MOLECULAR BREEDING OF GROUNDNUT FOR ENHANCED PRODUCTIVITY AND FOOD SECURITY IN THE SEMI-ARID TROPICS: OPPORTUNITIES AND CHALLENGES

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Advances in Agronomy, Volume 80

0065-2113/03S35.00

About 94% of the world groundnut (*Arachis hypogaea* L.) production comes from the rainfed crop grown largely by resource-poor farmers. Several biotic and abiotic stresses limit groundnut productivity, together causing annual yield losses of over US $ 3.2 billion. The *Arachis* species harbor genes capable of improving both seed yield and quality in addition to imparting high levels of resistance to diseases and insect pests. Many of the wild *Arachis* species are not cross compatible with cultivated groundnut. However, efforts to overcome incompatibility in wide crosses have started to liberate resistance genes in interspecific progenies. But these progenies carry a lot of linkage drag. Marker-assisted backcross breeding should minimize the linkage drag as it greatly facilitates monitoring of introgressed chromosome segments carrying beneficial genes from wild *Arachis* to cultivated groundnut. Transgenic groundnuts with resistance or tolerance to biotic and abiotic stresses have been produced and are in various stages of characterization under containment and/or controlled field conditions. Once favorable genes are introduced into cultivated groundnut through wide crossing and/or genetic transformation techniques, these genes will become ideal candidates for marker-accelerated introgression.

DNA marker based genetic linkage map should enable breeders to effectively pyramid genes for good seed quality and resistance to biotic and abiotic stresses into agronomically enhanced breeding populations in a much shorter time than would be possible by conventional techniques. To date 110 SSR markers detected genetic variation in a diverse array of 24 groundnut landraces. However, substantial efforts are still required to develop sufficient PCR-based markers, particularly SSRs and SNPs, for the construction of high-density genetic linkage map and for the routine application in the molecular breeding in groundnut. The use of automated technologies will become increasingly important for large-scale germplasm characterization and realistic scale marker-assisted selection in groundnut. An international legume genomics initiative has been formed between USA Universities and the International Agricultural Research Centers of the Eco-Regional Alliance on legumes to translate the benefits of the "consensus legume genome" for rapid impacts on the genetic improvement of tropical legumes.

1. INTRODUCTION

A. CROP PRODUCTION AND USES

Cultivated groundnut, also known as peanut (*Arachis hypogaea* L.), is grown on nearly 24 million hectares between latitudes 40° N and 40° S with a total

global production of 34.5 million tones (FAO, 2000) Although originating in South America, the vast majority of groundnut is produced in Asia and Africa: Asia 68% (23 Mt), Africa 24% (8 Mt). The remaining 8% (3.5 Mt) comes from North America, the Caribbean, Europe and Oceania. Approximately 94% of groundnut is produced in the developing world, mostly under rainfed conditions. Fig. 1 shows the proportion of groundnut area and production in each of the major groundnut growing regions of the world. The major groundnut producing countries are China, India, Indonesia, Myanmar, and Vietnam in Asia; Nigeria, Sudan, Democratic Republic of Congo, Chad, Mozambique, Zimbabwe, Burkina Faso, Uganda, and Mali in Africa; USA in North America; and Argentina, Brazil, and Mexico in Latin America and the Caribbean (Table I).

The average (FAO, 2000) yield of groundnut in Africa is 0.9 t ha^{-1} which is markedly lower than groundnut yields in Asia (1.7 t ha^{-1}) and in Latin America and the Caribbean (1.8 t ha^{-1}), while yields are by far the highest in North America (2.9 t ha^{-1}) and China (3.1 t ha^{-1}). The largest groundnut acreage in Asia occurs in India. However, India ranks below China in total production, as its average yield is 1.0 t ha^{-1}. The key factors contributing to higher yields in China are (1) introduction of improved varieties presently covering 90% of the total groundnut area, (2) adoption of improved cultural practices including crop rotation and polythene film mulching, (3) rewards to groundnut growers for producing higher yields, and (4) national policies for price support systems and marketing opportunities (Shuren *et al.,* 1996). In contrast, groundnut yields in Africa are very low with many countries reporting yields as low as 0.5-0.8 t ha^{-1}. Although the Latin American and the Caribbean regions contribute only 3.4% of the world groundnut production, high yields of 2.2 t ha^{-1} in Argentina and 1.8 t ha^{-1} in Brazil have been reported.

