area of considerable confusion for many years (Percy and Cronk, 2002). Recent focused efforts on defining phylogenetic relationships within the Genisteae have substantially clarified the situation (Cardoso *et al.*, 2012a, b, 2013; The Legume Phylogeny Working Group, 2013). The Genisteae tribe is currently considered to include 618 species in 25 genera (Cardoso *et al.*, 2013), and its diversity is centered in the Mediterranean region and in the Canary Islands (Cristofolini, 1997; Cristofolini and Chiapella, 1984). *Lupinus* is the largest Genisteae genus, comprising 267 species, and appears to be monophyletic in origin (Ainouche and Bayer, 1999; Drummond *et al.*, 2012). Chromosome numbers range between $2n = 24$ to $2n = 52$, and there are multiple lines of evidence showing that at least one polyploidy event has taken place since the divergence of Genisteae from other Papilionoid legumes (Wolko and Weeden, 1989; Gupta *et al.*, 1996; Naganowska *et al.*, 2003; Nelson *et al.*, 2006; Parra-Gonzalez *et al.*, 2012; Yang *et al.*, 2013b; Kroc *et al.*, 2014). The structural distinctiveness of *Lupinus* genomes from other Papilionoid genomes has been investigated by comparing genetic maps of *L. angustifolius* to the reference genome sequences of *Medicago truncatula* and *Lotus japonicus* (Nelson *et al.*, 2006; Nelson *et al.*, 2010) and by comparing the genetic map of *L. albus* to the genome of *M. truncatula* (Phan *et al.*, 2007a). These studies revealed that *Lupinus* genomes are highly rearranged relative to other Papilionoid genomes, with regions of gene collinearity extending over relatively short distances. Comparison between *Lupinus* genomes has so far been limited by low numbers of shared genetic markers, but initial results suggest that genome rearrangements have occurred even between the relatively closely related *L. angustifolius* and *L. albus* (Wolko *et al.*, 2011). A complete genome sequence for *L. angustifolius* is expected in the near future (Gao *et al.*, 2011) and will serve as a valuable reference for genomic studies within *Lupinus* and between *Lupinus* and other sequenced legume genomes, such as *Medicago truncatula*, *Lotus japonicus*, soybean, chickpea and pigeonpea (Sato *et al.*, 2008; Schmutz *et al.*, 2010; Varshney *et al.*, 2012, 2013a; Young *et al.*, 2011).

Lupinus has centers of diversity in the Old World and New World (Gladstone, 1970). Old World lupins comprise 13 annual species and include rough-seeded and smooth-seeded types distributed around the Mediterranean region and North Africa (Mahé *et al.*, 2011). Chromosome numbers range from $2n = 32$ to $2n = 52$, and nuclear DNA contents range from 2C = 0.97 pg to 2C = 2.44 pg (Naganowska *et al.*, 2003), although rare autopolyploids have been observed with $2n = 100$ and $2n = 104$ chromosomes (Ainouche and Bayer, 1999). The most strongly supported clade within the Old World lupins is the rough-seeded type, with four less well-defined smooth-seeded sections recognized (Ainouche and Bayer, 1999). Three smooth-seeded Old World species have been used regularly in agriculture: *L. albus,* as long ago as 2,000 BC; and *L. angustifolius* and *L. luteus* by the 19th century (Gladstone, 1970). Several other Old World lupin species have been used sporadically in agriculture, including the rough-seeded *L. pilosus* L., *L. atlanticus* Gladstone and *L. cosentinii* Guss. (Gladstone, 1970; Wolko *et al.*, 2011). Experimental hybridization studies have found that many rough-seeded types can intercross, albeit at a relatively low frequency, while crossing between smooth-seeded types (including the main cultivated species) is rarely successful (reviewed by Wolko *et al.*, 2011). Given the great difficulty in interspecific crossing between the cultivated species of lupin, it is perhaps unsurprising that there has so far been no example of the successful transfer of useful genes into lupin crop species. Therefore, for practical breeding purposes, the gene pool of the cultivated Old World lupin species is restricted to the species themselves.

New World lupins comprise over 250 annual and perennial species with centers in western North America (c. 100 species) and the Andes of South America (c. 85 species) (Hughes and

Eastwood, 2006). Despite the much larger number of *Lupinus* species in the New World, the diversity of chromosome numbers is remarkably less than in Old World species. Chromosome numbers are typically $2n = 48$ for Andean and North American species and $2n = 36$ for southeastern South American species, with a few exceptions, including putative autotetraploids (Conterato and Schifino-Wittmann, 2006). DNA contents range from 2C = 1.08 pg to 2C = 2.68 pg, with North American species showing the widest range of DNA contents (Naganowska *et al.*, 2006). *Lupinus* in the Andes has among the highest known rates of species diversification for any angiosperm genus (Hughes and Eastwood, 2006). The vast range of morphological variation (from tiny herbs to large trees) and ecological adaptation (from coastal sand dunes to montane forests) pose challenges for resolving phylogenetic relationships using taxonomic methods (Drummond *et al.*, 2012). Comparisons of nuclear and chloroplast DNA sequences (Ainouche and Bayer, 1999; Wink and Mohamed, 2003; Ainouche *et al.*, 2004; Ree *et al.*, 2004; Drummond and Hamilton, 2007; Drummond, 2008; Eastwood *et al.*, 2008b; Drummond *et al.*, 2012) have made some progress toward resolving *Lupinus* phylogeny, but ambiguities still remain. Current efforts are underway to sample large gene sets obtained by whole transcriptome sequencing across New World *Lupinus* (C. Hughes, G. Atchison, D. Filatov, personal communication), which should definitively answer these remaining questions. Transcriptome-based studies will also provide insights into the nature and age of polyploidy events that have shaped Genisteae genomes through the comparison of rates of synonymous and non-synonymous substitution in the coding regions of duplicated genes (Cannon *et al.*, 2010). The only New World species to be adopted in arable agriculture was *L. mutabilis* (Andean lupin). It was domesticated around 2,000-1,000 BC in the central Andes, where it was used by the Chavinoid culture and later by Tihuanacoid and Inca civilizations in their crop rotations (Wolko *et al.*, 2011).

1. *Crop lupin (*L. angustifolius*,* L. albus*,* L. luteus *and* L. mutabilis*)*

The world collection of *Lupinus* is estimated to comprise approximately 38,000 accessions, duplicates notwithstanding (Table 1). *Ex-situ* collections of *Lupinus* germplasm are extensive though focused primarily on the four cultivated species (Wolko *et al.*, 2011; Berger *et al.*, 2013). Lupin germplasm stands out in terms of the large proportion of wild (18%) compared to cultivated material. Due to its recent domestication the current focus is on collecting wild diversity. The largest repository exists in the Australian Lupin Collection (ALC), which holds 66 wild and 912 cultivated acc. of *Lupinus albus*, 1,327 wild and 729 cultivated acc. of *L. angustifolius*, 198 wild and 299 domesticated acc. of *Lupinus luteus*, 31 wild and 208 domesticated acc. of *Lupinus mutabilis* and 821 accessions of other *Lupinus* species. Significant collections are also found in the Russian Federation (2,450 acc.), USDA (1,183 acc.), Germany (1,969 acc.), and other European countries. New World species such as *L. mutabilis* are held in South American institutions (in Peru), but also in the USDA (79); the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany (987); the Institute for Agrobotany, Hungary; and the Vavilov Institute, Russia (129). Molecular marker-based analyses of genetic diversity in geographically defined and/or small germplasm sets of Old World cultivated *Lupinus* species have been reported (Talhinhas *et al.*, 2003, 2006; González-Andrés *et al.*, 2007; Raman *et al.*, 2008; Sbabou *et al.*, 2010; Nelson *et al.*, 2011; Berger *et al.*, 2012a). Systematic investigations that integrate both molecular and ecophysiological information are required for all four cultivated *Lupinu*s species.

