Chapter 2
Arachis Gene Pools and Genetic Improvement in Groundnut

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Abstract Groundnut (*Arachis hypogaea* L.) is an important oilseed and food crop in the world. The crop is predominantly grown in low input production systems in developing countries in Asia and Africa. There are several production constraints, both biotic and abiotic, to groundnut. Some of these are global in nature and the others are either regional or local. Four *Arachis* gene pools contain 80 species, distributed among nine sections are native to five countries of South America. Section *Arachis* contains tetraploid cultivated groundnut, divided into two subspecies and six botanical varieties and a number of cross-compatible diploid species with rich genetic diversity. International efforts have made significant progress in collection and conservation of these genetic resources, facilitating genetic improvement. Groundnut is an autogamous crop. The pedigree and bulk selection methods are more commonly used by the groundnut breeders. Conventional breeding, including cytogenetic manipulations introgressing genes from cross-compatible wild diploid species has been effective in some areas, while in others it has been tardy due to lack of proper and effective phenotyping tools and limited understanding of the genomics, genetics/inheritance, and underlying mechanisms influencing targeted traits. A greater diversification of parental resources (both cultivated and wild *Arachis* species) in breeding programs is required to develop new cultivars with diversified genetic backgrounds, which will enable them to perform better under the changing climatic/adverse conditions. Molecular breeding is in infancy. Infrequent and low polymorphisms have restricted the progress in the development and application of genetic maps, except in cases where polymorphic chromosomal regions have been introgressed from diploid wild *Arachis* species into *A. hypogaea*. Both conventional and nonconventional crop improvement efforts in groundnut need to concentrate on bridging

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the yield gap between the potential yield and the realized yield by alleviating major production constraints particularly in rainfed environment.

Keywords *Arachis hypogaea* · *Arachis* gene pool · Center of origin/diversity · Core collection · Genetic improvement · Molecular breeding · Genetic transformation

2.1 Introduction

Groundnut or peanut (*Arachis hypogaea* L.), an annual legume of indeterminate growth habit, is primarily grown for its high-quality edible oil (44–56 %) and easily digestible protein (22–30 %) in its seeds. Groundnut seeds also contain carbohydrates (10–25 %) and are a rich source of vitamins (E, K, and B complex), minerals (Ca, P, Mg, Zn, and Fe), and fiber. It ranks sixth in edible oil production among the oilseed crops and thirteenth among the food crops (production utilized directly as food or in confections) in the world. It is also the third most important source of vegetable protein in the world. It is grown predominantly for food use in North America, Southern Africa, West Africa, Southeast Asia, and Europe and predominantly for edible oil use in South America and Southwest Asia. In East Africa and East Asia, both food and edible oil uses are important. On a global basis, 41 % of the production goes for food use and 49 % for extraction of edible oil. The remaining 10 % is used as feed and seed or goes waste. The commercial production of groundnut occurs principally between 40°N and 40°S and about 114 countries grow groundnut. The crop is predominantly grown in low-input production system in Asia and Africa with yield ranging between 700 and 1000 kg/ha and in high input system in USA, Australia, Argentina, Brazil, China, and South Africa where yields of 2000–4000 kg/ha are obtained.

2.2 *Arachis* Gene Pool and Taxonomy

Genus *Arachis* gene pool contains 80 species (Krapovickas and Gregory 1994; Valls and Simpson 2005). Based on distribution, character clustering, and cross-compatibilities, Krapovickas and Gregory (1994) classified the genus into nine sections. Of these, section *Trierectoides* contains 2, *Erectoides* 14, *Extranervosae* 10, *Triseminatae* 1, *Heteranthae* 6, *Caulorhizae* 2, *Procumbentes* 10, *Rhizomatosae* 4, and *Arachis* 31 species. Section *Arachis* contains cultivated groundnut (*A. hypogaea*), another tetraploid species *A. monticola* and 29 diploid wild species. Based on high degree of genetic isolation and the comparative cytology (Fernandez and Krapovickas 1994), Krapovickas and Gregory (1994) inferred that five sections, *Trierectoides*, *Erectotoides*, *Triseminatae*, *Extranervosae,* and *Heteranthae*, are primitive compared

to sections, *Procumbentes, Caulorhizae, Rhizomatosae,* and *Arachis,* except for section *Erectoides*. Sections *Rhizomatosae* and *Arachis* have evolved feature of shorter peg length, while sections *Caulorrhizae* and *Rhizomatosae* have new methods of vegetative propagation: stolons and rhizomes, respectively, and appear to be advanced. Besides, the annual character represents an adaptive advantage that permits the species to avoid droughts in the northeast Brazil (*Heteranthae*) and in the foot hills of the Andes, as well as the flooding of the Paraguay River watershed (*Arachis*). Additionally, section *Arachis* appears to be spreading to new territories invading the areas of other sections. Its species grow intermixed with populations of *Extranervosae* in the upper Paraguay basin and occupy common ground with section *Procumbentes* in the Gran Pantanal. They have reached the shores of La Plata and the southeastern coast of Brazil and grow from Yala in northwest Argentina to the Tocantins in northeast Brazil, besides worldwide adaptation of *A. hypogaea*. Cross-compatibility recorded between *A. paraguariensis* ssp. *paraguariensis,* the southernmost taxon in the section *Erectoides, A. rigonii,* the westernmost species in the section *Procumbentes,* and *A. duranensis*, one of the most western species of section *Arachis* (Gregory and Gregory 1979) and recently between some more species of these sections (Singh 1998; Mallikarjuna 2005; Mallikarjuna and Hoisington 2009) and *A. glabrata* of *Rhizomatoseae* (Mallikarjuna and Sastri 2002) corroborate the closeness and advance nature of these sections. Figure 2.1 illustrates the overall phylogenetic relationships between various sections.

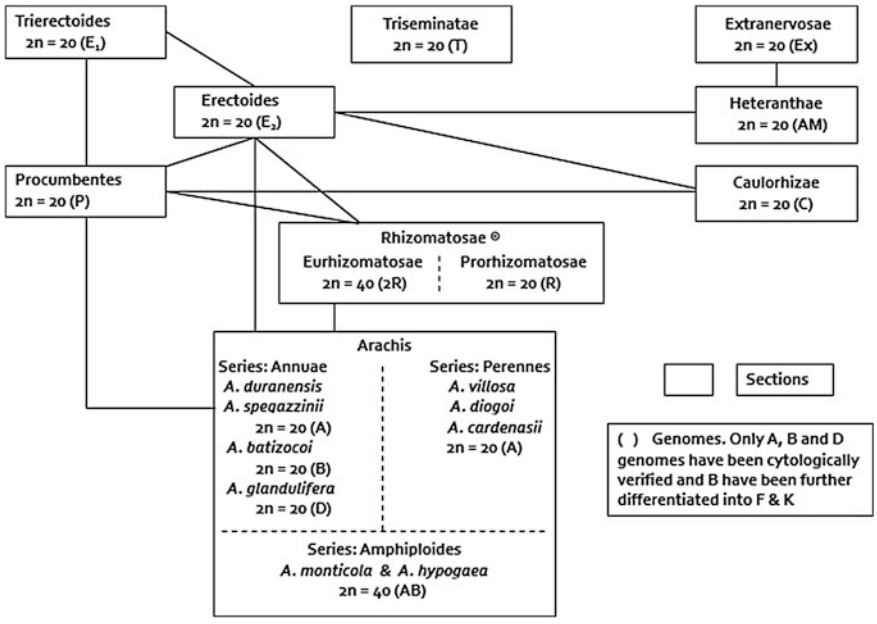

Fig. 2.1 The sections of genus *Arachis* with connecting lines displaying intersectional crossability. All species within a section are crossable, except *Eurhizomatosae* x *Prorhizomatosae*

Harlen and de Wet (1971) proposed the *gene pool* concept in order to provide a genetic perspective to relationship of cultivated plant species to other components of genetic diversity, the wild relatives, based on cross-compatibility into (1) primary gene pool (GP-1), (2) secondary gene pool (GP-2), and tertiary gene pool (GP-3). Application of this principle facilitates clearer understanding of phylogenetic relationships between the wild and cultivated species and helps to identify appropriate breeding strategies for incorporating desired genes into conventionally usable form of cultivated species for designing new cultivars. This helps to facilitate conventional cytogenetic manipulations to establish fertile hybrids, improve genetic recombination for incorporation of desirable genes into a usable form and hybridization using pre- or post-fertilization manipulations to establish hybrids. Alternatively, biotechnological approaches may be applied to access genes through sexual or parasexual means of genetic transformation. This approach has been used in groundnut classifying the genetic diversity into four gene pools (Smartt 1990; Singh and Simpson 1994):

1. The primary gene pool consists of landraces and traditional cultivars of groundnut from primary and secondary centers of genetic diversity in South America and other groundnut-growing countries and wild *A. monticola* found in northwest Argentina having free crossability with *A. hypogaea* producing normal segregants.
2. The secondary gene pool consists of diploid species from section *Arachis*, cross-compatible with *A. hypogaea*, despite ploidy differences, producing sterile to partially fertile hybrids.
3. The tertiary gene pool includes species of section *Procumbentes*, which have crossed with diploid species of section *Arachis* (Gregory and Gregory 1979; Mallikarjuna 2005; Mallikarjuna and Hoisington 2009) and probably coevolved with series *perennes* of section *Arachis*; *Erectoides,* whose species are weakly cross-compatible with diploid species of section *Arachis* and *A. hypogaea* (Singh 1998); and *Rhizomatosae*, whose tetraploid species can be crossed both with diploid species of section *Arachis* and *A. hypogaea* (Gregory and Gregory 1979; Mallikarjuna and Sastri 2002).
4. The quaternary gene pool of the remaining *Arachis* species that are cross-incompatible or very weakly cross-compatible to species of section *Arachis* and are classified into five other sections.

Based on heritable genetic variation observed in cultivated *A. hypogaea*, Krapovikas and Gregory (1994) divided it into the following two subspecies and six botanical varieties.

1. Subsp. *hypogaea*: Characterized by absence of flowers on main axis and regular alternation of vegetative and reproductive branches on the laterals and long life cycle.
2. Subsp. *fastigiata*: Characterized by presence of flowers on main axis and no specific order of vegetative and reproductive branches on the laterals and shorter life cycle.

Subsp. *hypogaea* is divided into two botanical varieties as follows:

i. Var. *hypogaea*: Characterized by leaflets with glabrous dorsal surface, short central or main axis, prostrate to erect growth habit, simple inflorescence, and 2–3 seeded pods.
ii. Var. *hirsuta*: Characterized by leaflets with entire dorsal surface hairy (1–2 mm), long central or main axis, prostrate growth habit, and 2–4 seeded pods.

Subsp. *fastigiata* is divided into four botanical varieties as follows:

i. Var. *fastigiata*: Characterized by leaflets with glabrous dorsal surface and hair only on the midrib, 3–5 seeded pods with smooth or lightly marked reticulation without highlighting the longitudinal ribs, reproductive branches mostly short and thin, little branched, curved branches, erect growth habit, and simple inflorescence.
ii. Var. *peruviana*: Characterized by leaflets with glabrous dorsal surface and hair only on the midrib, pods with very marked reticulation and with prominent longitudinal ribs and long and strong reproductive branches (5–10 cm) with strong central axis and lateral branches.
iii. Var. *aequatoriana*: Characterized by leaflets with entire dorsal surface hairy (1–2 mm), long reproductive branches, mainly the lateral branches, central axis mostly with short inflorescence and reproductive branches, deep pod reticulation, purple stems, more branched and erect growth habit.
iv. Var. *vulgaris*: Characterized by pods mostly 2-seeded, bunched fruits pointing to the base of the plant, erect growth habit, more branched and compound inflorescence.

Commercially, var. *hypogaea* is also known as Virginia type (large-seeded) or Runner type (small-seeded), var. *hirsuta* as Peruvian runner, var. *fastigiata* as Valencia type, and var. *vulgaris* as Spanish type.

Besides the variability of primary gene pool of cultivated *A. hypogaea*, the wild *Arachis* species have attracted groundnut workers because of their resistance to diseases and insect pests for which the genetic variation in primary gene pool is limited. The most accessible variability of primary and secondary gene pools have been successfully utilized in groundnut improvement and their potential value is now much more predictable and productive. The exploitation of tertiary and quaternary gene pools waits for advancement in the biotechnological techniques and policy decision with regard to release of transgenic varieties at global level.

2.3 Extent of Distribution, Center of Origin, and Genetic Diversity

The genus *Arachis* is naturally distributed in east of the Andes, south of Amazon, north of La Plata from northwest Argentina to northeast Brazil, including Argentina, Bolivia, Brazil, Paraguay, and Uruguay, i.e., from the mouth of the Amazon (0°) to south across the Sao Francisco and the Jequitinhonha, and into the mild temperate zone to 34° S on the shores of the South Atlantic in the southern Uruguay (Fig. 2.2). *Arachis* species grow from sea level to 650 m above mean sea level (amsl) on the Planalto, from southern Mato Grosso to southern Goias, to

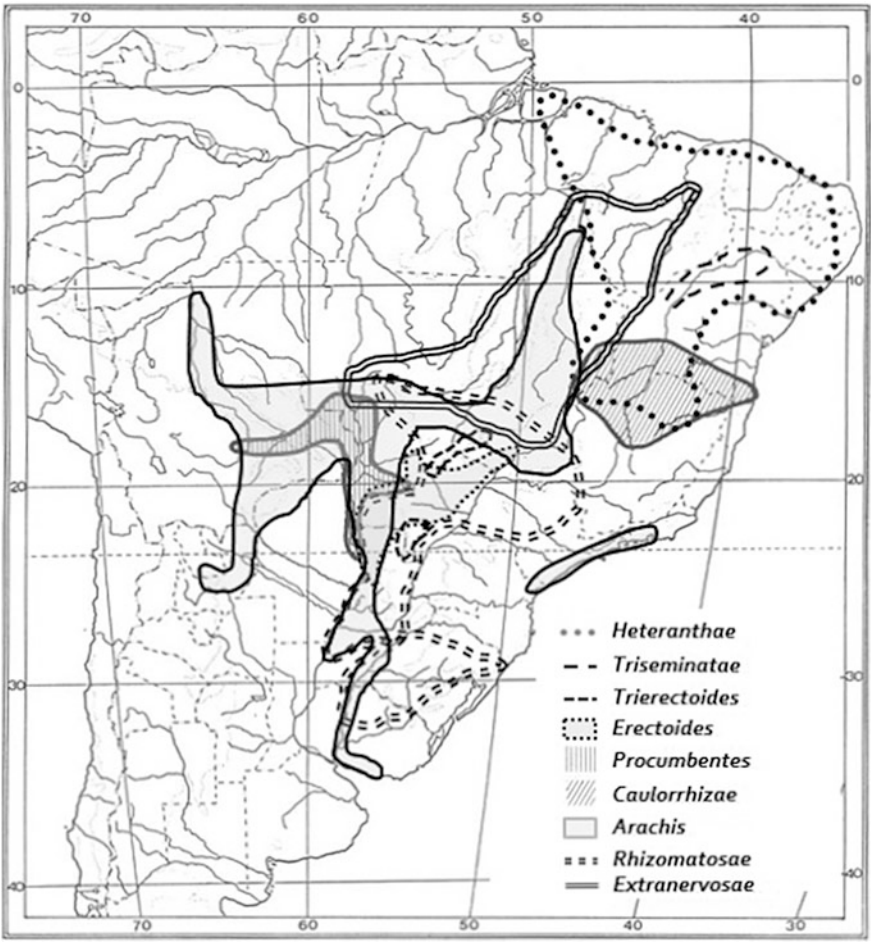

Fig. 2.2 Distribution and extent of various sections of genus *Arachis* in South America (based on Krapovickas and Gregory 1994/2007)

1450 m near Jujuy. They are found mixed in the vegetation of mixed forest to open grassland. The species may grow submerged, among stones bathed with water, in dry gravel and in flood plain alluvium. For these reasons *Arachis* species are found from semiarid region to the tropical locations receiving an average rainfall more than 2000 mm and subjected either to intense drought or flooding. Adaptation of wild *Arachis* species to such diverse conditions has resulted in generation of great genetic variability and resilience to grow under diverse and adverse conditions. This probably led to the development of geocarpy and tuberiform roots to overcome the harshness of dry conditions and to escape the seasonal fires. However, in cultivated groundnut (*A. hypogaea*), selection pressure against the tubiriform roots led to elimination of this trait, but the geocarpy providing protection to fruits from adverse external environment, ensuring regeneration was retained.