Groundnut (33 Mt) is one of the world's most important oilseeds crop, along side soybean (154 Mt), cottonseed (52 Mt), rapeseed (42 Mt), and sunflower (29 Mt) (FAO, 1999). It is also a rich source of edible oil and vegetable protein

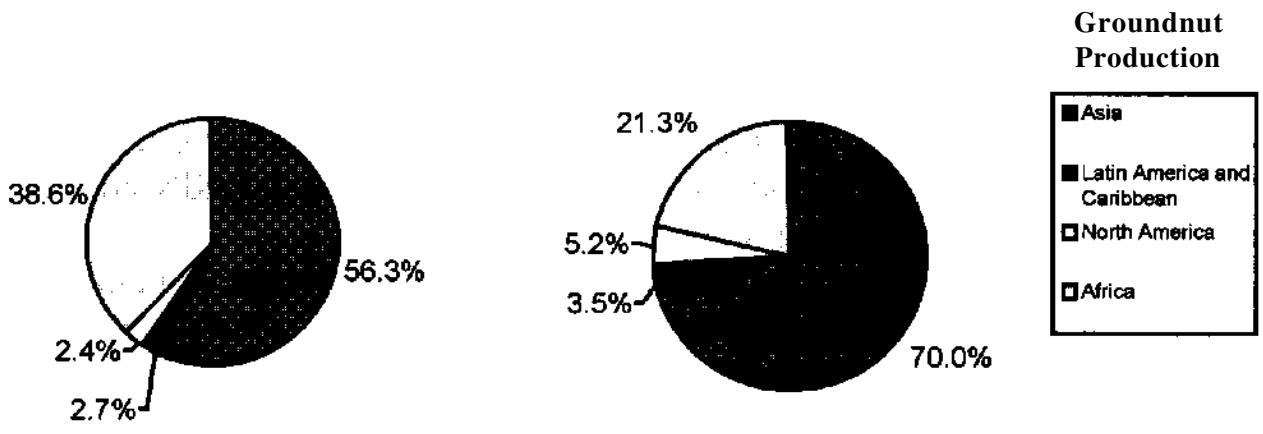

Figure 1 The average groundnut land area and yield production (expressed as %) of the major groundnut growing regions of the world for the period from 1998 to 2000.

Table I
The Major Groundnut Producing Countries in Asia, Africa, North America, and Latin America with the Caribbean and Proportionate Contribution (%) to the Global Groundnut Area and Production

Region	Country	Area in '000 ha[a]	(%)	Production in '000 t[a]	(%)
Asia	India	7207	30.5	7017	20.9
	China	4297	18.2	13243	39.5
	Indonesia	650	2.8	973	2.9
	Myanmar	489	2.1	580	1.7
	Vietnam	255	1.1	341	1.0
Africa	Nigeria	2643	11.2	2700	8.1
	Sudan	1417	6.0	934	2.8
	Congo	525	2.2	397	1.2
	Chad	419	1.8	471	1.4
	Zimbabwe	227	1.0	121	0.4
	Burkina Faso	215	0.9	215	0.6
	Uganda	198	0.8	139	0.4
	Mali	160	0.7	150	0.4
North America	USA	569	2.4	1675	5.0
Latin America and the Caribbean	Argentina	311	1.3	658	2.0
	Brazil	101	0.4	185	0.6
	Mexico	92	0.4	134	0.4
Developing countries		22919	97	31522	94
Developed countries		709	3	1941	6
World		23628		33493	

[a]Average of 1998-2000 figures of FAO data (http://www.fao.org).

(Weiss, 1983). Approximately 53% of the total global production of groundnut is crushed for high quality edible oil, 32% for confectionery consumption, and the remaining 15% is used for feed and seed production (FAO, 2000). However, there has been a gradual shift away from the use of groundnut as oil and meals to confectionery consumption, particularly in Asia, Latin America, and the Caribbean (Freeman *et al.,* 1999). Figure 2 shows the proportion of in-shell groundnut production used for oil extraction, confectionery, and feed/seed uses in the major groundnut producing regions in the world.