The global production of lupin in 2012 was 1.29 M tonnes, of which Australia was the largest producer (0.98 M tonnes) with mean yield of 1,445 kg/ha (FAOSTAT, 2012). The main use of *L. angustifolius* grain in Australia is as a high-protein sheep feed. However, there is increasing interest in using *L. angustifolius* as a human health food. When the seed coat is removed, the kernel contains 40–45% protein and 25–30% dietary fiber and has a low fat and carbohydrate content (Lee *et al.*, 2006). Including lupin kernel flour as part of a regular human diet could help address growing obesity and diabetes problems, since it has been shown to increase satiety, thereby reducing further caloric intake (Lee *et al.*, 2006).

Research is underway to understand how seed storage proteins are produced in *L. angustifolius* (Foley *et al.*, 2011), which may provide effective selection and/or transgenic tools for breeders to increase the quality and quantity of seed protein. A small proportion of the population is allergic to lupin kernel flour; consequently, research is underway to understand the components of lupin seed proteins associated with allergenicity (Goggin *et al.*, 2008). Breeders successfully addressed problems of late maturity caused by a strong vernalization requirement, excessive indeterminate branching and excessive height (Wolko *et al.*, 2011). Remaining constraints on the wider adoption of *L. albus* as a crop are susceptibility to anthracnose, BYMV, Pleiochaeta root rot, brown leaf spot, Fusarium wilt and grey mold. Most *L. angustifolius* cultivars are susceptible to a range of fungal diseases (anthracnose, phomopsis and pleiochaeta root rot) and viral pathogens (CMV, BYMC) but are resistant to aphids. As current cultivars are slow in establishment after sowing, herbicide tolerance is essential to reduce weed competition. *L. angustifolius* is tolerant of simazine and diflufenican, and some cultivars are partially tolerant to metribuzin (Si *et al.*, 2006; Wolko *et al.*, 2011). Breeding has achieved an estimated genetic gain in yield of 81% between the first early flowering variety, "Unicrop" (released in 1973), and "Mandelup" (released in 2004), a rate of gain of 2.6% per year (Stefanova and Buirchell, 2010). These yield gains were associated with increased main stem productivity and higher seed numbers (Berger *et al.*, 2012b). However, intensive breeding and domestication bottlenecks have reduced genetic diversity and restricted phenological adaptation of *L. angustifolius* in Australia, thus limiting the potential of future genetic gains (Berger *et al.*,

2012a). In Germany in the 1930s, von Sengbusch identified natural sweet-seeded mutants, which heralded the beginning of modern *L. albus* breeding (Gladstone, 1970). Modern *L. luteus* cultivars are resistant to pod shattering, though improvements are still necessary in Mediterranean-type environments, which experience hot, dry conditions at harvest time (Wolko *et al.*, 2011). Soft-seededness, removal of the vernalization requirement for flowering and restricted branching traits were also introduced. There has been excellent progress in increasing grain yield in Polish cultivars over the last decade (Wolko *et al.*, 2011).

Lupinus luteus has the highest protein content of the Old World cultivated lupin species (average 38.3%) with high S amino acids, which has driven its increased use in Chile's aquaculture industry (Wolko *et al.*, 2011). Constraints on its wider use include the narrow edaphic adaptation, aphid susceptibility in very low-alkaloid cultivars, and susceptibility to CMV, BYMV and anthracnose.

Lupinus mutabilis prefers mildly acidic to neutral loamy sands and loams, is tolerant of water-logging and has very high P-use efficiency (Wolko *et al.*, 2011). It has the highest grain quality of all the cultivated lupins, rivalling soybean with an average of 42% protein, 18% oil and a thin seed coat (Wolko *et al.*, 2011). It was an important part of the diet and farming practices of pre-Columbian civilizations but was marginalized after the European invasion of the Inca (Gross *et al.*, 1988). In recent years, efforts have been made to re-establish *L. mutabilis* as a crop and to adopt it outside South America (Caligari *et al.*, 2000). Low-alkaloid forms were initially developed by von Sengbusch in 1942 as a new variety, with $<0.05\%$ alkaloids reported (Gross *et al.*, 1988). However, the current adoption of *L. mutabilis* is limited by late maturity, low and unstable yields and frost susceptibility (Eastwood and Hughes, 2008a).

IX. ECO-GEOGRAPHICAL AND ECO-PHYSIOLOGICAL APPROACHES TO CONSERVING AND IDENTIFYING USEFUL GERMPLASM

Geographical and ecological information has been key to many successful germplasm-collecting forays, as well as to the preservation of extant diversity in *ex-situ* collections. Following collecting with the compiling of descriptor, disease and agronomic data adds value to germplasm collection and enables breeders to make more informed selections when requesting germplasm. Targeting germplasm for tolerance to abiotic stresses can be done through eco-geographical identification of the collection sites of landraces. By overlaying these with world climatic data to a resolution of 1 square km for the months corresponding to local vegetative and reproductive growth phases, landraces associated with sites highly stressed for frost, high temperature and drought can be identified. These landraces, being adapted to such sites, may have undergone natural selection for such stress tolerances. This knowledge enables specific targeting of germplasm for screening of tolerance to abiotic stresses, as conducted for the pea landraces from China (Li *et al.*, 2013).

A. Chickpea

Global chickpea distributions and habitat characteristics have been analyzed in detail using passport data from the ICRISAT, ICARDA, ATFCC and USDA collections, augmented by feedback from regional breeders (Berger and Turner, 2007; Berger, 2007; Berger *et al.*, 2012). Chickpea seasonal climates fall into two broad categories (Berger and Turner, 2007):

a) **Mediterranean-type**: cool, wet winters, where the crop is reliant on in-season rainfall, and the growing season is terminated by drought (Mediterranean Basin, western parts of Central Asia, southern Australia, western Americas (California, Mexico, Chile). The most arid Mediterranean production areas are found in central Iran, central Pakistan, parts of Afghanistan, the inner Eastern Mediterranean, parts of North Africa, California, northern Chile, and Western Australia (Berger and Turner, 2007).
b) **Summer dominant rainfall**: winter chickpea relies on stored soil moisture from the preceding monsoon, seasonal temperatures are relatively high, and growth is also terminated by drought (South Asia, East Africa). In South Asia, there is a very strong latitudinal winter temperature gradient, the south being considerably warmer than the north (22.1 and 16.8°C, respectively), leading to much shorter growing seasons (Berger and Turner, 2007).