Krapovickas and Gregory (1994) considered that the genus *Arachis* originated in the Sierra de Amambay, on the border between Mato Grosso do Sul (Brazil) and Paraguay, where grew, possibly, the oldest species of the genus, *A. guaranitica* (Gregory et al. 1980). It has been difficult to understand how the genus could have dispersed to some 4000 km, both toward northeast up to Amazon as well as to the west, up to the Andes. Fluvial system associated with rivers, streams and the deposits, and landforms created by them must have played an important role in dispersal, as many species have distribution associated with the watershed of the great Paraguay, Uruguay, and Parana or Sao Francisco rivers. The species generally live near watercourse, in places where the water evidently reaches only during the higher floods. The geocarpic habit also indicates possible support to long distance dispersal of species through the rivers and streams. For this reason, Gregory et al. (1973, 1980) postulated that most ancient species were found in higher elevations, their immediate descendants occupied the next lower eroded surfaces, while the distantly evolved species occupied still lower and more recently eroded surfaces. Further, as seeds moved to lower elevations, they became isolated in major river valleys; thus probably different sections of the genus evolved independently in parallel fashion. This perception, however, is changing with record of overlapped distribution of species belonging to some sections. Dispersion of species has also occurred by animal and human movement (Singh et al. 2004).

Based on Krapovickas and Gregory (1994), Fig. 2.2 presents the extent and distribution of genus *Arachis* and its various sections in South America. Section *Trierectoides* lives in the highest places of the divide between the watersheds of the Paraguay and Parana rivers, 400–700 m amsl. The northern limits are found in Jatai, in Goias at 700 m amsl between the Araguaia and Paranaiba rivers. Section *Erectoides* is characteristic of the 'cerrado' with red soil, which surrounds the Mato Grosso Pantanal and is nearly exclusive to Mato Grosso do Sul, with some species going beyond and others extending into Paraguay. The other group of this section lives in the southwest extreme of the section's range. All species of section *Extranervosae* live in state of Goias, Tocantins, the central part of Mato Grosso, and the northern part of the Mining Triangle in Minas Gerais. A few extend beyond these limits. *A. villosulicarpa*, the other cultivated species of genus, is grown by the indigenous people of west central Mato grosso. The majority of the species in this

section grow on a very special soil type, frequently encountered in the "cerrado", constituted by a thin layer of soil over a stony substrate. The lone member of *Triseminatae* grows in the state of Bahia, in the south of Pernambuco, in the north of Minas Gerais, and in the vicinity of the São Francisco River. Section *Heteranthae* is a typical of northeastern region of Brazil. Section *Caulorrhizae* grows in the border area between the Brazilian states of Goiás, Bahia, and Minas Gerais, reaching as far as the Atlantic coast, where the type specimen of *A. pintoi* was collected. Section *Procumentes* extends itself along the Paraguay River from Concepción on the Tropic of Capricorn, toward the north, flanking the Pantanal in Mato Grosso on the south and the north, and then expands westward as far as Santa Cruz de la Sierra, in Bolivia, living in soils that are periodically flooded. Section *Rhizomatosae's* tetraploid species occupy a central position within the overall range of the genus *Arachis* and the diploid *A. burkartii* growing more to the south. Section *Arachis* is distributed along an axis that coincides more or less with the 57th and 58th meridians, that encompasses the watersheds of the Paraguay and Uruguay rivers and ends at the La Plata River. It is the most widely distributed section invading/overlapping the areas of other sections. The perennial species of section are found along water house and some are adapted to flooding. Further, two arms of section extend toward the north and correspond to the basin of the Tocantins River to the east and to the Mamoré and Guaporé River system to the west, between Trinidad and Guayaramerín, in Bolivia (Fig. 2.2). In these two expansions, the species encountered are annuals, adapted to prolonged inundation. *A. stenosperma*, an annual growing on the sands of the Atlantic coast, isolated at the eastern extreme, evidently was carried by the humans (Singh et al. 2004). Expansion of section toward the southwest is constituted by annual species, adapted to conditions of periodic drought. They extend from the dry "chaco" up to the first foothills of the Andes: *A. batizocoi* (300–950 m amsl) and *A. duranensis* (250–1250 m amsl) together with *A. monticola* (1350–1560 m amsl) grow at the highest elevations.

Highest numbers of species representing eight sections of *Arachis* are reported from Brazil, of which four are nearly endemic. Bolivia has the second largest number of species followed by Paraguay, Argentina, and Uruguay. Most species occurring in Brazil are confined to the west central region, with a group of species endemic to the semiarid region of northeast. Further differentiation in patterns of genetic variability in different sections occurred as a result of their adaptation to different ecological niche, where they were caught with a series of land uplifts during their movement downstream in the associated drainage systems. Genetic isolation among the species of section *Arachis* is not that strongly marked as among the species of other sections.

Regarding the origin of cultivated groundnut, *A. hypogaea*, Krapovickas (1969) proposed southern Bolivia and northwestern Argentina, which is the range of the diploid species considered to be involved in its origin. As per Hammons (1994), it probably first occurred in the valleys of the Parana and Paraguay River systems in the Gran Chaco area. Krapovickas (1969) suggested the eastern foothills of the Andes for domestication, based on wide range of ecological diversity and uses of groundnut. This area is also an important center of diversity of primitive

subsp. *hypogaea*. Archeological evidence suggests that groundnut has been in cultivation for over 3500 years. Early European explorers found local Indians cultivating groundnut in many islands in the Antilles, on the northeast coasts of Brazil, in all the warm regions of the Rio de la Plata basin, extensively in Peru and sparsely in Mexico.

Of the two subspecies of *A. hypogaea*, the primitive subsp. *hypogaea* has its most important center of variation in Bolivia. In southeast Bolivia, on the first foothills of the Andes in the departments of Tarija and Chuquisaca, samples of cultivated groundnut with the greatest amount of primitive characters have been collected. *A. hypogaea* subsp. *hypogaea* var. *hirsuta* Köhler was found in the archeological deposits from the coast of Peru. *A. hypogaea* subsp. *fastigiata* var. *fastigiata* (Valencia types) has its most important center of variation in Paraguay and is the most widespread variety in all of South America. *A. hypogaea* subsp. *fastigiata* var. *peruviana* is grown in almost all of Peru, especially in the basin of the Marañón River, and is common in Ecuador. Its southern limit is found in northern Bolivia, where a few samples were found in Rurrenabaque on the Beni River and in the department of Pando. A few samples were also obtained in Acre state of Brazil. *A. hypogaea* subsp. *fastigiata* var. *aequatoriana* is nearly confined to Ecuador, primarily cultivated in the provinces of El Oro and Loja. It is also cultivated sporadically in northern Peru. *A. hypogaea* subsp. *fastigiata* var. *vulgaris* (Spanish types) is grown in South America in Uruguay, in Argentina (Santa Fe, Entre Ríos and Corrientes), in southern Brazil and to some extent, in Paraguay. Based on above occurrence, Krapovickas (1969) recognized five and Gregory and Gregory (1976) six centers of genetic diversity, while recent explorations added Ecuador as the seventh center with distinct group of landraces referred as var. *aequatoriana* (Singh and Nigam 1997). These centers (Fig. 2.3) are given below:

1. The eastern foothills of the Andes in Bolivia
2. The Guarani region
3. Goias and Minas Gerais (Brazil)
4. Rondonia and northwest Mato Grosso (Brazil)
5. Peru
6. Northeastern Brazil
7. Ecuador

These centers of diversity present a very high level of genetic variation due to natural introgressive hybridization between divergent types, followed by human selection resulting in production of typical hybrid swarms. The first center (eastern foothills of the Andes in Bolivia) is a center of diversity of subsp. *hypogaea* var. *hypogaea* with few landraces of var. *fastigiata*. In Bolivia, there are indications of introgression between the two subspecies, and 'Overo' and 'Cruceno' types of groundnut are probably the product of such introgression (Krapovickas 1969; Gregory and Gregory 1976). The second center of diversity is the Guarani region, dominated by the erect subsp. *fastigiata* (Valencia types) with rare occurrence of subsp. *hypogaea* and with little evidence of introgression between the two

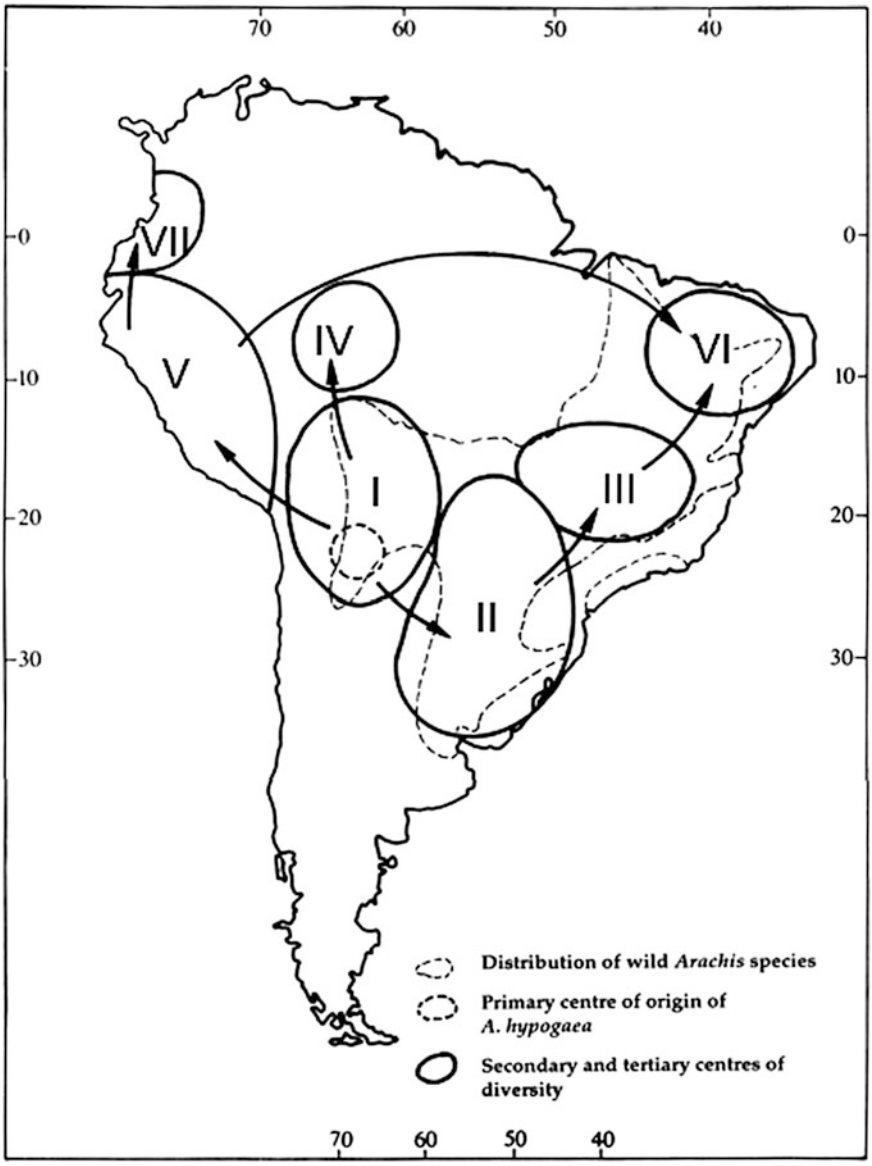

Fig. 2.3 Centers of origin and diversity of *Arachis hypogaea* in South America, I. The eastern foothills of Andes in Bolivia; II. The Guarani region; III. Goias and Minas Gerais; IV. Rondonia and northwest Mato Grosso; V. Peru; VI. Northeastern Brazil and VII. Ecuador

subspecies. However, hybrid swarms of intermediate landraces between the two botanical varieties of subsp. *fastigiata, fastigiata* and *vulgaris*, do exist, consequently both var. *fastigiata* (Valencia), Porto Alegre and var. *vulgaris* (Spanish)

Negrito are identified. It is possible that spread of Valencia types to other parts of the world might have occurred from Paruguay or central Brazil, but more likely point of embarkation is from the northeast coasts. The Guarani region is also center of diversity for var. *vulgaris*, the Spanish types, which probably were disseminated from this region (Krapovickas 1969; Gregory and Gregory 1976). The third center of genetic diversity, Goias and Minas Gerais, has distinct varietal pattern from the Guarani, but is still dominated by erect subsp. *fastigiata* (Valencia types), with very few representative of subsp. *hypogaea*. Landraces of botanical varieties, *fastigiata* and *vulgaris*, are found without much indication of introgression. Rondonia, in the fourth center of diversity represents the nambyquarae types of subsp. *hypogaea*.

The fifth center of diversity, Peru, is represented by the collection of three distinct types. One type includes like the one found in pre-Columbian tombs, with fruits having prominent constriction, veins, and beak and belongs to subsp. *hypogaea*, referred as Chinese type in USA and another with similar fruit characteristics, but belonging to subsp. *fastigiata* var. *fastigiata*. The two together have been referred as 'peruvian' type by Dubard (1906). And a third type with smooth pods, three to five seeds per pod and almost no beak, belonging to subsp. *fastigiata* var. *fastigiata* has also been collected. The sixth center, the northeast of Brazil, is regarded as the tertiary center of diversity (Krapovickas 1969; Gregory and Gregory 1976) with almost all botanical types. Seventh center, Ecuador, represents types similar to var. *fastigiata* from Peru, but morphologically distinct and might even be considered as intermediate between vars. *fastigiata* and *hypogaea*. Williams (1991) studied the region of the north Beni of Bolivia/Peru and collected some more extraordinary types, appearing to be intermediate between subsp. *fastigiata* and subsp. *hypogaea.*

The global dispersal of cultivated groundnut occurred in early 1500, at least in two distinct forms—a two-seeded Brazilian and three-seeded Peruvian types dispersed soon after the discovery of New World (Dubard 1906). Many authorities believe that the Portuguese carried two-seeded varieties from Brazil to Africa, to the Malabar Coast of southwestern India and possibly to the Far East. The Peruvian type (*A. hypogaea* var. *hirsuta*) went to the Western Pacific, to China, to Indonesia (Java), and to Madagascar. Their most plausible path was up the west coast from Peru to Mexico, thence across the Pacific as an item of trade between Acapulco and Manila. Gibbons et al. (1972) recorded cultivar clusters of subsp. *fastigiata* var. *vulgaris* representing both the Guariani region and the region of the eastern slopes of Andes in Bolivia and parts of western Brazil in Africa. In Africa and Asia, groundnut readapted to environment and specialized agricultural production systems. Africa received groundnut from Brazil in West Africa and probably from west coast of South America in the east coast through Philippines, China, and India and became important center of diversity. The Spanish type of groundnut was introduced into Europe from South America (Krapovickas 1969). Higgins (1951) speculated that variety *hypogaea* was introduced to the southeastern United States from Europe, while Simpson et al. (2001) suggested that cultivated peanut traveled in slave ships from Africa into the southeastern United States, Central America, and

northeast South America, thus returning as modified germplasm. By the nineteenth century, groundnut became an important food crop in West Africa, Southeast and South Asia, and USA, generating rich genetic diversity.

2.4 Collection, Conservation, and Ensuring Availability of Genetic Resources

Exploration for collecting seeds and living plants of cultivated groundnut varieties and wild *Arachis* species started in mid-twentieth century by USDA and CSIRO scientists. The first exploration dedicated to collection of germplasm was conducted in Argentina in 1945 with the initiation of plant breeding program at the Manfredi Agricultural Experiment Station (Cordoba) and with the organization of the Department of Plant Exploration and Introduction (DEIP) of the Ministerio de Agricultura de la Nación, under the direction of E. C. Clos. Since then to early 70s, extensive explorations were made by Krapovickas (CONICET) and Gregory (USDA) collecting live specimens of wild species and samples of cultivated groundnuts. It was followed with introductions of these collections to other parts of the world. Banks (1976) emphasized the need to make additional collections of the cultivated groundnut and the wild species before destruction of their habitats. Consequent to the support of the International Board for Plant Genetic Resources (IBPGR), FAO, and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), 17 expeditions were undertaken between 1976 and 1983 to the centers of origin and diversity of *Arachis* in South America, surveying almost entire area of distribution of the genus (Valls et al. 1985). These efforts continued, enriching the available genetic diversity/collections, till the time of enforcement of Convention on Biological Diversity (CBD), which provided ownership to the nations of their biological resources and made them responsible for their maintenance and conservation, to facilitate their use. Each expedition provided additional locations of both wild and cultivated groundnut, as a result the map of natural resources for different sections was greatly modified from the earlier one presented by Gregory et al. (1980). Additionally, cultivated groundnut accessions were collected from groundnut-growing areas of various countries, included landraces, farmers'/traditional varieties, material developed by the breeders and/or released varieties, and the genetic stocks identified with special features or sources of resistance to biotic and abiotic stresses, representing different botanical varieties and cultivar groups. Groundnut germplasm is conserved as pods or seeds, except for wild *Arachis* species belonging to section *Rhizomatosae*, which rarely produce seed and if produced, progenies are highly heterogeneous and therefore are conserved as live plants under controlled conditions providing an environment close to their habitat. Globally, several repositories have facilities for processing and ex situ conservation/storage of seeds, facilitating prolonged shelf life.