The cake remaining after groundnut oil extraction can be used in human food or incorporated into animal feeds (Savage and Keenan, 1994). Groundnut haulms constitute approximately 45% of the total plant biomass, and provide excellent forage for cattle. Haulms are rich in protein and more palatable than many other fodders (Cook and Crosthwaite, 1994). Wild *Arachis* species (*Arachis pintoi* and *A. glabrata)* have been used for pasture improvement in North America,

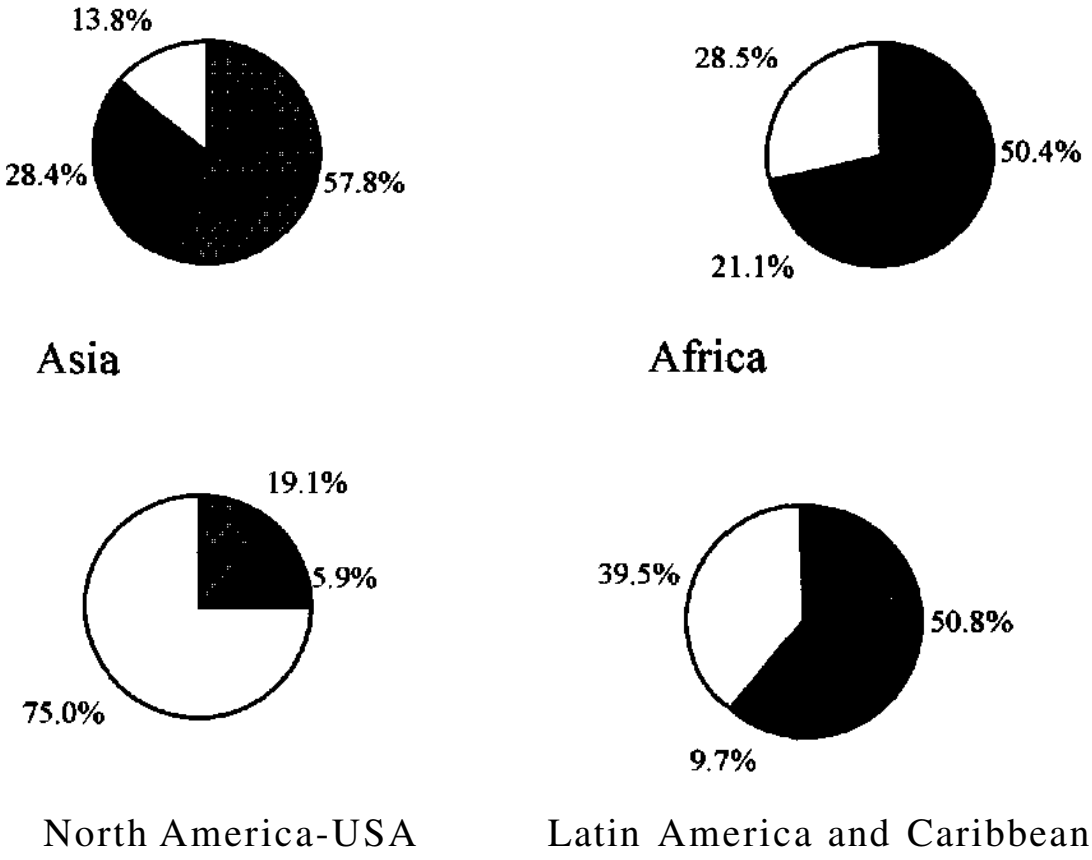

Figure 2 Average in-shell groundnut usage patterns in major groundnut producing regions in the world during the period from 1997 to 1999.

Central America and Mexico, South America, and Australia (Kerridge and Hardy, 1994). The greater adaptability of rhizoma perennial peanut (*A. glabrata*) to the tropical environment, and its high yield when harvested for hay, give it the potential of becoming one of the most important forages in the tropics (Ruiz *et al.*, 2000). The nutritive values of *A. glabrata* cultivar Florigraze and *A. pintoi* are higher than that of most tropical forage legumes of commercial importance (Kerridge and Hardy, 1994).