In both climatic regions, chickpea reproduction is timed to avoid chilling stress (see later discussion). However, notable exceptions include southern Australia, the western Mediterranean and Americas, and northern India (Berger, 2007). The combination of regionally appropriate farming practices and phenology facilitates avoidance of the principal abiotic and biotic stresses in chickpea. In Mediterranean regions, Ascochyta blight and vegetative frost are both long-standing stresses for the crop, graphically illustrated by ICARDA screening trials in the 1980s (Singh, 1990). Of 15,000 lines screened against Ascochyta blight and 4,500 against winter cold, only 18 and 15 accessions, respectively, were resistant, and there was no evidence of combined resistance (Singh, 1990). The traditional Mediterranean spring-sowing regime avoids both these stresses but comes with a considerable yield potential opportunity cost (Singh *et al.*, 1997). Terminal drought is an almost ubiquitous stress in both Mediterranean and South Asian-type climates. Although chickpea has deep roots (Saxena *et al.*, 1994), is able to extract water at depth (Zhang *et al.*, 2000), and is capable of osmotic adjustment (Morgan *et al.*, 1991; Basu *et al.*, 2007; Turner *et al.*, 2007), its principal adaptive strategy appears to be drought escape through early phenology (Silim and Saxena, 1993; Siddique *et al.*, 2001; Berger *et al.*, 2004, 2006). However, this must be balanced against its considerable chilling sensitivity, which causes chickpea to delay pod set until temperatures are warm enough. Delays in pod set are strongest between 11°C and 16°C,

and although tailing off after 17.5°C, remain statistically significant until 20.6°C (Berger *et al.*, 2012). In much of its global distribution, chickpea is exposed to terminal drought stress because low chilling tolerance delays the onset of pod formation (Berger, 2007; Berger *et al.*, 2012). Chickpea evolution has selected for regionally appropriate phenology to negotiate these various stresses (Berger, 2013). Thus, as seasonal temperatures increase from the Mediterranean through South Asia, chickpea cultivars become increasingly temperature responsive, flowering ever earlier to escape terminal drought, minimizing the risk of encountering sub-optimal chilling temperatures (Berger *et al.*, 2011). Modern autumn-sown Mediterranean germplasm is relatively unresponsive to temperature and compensates by a strong photoperiod response, flowering comparatively late to minimize both early low temperature and late terminal drought stress. An inverse relationship between photoperiod and temperature response in Mediterranean material (Berger *et al.*, 2011) made it possible for chickpea to colonize warmer areas to the south and southeast early in its domestication history, as photoperiod-initiated flowering is wholly maladaptive in low latitude, terminal drought-prone South Asian environments, where flowering occurs under reducing rather than increasing daylength.

B. Lupin

Collection site habitats of the Old World species housed in the Australian Lupin Collection (ALC) have been characterized by calculating site-specific bioclimatic variables, such as monthly mean rainfall; mean, minimum and maximum temperatures; relative humidity; rainy days per month; coefficients of variation for monthly precipitation; frost days per month; and sunshine percentage (Berger *et al.*, 2008a, b). Mapping the results of multivariate analysis demonstrates that in all species, accessions tend to align along latitudinal drought stress gradients. Thus, in the Mediterranean basin, cooler, higher rainfall/elevation sites are typically found in northerly locations, such as the Iberian Peninsula, while warmer, drier sites in are common in North Africa and the southern Levant. Material from these contrasting environments forms the basis of current efforts to understand specific adaptation in the genus, as outlined below. *L. albus* collection site climates are more complex than those of *L. angustifolius* and *L. luteus*, including low rainfall sites in central Anatolia, very warm irrigated locations along the Nile River Valley, and warm and wet locations in the Ethiopian highlands (Berger *et al.*, 2008b). Recent genotype by environment interaction studies highlighted the limited adaptive and genetic diversity of modern elite cultivars, demonstrating that matching cultivar phenology to target environment (late for long season, early for short season) was not possible throughout much of the current production range because of a confounding between vernalization response and later flowering (Berger *et al.*, 2012a, b). The idea that lupin yield could be increased by selecting appropriate adaptive traits for specific target environments has sparked interest in the adaptive strategies of wild germplasm, which, unlike domesticated material, has undergone natural selection in the contrasting Mediterranean environments described above. Long-season, high-rainfall habitats select strongly for delayed phenology, high above- and below-ground biomass production, high leaf area, seed yield and number, a combination of traits that leads to high water use, and the early onset of stress. *L. luteus* appears to ameliorate this aggressive competitive strategy with some degree of drought tolerance in high rainfall ecotypes, which can maintain higher leaf relative water content under lower critical leaf water potentials under water deficit. By contrast, lupins from terminal drought-prone environments are characterized by ruderal traits that facilitate drought escape/avoidance (early phenology, low biomass and water use, late stress onset) rather than tolerance which limit reproductive potential. Given that modern cultivars tend to express the ruderal traits of low-rainfall ecotypes, there appears to be considerable potential for lifting long-season productivity by introducing some of the competitive traits of high rainfall ecotypes.

C. Common Bean

The FAO-treaty germplasm-based core collection for cultivated common bean, housed at CIAT, was selected based on eco-geographical considerations, although not so formally as in other crops. The main purpose of the core collection was to sample the diversity across the two primary centers of origin for this crop, but only in the cultivated germplasm. Screening of this core collection for low phosphorus stress tolerance was successful, as was evaluation for some disease resistances, although many individual strain resistances or trait mechanisms are related to the overall differentiation of Andean and Mesoamerican phenotypes. This is especially clear when comparing the determinate plant type that occurs in the first genepool to indeterminate plants found in the both genepools, especially the bush beans of the second genepool. Wild germplasm of common bean has been used less often for screening but was the source of resistance to anthracnose and angular leaf spot in some cases. The multitude of pathogenic races for the fungi that cause these diseases makes it difficult to identify genes of any greater importance than those occurring in cultivated germplasm. The long history of introgression between wild and cultivated common beans and *vice versa* may explain why few novel disease-resistance genes have been found in the primary genepool. The use of secondary and tertiary genepool species, on the other hand, has proved promising for identifying resistances to both biotic and abiotic stresses. The sources of these traits are correlated with eco-geographical features even at the species level, since scarlet runner beans are from rain-leached, acid-soils of humid climates in Central America, and as such are resistant to fungal diseases and aluminum toxicity soil stress. In addition, tepary beans from the arid climates and sandy soils of northern Mexico and southwestern USA provide resistances to salinity and drought stress. Perhaps because of their evolution outside the wetter regions where bacterial and fungal pathogens occur, tepary beans also provide high levels of resistance to

specific *Xanthomonas* and rust infections, respectively. Recently, Cortés *et al.* (2012a, 2012b and 2013) analyzed the drought tolerance of wild common beans based on climatic data for each accession's collection site and found a correlation with allelic diversity in candidate genes for drought tolerance, such as the ASR and DREB transcription factors.