Short-term chambers: These are maintained at 20 ± 5 °C and relative humidity (RH) 35–45 %. Pods/seeds in these chambers remain viable for several years without much loss of viability.

Medium-term chambers: These are prefabricated modules maintaining temperature between 4 to 10 °C and RH between 30 to 40 %. The seeds are dried to 8–10 % moisture level and kept in moisture-proof containers. The seeds remain viable for 25–35 years without much loss of viability.

Long-term chambers: These are also prefabricated modules maintaining temperature around minus 18 °C and host around 1000–1500 seeds of each accession. The seeds are dried to a moisture level of 4–5 %, hermetically sealed in vacuum sealed aluminum pouches, and transferred to the chambers.

The major repositories of the world groundnut germplasm collections are at ICRISAT, India; in the USA at Southern Regional Plant Introduction in Georgia, at North Carolina State University, Raleigh, and at Texas Agricultural Experiment Station, Stephenville; in Brazil at Empressa Brasileria De Pesquisa Agropecuaria (EMBRAPA)/Centro Nacional de Recursos Geneticos (CENARGEN), Brasilia and Instituto Agronomico, Campinas; and in Argentina at Instituto Botanica del Nordeste (IBONE), Corrientes and Instituto Nacional de Technologia Agropecuaria (INTA), Manfredi. The germplasm collections include both cultivated and wild *Arachis* species accessions. ICRISAT maintains over 14,966 from 91 countries, while USDA and NBPGR (India), 9225 and 13,337 accessions, respectively, and provide basic genetic stocks to the international and national scientific community. Table 2.1 presents the germplasm status at some of the major repositories. The low seed multiplication rate and large seed size of groundnut are the major concerns in germpasm multiplication and storage.

Despite assembly of large collections, the use of germplasm accessions in groundnut improvement has remained limited, keeping the genetic base of most groundnut cultivars narrow and vulnerable to biotic and abiotic stresses and natural vagaries. Initially, this was circumvented by ensuring the availability and supply of global genetic resources. For example, ICRISAT since 1980 distributed 38,362 accessions to Indian researchers, leading to increased use of exotic germplasm in national breeding programs. Consequently, during 1985–1995, 46 % of new groundnut variety proposals in All India Coordinated Research Project on Oilseeds had exotic germplasm in their parentage, accruing an increase in national production from 794 kg in 1980 to 988 kg in 1994, about 1.4 % per annum (Singh and Nigam 1996). At the same time to improve information on agronomic and economic traits of each accession that requires extensive evaluation and for manageable quantification of genetic diversity, core collection concept advocated by Brown (1989) was applied, leading to creation of a set of 10 % of total collections retaining most variability of the entire collections. It was hoped that it would facilitate easier access to genetic resources, enhance their use in crop improvement and also simplify their management in genebank. Initially, core collections were developed by stratifying germplasm accessions by country of origin and botanical varieties, followed by the use of data on quantitative morphological traits for principal component/multivariate analysis and clustering, and randomly selecting 10 % of

Table 2.1 Groundnut germplasm holding at some important repositories

Repository	Number of accessions conserved		Additional information
	Primary gene pool	Other gene pools	
ICRISAT, India[a]	Var. *hypogaea* 6838 + *vulgaris* 5493 + *fastigiata* 2351 + *aequitoriana* 14 + *peruviana* 251 + *hirsuta* 19 = **14966**	Representing Section, *Arachis, Rhizomatosae, Extranervosae, Erectoides, Procumbentes Caulorhizae, Triseminatae* = **453**	Representing 91 countries
GRIN and USA[b]	*A. hypogaea* 6804 + ssp. *fastigiata* 361 + ssp. *hypogaea* 141 + var. *aequatoriana* 62 + var. *fastigiata* 1149 + var. *peruviana* 24 + var. *vulgaris* 128 + var. *hirsuta* 29 + var. *hypogaea* 527 = **9225**	Representing Section, *Arachis, Rhizomatosae, Procumbentes, Heteranthae, Extranervosae, Erectoides, Trierectoides, Triseminatae* = **641**	Texas A&M, Experiment Station, Stephenville, maintains 1200 acc. of 70 wild species, 400 hybrids and two mapping populations, while North Carolina State University, USA 740 acc. of primary and 406 of other gene pools
NBPGR, Delhi and DGR, Junagadh, India (*personal communication*)	**13337** at NBPGR, and var. *hypogaea* 2386 + ssp. *fastigiata* 4458 + others 2280 = **9129** at DGR Junagadh, India	Representing *Arachis, Caulorhizae, Heteranthae, Rhizomatosae, Procumbentes, Erectoides* = **112**, **105** respectively	Represent 90 and 84 countries respectively, NBPGR maintains duplicates of ICRISAT accession of Indian origin
Oil Crops Research Institute, Chinese Academy of Agricultural Sciences, and Crops Research Institute, Guaeglong Academy of Agricultural Sciences, China[c]	**7837** + **4210**	**246**	Core of 576 and mini-core of 298
CENARGEN, Brazil and Instituto Agronomicas Campinas, Brazil[c]	**1200** + **2140**	Representing Section, *Arachis, Caulorhizae, Rhizomatosae, Extranervosae, Erectoides, Triseminatae* **= 1220**	
INTA, Manfredi and IBONE, Argentina[c]	**3534**	**106** + **472**	

Source
[a]//ICRISAT// Groundnut Crop: www.icrisat.org/crop-groundnut-genebank.htm
[b]www.ars-grin.gov/npgs/cgc_reports/Status11.pdf
[c]Pandey et al. (2012)

collections to constitute a core collection. Using this methodology, first core collection of 831 accessions was developed on US germplasm collection of 7,432 by Holbrook et al. (1993); followed by the development of a core collection of 1,704 accessions on 14,310 world collections assembled at ICRISAT (Upadhyaya et al. 2003); a core collection of 576 from a collection of 6,390 accessions in China (Jiang et al. 2007) and another core collection of 576 accessions, and a mini-core collection of 298 accessions from a collection of 6,839 conserved at the Oil Crops Research Institute of Chinese Academy of Agricultural Sciences at Wuhan (Jiang et al. 2013). Using statistical methods it was ensured that these core collections retained the diversity index and phenotypic correlation of different traits to that of the entire collections so that they represented most spectrum of variability and were effective in the genetic improvement of groundnut. These core collections were further evaluated in multilocations for identification of regional core (Upadhyaya et al. 2005), development of mini-cores (Upadhyaya et al. 2002a), for identification of variability for specific traits (Upadhyaya et al. 2006; Jiang et al. 2013); characterizing the core collections using specific molecular markers to enable better quantification of genetic variability (Kottapalli et al. 2007), and identifying accessions with specific trait/resistance associated with molecular markers (Chamberlin et al. 2010). These efforts have been extended to characterization of diversity using association mapping for exploring the molecular basis of phenotypic variations, demonstrating a great potential of integrating the association analysis and marker-assisted breeding by utilizing the mini-core collection (Ren et al. 2014). Attempts are also made to purify the accessions of mini-core and register them on the basis of morphological, biochemical, and resistance traits (Chen et al. 2013a). Comparison of core collections developed in different parts of the world showed different traits contributing to variability in different set of collections, associated to the dominance of subspecies and botanical varieties in a collection and selection pressure (Jiang et al. 2008), indicating want of a universal core collection for groundnut improvement meeting everyone needs. Most cores are proportionally limited in variability from vars. *hirsuta, peruviana,* and *aequatoriana*.

2.5 Major Constraints to Groundnut Production

Groundnut suffers from several biotic and abiotic production constraints. Some of them are global in nature; and others are either regional or local.

Biotic constraints: Among the foliar fungal diseases, early leaf spot (ELS; *Cercospora arachidicola* Hori.), late leaf spot [LLS; *Phaeoisariopsis personata* (Berk.&M.A. Curtis) Van Arx], and rust (*Puccinia arachidis* Spegazzini) are wide spread and are prevalent wherever groundnut is grown. Other foliar fungal diseases, which could be important in certain regions/countries, include web blotch (*Phoma arachidicola* Marasas, Pauer & Boerema) and pepper spot and leaf scorch [*Leptosphaerulina crassiasca* (sechet) Jackson &Bell]. Among the seed and seedling fungal diseases, preemergence seed and seedling rots [*Aspergillus flavus*

Link ex Fries, *A. niger* van Tieghem, *Macrophomina phaseolina* (Tassi) Goidanich, *Sclerotium rolfsii* Saccardo, *Rhizoctonia solani* Kühn, *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl., *Rhizopus* spp., *Penicillium* spp., *Phythium* spp., and *Fusarium* spp.], Aspergillus crown rot/ collar rot (*A. niger* van Tieghem), yellow mold (*A. flavus* Link ex Fries), and Rhizoctonia damping off (*Rhizoctonia solani* Kühn) are wide spread. Important stem, root, and pod diseases caused by fungi include stem and pod rots (*Sclerotium rolfsii* Saccardo), Sclerotinia blight [*Sclerotinia sclerotiorum* (Lib.) de Bary], Cylindrocladium black rot [CBR; *Cylindrocladium crotalariae* (Loos) Bell & Sobers], Botrytis blight (*Botrytis cinerea* Pers. Ex Fries), Fusarium wilt (*Fusarium oxysporum* Schlechtend. Emend Snyder & Hans.), charcoal rot [*Macrophomina phaseolina* (Tassi) Goidanich], and pod rot [*Pythium myriotylum* Dreschler, *Rhizoctonia solani* Kühn, *Fusarium solani* (Mart.) Saccardo f. sp phaseoli (Burkholder) Snyder & Hans., *Fusarium oxysporum* Schlechtend. Emend Snyder & Hans., and *Macrophomina phaseolina* (Tassi) Goidanich] are important. The groundnut pod and kernels can also get infected while developing with *A. flavus* Link ex Fries*/A. parasiticus* Speare leading to their contamination by aflatoxin. The only bacterial disease of significance is bacterial wilt [BW; *Ralstonia solanacearum* (E.F. Smith)], which is wide spread in East and Southeast Asia.

Significant virus diseases include peanut stripe (PStV; *Peanut stripe virus*) in East and Southeast Asia, peanut clump (PCV; *Peanut clump virus*) in West Africa, peanut bud necrosis (PBND; *Peanut bud necrosis virus*) in South Asia, tomato spotted wilt (TSWV; *Tomato spotted wilt virus*) in North America, peanut stem necrosis (PSND; *Tobacco streak virus*) in South India, and groundnut rosette disease (GRD; a complex of *groundnut rosette virus*, *groundnut rosette assistor virus,* and a satellite RNA) in Africa. Important diseases caused by nematodes are root knot [*Meloidogyne arenaria* (Neal) Chitwood, *M. hapla* Chitwood, *M. javanica,* and *M. incognita*; the first two are wide spread], root lesion [*Pratylenchus brachyurus* (Godfrey) Filipjev & Sch. Stekh.], and Kalahasti malady (*Tylenchorhynchus brevilineatus* Williams) in Andhra Pradesh in India.

Defoliators, tobacco caterpillar/tobacco armyworm (*Spodoptera litura* Fab.), hairy caterpillars (*Amsacta albistriga* Walk., *A. moori* Butler), Bihar hairy caterpillar [*Spilosoma* (*Diacrisia*) *oblique* (Walk.)], gram pod borer (*Helicoverpa armigera* Hübner) and groundnut leaf miner (*Aproaerema modicella* Deventer), sucking pests, aphids (*Aphis craccivora* Koch.), thrips (*Scirtothrips dorsalis* Hood., *Thrips palmi* Karny., *Frankliniella schultzei* Trybom) and *Caliothrips indicus* Bagnall and jassids/leaf hopper (*Empoasca kerri* Pruthi), root and pod feeders, white grub [*Lachnosterna* (= *Holotrichia*) *consanguinea* Blanch.] and *L. serrata* (Fab.), termites/white ants (*Microtermes* spp. and *Odontotermes* spp.) and earwig (*Anisolabis stali* Dohrn) and storage pests groundnut, bruchid (*Caryedon serratus* Oliver), and red flour beetle (*Tribolium castaneum* Herbst) are the major insect pests of groundnut.

Abiotic constraints: As a majority of groundnut is grown under rainfed conditions, drought is the most significant abiotic stress affecting groundnut production. Drought can occur at any stage—early-season, mid-season, end-of-season, and intermittent. Drought also predisposes groundnut pods to aflatoxin contamination

by *A. flavus*. Other abiotic constraints include low soil fertility, salinity, iron chlorosis, aluminum toxicity, cold temperature at germination, and high temperature at podding and harvest.

2.6 Searching Potential Genetic Resources and Managing Constraints with Genetic Improvement

For assessment of genetic variability and identification of genetic resources with desired features, the groundnut germplasm assembled at various places have been characterized and evaluated based on the common groundnut descriptors developed by IBPGR/ICRISAT (1992). Variability analysis has shown greater variation in landraces and in the accessions collected from the primary and secondary centers of diversity in South America, particularly for resistance to biotic and abiotic stresses and agronomic features like seed mass (Singh and Simpson 1994). An assessment of genetic diversity on world collection at ICRISAT for 16 morphological and 10 agronomic traits has shown vast diversity in size and shape of pods and seeds. Principal Component analysis using 38 traits and clustering on first seven PC scores produced three clusters; consisting North America, middle East, and East Asia in the first cluster, South America in the second cluster, and West Africa, Europe, Central Africa, South Asia, Oceania, Southern Africa, Eastern Africa, Southeast Asia, Central America, and Caribbean in the third cluster. The means for different agronomic traits differed significantly among regions, while the variances for all the traits among regions were heterogeneous. South America cluster showed 100 percent range variation for 12 of the 16 morphological traits and revealed highest range of variation. Assessment of phenotypic diversity in core collection revealed significant variation. The average phenotypic diversity index was higher in the *fastigiata* group (0.146) than the *hypogaea* group (0.141). The *hypogaea* group showed significantly greater mean pod length, pod width, seed length, seed width, yield per plant, and 100-seed weight than the *fastigiata* group in both rainy and postrainy seasons whereas it was opposite for plant height, leaflet length, leaflet width, and shelling percentage with *fastigiata* group showing significantly greater means. Principal coordinate and principal component analyses showed that 12 morphological descriptors and 15 agronomic traits were important in explaining multivariate polymorphism. Leaflet shape and surface, color of standard petal markings, seed color pattern, seed width, and protein content did not significantly account for variation in the first five principal coordinates or components of *fastigiata* and *hypogaea* types, indicating their relatively low importance. The average phenotypic diversity index was similar in both subspecies. The Shannon–Weaver diversity index varied among traits between the two and the diversity within a subspecies/group depended upon the season and traits recorded. Molecular profiling of joint composite collection developed by ICRISAT and EMBRAPA, using 21 SSRs showed rich allelic diversity, group-specific unique alleles, and common

alleles sharing between subspecies and geographical groups. Gene diversity ranged from 0.559–0.926, with an average of 0.819. Group-specific unique alleles were 101 in wild *Arachis*, 50 in subsp. *fastigiata*, and only 11 in subsp. *hypogaea*. Accessions from Americas revealed the highest number of unique alleles (109), while Africa and Asia had only six and nine, respectively. The two subsp. *hypogaea* and *fastigiata* shared 70 alleles. In contrast, the wild *Arachis* shared only 15 alleles with *hypogaea* and 32 alleles with *fastigiata* (//ICRISAT// Groundnut Crop: www.icrisat.org/crop-groundnut-genebank.htm). Greater genetic diversity among the landraces originating from primary and secondary centers of diversity in South America is corroborated by the molecular characterization using various markers, for example, in Bolivian landraces (Husain and Mallikarjuna 2012).

For many traits, the primary gene pool has been found limited, but the wild *Arachis* species have been found with desired variability; for example, for PStV no resistant line was found in cultivated groundnut despite screening of 9,000 accessions, but several accessions of wild *Arachis* showed negative reaction (Culver et al. 1987; Prasada Rao et al. 1991). Often wild *Arachis* species have shown higher level of resistance than primary gene pool. Variability observed among the accessions of wild species for their reaction against specific constraints (Singh et al. 1996) demands thorough investigation for useful exploitation. Table 2.2 presents the number of accessions identified with useful diversity and used in breeding programs, and Table 2.3 lists representative wild species with multiple resistances.