Figure 3 shows the distribution of market shares for shelled groundnut seeds entering international trade from the groundnut producing regions of the world

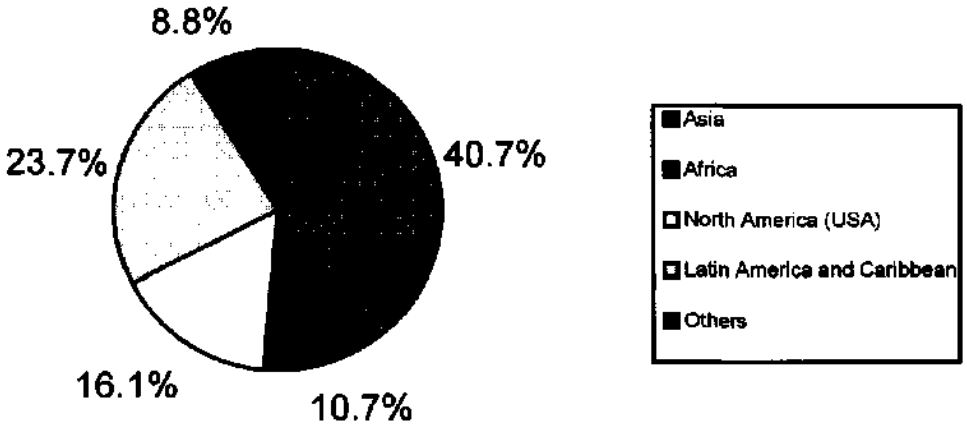

Figure 3 The average distribution of international trade market share for shelled groundnut seeds exported from the major groundnut producing regions of the world for the period from 1997 to 1999.

(FAO, 2000). The major exporting countries are China, India, and Vietnam in Asia; South Africa, Sudan, Zimbabwe, and Senegal in Africa; USA in North America; and Argentina in Latin America and the Caribbean.

B. CONSTRAINTS TO PRODUCTION

Groundnut is extensively grown in the semi-arid tropics (SAT) by resource-poor farmers where many abiotic and biotic factors limit its productivity and seed quality. The major abiotic factors affecting groundnut production include drought, low availability of phosphorus especially under acidic soil conditions, and non-availability of iron in calcareous soils. The major biotic constraints to groundnut production are

Diseases	Fungi	Rust (*Puccinia arachidis* Speg.), early leaf spot (ELS) (*Cercospora arachidicola* Hori), and late leaf spot (LLS) [*Phaeoisariopsis personata* (Berk, and Curtis) Deighton]
	Virus	Groundnut rosette disease (GRD), peanut clump virus (PCV), peanut bud necrosis virus (PBNV), and tomato spotted wilt virus (TSWV)
	Bacterial	Bacterial wilt [*Burkholderia solanacearum* (E.F. Smith) Yabuuchi *et al.*]
	Nematodes	*Meloidogyne, Scutellonema, Pratylenchus, Helicotylenchus, Aphelenchoides, Telotylenchus,* and *Paralongidorus* species
Insect pests	Field pests	Leaf miner [*Aproaerema modicella* (De-venter)], army worm (*Spodoptera litura* Fab.), corn earworm (*Helicoverpa armigera* Hubner), lesser corn stock borer (*Elasmopatpus lignosellus* Zeller), southern corn rootworm (*Diabrotica undecimpuctata howardiJlaiber*), thrips (*Frankliniella* and *Scirtothrips* species), jassids (*Empoasca kerri* Pruthi), aphids (*Aphis craccivora* Koch.), and termites (*Microtermesand Odontotermes* species)
	Storage pests	Bruchid (*Caryedon serratus* Olivier), red flour beetle (*Tribolium castaneum* Herbst), rice moth (*Corcyra caphalonica* Stainton), and pod-sucking bug (*Elasmolomus* (*Aphanus*) *sordidus* Fab.)