X. WILD RELATIVES AS A SOURCE OF NOVEL VARIATION

Most researchers agree that wild relatives of crop plants are a useful source of novel variation for potential breeding (McCouch *et al*., 2013). The challenges now are to reintroduce traits that have been lost or not used during the domestication process and subsequent breeding, including disease and resistance genes to make use of the wild allelic diversity that exists in germplasm collections. Highly variable germplasm is found in the secondary and tertiary pools of crop plants. This exotic material has largely remained uncharacterized and underutilized. Fortunately, there is a rising concern surrounding CWR use, and it is now a priority for GCDT. Genetic improvement of many crop plants has already benefited from the incorporation of traits from related wild species and other exotic germplasm sources. The development of pre-bred lines has long been advocated as a means of facilitating the transfer of genes from wild species. However, the majority of published results have been achieved with dedicated crosses and specific selection; thus they need to be made in trait-by-trait manner, which is a time-consuming and expensive process. The synthesis of exotic libraries, such as introgression lines (IL) or chromosome segment substitution lines (CSSL) and near isogenic lines (NIL), containing chromosome segments defined by molecular markers from wild species in a constant genetic background of the related cultivated species, has made the use of alien genomes more precise and efficient (Zamir, 2001; McCouch, 2004; Gur and Zamir, 2004). Establishment of such a permanent introgression library with characterized genomic fragments of wild crop relatives in a defined genetic background will allow phenotypic characterization of an unlimited number of target traits, which, coupled with molecular tools, will provide a means of final gene identification and their subsequent incorporation, pyramiding in desired genotypes, ultimately leading to better performing commercial cultivars. So far, not many such series of lines have been developed in grain legumes, but there are several ongoing efforts to establish them in pea (Smýkal and Kosterin, 2010; Smýkal *et al.*, unpublished), beans (Muñoz *et al.*, 2004; Blair *et al.*, 2006; Blair and Izquierdo, 2012), groundnut (Foncéka *et al*., 2009) and other legumes (reviewed in Upadhyaya *et al.*, 2011). Intergeneric legume hybrids have been critically reviewed in McComb (1975), which found insufficient evidence for all reported crosses due to misleading paper titles, confusion of vegetative with generic hybrids, the occurrence of patrocliny, and the frequent occurrence of misplaced generic boundaries. Sobolev *et al.* (1970, 1971) even reported hybrids between *Vicia faba* and pea with chromosome numbers of 2n = 12 and 16, respectively. This result is doubtful today in light of unsuccessful hybridization attempts between *Vicia faba* and several of its relatives, such as *V. narbonesis* and *V. johannis*. By contrast, Golubev (1990) reported a well-documented example of a successful intergeneric cross between *Vavilovia formosa* and *Pisum sativum* (reviewed in Mikič *et al.*, 2013), which may not surprising given that they are sister lineages that diverged only c. 8 Mya ago (Schaefer *et al.*, 2012). Ben Ze'ev and Zohary (1973) were the first to perform systematic crosses within and between pea species and between subspecies and noted cytological behavior at meiosis. Hybrids between *P. sativum* subsp. *sativum* (*P. humile*) and *P. sativum* subsp. *elatius* had reduced fertility as a consequence of meiotic irregularities, and this was more pronounced in hybrids with *P. fulvum*. They noted in reciprocal crosses that it was only possible to use *P. fulvum* as the male parent. Due to translocation, the hybrids between cultivated *P. sativum* and *P. sativum* subsp. *elatius*, as well as southern "*P. humile*," had also reduced fertility, while with northern "*P. humile*" were normal as a result of a standard karyotype. Two reciprocal translocations (T1-7) and (T3-5) account for reduced fertility and distorted segregation of hybrids between cultivated *P. sativum* and *P. fulvum* (Errico *et al.*, 1991, 1996; Campbell 1997), together with different numbers of nucleolus-organizing chromosomes (De Martino *et al.*, 2000). Durieu and Ochatt (2000) have tested protoplast fusion and regeneration of calli between *Pisum sativum* and *Lathyrus sativus*, and although heterokaryons were detected and up to 6 cell divisions were observed, no further growth or plant regeneration could be achieved. *Pisum fulvum* was used to introduce resistance to powdery mildew (Fondevilla *et al.*, 2007), bruchid pests (Clement *et al*., 2002, 2009; Byrne *et al.*, 2008) and *Orobanche crenata* (Rubiales *et al.*, 2009), while primitive landraces were used in order to incorporate virus and *Fusarium* resistances (Providenti, 1990; McPhee *et al.*, 1999). Wild accessions of *P. sativum* subsp. *sativum* or subsp. *elatius* (variously named *P. humile* or *P. syriacum* in papers) have often found to be resistant to various biotic stresses (reviewed in Smýkal *et al.*, 2013). Attempts to cross *Pisum* with *Lathyrus sativus* did not result in fertile, viable plants (Ochatt *et al.*, 2004), although the phylogenetically closest *L. ochrus*, *L. clymenum*, and *L. neurolobus* (Schaefer *et al.*, 2012) have not been tested. The development of backcross recombinant inbred lines containing chromosome segments of the wild pea *P. fulvum* or *P. sativum* subsp. *elatius* in a cultivated pea (*P. sativum* subsp. *sativum*) genetic background defined by molecular markers is currently being performed by Smýkal and Kosterin (2010 and unpublished).

The wild *Lens* taxa are known to possess resistance to biotic and abiotic stresses (Bayaa *et al.*, 1994, 1995; Hamdi and Erskine, 1996; Hamdi *et al*., 1996; Gupta and Sharma, 2006). Incorporation of diverse genetic material from wild relatives using intensive hybridization would make it possible to recreate some of the lost variability while still respecting productivity and other desirable traits in lentil. Intraspecific hybridization

between cultivated lentil and *L. culinaris* subsp. *orientalis*, *L. odemensis*, *L ervoides* and *L nigricans* has been attempted in the past (Ahmad *et al*., 1996; Gupta and Sharma, 2007). *Lens culinaris* subsp. *orientalis* is readily crossable with the domesticated lentil, although the fertility of the hybrids depends on the chromosome arrangement of the wild parent. Pod abortion took place when the cultivated lentil was crossed with either *L. ervoides* or *L. nigricans* (Abbo and Ladizinsky, 1991). *In vitro* methods of embryo-ovule rescue are used overcome the post-fertilization interspecific barrier (Fratini and Ruiz, 2006; 2011).

In case of *Lathyrus*, among 1,555 accessions of 45 wild species conserved at ICARDA, a toxin-free gene has been identified in *L. tingitanus*, which can be used to develop toxin-free grass pea cultivars, providing its hybridization with *L. sativus* is possible. *Lathyrus* species, such as *L. ochrus* and *L. clymenum* and *L. cicera* (Fernández-Aparicio *et al*., 2009; 2010), have been identified as possessing resistance to *Orobanche*, a resistance that is not available within cultivated germplasm. *Lathyrus cicera* is also a good source for earliness and cold tolerance. However, alien gene transfer has hardly been attempted in grass pea in spite of the success of interspecific hybridization between *L. sativus* and two wild *Lathyrus* species (*L. cicera* and *L. amphicarpos* L.) with viable seeds (Yunus, 1991; Addis and Narayan, 2000). Other tested species formed pods but did not produce fully developed, viable seeds. It may be concluded that breeding strategies involving alien genetic transfer for the improvement of grasspea are possible through the readily crossable species *L. cicera* and *L. amphicarpos*, but biotechnology tools will be needed to assist in gene transfers among other species (Ochatt *et al.*, 2004).