2.6.1 Genetic Improvement Using Resources of Primary Gene Pool Through Conventional Breeding

Groundnut is a highly self-pollinated crop, though cross-pollination can reach as high as 10 % at locations and in seasons, where bee activity is high. Standard breeding methods, followed in groundnut for developing a cultivar, can be placed into two groups—(a) methods without hybridization, and (b) methods after hybridization. The former includes introduction, pure line/ mass selection and mutation breeding and the latter bulk selection, pedigree selection, bulk pedigree selection, single seed descent method, backcross method, and recurrent selection. Among these, pedigree and bulk selection methods are more commonly used by the breeders. Some breeders use a combination of breeding methods or make modification to conventional methods.

Examples of release of cultivars following introduction and selection include, among others, release of JL 24 in India, release of Indian cultivars, TMV 2 and JL 24, under different names in many countries in Southeast Asia and Africa, release of Makulu Red, Apollo, Egret, Chalimbana, Mani Pintar, and Malimba in Africa, and New Mexico Valencia C in the USA. Mutation breeding uses X-rays, gamma rays, and various chemicals to create mutations breaking specific linkages and enhancing variation for specific character in a genotype. Bhabha Atomic Research Centre

Table 2.2 Primary Gene Pool Genetic diversity for useful traits in world collections at ICRISAT

Stress/trait	Acc. screened	Acc. with desirable variability	Additional information
Fungal and bacterial diseases			
Early leaf spot	7000	37 (2)	15 (India) + 4 (Malawi) + 18 (West Africa)
Late leaf spot	13000	69 (26)	
Rust	13000	169 (35)	
Aflatoxin production	582	4	
Aflatoxin seed invasion	580	39 (4)	
Pod and stem rot	3222	24/9 (6)	4 (India) + 5 (USA)
Bacterial wilt		24	Screening in Indonesia and China
Viral diseases			
PBNV	7400	23	
PMV	6944	2	Promise in wild *Arachis* spp.
Insect pest			
Thrips	5345	15 (7)	Promise in wild *Arachis* spp.
Jassids	136	30/6 (7)	
Termites	520	20/9 (6)	
Leaf minor	600	18/4 (6)	
Aphids	300	4 (1)	
Abiotic stress			
Drought	820	46 (8)	
N fixation	342	4 (2)	
Nutritional traits			
High oil content	8868	20/44 (10)	
High protein content	8868	117/51	

Source Singh and Nigam (1997), Singh et al. (1997) Figure in parenthesis indicate number of commonly used source in breeding program

(BARC), Mumbai, India used gamma rays to create desired variation for further use in conjunction with other breeding methods and released 15 groundnut cultivars till date. Some of these are TG #s 19, 37A, 38B and 51, TAG 24, TGB 39, TPG 41, TLG 45.

Hybridization provides opportunity to combine genes from different parents and recombine them in a single genotype via single cross, three-way cross, four-way cross, convergent cross, diallel mating, and diallel selective mating. Selection is practiced in segregating generations following the method of selection of choice. Generally, this process takes 12–15 years, but can be expedited by taking multiple crops in a year under controlled greenhouse conditions or raising off-season nursery at other locations where environmental conditions are favorable to raise a crop.

Table 2.3 Representative desirable genetic diversity in secondary, tertiary, and quaternary gene pool of *Arachis*

Species/gene pool[a]	Early leafspot	Late leafspot	Rust	PStV[b]	GRD[c]	Thrips	Leaf hopper	Lepidoptera
Secondary gene pool (Sect. *Arachis*)								
A. diogoi	R	R			R			
A. duranensis	MR	–	I	I	–	S	I	HR
A. spegazzini	MR	_	I	R	–	R	HR	HR
A stenosperma	HR	HR	HR	–	R	HR	HR	HR
A. villosa	R	R	I	S	R	–	–	–
A. correntina	–	–	I	R	–	HR	HR	HR
A. cardenasii	HR	HR	I	R	R	HR	HR	HR
A. chacoense	HR	HR	I	S	–	HR	HR	HR
A. kempff-mercadoi	R	R	–	–	–	–	R	R
Tertiary gene pool								
A. appressipila (P)	R	–	R	–	R	–	–	–
A. rigonii (P)	–	–	–	S	–	HR	I	HR
A. benthamii (E)	MR	MR	–	I or R	–	–	–	–
A. paraguariensis (E)	R	MR	R	R	–	–	R	–
A. glabrata (R_2)	S or MR	S or MR	I	R or I	–	I	HR	HR
Quaternary gene pool								
A. repens (C)	R	R	R	I	–	I	HR	HR
A. lutescens (Ex)	R	HR			–			
B. macedoi (Ex)	R	–	–	–	–	I	I	–
A. villosulicarpa (Ex)	HR	HR	I	–	–	–	–	–
A. pusilla (Tri)	R	R	I	–	–	I	I	HR
A. triseminata (Tri)	R	R	R		R		R	R

Source Stalker and Moss (1987), Upadhyaya et al. (2011)

[a]Symbol in parenthesis for section; Reaction- *MR* Moderately resistant, *R* Resistance, *HR* Highly resistant, *I* Immune, *S* Susceptible, it may vary between accessions of same species

[b]PStV = Peanut stunt virus

[c]GRD = Groundnut rosette disease

In spite of limited DNA polymorphism, there is abundant morphological variability present for most of the traits among germplasm accessions of the cultivated species. However, only an insignificant portion of this large variability has been utilized for crop improvement for reasons described earlier. To promote intensified and diversified use of genetic resources in crop improvement, recently, core and mini-core collections in groundnut have been developed (Holbrook et al. 1993;

Upadhyaya et al. 2002a, 2003, 2010), which capture representative variability in cultivated groundnut germplasm collection. However, in any applied breeding program where breeders have to maintain physical, chemical, and esthetic quality parameters as per the market requirements, breeders are often reluctant to use primitive germplasm because of linkage drag, which takes a long time to get rid off. Any variation in these qualities discourages processors to accept new genotypes as these variations affect the quality of their products and efficiency of their processing operations. Having used primitive germplasm in the beginning of the program, the breeders prefer to use second- or third-generation breeding lines with desired genes for use in breeding programs. In a recent publication, Janila and Nigam (2013) have reviewed the phenotyping protocols for various biotic and abiotic stresses, which are being followed in groundnut improvement programs. Murthy and Reddy (1993) and Reddy and Murthy (1996) have summarized the results of various genetic and inheritance studies covering most of the traits in groundnut. For details, readers are advised to refer to these publications. The status of up-to-date efforts, made for genetic improvement of groundnut in relation to various traits of significance for an overall engineering of cultivars incorporating both desirable agronomic features and resilience to stress factors, is described below.

Yield and yield-related traits: Yield is a complex trait with quantitative inheritance. In addition to yield, pod and seed characters are also important for esthetic and commercial considerations. Most of the pod and seed characters with few exceptions are governed by a few genes. Selection either for higher pod yield or for greater harvest index is essential for improvement of yield potential in future cultivars. Remobilization of reserves from vegetative biomass to pods under conditions of source limitations (falling temperature, defoliation by pathogens or water stress) is likely to be significant in maintaining yields but may limit response to improved conditions specially with high partitioning. Newer high-yielding cultivars in the USA allocate a greater proportion of biomass to reproductive tissue early in the growth cycle with greater reproductive efficiency and have more spreading growth habit and greater seed and pod weight than older cultivars (Wells et al. 1991; Seaton et al. 1992). However, the crop duration in the USA is much longer (140–160 days) than the one available to the crop in South and Southeast Asia and West Africa (<100 days).

Between 1944 and 1987, the average yearly genetic gain for yield in Virginia market type cultivars in the USA was 14.7 kg per ha. However, when the emphasis in breeding programs shifted to pest resistance, earliness, and quality, the new cultivars improved upon these traits but failed to combine them with increased yield potential (Mozingo et al. 1987). During 1980s and mid-1990s, the groundnut yield in India increased by 1.4 % per annum (Nigam et al. 1991). New Spanish-type cultivars in India have greater seed size, seed weight, and pod numbers per plant than the older cultivars (Rathnakumar et al. 2012). Increase of 0.43 % per year in seed yield, of 0.29 % per year in seed weight, and of 0.52 % per year in pod growth rate during 1948–2004 were obtained in Argentina (Haro et al. 2013).

Resistance to foliar fungal diseases: ELS, LLS, and rust are the most widely distributed and economically important diseases of groundnut in the world. Only

one leaf spot dominates in a region, however, both pathogens can be observed in the same field. LLS and rust often occur together. Breeding for resistance to foliar diseases in groundnut got a real boost in the late 1970s and early 1980s when a massive field screening program for resistance to foliar fungal diseases (rust and LLS) of more than 13,000 germplasm accessions from 89 countries was launched at ICRISAT, Patancheru, India. Subsequently, many sources of resistance were identified and used in breeding programs (Singh et al. 1997). Most of these resistant sources are landraces from South America and have undesirable agronomic characters (low yield, poor pod and seed traits, and longer crop duration). The components of resistance include longer incubation period and latent period, reduced sporulation, smaller lesion diameter, lower infection frequency, and less defoliation in resistance sources. Combining high levels of resistance to ELS and LLS into high-yielding cultivars with acceptable market traits continues to be difficult.

The first-generation cultivars emanating from foliar diseases resistance programs in India, ICG (FDRS) 10 and Girnar 1, did not find acceptance among the farmers and traders in spite of their higher yields under heavy disease pressure due to unattractive pod and seed characteristics. However, when these cultivars were recycled again in breeding programs, the resultant second-generation genotypes had better pod and seed characteristics and more acceptability among farmers and traders in spite of some dilution in their levels of resistance.

ELS, is more serious in Southern Africa and the USA. Resistant/tolerant *A. hypogaea* genotypes have been identified in Malawi, West Africa, India, and the USA with a disease score ranging between 3.6 and 6.3 on a 1–9 scale, where 1 = no disease and 9 = more than 81 % foliage destroyed. However, resistant sources reported from the USA (NC 3033 and PI #s 270806, 259747, and 350680) were found susceptible in India and Malawi. Excessive use of chemicals to control the disease in the USA is suspected to have led to variation in pathogen. Genotypes ICG #s 6284, 6902, 7878, 10000, 10948, and 13917 show some resistance at more than one location. Rate-reducing resistance is quantitative in nature and controlled by both additive and nonadditive gene effects including maternal effects. Duplicate recessive inheritance is also observed. Narrow sense heritability varies from low to high. Some of the ELS tolerant cultivars released in India are ICGS 44, ICGS 76, M 335, BG 3, Somnath, CSMG 84-1, M 522, Prutha, and GG 7 and in the USA are VA 81B, DP 1, Georganic, C-99R, Bailey, Florida 07, and Sugg.

LLS is predominant in warmer areas. Sixty-nine *A. hypogaea* genotypes tolerant to LLS with disease score ranging between 3 and 5 on a 1–9 scale (described earlier) have been identified. Forty-nine of these resistant sources are landraces belonging to var. *peruviana* with low yield and shelling outturn and other undesirable pod and seed characters. Resistance to LLS is quantitative in nature and governed by both additive and nonadditive gene effects including maternal effects. Duplicate recessive inheritance is also reported. Tolerant cultivars released in India include RG 141, ICG(FDRS) 10, ICGV #s 86590 and 86325, K 134, Girnar 1, GBPD 4, R 8808, ALR #s 1, 2, and 3, BSR 1, VRI 5, and CSMG 84-1 and in the

USA, Southern Runner, Florida MDR 98, TUFRunner TM '727', Florida 07, and C-99R, among others.

For rust, of the 169 *A. hypogaea* genotypes reported resistant (a score of five or less on a 1–9 scale), 135 are landraces belonging to var. *peruviana*. Many of these (ICG #s 7896, 7897, 7899, 10014, 10030, 10052, 10053, 10067, 10933, 10939, 10940, and 10943) have a disease score of <3 but are agronomically poor (low shelling outturn, thick pod shell, strong pod reticulation, and unacceptable seed coat color). New sources of resistance—ICG #s 10056, 10567, 10925, 10932, 11108, 12059, 12112, and 12113 and the interspecific derivatives involving *A. batizocoi* and *A. duranensis*—have high levels of resistance with good agronomic potential and resistance to other biotic stresses. Resistance to rust is reported to be recessive, partial dominant, or dominant with duplicate recessive, digenic, trigenic, or multigenic inheritance. Resistant cultivars released in India include ICG (FDRS) 10, ICGV 86590, and GBPD 4, among others.

Resistance to rust and LLS is correlated ($r = 0.48–0.60$). Forty-two LLS resistant genotypes are also resistant to rust. Of these, ICG #s 1703, 4995, and 10920 and interspecific derivative ICG 13917 [259-2 (red)] are useful in multiple resistance breeding, the last one being resistant to all the three pathogens. Other useful sources of resistance to both LLS and rust with agronomic potential are *A. hypogaea* genotypes ICG #s 6330, 7884, 10023, 10035, and 11182 and interspecific derivatives ICG #s 11312, 11317 (also resistant to ELS), 11321, 11325, 11337, 13916, 13917, 13919, 13920, and 13922. Cultivars reported with multiple resistances to foliar diseases, among others, are ICG (FDRS) 4, ICG (FDRS) 10, Girnar 1, ICGV 86590, Somnath, GBPD 4, VRI 2, VRIGn 5, and ALR #s 1, 2, and 3 in India and Azivivi, Nkosour, Adepa, and Jenkaa in Ghana.

Resistance to soil-borne fungal diseases: Breeding for resistance to soil-borne fungal diseases continues to be difficult as creating uniform disease pressure in the disease screening nursery remains challenging. Breeding for resistance to *A. flavus/A. parasiticus* and aflatoxin contamination has received the most attention among the soil-borne fungal diseases. Other diseases, where breeding efforts are in progress, include pod and stem rots, cylindrocladium black rot (CBR), and sclerotinia blight.

Efforts on breeding for resistance to *A. flavus/A. parasiticus* invasion and aflatoxin production in the USA, where *A. parasiticus* is dominant, and in other countries in Asia and Africa, where *A. flavus* predominates, are in progress. However, they have not yet succeeded in ensuring complete freedom from *A. flavus/A. parasiticus* infection and aflatoxin contamination in groundnut cultivars. Liang et al. (2009) and Nigam et al. (2009) have reviewed the progress in breeding for resistance to *A. flavus* invasion and aflatoxin contamination at ICRISAT, India/West Africa and Guangdong Academy of Agricultural Sciences in China, respectively.

There are three barriers to *A. flavus/A. parasiticus* infection and aflatoxin production in groundnut seed—pod wall, seed coat, and cotyledons. Resistance to pod infection is attributed to shell wall structure and that of seed coat to thickness and density of palisade layers, absence of fissures and cavities, and presence of wax and

cutin layers on the seed coat. Cotyledons are where the toxin is produced. Three resistance mechanisms—preharvest resistance, seed coat resistance [in vitro seed colonization (IVSC)], and cotyledon resistance (aflatoxin production) are independently inherited and provide opportunity for gene pyramiding (Upadhyaya et al. 2002b). The genetics of resistance is not clearly understood. There are a few published reports on broad sense heritability of three mechanisms of resistance (low to moderate) and combining ability of resistance sources (Rao et al. 1989; Upadhyaya et al. 1997a). A pair of major genes with additive value of 0.38 and a pair of minor genes with additive value of 0.12 were reported to be responsible for resistance to seed infection by *A. flavus* (Zhou et al. 1999; Zhou and Liang 2002). Predominantly, nonadditive genetic variance for aflatoxin production is also reported. Sources of resistant to preharvest infection [≤2 % infection; 21 genotypes —ICG #s 1122, 1173, 1323, 1326 (J 11)*, 1859, 1994, 3263 (U 4-47-7)*, 3267, 3336*, 3700*, 4589, 4749 (PI 337394 F)*, 4888, 7633 (UF 71513)*, etc.; *consistent across locations], IVSC (≤15 % seed colonized; PI #s 337394F* and 337409*, UF 71513, Ah 78223, J 11*, US-47-7, Var 27, Faizpur, Monir 240-30; * consistent across locations and pathogen pressure), and aflatoxin production (<0.7 μg per kg: ICG #s 10609, 11682, 10615, 6760, 9610) are available, but none of these is completely free from infection or aflatoxin production. Containment of preharvest infection is essential as once infected, the seed cannot be disinfected and the infection is carried forward. Seed coat resistance provides postharvest protection in storage. Recommended genotypes for use in breeding because of their multiple resistances include ICG #s 1326, 1859, 3263, 3336, 3700, 4749, 7633, 9407, 9610, 10094, etc.