Rust, early leaf spot, and late leaf spot are widely distributed foliar diseases of groundnut (Subrahmanyam *et al.,* 1984; 1985c; Waliyar, 1991). Groundnut rosette disease is the most destructive disease of groundnut in sub-Saharan Africa. It is not present in Asia or in Latin America or the Caribbean. The two main forms of the disease are chlorotic and green rosette (Hayes, 1932; Smart, 1961; Hull and Adams, 1968). Chlorotic rosette is the most common in southern,

eastern, and central Africa whereas green rosette is the most common in West Africa (Subrahmanyam *et al.,*1977; 1991). There are three agents that interact to produce rosette disease syndrome in groundnut: groundnut rosette virus (GRV), groundnut rosette assister virus (GRAV), and satellite RNA (sat RNA) (Bock *et al.,* 1990). GRV is transmitted by aphids but only from the plants that also contain GRAV. GRAV is not mechanically transmissible and causes no apparent symptoms in groundnut. The sat RNA, which is dependent on GRV for multiplication and on GRAV for aphid transmission, is largely responsible for rosette symptoms (Murant *et al.,* 1988). Variation in sat RNA has been correlated with the different forms of rosette disease (Murant and Kumar, 1990). Peanut clump virus is an economically important soil-borne virus disease of groundnut in West Africa (Thouvenel *et al.,* 1988). It has an extremely wide host range including monocots (Reddy *et al.,* 1988), and is transmitted by the fungus vector *Polymyxa graminis* Lendingham (Ratna *et al.,* 1991). The two isolates of peanut clump virus, Indian peanut clump virus (IPCV) and West African peanut clump virus (WAPCV), are not serologically related (Reddy *et al.,* 1983). Peanut bud necrosis virus is prevalent in south Asia (Reddy *et al.,* 1995) and tomato spotted wilt virus predominates in North America (Reddy *et al.,* 1991). Root-knot diseases caused by *Meloidogyne* species of nematode are widely distributed in Asia, Australia, and North America. The widely distributed nematode species causing substantial damage in groundnut in Africa are *Scutellonema, Pratylenchus, Helicotylenchus, Aphelenchoides, Telotylenchus,* and *Paralongidorus* (Sharma *et al.,* 1991; 1992). Bacterial wilt of groundnut is prevalent in South East Asia, the Far East, and Uganda (Hayward, 1990). It also infects many other crop plants including potato *(Solarium tuberosum* L.), tomato (*Lycopersicon esculentum* Mill.), tobacco (*Nicotiana* sps.), pepper (*Capsicum* sps.), eggplant (*Solarium melongena* L.), and ginger (*Zingiber officinale* Rose). The species is highly heterogenous (Bradbury, 1986). Isolates are classified into five races based on host range (Buddenhagen and Kelman, 1964; He *et al.,* 1983), and into five biovars based on biochemical characteristics (Hayward, 1964; He *et al.,* 1983). Race 1 isolates cause wilt in groundnut and in many other leguminous and solanaceous plants. Biovar 1 isolates cause wilt of groundnut in the USA; biovar 3 and to a lesser extent biovar 4 isolates cause wilt of groundnut in Asia and Africa (Hayward, 1991). Aflatoxins are a serious quality problem because they are carcinogenic and immunosuppressive agents. Their presence, therefore, influences marketing of groundnut kernels as well as cake. Aflatoxins are produced by *Aspergillus flavus* Link ex Fries. The harmful effects of aflatoxin contaminated confectionery and groundnut cake have been reported (Mehan *et al.,* 1991). Aflatoxin contamination in food and livestock feed is particularly severe in the developing countries of Africa, and South and South East Asia.

Unlike the diseases listed above, insects are occasional pests of groundnut, and their distribution is erratic and localized even within regions. The only groundnut insect pests of economic significance are leaf miner in South Asia, armyworm in

South East Asia, and termite in Africa (Wightman *et al.,* 1990). The major pests in North America are corn earworm, lesser corn stock borer, and southern corn rootworm (Campbell and Wynne, 1980). The important vectors of groundnut virus diseases are *T. palmi* for peanut bud necrosis (Wightman *et al.,* 1995), *F. occidentalis* and *F. fusca* for tomato spotted wilt virus (Culbreath *et al.,* 1992), *and Aphis crassivora* for groundnut rosette virus (GRV) (Hull and Adams, 1968). However, thrips, jassids, and aphids are not themselves considered economically important pests of groundnut.