Numerous studies have attempted to facilitate the useful gene transfer from wild *Cicer* species to the cultivated chickpea and *vice versa*. Successful hybridizations between the cultivated chickpea and *C. reticulatum* or *C. echinospermum* and their reciprocals have been reported (Ladizinsky and Adler, 1976ab; Jaiswal and Singh, 1986; Singh and Ocampo, 1993; Croser *et al.*, 2003; Ahmad and Slinkard, 2004; Singh *et al.*, 2005; Clarke *et al.*, 2006; Knights *et al.*, 2008; Malikarjuna *et al.*, 2011; Thompson *et al.*, 2012). Although some of the accessions of *C. bijugum*, *C. judaicum* and *C. pinnatifidum* used as pollen donors were crossed with the cultivated chickpea, hybrids were available via embryo rescue techniques (Ahmad and Slinkard, 2004). So far, there have been no successful gene transfers between the cultivated chickpea and perennial wild *Cicer* species due to post-zygotic hybridization barriers. Hybrids between *C. arietinum* and *C. pinnatifidum* (Badami *et al.*, 1997; Mallikarjuna, 1999), *C. arietinum* and *C. judaicum* (Verma *et al.*, 1995), and *C. arietinum* and *C. bijugum* (Mallikarjuna *et al.*, 2007) were obtained via embryo rescue and tissue culture techniques. Some hybrids between *C. judaicum* and *C. bijugum*, as well as between *C. cuneatum* Hochst. ex A. Rich. and *C. canariense* A. Santos & G.P. Lewis, were produced by Abbo *et al.* (2011). Other hybrids between *C. arietinum* and *C. judaicum*, *C. arietinum* and *C. pinnatifidum*, and reciprocal crosses were obtained by Clarke *et al.* (2011).

As pigeonpea suffers limited genetic diversity within the cultivated gene pool, it is imperative to increase genetic diversity by using wild relatives from different gene pools. A number of species from the secondary gene pool (*C. sericeus*, *C. albicans* (Wight & Arn.) Maesen, *C. lineatus* (Wight & Arn.) Maesen, *C. trinervius* (DC.) Maesen, *C. cajanifolius* and *C. scarabaeoides*) have shown crossability with the cultivated type. Several interspecific crosses have produced hybrids that showed shrivelled and non-viable seeds, proving that crossability barriers exist within the genus (Yadav and Padmaja, 2002). Some of these wild species have been found to be sources of resistance/tolerance to various biotic and abiotic stresses and of agronomically important traits, such as sterility mosaic disease resistance, high protein content, high fruit set, pod borer resistance, salinity tolerance, etc. (see Bohra *et al.*, 2011b). Inter-specific hybridization has played an important role in the development of the cytoplasmic male sterility (CMS) system in pigeonpea (see Saxena *et al.*, 2010). Therefore, some of the secondary gene pool species have been used successfully. However, few of the wild relative species from the tertiary gene pool have shown promising crossability and are difficult to use for pigeonpea improvement.

Even though wild soybean is considered the closest relative of the cultivated soybean (Hymowitz, 1970), it has significant phenotypic differences. The large phenotypic diversity in soybean is genetically controlled in both qualitative and quantitative aspects. For example, wild soybean has mainly tiny, black seeds in contrast to the large, yellow seeds of cultivated soybean. There are also significant differences in the seed oil and protein concentration between wild and cultivated soybeans (Xu and Gai, 2003; Chen and Nelson, 2004). Several studies suggest that wild soybean has important phenotypic characteristics and specific alleles that are not present in cultivated soybean (Carter *et al.*, 2004). Major traits of agricultural importance, including yield and stress tolerance, are polygenic, and the presence of these favorable alleles in *G. soja* will help breeding programs introduce beneficial traits into soybean (Tanksley and McCouch 1997; Li *et al.*, 2008). Therefore, wild soybeans are important sources of novel alleles that can be used to broaden the genetic base of cultivated soybean, which is necessary due to the fact that diversity in soybean has been greatly reduced by the genetic bottleneck of domestication (Guo *et al.*, 2010; Lam *et al.*, 2010; Li *et al.*, 2010).

Cowpea has an intrinsically narrow genetic base that limits breeders' progress today. However, there are few reports in published literature on the use of wild cowpea relatives for the genetic improvement of cultivated cultivars. The relatively low level of utilization of wild cowpea relatives in the development of improved cowpea cultivars may be due to factors like linkage drag. The basic need for exploiting the wild relatives is its cross compatibility with cultivated cowpea. It is possible that some of the available wild cowpea lines belong to the same or different gene pools. The subspecies or cultivars that constitute the

primary and secondary gene pools for cowpea are not yet well defined (Table 1).

Among all the genetic barriers, the difference in ploidy level is cultivated groundnut's main obstacle in sharing alleles with its wild relatives. Even though there has been a continuous effort to tackle this genetic barrier via three main pathways (the hexaploid, the autotetraploid and the allotetraploid routes), very limited success has been achieved. The hexaploid route involves crossing between diploid and tetraploid genotypes, followed by chromosome doubling through colchicine treatment achieving hexaploid (60 chromosomes). This hexaploid was used for repeated backcrossing with cultivated species (*A. hypogaea*), and resultant progenies were used for several genetic and breeding applications, such as introgression lines/populations, genetic maps and even germplasm releases or cultivars with disease resistance (see Burrow *et al.*, 2013). The second route involves the creation of synthetic autotetraploides (AAAA or BBBB) through colchicine treatment of diploid species (AA or BB genome) and their use in crossing with cultivated genotype (Singh, 1985; Mallikarjuna *et al.*, 2011). The third route involves the creation of synthetic allotetraploides (AABB) through crossing two diploid species (AA and BB genomes), followed by colchicine treatment. Several allotetraploid synthetics were successfully developed using this method and were used for introgressing wild alleles into cultivated germplasm (Simpson, 1991; Simpson *et al.*, 1993; Fávero *et al.*, 2006; Mallikarjuna *et al.*, 2011). The development and use of the allotetraploid "T*x*AG-6 ({*A. batizocoi* Krapov. & W.C. Greg. × [*A. cardenasii* Krapov. & W.C. Greg. × *A. diogoi* Hoehne]}^{4x})" presents one notable example for wide applications, such as introgression of resistance for root-knot nematode and genetic maps using mapping populations (cultivated Florunner × amphidiploid TxAG-6). Resistance to root-knot nematode and foliar diseases (rust and late leaf spot) was introduced into the cultivated genepool from *A. cardenasii* via the hexaploid route (Garcia *et al.*, 1996; Gowda *et al.*, 2002), while root-knot nematode resistance was introduced via the tetraploid route (Simpson, 1991). Development and release of root-knot nematode resistant cultivar "COAN" (Simpson and Starr, 2001) and foliar disease (rust and late leaf spot) resistant cultivar "GPBD 4" (Gowda *et al.*, 2002) are other notable examples. TxAG-6 amphidiploid was used for developing root-knot nematode resistant cultivar "COAN" by crossing with cultivated Florunner (Simpson and Starr, 2001). Similarly, an interspecific line (CS 16 or ICGV 86855) derived from the cross between *A. hypogaea* and *A. cardenasii* was used as a parent in the development of GPBD-4 (KRG 1 × ICGV 86855) (Gowda *et al.*, 2002). Thus far, 12 wild relatives have been deployed for the development of synthetics for enriching the primary gene pool in groundnut. These include *A. cardenasii, A. diogoi, A. batizocoi*, *A. ipaënsis*, *A. duranensis*, *A. gregoryi* C.E. Simpson, Krapov. & Valls, *A. linearifolia* Valls, Krapov. & C.E. Simpson, *A. magna* Krapov., W.C. Greg. & C.E. Simpson, *A.valida* Krapov. & W.C. Greg., *A. kempff-mercadoi* Krapov. & W.C. Greg., *A. stenosperma* Krapov. & W.C. Greg., and *A. hoehnei* Krapov. & W.C. Greg. In addition to above-mentioned cultivars, several other elite lines have been bred using wild relatives from across the world, and these elite lines possess resistances to different diseases and pests in groundnut (see Sharma *et al.*, 2013).