Drought predisposes groundnut to aflatoxin contamination. Some drought-tolerant lines also show low preharvest seed infection and aflatoxin production (Holbrook et al. 2000a). Fatty acid composition is also reported to influence directly or indirectly aflatoxin contamination (Holbrook et al. 2000c; Xue et al. 2005). N_2 fixation and related traits have negative and significant effects on kernel infection and aflatoxin contamination especially under drought conditions (Arunyanark et al. 2012). Girdthai et al. (2010) suggested inclusion of SLA [specific leaf area; positively correlated with aflatoxin traits (seed infection and aflatoxin contamination)] and SCMR (SPAD chlorophyll meter reading; negatively correlated with aflatoxin traits), among other traits, in selection for resistance to aflatoxin contamination. It is advisable to have more number of replications in field screening nursery as plot to plot and plant to plant variations within a plot for preharvest seed infection, despite sufficient fungal propagules being present in the soil, which is often large. Screening for resistance to in vitro seed colonization and aflatoxin production is done in laboratory following protocols prescribed by various researchers. During field and laboratory screening, it is not unusual to find nil preharvest infection but presence of aflatoxin in the same genotype and the reverse is also observed. Conventional breeding alone does not ensure complete freedom from aflatoxin contamination; at best it is able to combine the level of resistance available in resistant parents with high yield and other agronomic characters. Attempts to pyramid resistance genes of different resistance mechanisms have also

not changed the situation much. Elite breeding lines giving good performance in India and Mali/Niger include ICGV #s 88145, 89104, 91278, 91283, 91284, 87084, 87094, and 87110 and in China include ICGV #s 95440, 95422, 94435, and 95435 and UF 71315. Yueyou #s 9 and 20 are released cultivars in China which are resistant to *A. flavus* invasion (Liang et al. 2009).

Stem and pod rots (stem rot also known as white mold, southern blight, sclerotium rot or white mold), caused by *Sclerotium rolfsii*, is wide spread in major groundnut-growing areas in the world. Some screening techniques have been described by Mehan et al. (1995). Field screening is more consistent than screening in the greenhouse. Uniformity and level of inoculum in the sick plot can be enhanced by adding sterilized oat seed inoculum of *S. rolfsii*, but individual plants may still escape the infection. The 'agar disk technique' is used to screen individual plants. Sources of moderate resistance include NC 2, NC Ac #s 18016 and 18416, ICG #s 15233, 15234, 15235, and 15236, and ICGV #s 86590 and 87160, among others. Bera et al. (2014) screened 286 interspecific derivatives in a sick plot in the field and in concrete blocks and pots filled with sick soil and found NRCGCS #s 47, 99, 131, and 319 highly promising. Cultivars with moderate resistance released in the USA are Southern Runner, Toalson, Pronto, Georgia Browne, Sunbelt Runner, and Tamrun 96.

Cylindrocladium black rot (CBR), caused by *Cylindrocladium parasiticum*, is largely reported from the USA, particularly from North Carolina. The screening for resistance to CBR is done at naturally infested hot spot locations. In general, the Spanish cultivars are most resistant, the Valencia cultivars most susceptible, and the Virginia cultivars moderately susceptible. The inheritance of resistance is complex (Green et al. 1983). The resistance delays the onset of epidemics rather than the rate of disease progress (Culbreath et al. 1991). NC #s 8 C, 10 C, and 12 C are the partial resistant cultivars released in the USA.

Sclerotinia blight (SB), caused by *Sclerotinia miner* Jagger, is important in Virginia and Oklahoma in the USA. 'Detached shoot technique', which relies on rate of lesion growth and development and disease infected fields (hot spot) are used for screening. In general, cultivars with Spanish ancestry are more resistant than those with Valencia and Virginia ancestries (Akem et al. 1992). Resistance to the disease is quantitative (Wildman et al. 1992). Interspecific lines derived from *A. hypogaea* × *A. cardenasii* cross are highly resistant to the disease. Spanish cultivars Toalson and Tamspan 90 have good resistance to sclerotinia blight.

Resistance to virus diseases: The status of genetic management of virus diseases in groundnut has recently been reviewed by Nigam et al. (2012). The conventional breeding efforts have concentrated only on three virus diseases—peanut bud necrosis disease (PBND) in India, tomato spotted wilt virus (TSWV) disease in the USA, and groundnut rosette disease (GRD) in Africa.

PBND, caused by peanut bud necrosis virus (PBNV), is economically important in South and Southeast Asia. It is transmitted by thrips species *Thrips palmi*; the virus is acquired by the larvae but transmission is done exclusively by the adults in a persistent manner. The virus is not seed transmitted. Several germplasm accessions with consistently low disease incidence in the field (ICG #s 848, 851, 852,

862, 869, 885, 2271, 2306, 2307, 2323, 2741, 3042, 3806, 3873, 5030, 5024, 5043, 5044, 6135, 6317, 6323, 7676, 7892, and others) and breeding lines/cultivars DRG 18, ICG 7812, ICG (FDRS) 10, JSSP 3, KNG 22, PI 393516, and ICGV #s 80325, 86031, and 86388, among others, have been identified at ICRISAT. The last two breeding lines (ICGV #s 86031 and 86388) are resistant to both, the vector and the virus (Dwivedi et al. 1995). Sources of resistance to the vector include NC Ac #s 2242, 2214, 2243, 2240, 2232, 2230, and others. The resistance is stable across environments.

Three factors with additive gene effects are reported to be responsible for low disease incidence (Buiel 1996). Significant gca, sca, and reciprocal effects are also observed for disease incidence with the gca effects being predominant (Pensuk et al. 2002). Because of significant reciprocal effects, the resistant source should be used as female parent in hybridization. Nonadditive gene effects are also reported for low PBND incidence (Pensuk et al. 2004). In another study, additive gene effects were found to be major contributors to PBND resistance besides additive × additive and dominance gene effects (Poledate et al. 2007). Resistant cultivars released are CO 3, ICGS #s 11, 44 (ICGV 87128), and 37 (ICGV 87187), R 8808 (KRG 2), R 9251, K 134, DRG 12, RSHY 1, and Kadiri 4 in India and Khon Kaen 6 in Thailand.

Culbreath et al. (2003) have done an extensive review of epidemiology and management of TSWV disease of groundnut in the USA, where it is a major production constraint. TSWV is transmitted by thrips species, *Frankliniella fusca* (Hinds) (tobacco thrips), *F. occidentalis* (Pergande) (western flower thrips), *F. intonsa*, *F. schultzei*, *S. dorsalis*, *Thrips tabaci*, *T. palmi,* and *T. setosus*, in a persistent manner; the first two are the primary vectors. The virus is not seed or pollen borne. Sources of resistance in cultivated groundnut include PI #s 203396 (also resistant to LLS), 196621, 339967, and 341267. Significant gca and sca (Anderson et al. 1990) and transgressive segregation for TSWV resistance (Holbrook et al. 2003) are reported. However, genetic mechanism of resistance is not elucidated. Breeding lines derived from var. *hypogaea* and var. *hirsuta* have higher resistance to TSWV (Culbreath et al. 2005). TSWV resistant/tolerant cultivars released in the USA are Southern Runner, Georgia Browne, Georgia Green, Tamrun 96, Georgia Bold, Georgia Hi-O/L, Georgia 01R, C-99R, Florida MDR 98, Tifguard, Georganic (highest level of field tolerance among cultivars), and others. However, they may suffer significant damage during extreme epidemics.

Waliyar et al. (2007) have summarized a century of research on GRD and its management. GRD is confined to the African continent and its surrounding islands. It has a complex of three causal agents—groundnut rosette assistor virus (GRAV), groundnut rosette virus (GRV), and a satellite RNA (SatRNA). These three agents synergistically act with each other for survival and spread. GRV is dependent on GRAV for transmission by aphid vector *Aphis craccivora* and SatRNA, which is responsible for rosette symptoms, is itself dependent on GRV for replication. GRV and SatRNA alone do not produce GRD symptoms. GRAV on its own can cause mild yellowing/chlorosis of leaves and can cause reduction in plant growth and yield. GRV and SatRNA must be packaged within GRAV coat protein to be aphid transmissible. GRV is dependent on its SatRNA for encapsidation in coat protein.

GRV on its own produces transient symptoms only. GRV and SatRNA are always found together in nature. These three causal agents are not seed borne. There are two variants of GRD symptoms—chlorotic rosette and green rosette. Chlorotic rosette occurs throughout sub-Saharan Africa and green rosette, which earlier was largely confined to West Africa, is now also reported from Southern and Eastern Africa. SatRNA is responsible for variation in symptoms.

Using viruliferous aphids and grafting, genotypes can be evaluated for resistance to all the three causal agents (Olorunju et al. 1992) in greenhouse. Mechanical sap inoculation can be used only for screening for resistance to GRV and SatRNA. Resistance to GRAV can be evaluated using vector aphids fed on GRAV-infected groundnut plants or by grafting scions on to plants under test from these plants. Resistance to GRD was first found in groundnut germplasm originating from Burkina Faso and Côte d'Ivoire in mid-1950s. Several pure line selections made in late maturing Virginia landraces in Burkina Faso, such as 48-7, 48-14, 48-15A, 48-21, 48-34, 48-35, 48-36, 48-37, 48-44, 48-45, and 48-70A, were resistant to GRD. Subsequently, evaluation of 12,500 germplasm accessions form ICRISAT's gene bank resulted in identification of 150 resistant sources (130 long-duration Virginia types and 20 short-duration Spanish types) (Subrahmanyam et al. 1998; Olorunju et al. 2001). Sources of resistant to aphid vector, EC 36892 (ICG 5240), and ICG 12991, show less GRD but they are susceptible to all the three agents of GRD.

All the sources of resistance to GRD are resistant to GRV and its SatRNA but they are susceptible to GRAV. The resistance to GRAV in cultivated groundnut is yet to be found. Resistance to GRD (effective against GRV and its SatRNA) in cultivated types is governed by two independent recessive genes which are effective against both chlorotic and green rosette (De Berchoux 1960; Nigam and Bock 1990; Olorunju et al. 1992). Resistant cultivars released in Africa include RMP #s 12 and 91, 69-101, KH #s 241D and 149A, RG 1, Nyanda (ICGV 93437), ICG 12991, ICGV-SM #s 90704, 99568, 99555, 99557, 01711, and 01721, and Samnut #s 23 (ICGV-IS 96894), 21 (UGA 2), and 22 (M572.801).

Resistance to bacterial wilt disease: Bacterial wilt, caused by *Ralstonia solanacearum*, is one of the major production constraints in groundnut in Southeast and East Asia. Hot spot locations with naturally infested soils are used to screen germplasm and breeding populations. Breeding for resistance to bacterial wilt was probably the first disease resistance breeding activity in groundnut which was initiated in Indonesia. It led to release in 1925 of Schwarz 21, a bacterial wilt resistant variety selected from a local population, in Indonesia. Since then, several sources of resistance, mostly belonging to subspecies *fastigiata*, have been reported from Indonesia and China (Mehan et al. 1994). These resistance sources belonging to the subspecies *fastigiata* are also early maturing and tolerant of acid soils and poor soil fertility. Nature of the resistance is dependent on the genetic background. In the Chinese dragon type groundnut, the resistance is reported to be partially dominant with cytoplasmic effect (Shan et al. 1998). In *fastigiata* types, the resistance is reported to be partially dominant involving three pairs of major genes and some minor genes (Liao et al. 1986) and partially dominant in some crosses and partially recessive in some crosses (Shan et al. 1998). Several bacterial wilt resistant

cultivars have been released—such as Xiekongchung, Teishansanliyue, Yue You #s 13, 589, 92, 256, 200, 256, and 79, Wu You 4, Gui You 28, E Hua 5, Zhong Hua 2, Lu Hua 3, Yuanza 9307, and others in China and Schwarz 21, Gajah, Matjan, Kidang, Banteng, Macan, and others in Indonesia.

Insect pest resistance: Breeding for resistance to insect pests has received limited attention due to difficulty in screening large number of germplasm lines and segregating breeding populations under sporadic and variable natural insect pressure. In most cases, limited screening under field and laboratory or controlled conditions has been carried out leading to identification of sources of tolerance/resistance to major insect pests and characterization of reaction of advanced breeding lines (Amin et al. 1985; Lynch 1990; Wightman and Ranga Rao 1994). Many genotypes with resistance to multiple insect pests are also reported (Nigam et al. 1991). To enhance the natural pressure of insect pests, rows of susceptible genotypes (infester rows) are planted at regular intervals with test materials. The cultured population of the insect pests is also released to raise the levels of insect pressure in the screening nursery. The resistance mechanisms may involve any one of the following or their combinations: repellence, antibiosis, tolerance, physical structures, and avoidance.

Sucking pests such as thrips, jassids, and aphids not only cause direct yield losses but some of them (thrips and aphids) also act as vectors of the virus diseases. Several genotypes resistant to thrips and jassids are reported. Some of the thrips resistant/ tolerant genotypes are listed in sections of PBND and TSWV virus diseases. High density, distribution and length of trichomes (NC Ac #s 2214, 2230, and 2240), and thick leaf cuticle (NC Ac #s 2242 and 2243) are important factors associated with resistance to thrips and jassids. In aphid resistant genotypes, NC Ac 343, EC 36892, and ICGV 86030, antibiosis operates by reducing growth and fecundity (Padgham et al. 1990). Nonadditive genetic variance was predominant for all trichome characters; for trichome length and jassid damage additive genetic variance was also important (Dwivedi et al. 1986). For resistance to complex of pests (thrips, jassids, and *Helicoverpa*) in North Carolina, USA, additive genetic variance was predominant (Holley et al. 1985). Breeding lines tolerant to jassid are ICGV #s 86388, 86462, 86252, 86393, and 86455, among others.

Among defoliators, leaf miner (*Aproaerema modicella* (Deventer)) and tobacco caterpillar (*Spodoptera litura* F.) are important. Screening for resistance to defoliators under natural field conditions is difficult because of variation in infestation in space and time. No-choice cage technique is used to screen for resistance to *S. litura*. Nuclear insect culture is maintained on artificial diet. A known number of first- or third-instar larvae are released for varying period of time on 15-day old greenhouse grown plants which are kept inside a plastic jar cage with wire mesh screen windows. Observations on insect survival (number of surviving larvae and larval weight) and leaf area damage are recorded. For leaf miner, natural infestation is relied upon, which can be enhanced by planting soybean as an infestor crop and creating prolonged drought. It is difficult to devise no-choice cage screening for leaf miner. Breeding lines, ICGV #s 86031, 87154, and 87160, and germplasm accessions, ICG #s 2271 and 1697, showed resistance to both tobacco caterpillar

and leaf miner. Other genotypes showing promise against leaf miner are NC Ac #s 343 and 17090 and ICG (FDRS) 4.

Nematode resistance: Breeding for resistance to nematodes has received little attention elsewhere except in the USA, China and to some extent in India. Screening for resistance to *Meloidogyne arenaria* (root knot nematode) in the USA resulted in identification of several genotypes that supported less egg production per gram of fresh root weight (Holbrook and Noe 1992; Holbrook et al. 2000b). COAN was the first groundnut cultivar resistant to *M. arenaria* in the USA. The resistance in COAN was conditioned by a single dominant gene from TxAG 7, which is a backcross derivative of TxAG-6, a complex interspecific derivative involving *A. cardenasii*, *A. batizocoi,* and *A. diogoi*. But it was susceptible to TSWV. In the USA, root knot nematode resistant variety Nema TAM was the first variety developed using marker-assisted selection (MAS), but it was also susceptible to TSWV. Subsequently Tifguard, resistant to both root knot nematode and TSWV, was developed following conventional breeding. 'Kalahasti disease' caused by stunt nematode (*Tylenchorhynchus brevilineatus*) was first noticed in 1975/1976 in Kalahasti area of Andhra Pradesh, India. From replicated screening of 1599 genotypes in a hot spot location in a farmer's field in Kalahasti during 1985/86–1986/87, 14 resistant genotypes were identified. Most of these genotypes had undesirable pod/seed characteristics with the exception of TCG 1518, an advanced Virginia bunch breeding line, which was later released as Tirupati 3 for cultivation in disease-affected areas (Mehan et al. 1993). In another screening exercise of 39 genotypes during 1992–1994, TCGS #s 307, 313, and 320 (released as Kalahasti) were also identified as resistant to the disease with the last two having pod yield exceeding 3 t/ha (Naidu and Moses 2000).

Resistance to abiotic stresses: Drought is the overriding stress factor in rainfed groundnut. Other emerging issues are salinity and heat tolerance. Although considered a drought-tolerant legume, it can still suffer early-season, mid-season, end-of-season, or intermittent droughts impacting adversely on yield and yield-related traits including quality of the produce due to reduced photosynthesis, N_2 fixation, and calcium uptake by developing pods. The impact will depend on the timing of occurrence, duration, and intensity of drought. A 20/25-day moisture stress soon after crop emergence is beneficial to the crop as it forces roots to go deeper into the soil in search of moisture and when the moisture stress is released, it induces profuse flowering resulting in synchronized and uniform maturity and increased yield. The adverse effect of end-of-season drought can be overcome by developing short-duration varieties with their life cycle matching the period of soil moisture availability. It is the mid-season drought that is a cause of worry as insufficient water at the time of flowering and fruiting reduces the yield significantly. Direct selection for yield under drought is effective but it is resource consuming and lacks repeatability across different environments. Drought tolerance can be enhanced by improvements in soil water extraction ability (T) or improvements in water-use efficiency (TE). Genetic variation for root system (Songsri et al. 2008b) and transpiration efficiency (g dry matter per kg of water transpired) is reported, but these traits are difficult to measure. Easily measurable surrogates for

these traits are needed for use in a large-scale breeding programs. Transpiration efficiency is negatively correlated with $\Delta\ ^{13}C$ (carbon isotope discrimination) in leaves, which is rapid but expensive to measure. $\Delta\ ^{13}C$ is highly positively correlated with specific leaf area (SLA, ratio of leaf area to leaf dry weight), which is easy and inexpensive to measure (Wright et al. 1994; Nageswar Rao and Wright 1994). SLA has inverse relationship with relative leaf water content (RWC) and the low SLA types are drought tolerant as they are able to maintain higher RWC. However, SLA is influenced by the time of sampling and age of the leaf (Wright et al. 1996). SLA is inversely correlated with SPAD chlorophyll meter reading (SCMR) (Nageswar Rao et al. 2001), which, in turn, is positively correlated with TE. SCMR is measured by a hand held device which is easy to operate and can rapidly record observations. Thus, for fast screening, SCMR can be used in a large-scale breeding programs aiming to improve drought tolerance in groundnut. SLA and SCMR can be recorded any time after 60 days of crop growth, preferably under moisture deficit conditions (Nigam and Aruna 2008a). However, the utility of SLA and SCMR in screening for drought tolerance has been questioned in some studies (Devi et al. 2011). Sufficient variation for physiological traits such as SLA, T, TE, and HI (Nageswar Rao and Wright 1994; Wright et al. 1994, 1996; Nageswar Rao and Nigam 2001) and in tolerance to mid-season and/or terminal droughts is reported (Nageswar Rao et al. 1989; Nigam et al. 2003). High heritability for HI, SCMR, and $\Delta\ ^{13}C$ and medium to high heritability for SLA are reported (Songsri et al. 2008a; Chen et al. 2013b). Both additive and additive × additive gene effects for SLA and HI and additive gene effects for $\Delta\ ^{13}C$ are reported (Jayalakshmi et al. 1999; Nigam et al. 2001). The segregating populations are screened in the field under imposed drought conditions and selections are made based on pod yield, pod number, and pod filling. In selected populations, surrogates SCMR or SLA can also be used along with pod yield and other characters. Both empirical (yield-based) and trait-based approaches are effective in selecting for drought tolerance (Nigam et al. 2005). In the case of trait-based approach, TE is the major contributor to pod yield, which indicates more efficient utilization of available water. However, in the case of empirical approach, it is T which is a major contributor to pod yield, which indicates better mining of water from soil layers. The better mining does not necessarily mean better utilization of water. In case of limited water availability, enough T may not occur thus impacting on pod yield. It is advisable to integrate surrogates of TE in the selection scheme for drought tolerance. Some of the drought-tolerant breeding lines/cultivars released are ICGS #s 44 and 76, ICG(FDRS) 10, ICGV #s 91114 and 00351, R 8808, GPBD 4, Dh 86, and Kadiri 5 in India, 796, 55-437, and TS 32-1 in West Africa, and BARI 2011 in Pakistan.

When drought occurs, temperature also rises. Drought and heat tolerance appear to be correlated. Besides, breeding for tolerance to high temperatures has also become essential to meet the challenges of changing climate. In vitro pollen germination, pollen tube growth and membrane thermostability, growth rates, fruit set, and partitioning have been used to measure response of groundnut genotypes to high temperature (Craufurd et al. 2003; Ntare et al. 2001; Hamidou et al. 2013). The

heat tolerant genotypes are 796, 55-437, ICG 1236, TMV 2, ICGS 11 and ICGV #s 86021, 87281, and 92121, among others.

Breeding for adaptation traits: Growth and development in groundnut is largely driven by temperature. The optimum temperature (T_0) for growth and development in groundnut ranges between 27 and 32 °C. The base temperature (T_b) in groundnut ranges between 9 and 13 °C below which the growth ceases (Williams and Boote 1995). There is variation in T_b for different phenological stages and among genotypes. At lower temperatures, growth is slowed down and it takes longer for crop to mature. The reverse is observed at relatively higher temperatures. But, the growth stops at temperatures exceeding 45 °C as protein gets denatured. At temperatures above the optimum, significant reduction in dry matter production and partitioning of dry matter to pods are observed but flower production is not affected. Photoperiod does not affect flowering in groundnut but it affects partitioning (Nigam et al. 1994), however, these effects are genotypic specific. Irradiance also plays a role together with temperature in determining the crop duration.

Short duration: Breeding for early maturity in groundnut has been reviewed by Nigam and Aruna (2008b). Selection based on days to first flower alone is ineffective in identifying early maturing lines as there are other processes also involved in reaching to maturity. Instead of calendar days, use of cumulative thermal time (CTT) measured in day-degrees (°Cd), is recommended for selecting for early maturity at a given location (Rao et al. 1991). The CTT is measured in day-degrees (°Cd) above the base temperature and is calculated on successive days by subtracting the base temperature from the mean daily temperature and adding each value to the subtotal accumulated since the seed was sown ($\mathrm{CTT}(^{\circ}\mathrm{Cd}) = \sum((T_{\max} + T_{\min})/2 - T_b)$). In photoperiod-insensitive genotypes the CTT for maturity does not differ across environments barring the influence of environmental factors other than photoperiod. For photoperiod-sensitive genotypes, the CTT will vary with photoperiod over the photoperiod-sensitive range. It must be remembered that early maturity is a relative term; in India early maturing varieties are less than 100-day duration whereas in China and USA a variety of 120-day duration will qualify as early maturing variety.

Incorporating large seed size in short-duration cultivars is unlikely to succeed as large seeds take more time to emerge on sowing, and to develop and mature. Similarly, combining higher levels of resistance to foliar diseases and short duration will be difficult to achieve through conventional breeding. On the other hand, a moderate level of resistance will have only limited influence on crop duration and would also stabilize productivity in a cropping system. In breeding for early maturity, it is helpful to partition crop duration into different segments/stages and examine the possibility of shortening their duration individually and collectively with an overall aim to reduce crop duration. These segments/stages include days to germination and emergence, days to first flower after emergence, days from opening of first flower to opening of a given number of flowers per plant, and days from opening a flower to maturation into seeds. Based on the botanical characteristics and physiological behavior of the crop, the following characteristics could be visualized for attaining short duration of the crop: short plant stature (plant height in case of

subspecies *fastigiata* and plant spread in case of subspecies *hypogaea*) with smaller internodal length, faster germination and emergence, fewer days to first flowering, and accumulation of a maximum number of early flowers, more flowers per node, absence of late flowers, fewer days after fertilization for a peg to enter soil, faster pod and seed growth, high seed partitioning, and high shelling turnover. To capitalize on the full potential of the genotypes with aforementioned traits, it would be essential to modify crop husbandry to accommodate larger numbers of plants per unit area to provide quick ground cover and to provide plant with required nutrients and other inputs. The following considerations in breeding strategy will help to achieve the objective of early maturity along with high yield: (i) Selection for low T_b and CTT for various phenological stages, (ii) Selection for tolerance to high temperature, (iii) Selection for photoperiod-insensitive genotypes, (iv) Selection for high crop growth rate and partitioning, (v) Selection for high water-use efficiency, and (vi) Evaluation in target environments/cropping systems. Inheritance of earliness and its components has been reviewed by Nigam and Aruna (2008b). From a single gene to 4–5 genes, from complete dominance to incomplete dominance of late maturity over early maturity, epistatic gene effects, absence of reciprocal differences, higher gca variance than sca variance, additive genetic variance, additive and dominance gene effects, and generally high heritability are reported in the literature. Various sources of early maturity identified are Chico, Gangapuri, JL 24, and ICG #s 3540, 3631, 4558, 4729, 4890, 9427, 9930, and 11605, 91776, 91176, Dh 40, ALG (E) 57, TG #s 1E, 2E, and 3E, etc. Of these, Chico, which matures in 75–80 days, has been very extensively used in the breeding programs. Some of the early maturing cultivars released in different countries are Pronto and Spanco in the USA, Dh 40, TNAU 97, ALG (E) 57, GG #s 3, 5, 7, and 12, TG 26, R 9251, M 522, RS 138, K 134, JL 220, VRI 3, and C0 4 in India and 55-437, TS 32-1, 73-30, KH #s 149A and 241D, Te 3, and Fleur 11 in West Africa in different habit groups.

Seed dormancy: A majority of the groundnut in developing countries is grown under rainfed conditions characterized by uncertain and irregular rainfall. The groundnut crop is very often caught in rains at the time of harvest, which results in *in situ* germination in Spanish and Valencia cultivars, thus causing significant losses in yield and quality of the produce. Incorporation of 2–3 weeks fresh seed dormancy in Spanish and Valencia cultivars will help to avoid these losses, which could reach up to 40 % (Reddy et al. 1985). Depending on their genetic constitution, different seed parts—seed coat, cotyledons, and embryo—have been reported to have a role in imparting dormancy (Bandyopadhyay et al. 1999; Nautiyal et al. 2001). Fresh seed dormancy is more under control of testa than cotyledons. Complexity arises in studying the inheritance of seed dormancy when both maternal (testa) and zygotic (cotyledons) tissues are involved in its control. From monogenic control with seed dormancy dominant over nondormancy (Upadhyaya and Nigam 1999; Yaw et al. 2008) to quantitative inheritance with additive, dominance, and digenic epistatic effects (Khalfaoui 1991; Nautiyal et al. 1994) are reported. Several Spanish breeding lines/cultivars with fresh seed dormancy are available now (Upadhyaya et al. 1997b). Most of these originate from

Virginia × Spanish/Valencia crosses. Instead of screening for seed dormancy in early generations, the advanced generation Spanish/Valencia breeding lines are screened for fresh seed dormancy in laboratory and under field conditions.

Salinity: There is no targeted program in progress to breed groundnut tolerant to soil salinity. In limited studies, genotypes have been screened and tolerant genotypes based on plant survival and seed yield per plant have been identified. The tolerant genotypes include germplasm, breeding lines, and cultivars such as NRCG #s 2588, 4659, 5513, 6131, 6450, 6820, 6919, and 7206, TMV 2 NLM, TG 33, JNDS-2004-15, VRI 3, UF 70-103, TKG 19 A, S 206, Tirupati 4, M 522, Punjab 1, BG 3, Somnath, and ICGV 86590 (Singh et al. 2008, 2010).

Quality traits: Oxidative stability and shelf life of groundnut and its products can be enhanced by improving oleic-to-linoleic fatty acid ratio, which normally ranges between 0.8 and 2.5 in old commercial cultivars. These two fatty acids constitute about 80 % [55 % oleic acid (18:1) and 25 % linoleic acid (18:2)] of the oil content of groundnut (Knauft et al. 1993). Of these two, linoleic fatty acid is less saturated and less stable than oleic acid. In peanut breeding program at the University of Florida in 1987, two breeding lines originating from F 435, a high oleic acid spontaneous mutant, with 80 % oleic and 2 % linoleic acid composition were identified (Norden et al. 1987). With simple inheritance (single recessive or two recessive genes and some possible modifiers depending upon the parents involved in the crosses), it is easy to transfer high-oleate trait to other genotypes through backcross breeding program (Moore and Knauft 1989; Knauft et al. 1993; Lopez et al. 2001). Cultivars developed with high O/L ratio in the USA through conventional breeding are SunOleic 95R, SunOleic 97R, Tamrun OL01, Georgia 04S, Andru II, Florida-07, and Hull, through chemical mutagenesis are Mycogen-Flavorunner and M 2-225 and through Gamma radiation are Georgia-02 C and Georgia Hi-high. Varieties with high levels of oleic acid, when consumed, have beneficial effect on human and animal health.

Improved flavor: Since 1980, the flavor of roasted groundnut has become an important consideration in breeding programs engaged in developing Virginia varieties for direct consumption as it influences consumers' acceptance. Several roasted groundnut quality sensory attributes are heritable (Pattee et al. 1998). Thus, choice of parents becomes critical in ensuring good flavor of roasted groundnut in breeding lines. Jenkins Jumbo, one of the ancestors of USA-bred Virginia varieties, was found responsible for their poor roasted flavor. The parents selected for hybridization should have at least acceptable roasted flavor to ensure consumers' acceptability for new cultivars. During the selection process all plants with off-type flavor should be rejected.

2.6.2 Genetic Improvement Using Resources of Secondary Gene Pool

2.6.2.1 Phylogeny of *A. hypogaea*

Information on phylogenetic relationship between cultivated and the species of other gene pool is an essential prerequisite to facilitate gene transfer. A series of initial cytogenetic investigations in section *Arachis* that includes tetraploid ($2n = 40$) cultivated groundnut, *A. hypogaea*, wild tetraploid *A. monticola,* and 29 diploid ($2n = 20$) species crossable with *A. hypogaea,* falling in secondary gene pool revealed that basically there are two genomes, A and B distributed among the diploid species of section *Arachis*, which together contribute to the evolution of cultivated *A. hypogaea* with genomic constitution AABB (Smartt and Gregory 1967; Smartt et al. 1978; Singh and Moss 1982, 1984b; Gardner and Stalker 1983; Singh 1988). These and further studies indicated that most diploid species of section *Arachis* contain A genome, while *A batizocoi*, *A. ipaënsis* and four more, including *A. hoehnei* contain B genome (Mallikarjuna et al. 2006), and K30091, 30098, 30099, and 30100 (*A. glandulifera*), probably another genome D (Stalker 1991). Recently, based on FISH mapping of rDNA loci and heterochromatin detection, two new genome types (F and K) have been described for some of the species formerly considered in the B genome group (Robledo and Seijo 2010). *Arachis benensis* and *A. trinitensis* are now classified as having an F genome and *A. batizocoi*, *A. cruziana,* and *A. krapovickasii*, a K genome. These two genomes have centromeric bands on most of the chromosomes, differing from each other in the amount and distribution of heterochromatin. However, the exact phylogenetic relationships of the F, K, and D genomes with the A and the B genomes need further study. Cross-compatibility, chromosome pairing, and hybrid fertility suggest that A and B genomes are homoeologus and they together evolved *A. hypogaea*, a segmental allopolyploid, with A. *batizocoi* or *A. hoehnei* contributing B genome and *A. duranensis*, *A. villosa,* or *A. cardenasii* A genome (Smartt et al. 1978; Singh and Moss 1984b; Singh 1986a, 1988; Mallikarjuna et al. 2006). Molecular markers affinity suggested *A. ipaënsis* as contributor of B genome, supported by genomic in situ hybridization (Raina and Mukai 1999; Seijo et al. 2004) and *A. duranensis* of A genome (Kochert et al. 1991, 1996; Burow et al. 2009; Moretzsohn et al. 2013), though needing response to some basic questions raised by Singh and Smartt (1998). All studies, including biochemical profile (Singh et al. 1991) supported broad genomic grouping of section *Arachis*. Thus based on cross-compatibility, chromosome pairing, and hybrid fertility, direct introgression of genes from section *Arachis* diploid wild species is possible through direct hybridization with tetraploid *A. hypogaea,* with or without ploidy and cytogenetic manipulations. The other sections species are genomically distant for direct introgression of gene(s).