Due to unique adaptations, alfalfa CWR have made substantial contributions to alfalfa breeding. Cold-hardy and drought-tolerant *M. sativa* subsp. *falcata* has been used to expand the adaptive range of alfalfa into colder and drier locations (Small, 2011; Barnes *et al.*, 1977). There have also been breeding efforts to capitalize on heterosis between subsps. *M. sativa* subsp. *sativa* and *falcata* (Riday et el., 2002a,b; Riday and Brummer, 2005). The glandular hair trait found in *M. sativa* subsp. *falcata* var. *viscosa*, M. *sativa* subsp. *glomerata* and *M. sativa* subsp. *sativa* × *M. sativa* subsp. *glomerata* is considered an adaptation that conveys insect resistance (Small, 1986; Small and Brooks, 1986). In the United States, CWR introductions with glandular hairs have given rise to proprietary alfalfa cultivars that are resistant to potato leafhopper (*Empoasca fabae* Harris), a serious pest in the Eastern United States (Shockley, 2002). Fertile interspecific hybrids are difficult to obtain in *Trifolium* (Taylor *et al.*, 1980), and generally success occurs between closely related taxa only (Taylor and Quesenberry, 1996). There are some exceptions: allotetraploid white clover originated as a hybrid between *T. pallescens* Schreb. and *T. occidentale* D. E. Coombe (Williams *et al.*, 2012).

An introgressive crossing strategy was proposed by Cowling *et al.* (2009) to increase genetic diversity in the Australian *Lupinus angustifolius* breeding program. The strategy involves crossing wild donor accessions with a domesticated variety three times, followed by single-seed descent. Only targeted selection of domestication traits is applied before the BC_2S_3 generation (two backcrosses of the F1, followed by three generations of single-seed descent) to maximize the probability that most of the wild-donor genome is represented. Early yield trial data indicated that this strategy is effective, with some introgression lines yielding almost 30% higher than the recurrent domesticated variety (Berger *et al.*, 2013). A simplified version of this approach, whereby European cultivars acted as donors, appeared to be even more effective, with up to 44% higher yields than the recurrent Australian variety (Berger *et al.*, 2013). However, given the close genetic relationship between Australian and European breeding material, it is likely that such gains will be less sustainable compared to introgressive crossing with the much more diverse wild germplasm (Berger *et al.*, 2012a). In addition to their role in increasing yield, these genetically diverse populations will be grown in multi-environment trials to study specific adaptations in a domestic framework, linking adaptive traits to QTLs where possible. Interspecific crossing of *L. mutabilis* has been successfully achieved with other New World lupins with $2n = 48$ chromosomes, most notably *L. tomentosus* DC., *L. mexicanus* Cerv. ex Lag, and *L. hartwegii* Lindl. (Clements *et al.*, 2008). Indeed, the ability to intercross New World lupin species was the basis of the development of ornamental Russell lupins with a wide variety of flower colors (Wolko *et al.*, 2011).

Therefore, unlike the Old World lupin crop species, where inter-specific crossing is extremely challenging, *L. mutabilis* breeders have access to a broad secondary genepool of related species for introgressing traits not available within the primary genepool.

Two novel techniques for introgression of wild germplasm diversity into breeding programs have been pioneered in common bean. *P. vulgaris* was the first legume in which the advanced backcross (AB)-QTL method was applied to incorporate agrononomically valuable alleles from the wild into the cultivated form (Blair *et al.*, 2006). In another study, Blair and Izquierdo (2012) found that genes from the small-seeded, wild common beans can increase the seed concentration of mineral elements of nutritional importance, such as iron and zinc, in an AB-QTL breeding program of large-seeded Andean beans. However, further research summarized in Blair (2013) found that wild beans concentrate many minerals in their seed coats, and that this is the mechanism of higher mineral concentration in the chromosome segment substitution lines developed by the AB breeding method. These results build on the transfer of other seed characteristics, such as the arcelin and APA cotyledonary proteins that confer insect resistance from wild to cultivated beans by marker-assisted selection, even in regions of low linkage disequilbrium (Blair *et al.*, 2010). In terms of inter-specific crosses, certain common bean advanced lines have been improved from embryo-rescued hybrids between *P. vulgaris* and *P. acutifolius,* with introgression confirmed by AFLP analysis of congruity backcross derived lines compared with standard backcross lines (Muñoz *et al.*, 2004, 2006). A similar program, but with limited backcrossing, has been initiated for common bean using *P. coccineus* and *P. dumosus* accessions and has resulted in limited introgression in need of confirmation through marker analysis. More focused and concentrated introgression of *P. acutifolius* or *P. parvifolius* genes may be useful for incorporating drought and heat tolerance into common beans. Meanwhile, *P. lunatus* and its relatives have never been used for common bean improvement, although they may be valuable for climate change adaptation. Another alternative is to use lima beans and tepary beans in place of common beans. This will require breeding of these wilder species into more widely adapted modern crops for a range of climates and markets. One major goal of breeding in tepary beans is to increase seed size and to produce more variable seed colors, while the bush bean habit still needs to be improved in lima beans.

The wild, related species and other cultigens of *Vigna* do not form a particularly extensive or accessible gene pool (Smartt, 1990). Even the two closest relatives, *V. radiata* and *V. mungo*, have some structural differentiation among their genomes. Despite the phylogenetic proximity of *V. vexillata* and cowpea, there exists a strong barrier to cross compatibility between them (Fatokun, 2002). Lawn (1995) proposed that the Asian Vigna consists of three more or less isolated genepools, based on cross-compatibility studies, which correspond with groups based on seedling characteristics proposed by Tateishi (1996).

XI. IMPACT OF GENOMICS FOR CROP LEGUME GERMPLASM UTILIZATION

Until recently, a very limited number of genomic resources–—a few hundred molecular markers, some fragmentary genetic maps–were available in most of the legumes. Over the last decade, various types of genomic resources, such as microsatellites or simple sequence repeats (SSR), expressed sequence tags (ESTs), single nucleotide polymorphism (SNP), cleaved amplified polymorphic sequences (CAPS), conserved intron spanning primers and diversity array technology (DArT) markers have been developed. Molecular marker technologies, however, are currently undergoing a transition from largely serial technologies based on separating DNA fragments according to their size (SSR, AFLP) to highly parallel, hybridization-based technologies that can simultaneously assay hundreds to tens of thousands of variations, especially in genes. With completed and annotated genomes of model legumes, such as the 373 Mb genome of *Medicago truncatula* (Young *et al.*, 2011), the 472 Mb genome of *Lotus japonicus* (Sato *et al.*, 2008), and of three legume seed crops: the 1,112 Mb genome of *Glycine max* (Schmutz *et al.*, 2010), the 833 Mb genome of pigeonpea (*Cajanus cajan*) (Varshney *et al.*, 2012), the 738 Mb genome of *Cicer aerietinum* (Jain *et al*., 2013; Varhsney *et al.*, 2013), and the ongoing genome sequencing efforts in *Phaseolus vulgaris* (550 Mb), *Pisum sativum* (4,600 Mb), *Lupinus angustifolius* (924 Mb), *Trifolium praetense* (440 Mb) and *Arachis hypogaea* (2,800 Mb). There is strong potential for comparative genomics and its applications, including specific gene/allele mining and deeper diversity studies of legume germplasm collections. One example is that the sequencing of 90 chickpea accessions, composed of landraces and five wild species, has provided information related to domestication and diversification (Varhsney *et al.*, 2013). This information and many other re-sequencing efforts in chickpea and pigeonpea will be used to gather insight into genome evolution and phylogeny and gene-to-trait identification. Moreover, comparative sequencing of wild crop progenitors, such as studies involving *Glycine* and *Cicer*, should provide clues to the domestication process and enable practical exploration of CWR.

A chromosome-scale draft sequence of cultivated soybean (var. Williams 82) with 46,430 deduced protein-coding genes has been available since 2010 (Schmutz *et al.*, 2010). Using the genome of Williams 82 as a reference, a wide range of nucleotide and structural variations between wild and domesticated soybean have been catalogued (Kim *et al.*, 2010; Lam *et al.*, 2010; Li *et al.*, 2013b). However, some genomic regions present in wild soybean but absent in the cultivated reference need to be uncovered by *de novo* sequencing of wild soybean (Stupar, 2010). Therefore, it is necessary to sequence a set of diverged wild soybean accessions and build up a pan-genome of wild soybean for uncovering their specific genes for soybean improvement (Qiu *et al.*, 2013). TILLING populations have also been made for this crop in order to discover mutant alleles in the

small-seeded common bean advanced line BAT93 (Blair *et al.*, 2008; Porch *et al.*, 2009).

The reference genome of an Andean genepool common bean (*Phaseolus vulgaris*) G19833 line has been obtained by re-sequencing various other genotypes, which will lead to faster gene discovery or characterization and development of markers for the selection of specific genes with known functions (Blair *et al*., 2013). The missing ingredients for rapid advances in breeding of common bean are i) the lack of genomic or transcriptomic sequences for the other cultigens within the genus, such as lima bean, scarlet runner bean and tepary bean; ii) the small number of accessions of wild germplasm collected for each of the cultivated species and their fast disappearance in regions of heavy urbanization across the mid-elevation valleys of Latin America; and iii) the small number of inter-specific and even inter-varietal crosses that have been made for each of the cultivated groups (Blair *et al.*, 2012a, 2012b). Phenotyping, while challenging to carry out on a large scale, is quite advanced in common bean; therefore, common bean is not subject to the tremendous limitation predicted for other legume species. However, some of the cultivated species with long-season production cycles are indeed difficult to phenotype. These include climbing (or pole) common and lima beans, as well as scarlet runner beans, which are, for the most part, very late maturing and limited in adaptability.

Comparably, genomic study of *Vigna* crops have has lagged. The utilization of cowpea germplasm has gradually been strengthened through the application of molecular breeding technology (Undal *et al.*, 2011; Kumar *et al.*, 2012; Kaewwongwal *et al.*, 2013) and QTL analysis (Sholihin and Hautea, 2002; Humphry *et al.*, 2005; Kasettranan *et al*., 2010; Kongjaimun *et al.*, 2012; Chankaew *et al.*, 2014; Kajonphol *et al.*, 2012). The similarity of the cowpea and common bean genomes is well documented, and this should help to transfer genetic knowledge between genera and from one crop to the other. Sequencing of the cowpea genome is underway, and large transcriptome, SNP marker and physical mapping resources are available for the crop. Through the Tropical Legumes I project in the Generation Challenge Program at the University of California, Riverside, cowpea genomics activities are being conducted, and the tools developed there will be used in cowpea breeding programs. A high-throughput SNP genotyping platform based on Illumina 1536 GoldenGate Assay was developed. The result was a cowpea consensus map containing 928 SNP markers on 619 unique map positions distributed over 11 LGs, covering a total genetic distance of 680 cM (Muchero *et al.*, 2009). This offers the framework for QTL identification, map-based cloning, and assessment of genetic diversity, association mapping and applied breeding.

Until recently, lentil molecular breeding relied on other legume species' genomic resources for the development of new markers (Pandian *et al.*, 2000; Reddy *et al.*, 2010; Alo *et al.*, 2011; Datta *et al.*, 2011). This was a successful strategy because of the synteny between lentil and the model legume *Medicago truncatula* (Phan *et al.*, 2007b). With the publication of three transcriptomes of lentil (Sharpe *et al.*, 2013; Verma *et al.*, 2013; Kaur *et al*. 2011), this is rapidly changing. One transcriptome targeted SNP discovery, resulting in the publication of a SNP-dense genetic linkage map (Sharpe *et al.*, 2013). New EST-SSRs (2,393 and 8,722) were discovered using unigene sets of 20,419 and 20,009 (Kaur *et al.*, 2011; Verma *et al.*, 2013). Many of the main lentil breeding objectives are quantitative (yield, quality, disease and stress tolerances), and the development of useful maps can assist in effective QTL identification for marker-assisted selection. Moreover, mapping the new SNPs and EST-SSRs moves lentil a step closer to genome wide association studies (GWAS) (Sharpe *et al.*, 2013).

Yang *et al*. (2012) reported a total of 162,448,842 base pairs of genomic sequences from SSR enriched libraries constructed with genomic DNA from 247 faba bean accessions. Next-generation sequence technology has been applied to generate faba bean genomics resources for large-scale SSR identification (Yang *et al*., 2012). A high throughput SNP genotyping array targeting 887 loci has been developed for genomic-assisted breeding in faba bean (Cottage *et al.*, 2012). Limited gene sequence homologies and synteny to *Medicago truncatulla* have been applied to anchor gene-based markers in the faba bean and lentil linkage groups (Ellwood *et al.*, 2008). However, genome-wide comparison between these two species has not yet been carried out due to the scarcity of faba bean genome sequence data.

In groundnut, identified linked markers to root-knot nematode were used to transfer resistance from amphidiploid to cultivated groundnut, which resulted in the development of the first molecular breeding product in groundnut, NemaTAM (reviewed in Varshney *et al.*, 2013b). The use of markers proved helpful in selecting plant progenies under varied soil and fluctuating environmental conditions. Parallel efforts also led to the development of cleaved amplified polymorphic sequence (CAPS) markers for the high-oleate trait, which provided an opportunity to improve both traits (nematode and high oleate), together leading to the development of another molecular breeding product, "Tifguard High O/L" (reviewed in Varshney *et al.*, 2013b). Superior lines with desirable yield and higher rust resistance were identified and subjected to yield evaluation in replication for further multiplication and multilocation trails (Varshney *et al.*, 2014). However, in the case of drought tolerance and yield components, several QTLs contributing only small phenotypic variation were identified using family-based mapping populations. Recent advances in genomic technologies have opened avenues of research and marker development in 'orphan' legume species that were previously the preserve of well-resourced model species (Varshney *et al.*, 2009b).

In case of alfalfa, genomics can use the most directly knowledge of *Medicago truncatula* model. Exploiting genetic diversity in alfalfa genetic resources is being advanced by the development of molecular markers for important abiotic and agronomic traits, such as aluminium tolerance (Ku *et al.*, 2013),

biomass (Robins *et al.*, 2007a), persistence (Robins *et al.*, 2008), yield, plant height and regrowth (Robins *et al.*, 2007b). More recently, a large number of genome-wide EST and SNP markers have been developed using transcriptome sequencing (Li *et al.*, 2012). These markers, available through the Legume Information System (http://medsa.comparative-legumes.org/), will support marker-assisted breeding efforts and may be helpful in guiding introgression efforts.