2.6.2.2 *Accessing Secondary Gene Pool with or Without Ploidy Manipulations of Hybrids*

The cytogenetic information generated on genomic constitution and relationship between cultivated tetraploid *A. hypogaea* and the diploid species of section *Arachis* helped to visualize the implications of direct hybridization (*A. hypogaea* 4x × *A.* sp. 2x) and with autotetraploid and amphidiploid of diploid species with different genomic combinations, on the hybrid fertility, levels of meiotic recombination and on gene transfer, illustrating merits of various options (Singh 1985; Singh and Gibbons 1985; Singh et al. 1990; Simpson 1991). Direct hybridization is the first logical option for transfer of genes into cultivated groundnut from diploid species. Krapovickas and Rigoni (1951) were the first to report hybrid between *A. hypogaea* and *A. villosa*. Subsequently, triploid were produced involving a number diploid *Arachis* species (Smartt and Gregory 1967; Singh et al. 1980; Singh 1985) with the objective of gene transfer. Triploids produced some seeds and seedlings (Smartt and Gregory 1967, Singh and Moss 1984a) consequent to production of haploid, hyperdiploid, and unreduced gametes. Eighty-two percent F_2 of these seedlings were hexaploid, while other had chromosome ranging from 40 to 58 (Singh and Moss 1984a). However, fertility in triploid hybrids was restored by doubling of chromosomes to produce hexaploids (Smartt and Gregory 1967; Singh et al. 1980; Singh 1985). At ICRISAT, triploids were initially produced with the objective of incorporating genes conferring resistance to foliar diseases, involving cultivars of tetraploid *A. hypogaea* and eight diploid species such as *A. cardenasii* (resistant to LLS, rust and groundnut rosette), *A. diogoi* (called *A. chacoense* earlier) (resistant to ELS, rust, and groundnut rosette), *A. stenosperma* (field resistant to both leaf spots), *A. batizocoi* and *A. duranensis* (resistant to rust). Both synthetic hexaploids and the partial fertile triploids were backcrossed to recurrent *A. hypogaea* parents to effect gene transfer, which produced progenies with chromosomes ranging from 40 to 60. Backcrossed progenies were further backcrossed with recurrent *A. hypogaea* parents and intermittently selfed to regain agronomic traits of cultivated groundnut, and the produced backcross and selfed progenies were screened to select and progress with progenies incorporating desired resistance without dilution (Singh and Gibbons 1985; Singh et al. 1990; Ouedraogo et al. 1994; Simpson 2001).

2.6.2.3 Accessing Gene Pool with Ploidy Manipulations of Diploid Species or Hybrids

Autotetraploids and amphidiploids of various diploid species of section *Arachis* were produced in intra- and intergenomic combinations and crossed with tetraploid *A. hypogaea* (Gardner and Stalker 1983; Singh 1985, 1986a, b). It was expected that the resultant hybrids would have improved fertility with removal of ploidy difference and more so in complementary genomic combination. Further, as visualized, use of autotetraploid helped in increasing the dosage of desired trait

exploiting homologous intergenomic pairing, while hybridization with amphidiploids from crosses between "A" and "B" genome species produced relatively more fertile hybrids with greater recombination through preferential autosyndetic pairing between wild and cultivated species chromosomes, effecting gene transfer (Singh 1986a, b; Srikanth et al. 2012). Autotetraploids were initially established in eight diploid species, of which six were crossed with *A. hypogaea* as male parents. Similarly, amphidiploids were produced involving eight diploid species of section *Arachis* in 31 combinations, both in intra- (AAAA) and intergenomic (AABB), and 23 were successfully crossed with *A. hypogaea*. As expected, the intergenomic amphidiploids produced greater number of seeds than intragenomic (Singh 1985, 1986b; Mallikarjuna et al. 2011). A number of resultant hybrids from these crosses were backcrossed with groundnut cultivars and intermittently selfed resulting in production of *A. hypogaea*-like stable tetraploid derivatives, which were screened against various pathogens (Singh et al. 1990). These approaches were effective in incorporating resistance to rust and LLS and ELS from several of wild *Arachis* species (Gardner and Stalker 1983; Singh and Gibbons 1985), giving encouragement for full exploitation of the secondary gene pool with concerted efforts on target genes in future.

Using these breeding options by 1989, 209 *A. hypogaea*-like interspecific derivatives incorporating genes conferring resistance to various groundnut diseases were produced at ICRISAT, in addition to hybrid populations received North Carolina State University, produced by Smartt and Gregory (1967). Screening and multilocation yield trials of these interspecific derivatives were conducted in collaboration of national agricultural research systems (NARS) in India and abroad, identifying genotypes well adapted, high yielding, and resistant to prevailing stresses (Singh and Gibbons 1985). Many of these were dual-purpose types with potential for both haulm (fodder) and kernel yield. Interspecific derivatives, 83/372-2-2-22-B1 with resistance to groundnut rosette virus (Moss et al. 1993), ICGV 86699 with multiple disease and insect resistance (Reddy et al. 1996), ICGV 87165 with multiple disease resistance (Moss et al. 1997), ICGV 86715 with foliar disease resistance (Moss et al. 1998), and ICGV #s 99001, 99003, 99004, and 99005 with LLS and rust resistance (Singh et al. 2003) were registered and form the basis of foliar disease resistance breeding programs worldwide. Some, like ICGV 86775 was released as variety in Mauritius. The resulting increase in harvest due to this work is estimated to be some US$ 500 million (Sasson 1996).

2.6.3 Accessing Tertiary Gene Pool and Beyond with Alternative Manipulations

2.6.3.1 Bridge Crosses

The successful hybridization between diploid species of section *Arachis* and those belonging to section *Erectoides* and *Procumbentes* (Gregory and Gregory 1979), but without development of normal seed (Singh 1998), suggests that such cross-ability can be exploited in establishing hybrids with or without pre-fertilization manipulations and/or embryo rescue, that can provide access to significant portions of tertiary gene pool. Such hybrids between diploid species of section *Arachis* and those of *Erectoides* and *Procumbentes* have potential to work as bridge to carry genetic information to *A. hypogaea* from other cross-incompatible species of *Trierectoides*, *Heteranthae,* and *Caulorhizae* (Fig. 2.1). However, the usefulness of such manipulations in genetic improvement of groundnut is yet to be tried and established.

2.6.3.2 *Nonconventional Manipulations and Embryo Rescue*

Several methods, such as mentor pollen, in vitro fertilization, hormone treatments after pollination to overcome prezygotic incompatibility and embryo rescue are possible for direct access the gene conferring resistance to various biotic and abiotic stresses from diploid species section *Procumbentes, Erectoides,* and tetraploid species of *Rhizomatosae*. Interspecific hybrids were produced between *A. hypogaea* and *A. chiquitana* and *A. kretschmeri* of *Procumbentes* by applying growth regulators to pollinated pistils, and hybrid plants were obtained by germinating embryos in vitro (Mallikarjuna 2005; Mallikarjuna and Hoisington 2009). The possibility of establishing hybrids between diploid *Erectoides* and diploid and tetraploid species of section *Arachis* has been corroborated using such manipulations (Singh 1998). In vitro embryo rescue overcoming postzygotic incompatibility has helped establish hybrids between *A. hypogaea* cv. MK 374 and *A. glabrata* (Mallikarjuna and Sastri 2002). These approaches has also helped improve the success rate between some difficult crosses within section *Arachis*, like the success rate in cross, *A. hypogaea* ($2n = 40$) × *A. kempff-mercadoi* ($2n = 20$) increased significantly by culturing immature seeds in vitro (Mallikarjuna et al. 2004). Thus approaches to access the genetic resources (diversity) from tertiary gene pool are under initial stages of hybrid establishment and need further efforts for incorporation of desired genes into stable tetraploid *A. hypogaea*-like interspecific derivatives for use in conventional breeding efforts.

2.6.4 Molecular Breeding

Molecular markers and dense genetic linkage map are necessary for the application of marker-assisted breeding in crop improvement. Infrequent and low polymorphisms have restricted the progress in the development and application of genetic maps in groundnut breeding except in cases where polymorphic chromosomal regions have been introgressed into *A. hypogaea* from diploid relatives. Pandey et al. (2012) reviewed the advances in *Arachis* genomics. Their publication lists *Arachis* markers in public domain, main populations used in *Arachis* genomics research, details of some major genetic maps constructed in *Arachis* species and QTLs identified for some economically important traits in groundnut.

2.6.4.1 Genetic Maps of Cultivated Groundnut

A few maps constructed earlier were based on diploid or interspecific tetraploid populations (Halward et al. 1993; Moretzsohn et al. 2005, 2009). Varshney et al. (2009) were the first to report the construction of a genetic map for cultivated groundnut by screening 1145 SSR markers on two genotypes (TAG 24 and ICGV 86031), which are the parents of a recombinant inbred line (RIL) population. A total of 135 SSR loci were mapped into 22 linkage groups. Hong et al. (2010) constructed a composite linkage map from three individual linkage maps constructed from each of the three RIL populations which had common female parent Yueyou 13. The composite linkage map consisted of 22 composite linkage groups with 175 SSR markers covering a composite map length of 885.4 cM with an average marker density of 5.8 cM. Based on segregation data from RIL population of cross TAG 24 × GBPD 4, Khedikar et al. (2010) developed a partial linkage map with 56 SSR loci over 14 linkage groups. In an integrated map derived from two cultivated × cultivated RIL populations, Qin et al. (2012) anchored 324 SSR markers covering 1352.1 cM map distance with 21 linkage groups. Gautami et al. (2012b) constructed a consensus genetic map for drought tolerance traits based on three genetic maps developed from three RIL populations—reference map based on TAG 24 × ICGV 86031RIL population with 191 SSR loci (Varshney et al. 2009) and two other new maps based on—ICGS 76 × CSMG 84-1 RIL population with 119 SSR loci and ICGS 44 × ICGS 76 RIL population with 82 SSR loci. The consensus map spanned 2840.8 cM map distance with 293 SSR loci distributed over 20 linkage groups. Based on 11 populations, Gautami et al. (2012a) constructed an international reference consensus map for tetraploid groundnut with 897 marker loci (895 SSR loci and two cleaved amplified polymorphic sequence (CAPS)) distributed on 20 linkage groups and spanning a map distance of 3863.6 cM with an average map density of 4.4 cM.

2.6.4.2 Marker-Assisted Breeding

Identification of molecular markers associated with traits of interest and detection of QTLs through linkage mapping are the two prerequisites for application of marker-assisted breeding in crop improvement program. Stalker and Mozingo (2001) and Dwivedi et al. (2003) have comprehensively reviewed the history of marker development in groundnut. Initially, RAPD and RFLP markers were used to screen groundnut germplasm and/ or tetraploid interspecific breeding lines. However, they were not ideal for marker-assisted breeding for various reasons. Now simple sequence repeat (SSR, also known as microsatellites) are the markers of choice for molecular breeding in most crops. The SSR markers are preferred because of their abundance and uniformity of distribution throughout most of the genome, their multiallelic, codominance inheritance, and their highly polymorphic and reproducible nature where analysis is simple and readily transferable (Weber 1990). Different types of markers have been reported for almost all biotic stresses [root knot nematode (Burow et al. 1996), ELS and LLS (Stalker and Mozingo 2001; Khedikar et al. 2010), rust (Varma et al. 2005; Mondal et al. 2008, 2012), aflatoxin contamination (Milla et al. 2005), sclerotinia blight (Chenault and Maas 2005), aphids (Herselman et al. 2004), bruchid (Mondal et al. 2014)] and other traits [high oleic trait (Patel et al. 2004)] in groundnut. The number of polymorphic SSR markers for different traits are increasing fast.

Marker-assisted backcrossing (MABC) is extensively used to introgress transgene or major loci or a major QTL into a cultivar. Depending on the population size and considering one or two target loci, two to three backcrosses are generally sufficient to recover most of the recipient genome. The marker-assisted recurrent selection (MARS) and genomic selection (GS) approaches are practiced to accumulate favorable alleles with small effects in a genotype under improvement. The latter rather than relying on mapped loci uses breeding values, which are calculated based on high density genotypic data and historical phenotypic data from a 'training population' usually made up of breeding lines. The status of marker-assisted breeding for different traits in groundnut is summarized below.

Foliar fungal diseases: From composite interval mapping based on genotypic and phenotypic data from RIL population of TAG 24 × GPBD 4 cross, Khedikar et al. (2010) identified 11 QTLs for LLS in three environments explaining only 1.7–6.5 % phenotypic variation. Employing bulk segregant analysis, Shoba et al. (2012) identified three primers among the polymorphic SSR markers, which were able to distinguish between LLS resistant and susceptible bulks and individuals in $F_{2:3}$ progenies of TMV 2 (susceptible parent) × COG 0437 (resistant parent) cross. In single marker analysis, they found seven markers linked to LLS severity score, which explained 32–59 % phenotypic variation. They recommended use of PM 384 marker in marker-assisted breeding over a wide range of genetic backgrounds. Shoba et al. (2013) identified one QTL each for 100-kernel weight and LLS severity score. The former explained 6.1 % variation and the latter 37.9 % phenotypic variation in respective characters. The QTL for LLS can be effectively utilized in marker-assisted breeding for resistance to LLS.

Varma et al. (2005) studied F_2 populations of ICGV 99003 × TMV 2 and ICGV 99005 × TMV 2 crosses and identified two SSR alleles in the former and seven in the latter associated with rust resistance. Mondal et al. (2008) studied F_2 population of 117 individuals of VG 9514 × TAG 24 cross. Contrary to the earlier published reports of rust resistance being recessive and governed by a few genes, they reported it to be dominant and governed by a single gene in this cross between cultivated types. In their study, only 11 RAPD markers out of 160 showed polymorphism between two parents. Using bulk segregant analysis, they identified J 7 (1300) as a suitable marker for marker-assisted selection. From another study, Mondal et al. (2012) identified two EST-SSR markers (SSR_GO340445 and SSR_HO115759) closely linked to rust resistance, which were suitable candidates for marker-assisted selection.

Aflatoxin contamination: Using microarray analysis in A 13 cultivar, which is resistant to drought and preharvest aflatoxin contamination by *A. parasiticus*, Lu et al. (2005) identified 25 upregulated, commonly expressed genes when the cultivar was challenged by both drought and preharvest *A. parasiticus* infection. Of these, 20 were validated by real-time PCR. After characterization of each of these genes, appropriate gene probes can be developed for application in breeding programs. Liang et al. (2009) reported six QTLs, each located on a different linkage group, for resistance to *A. flavus* invasion, which could explain phenotypic variation ranging from 6.2 to 22.7 %.

Tomato spotted wilt virus (TSWV): Qin et al. (2012) identified two major QTLs for resistance to TSWV disease.

Insect pests: Mondal et al. (2014) identified two main QTLs for component traits associated with bruchid resistance. The QTL for total developmental period (TDP) explained 57–82 % phenotypic variation and that for adult emergence (AE) explained 13–21 % phenotypic variation. Additionally, three QTLs for TDP, AE and number of holes and one QTL for pod weight loss, which were also identified, explained 14–39 % phenotypic variation.

Nematode resistance: Marker-assisted selection in groundnut was first used in breeding for resistance to root knot nematode (*M. arenaria*). Burow et al. (1996) identified three RAPD markers linked to root knot nematode resistance, which was due to a single dominant gene. Subsequent studies by Choi et al. (1999), while confirming the single dominant gene nature of the resistance in some populations, also indicated the possibility of a second gene for resistance and evaluated the utility of these markers as selectable markers. Using marker-assisted selection, Chu et al. (2011) combined the root knot nematode resistance and high oleic trait leading to the development of Tifguard High O/L genotype. In addition to saving time, they also reported a significant reduction in the amount of breeding material carried through the breeding program by following marker-assisted selection.

Drought: Varshney et al. (2009) reported 2–5 QTLs for T, TE, SLA, and SCMR, which explained only 3.5–14.1 % phenotypic variation for these traits. Based on identification of few major and many minor QTLs and QTL × QTL interactions, Ravi et al. (2011) confirmed the complex and quantitative nature of drought tolerance in groundnut. Gautami et al. (2012b) identified 153 main effect QTLs and 25

epistatic QTLs with drought-tolerance-related traits. As no major QTL for drought adaptation was identified, Ravi et al. (2011) and Gautami et al. (2012b) recommended adoption of MARS and GS approaches to introgress a large number of QTLs to breed drought-resistant groundnut genotypes.

High oil/oleic acid content: Huang et al. (2012) reported that three SSR alleles associated with high oil content in wild *Arachis* species, are absent in cultivated groundnut. Using wild *Arachis* species, the oil content of cultivated groundnut can be increased. From the study of Yuanza 9102 × Zhonghua 5 RIL population, Huang et al. (2011) found 2A5-250/240 SSR marker tightly linked to oil content trait (2A5-250 with low oil content; 2A5-240 with high oil content). High O/L trait is reported to be dependent on two homeologous oleoyl-PC desaturase genes, *ahFAD2A* and *ahFAD2B* (Chu et al. 2009). The 4th backcross progenies, developed following marker-assisted selection, had all combinations of the two genes except ol_2ol_2 homologous mutant. The highest oleic acid content was found in progeny with all four mutant alleles (ol_1ol_1 ol_2ol_2) (Mienie and Pretorius 2013). Chu et al. (2011) developed Tifguard High O/L cultivar after three accelerated backcrossing and following marker-assisted selection among progenies to combine nematode resistance from Tifguard and high O/L trait from Georgia-02C and Florida-07.

2.6.5 Genetic Transformation

In a recent publication, Sunkara et al. (2013) discussed the progress and prospects of transgenic interventions in the improvement of groundnut. They have also listed responses of various explants and hormones on in vitro shoot regeneration and an update on genetic transformation of groundnut. The commonly used methods for DNA delivery or gene transfer into organogenic or embryogenic cultures of groundnut are either biological using *Agrobacterium tumefaciens* or by direct gene transfer using microprojectile/particle bombardment or by electroporation. The choice of method depends on several factors including laboratory facilities and technical skills available and the cultivar and regeneration system used. The first successful transformation and accompanying plant generation using microbombardment technique in groundnut was reported by Ozias-Akins et al. (1993). However, the efficiency of genetic transformation was low and the process took many months for plants to mature. Sharma and Anjaiah (2000) developed a different protocol for genetic transformation with *Agrobacterium tumefaciens*, which works with a wider range of groundnut genotypes. The direct regeneration system adopted in the above protocol favors genetic transformation because of advantages of de novo production of shoot primordial synchronous with the period of cellular differentiation, rapidity of morphogenesis and lack of requirement for frequent subcultures.

Ozias-Akins (2007) compiled a list of stable transformation up to 2005 in cultivated groundnut. Genetic transformation efforts in groundnut cover a wide range of abiotic and biotic stresses. These include drought and salinity in abiotic stresses

and LLS, ELS, rust, *Aspergillus flavus* and sclerotinia blight in fungal diseases, GRD, PSND, PBND, TSWV, PStV, and PCV in virus diseases, bacterial wilt, *Spodoptera litura*, *Helicoverpa armigera* and lesser corn stalk borer in insect pests and vitamin A biofortification, oil quality, and herbicide tolerance. The genetic transformation research in groundnut is at a slow pace because of the restriction in testing and ban on commercializing transgenics in many countries.

Biotic stresses: In most cases, the level of resistance achieved through transgenic is more or less similar to that achieved through conventional breeding. However, transgenics do provide opportunity to combine conventional resistance with that of nonconventional resistance to improve the level of protection against pathogen or stress factors.

Several genes have been used to develop transgenic events with resistance to fungal diseases in groundnut. These are listed in the paper by Sunkara et al. (2013) and include glucanase, chitinase, SniOLP, and Rs-AFP2 for LLS and ELS, chitinase for rust, oxalate, glucanase, and chitinase for sclerotinia blight and Stilbene synthase, glucanase, chitinase, mod1, anionicperoxidase, synthetic peptide D4E1, LOX 1, Nonheme chloroperoxidase (cpo), and Pn LOX 3 for *A. flavus* infection and aflatoxin biosynthesis. These genes suppressed the disease, delayed the onset of disease, enhanced resistance, and decreased disease incidence. In the case of sclerotinia blight, reduced lesion area and in the case of *A. flavus,* reduced aflatoxin contamination was also observed. Transgenic lines of Okrun cultivar with rice chitinase and an alfalfa glucanase gene showed up to 43–100 % reduction in incidence of sclerotinia blight compared to the parent variety in the field (Chenault et al. 2005).

Virus disease: Compared to fungal diseases, virus diseases have received greater attention in transgenic research. The protein-mediated resistance, in general, offers only moderate protection against a broad range of related viruses, while RNA-mediated resistance offers high levels of protection, but only against closely related strains of a virus (Dawson 1996). RNAi technology (RNA silencing or cosuppression of homologous genes) provides a significant tool for developing virus resistant groundnut genotypes (Wang et al. 2000).

In case of PBND, both *A. tumefaciens*- and microprojectile-mediated genetic transformation approaches using PBNV nucleocapsid gene encoding for viral coat protein are being pursued. Transgenic events with $PBNV_{np}$ gene, developed at ICRISAT, showed lower incidence and delayed onset of disease and also recovery from disease suggesting only a modest tolerance to PBNV. Currently, RNAi-mediated approach is being followed to counter the effect of nonstructural silencing suppressor gene (NSs gene) in the PBNV genome.

For TSWV, the protection of transgenic plants is under both RNA- and protein-mediated control (Yang et al. 1998). These approaches include using both sense and antisense TSWV nucleocapsid protein gene (N gene) expression. Nucleocapsid protein gene (NP) has been introduced via microprojectile bombardment into New Mexico Valencia A cultivar (Li et al. 1997) and a runner cultivar (Chenault and Payton 2003). *A. tumefaciens*-mediated transformation is also followed. AT 120 (with antisense nucleocapsid gene) (Magbanua et al. 2000)

and Marc 1 (with coat protein gene) (Ozias-Akins et al. 2002) cultivars were also transformed. Expression of sense or antisense NP gene from TSWV delayed expression of symptoms and prevented systemic virus infection but did not provide complete resistance to the disease. This single gene resistance may be short-lived because of highly heterogeneous population of the virus. Use of stable pathogen-derived resistance based on homology dependent RNA silencing for durable TSWV resistance has been suggested by Bucher et al. (2003).

For PStV, transgenic plants of Gajah and NC 7 cultivars containing one of the two forms of PStV coat protein gene (*cp* 2 or *cp* 4) exhibited high levels of RNA-mediated resistance (Higgins et al. 2004). The PStV resistance in transgenic groundnut cv. Gajah was stable up to seven generations of selfing (Hapsoro et al. 2005, 2007).

PSND transgenics produced following *A. tumefaciens*-mediated transformation with TSV coat protein gene (TSV_{cp} gene) showed three symptoms—blockage of systemic movement of the virus within the plants, recovery from an initial infection and subsequent new growth devoid of disease symptoms and susceptible reaction. Transgenic lines cv. JL 24 containing sense and antisense coat protein gene of TSV were developed using *A. tumefaciens*-mediated transformation (Bag et al. 2007). However, these lines are yet to be tested for disease reaction at hotspot locations under field conditions.

Transgenic lines having $IPCV_{cp}$ and $IPCV_{rep}$ genes of Indian peanut clump were produced following *A. tumefaciens*-mediated transformation and tested under containment facilities at ICRISAT. Some events showed resistant phenotype where the virus titer declined with maturity.

For GRD, pathogen-derived resistance (introduction of GRAV or GRV genomic sequences or genes or *Sat*RNA-derived sequences that down regulate GRV replication) is a potential strategy for controlling the disease through generation of transgenic plants (Taliansky et al. 1996). Groundnut transgenics having $GRAV_{cp}$ gene were developed at ICRISAT and are currently being tested in South Africa.

Insect pests: Synthetic genes, *cry1 EC* against *Spodoptera litura* (Tiwari et al. 2008), *cry1 X* against *Helicoverpa armigera* and *S. litura* (Entoori et al. 2008), and *cry1 Ac* against lesser cornstalk borer (Singsit et al. 1997) have shown good promise against respective insect pests.

Abiotic stresses: In drought, the DREB group of transcription factors has received greater attention in developing drought-tolerant varieties in various crops through transgenic research. Selected transgenic events of JL 24 cultivar containing DREB 1A transcription factor driven by rd29A promoter showed higher TE under both well-watered and water-limiting conditions with one event recording as high as 40 % more TE over untransformed control (Bhatnagar-Mathur et al. 2007). All DREB 1A transgenic events had significantly higher seed filling under drought and displayed 20–30 % lower pod yield reduction than their untransformed counterpart under drought stress (Bhatnagar-Mathur et al. 2014). Water stress promotes rooting growth more strongly in DREB 1A transgenic events than in the wild type especially in deeper soil layers leading to increased water extraction. Qin et al. (2011) reported that regulated expression of isopentenyltransferase gene (IPT) significantly

improved drought tolerance in groundnut. Transgenic plants maintained higher photosynthetic rates, higher stomatal conductance, higher transpiration and recorded higher yields than wild types under reduced irrigation conditions.

For salinity, transgenic events with AtNHX1 gene have been studied in a limited way. Asif et al. (2011) reported that over expression of AtNHX1 gene, isolated from Arabidopsis and driven by 35S promoter, in groundnut not only improved salt tolerance but also drought tolerance in transgenic events. Banjara et al. (2012) also reported increased tolerance of salt in transgenic events carrying AtNHX1 gene in groundnut. AhNHX1 gene from groundnut has been isolated and its important role in salt tolerance in groundnut has been confirmed.

Nutritional quality: Zmpsy 1 gene from maize and *β*-lycopene cyclase gene from tomato are being used to enrich groundnut seeds with *β-carotene* (pro- vitamin A). Second-generation transgenic events showed many fold increase in vitamin A content (Bhatnagar-Panwar et al. 2013). For Oleic/Linoleic fatty acid ratio (O/L ratio), an FAD2 gene RNAi construct was transformed into groundnut to reduce content of linoleic acid and increase the stability of groundnut oil (Zhang et al. 2007; Huang et al. 2008; Yin et al. 2009). Seeds from the transgenic plants showed an increased O/L ratio (Huang et al. 2008). Endogenous *allergens*, Ara h 2 and Ara h 6, were silenced by introducing RNAi construct targeting homologous coding sequence and human IgE binding to these proteins was greatly reduced (Dodo et al. 2008; Chu et al. 2008)

Herbicide tolerance: *Agrobacterium*-mediated transgenic groundnuts over expressing pEGAD-EPSPS with altered kinetics of enzyme showed improved tolerance to glyphosate (Manjunatha et al. 2008).

2.7 Conclusions

Arachis gene pool consisting of cultivated groundnut from 95 countries and 80 wild relatives naturally distributed in five major countries of South America offers a reservoir of genetic diversity for genetic improvement of groundnut crop. Significant progress has been made in collection and conservation of the available natural genetic variation in the repositories located in major groundnut-growing regions/countries. However, the assembled genetic variation is skewed and is limited in case of vars. *aequatoriana, peruviana* and *hirsuta.* Similarly, wild species gene pool that offers significant variability, particularly for biotic and abiotic stresses, has been understood very little in terms of genetic diversity within species. Collection of large amount of genetic diversity/collections has created a problem of plenty and use of genetic variability has been very limited, producing cultivars with very narrow genetic base. To improve understanding and quantification of genetic diversity, core collection approach has been vigorously advocated in the last two decades. However, there is no hard data to suggest that it has improved use of genetic diversity and needs further look to make these core collections more dynamic and true representative of total genetic diversity,

particularly useful diversity of breeding value to facilitate management of yield constraints, and to meet the needs of diverse agroclimatic and production conditions. The successful exploitation of several wild species of secondary gene pool, incorporating gene(s) conferring resistance to major biotic stresses once again highlight the importance of wild relatives in genetic enhancement/improvement of crop species. However, access to genes from tertiary gene pool is still limited, confined to initial hybrids, while the quaternary gene pool is yet to be tapped.

Conventional breeding has been effective in some areas, while in others it has been tardy due to lack of proper and effective phenotyping tools and limited understanding of the underlying mechanisms influencing targeted traits. Being largely a rainfed crop, the genetic gains in yield potential are likely to be low and slow to come by. In such situations, resistance breeding efforts are going to be more rewarding in improving realized yield. Resistance to soil-borne diseases including *A. flavus* infection and aflatoxin contamination and insect pests requires greater attention in groundnut improvement programs. However, for effective genetic enhancement in these areas, better and effective screening methods/tools and a clear understanding of underlying mechanisms of resistance are required. Information on inheritance/genetics of several traits is either lacking or limited. This knowledge gap needs to be filled in to devise better strategies for crop improvement. A greater diversification of parental resources in breeding programs is required to develop new cultivars with diversified genetic backgrounds, which will enable them to perform better under adverse conditions. Along with crop improvement research, the crop management research also needs to be pursued vigorously to harness the full potential of improved cultivars in a synergistic manner.

2.8 Future Perspective

More exploration is required in areas of distribution of *aequatoriana, peruviana,* and *hirsuta* varieties to obtain their comparative representation in collections and in core collection of global genetic diversity. Recognizing the presence of higher genetic variation, allelic diversity and presence of greater unique alleles in wild *Arachis,* greater efforts are needed for searching new genes/alleles in wild *Arachis* with intensive evaluation and proper characterization.

To improve the use of genetic diversity in groundnut improvement, the core collection needs to be made more dynamic. To achieve this the gene pool concept can be extended to total collections, stratifying them for specific diversity of breeding value, such as early maturity, accessions with genes conferring resistance to various biotic and biotic stresses, nutritional characters, etc. This is followed by principal component/multivariate analysis on quantitative agronomic traits and clustering, and selective picking of accessions representing taxonomic and geographic affinities, facilitating encompassing of total spectrum of useful variability to formulate an *active core collection* that can meet most requirements for genetic improvement of groundnut with precise breeding.

Crop improvement efforts, both conventional and nonconventional in groundnut needs to concentrate on bridging the yield gap between the potential yield and the realized yield, by alleviating major production constraints particularly in rainfed environment. The specific issues that require attention are listed below.

- Most of the foliar diseases resistant cultivars have a high level of resistance to rust. However, levels of resistance to both leaf spots in cultivars need further improvement without compromising on agronomic characters including crop duration as it often gets enhanced with higher levels of resistance. It may be desirable to intermate foliar diseases resistant second- or third-generation advanced breeding lines originating from different parents including interspecific derivatives to improve the level of resistance without bringing in linkage drag. Further, resistance to foliar diseases needs to be incorporated in short-duration cultivars without affecting their duration.
- To enhance effectiveness of aflatoxin resistance breeding, sampling procedures and screening methods need major refinement to improve characterization and precise estimation of infection and aflatoxin production. Ascertaining allelic relationship among resistant sources would help gene pyramiding.
- Breeding for resistance to soil-borne diseases needs impetus as these have increased over time resulting in significant plant mortality in the field. For this to happen, sources with higher levels of resistance and effective screening techniques are required. Resistance of wild *Arachis* species, where available, should be effectively exploited.
- Combining virus resistance with that of the vectors shall help reinforce the resistance against virus diseases. This may include application of newer approaches such as RNAi technology. In the case of GRD, the off-season survival of the disease causing agents is still a mystery and needs to be investigated for better disease management. There is a need to look for diversified sources of resistance to GRD and identify sources of resistance to GRAV in primary gene pool. Efforts for incorporation of GRAV resistance from wild *Arachis* species needs to be initiated. Additionally, allelic relationship between *A. hypogaea* sources and wild *Arachis* species should be studied to identify new resistance genes. For further reinforcement of resistance, aphid resistance should be incorporated. In Africa, developing GRD-resistant, short-duration, and high-yielding varieties with traits acceptable to farmers, traders and consumers should remain a high priority.
- More studies are needed to understand genetics and mechanisms of resistance to bacterial wilt disease. To obtain stable resistance against the disease, harnessing genes from diverse sources including wild *Arachis* species is required, besides combining it with resistance to rust and leaf spots.
- To breed resistance to insect pest, wild *Arachis* species, which show high levels of resistance, should be accessed with refined field screening techniques ensuring uniform desired pressure of insect pests. The resistance to nematodes may be combined with resistance to other stresses to derive larger benefits.

- Drought-tolerant cultivars are needed in different maturity groups along with resistance/tolerance to aflatoxin contamination. Adoption of marker-assisted recurrent selection (MARS) to accumulate several QTLs with small effects on drought tolerance in a single genotype will be helpful.
- Diversification of sources of earliness and studies on their genetic constitution and allelic relationships is needed to identify different genes for earliness which could be accumulated in a desired genotype.
- More efforts are needed in genomics research to saturate the linkage map of groundnut so that effective use of marker-assisted selection could be made in groundnut improvement.

The success achieved in genetic improvement of groundnut using wild species of secondary gene pool emphasizes the need for utilization of more wild species in genetic enhancement of *A. hypogaea* to produce better genetic resource of genes/alleles that can help in widening the genetic base of crop with sustainable resilience against biotic stresses and thereby yield. To access genes from tertiary and quaternary gene pools, efforts need to be extended to recombinant DNA technology using cis-transgenic approach, which shall partially dispel the negative apprehensions of environmentalists.

Emerging molecular tools provide an opportunity to enhance efficiency and effectiveness of the conventional breeding particularly for complex traits, which are multigenic. A holistic approach integrating conventional breeding, molecular breeding and transgenics will provide solutions to complex problems being currently faced in groundnut improvement. However, in the case of transgenic research, issues related to biosafety need to be dealt appropriately. In future, breeding programs will have to focus on developing customized cultivars to meet the requirements of the food industry. The new cultivars will have to be climate resilient to face the looming challenges of the climate change felt across the world.

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