Large insert clone libraries of the *Lupinus angustifolius* genome have been developed from European and Australian cultivars (Kasprzak *et al.*, 2006; Gao *et al.*, 2011). Transcriptome sequencing has been reported for *L. albus* and *L. luteus* (Parra-Gonzalez *et al.*, 2012; O'Rourke *et al.*, 2013) and is underway for *L. angustifolius* and a range of New World lupin species. A reference genome sequence assembly for *L. angustifolius* is currently under construction (Gao *et al.*, 2011), and a genome survey has been reported (Yang *et al.*, 2013b). Genotyping-by-sequencing has been used to develop improved markers for anthracnose and phomopsis resistance in *L. angustifolius* (Yang *et al.*, 2012; Yang *et al.*, 2013a). These resources are being used to address basic questions relating to genome evolution, *Lupinus* phylogeny, seed storage protein synthesis, specific adaptation and identification of domestication genes, as well as developing markers for applied breeding purposes. Knowing the genes underlying important agronomic and quality traits paves the way for refining traits by reverse genetic and transgenic approaches (Berger *et al.*, 2013).

With advances in model legume sequencing and genomic knowledge, there has been a switch to gene-based markers in pea (Aubert *et al.*, 2006; Jing *et al.*, 2007; Deulvot *et al.*, 2010; Bordat *et al.*, 2011). Recently, a comprehensive transcriptome of pea was published (Franssen *et al.*, 2011), and another RNA-seq atlas is being established at INRA, France (http://bios.dijon.inra.fr). This trend can be expected to further proliferate in conjunction with rapid advances in high-throughput single-nucleotide polymorphism (SNP) generation and detection assays (Deulvot *et al.*, 2010; Bordat *et al.*, 2011). In pea, a transcription atlas (RNAseq) and gene-based maps (Bordat *et al.*, 2011) will aid translation of genomic knowledge to practical breeding. Moreover, the pea variety Cameor was used to develop the TILLING mutant population (Dalmais *et al.,* 2008) and to construct a BAC library, both essential tools for positional cloning and pea genome sequencing (reviewed in Smýkal *et al.*, 2012; Smýkal and Konečná, 2014). Increased knowledge of the pea genome has not only a scientific but also a great educational and social impact, owing to seminal work of J. G. Mendel (1865–66) (Schwarzbach *et al.*, 2014).

Because of the limited amount of genomic resources and low polymorphism in cultivated germplasm, initial genetic mapping studies were restricted to inter-specific mapping populations. For trait mapping, however, it is important to develop genetic maps based on intra-specific mapping populations. However, the translation of genomics (QTLs/ markers identified) to legume breeding is still in its infancy, and, despite the efforts and progress made in developing molecular resources, their use in breeding has been limited (see Varshney *et al.*, 2013b, this issue). Several factors limit the direct application of QTLs and their associated markers, including: i) high genotype x environment interactions on expression; ii) the necessity of testing the polymorphism of the molecular markers in different genetic backgrounds; iii) large (5–10 cM on average) genetic distances between markers and the QTLs; iv) imprecise phenotypic description that has resulted in inaccurate marker-trait associations; v) the use of small mapping populations (50–200 individuals) that has resulted in limited genetic resolution; vi) the lack of common reference markers across QTL studies; vii) the limited range of variation in the cultivated genepool; viii) trait and marker validation in different genetic backgrounds; and ix) inadequate investment in many of legume crops, which has created a lag in the development of molecular tools for breeding (Smýkal *et al.*, 2012). The availability of a high-throughput genotyping platform on the appropriate germplasm collections mentioned will facilitate the use of the association genetics approach for identification of genes/markers associated with traits of interest to breeders. However, the association of genomic sequences/haplotypes with traits of interest to breeders would require multi-location and precise phenotyping data, as well as appropriate analytical tools on a high-computing bioinformatics platform.

Genetic characterization raises new issues for the management of genetic diversity within accessions, since preserving the original genetic composition of sample accessions is usually required. In many cases, particularly for wild relatives and traditional cultivars, this involves conserving genetically heterogeneous populations in a form that is difficult to use for gene discovery. It has been recommended that wherever possible, single plants should be used as the source of DNA for sequencing, and seed derived from these single plants should be set aside as "reference seed stocks." These stocks will also serve as the source of material for phenotyping and ensure that phenotypic information can be associated with the sequence information in a meaningful way. However, creating a new accession for each genotyped accession has significant consequences over the cost and size of germplasm maintenance. A coordinated effort to characterize germplasm collections is needed, along with advanced analytical methods that allow for three-way testing of diversity in genotypes, locations and quantitative traits to provide dynamic characterization of genotypic and phenotypic diversity. Such dynamic characterization could be used to study adaptation across a range of different ecological locations. Such a core set would provide a useful and powerful resource for next-generation markers, such as SNPs or whole-genome sequencing (WGS), and, more importantly, for phenotypic analysis of agronomic traits. Recent advances in genomic technology, the impetus to exploit natural diversity, and the development of robust statistical analysis methods make association mapping affordable for most legumes (reviewed in Smýkal *et al.*, 2012). Genomics-assisted breeding has already proved to be a very useful approach, which provides much-needed

precision in the selection of target traits and significantly reduces the duration of cultivar development. Compared to conventional linkage-mapping based on time-consuming biparental mapping population development, linkage disequilibrium (LD)-mapping using the non-random associations of loci in haplotypes is a powerful, high-resolution tool for complex quantitative traits.

XII. FUTURE OUTLOOK

Next-generation sequencing and high-throughput genotyping platforms promise to further revolutionize our understanding of genetic diversity and to assist in designing strategies to utilize the genomic information for legume crop improvement. It is possible to sequence large-scale germplasm collections of legumes held in genebanks of CGIAR centers and national genebanks of different countries. Genome-wide sequence data for these germplasm collections will provide an opportunity to develop a "hapmap" for the given species. These "hapmaps," on one hand, can be used for genome wide association analysis if, provided precise, large-scale phenotyping data for traits of interest to breeders is available. Therefore, there is an urgent need to establish a global phenotyping network for comprehensive and efficient characterization of legume crop germplasm for an array of target traits, particularly for biotic and abiotic stress tolerance and nutritional quality. Genome-wide sequence data can be stored in user-friendly databases that can serve as "digital genebanks." Such "digital genebanks" can be helpful in designing the primer pairs and amplifying gene(s) of interest. Low utilization of germplasm use, despite its accessibility, in crop breeding has always been debated, and it is anticipated that genome-wide sequence information and, most importantly, the association of alleles with targeted phenotyping traits potentially will provide sufficient knowledge to the crop community to decide which accession(s) and which genomic segment(s) they need to target for improving a given trait in a particular legume crop species. It is also important to mention that information generated regarding germplasm of, whether genotyping, genome sequencing or phenotyping, should be made available as open access data." This would link seeds and genetic stocks directly to passport, genomic and phenotypic information, thereby engaging the creativity of geneticists and breeders. This will help crop communities across the world make the best use of the information generated/ available for crop improvement.

FUNDING

P.S. acknowledges fruitful discussions with numerous colleagues worldwide and financial support from the Grant Agency of Palacký University, IGA PrF-2013-003. T.M.'s work is funded as part of a long-term project by Agricultural Research, Ltd., and by MSM 2629608001 project. R.K.V. would like to thank US Aid for International Development (USAID), the Australian Indo Strategic Research Fund (AISRF) of Ministry of Science & Technology and the CoE Grant from the Department of Biotechnology, Government of India, for sponsoring research related to the topics discussed in this article at ICRISAT.

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