Table II lists the important abiotic and biotic constraints to groundnut production in major groundnut producing regions of the world. These abiotic and

Table II
Constraints to Groundnut Production in South Asia, South East Asia, Southern and Eastern Africa, Western and Central Africa, North America, and Latin America and the Caribbean Regions

Constraints	South Asia	South East Asia	Southern and Eastern Africa	Western and Central Africa	North America	Latin America and Caribbean
Rust	*	*	*	*	*	*
Early leaf spot		*	*		*	*
Late leaf spot	*	*	*	*	*	*
Aflatoxin	*	*	*	*		*
Drought	*	*	*	*		*
Groundnut rosette virus			*	*		
Nematodes				*	*	
Spodoptera	*	*				
Termites			*	*		
Sclerotium rolfsii	*				*	
Sclerotinia minor	*				*	
Pythium myriotylum	*				*	
Acidic soils		*				*
Low temperature	*	*				
Bacterial wilt		*				
Peanut bud necrosis virus	*					
Tomato spotted wilt virus					*	
Peanut clump virus				*		
Leaf minor	*					
Rhizoctonia solani					*	
Corn earworm					*	
Lesser corn stock borer					*	
Southern corn rootworm					*	

biotic stresses often occur in combinations and their severity and extent of distribution vary with cropping systems, growing seasons, and regions. The estimates of the global annual yield losses caused by these stresses and the economic value that could be brought by genetic amelioration of these in the groundnut crop are projected in Table III. High yielding, well-adapted cultivars with multiple resistances to biotic stresses and tolerances to abiotic stresses would provide enhanced and sustainable groundnut production to subsistence farmers in the SAT regions. Enhanced pest and diseases resistance would allow reduced agrochemical use while resistance to aflatoxin contamination would facilitate the production of food and feed products with reduced health risks that would be accepted for international trade.

As in other crops, weeds compete with groundnut for soil moisture, nutrients, and light and may thereby dramatically reduce yields (Wilcut *et al.,* 1995). They also harbor pests and diseases, and serve as alternate hosts. Weed competition is most severe during early crop growth stages because of the slow initial growth of the groundnut. Weeds can be effectively controlled by the application of herbicides coupled with one to two weedings at critical groundnut growth stages. However, this approach is both labor intensive and expensive. Moreover, the effectiveness of chemical weed control depends on environmental conditions, the physiological stage of the crop and weeds, soil type, moisture, organic matter, clay content and pH, and atmospheric temperature and humidity. Thus, the use of herbicides has been very limited in rain-fed groundnut in the SAT. An alternative strategy to minimize losses due to weed competition is to introduce genes for herbicide tolerance and/or early vigour into groundnut.

Table III
Economic Values of Yield Losses Associated with Abiotic and Biotic Stresses and Potential Gains that can be Realized by Genetic Enhancement in Groundnut[a]

Trait	Yield loss (US$ m)	Potential yield gain by genetic enhancement (US$ m)
Rust	467.0	242.0
Early Leaf Spot	326.0	82.0
Late leaf spot	599.0	300.0
Aflatoxin	264.0	62.0
Groundnut rosette virus	156.0	121.0
Peanut clump virus	38.0	22.0
Peanut bud necrosis virus	89.0	45.0
Leaf miner	164.0	82.0
Spodoptera	97.0	-
Drought	520.0	208.0
Low yield potential	388.0	388.0
Lack of adaptability	44.0	44.0

[a]ICRISAT Medium Term Plan, 1994-98. Volume 1, Main Report.

II. GENETIC VARIABILITY IN GROUNDNUT

The origin of genus *Arachis,* its taxonomy, cytogenetics and genomes relationships, the botanical classification, and reproductive development have been extensively covered in a recent review article by Holbrook and Stalker (2003). They also discussed in brief about the domestication of groundnut across continents, the methods and sampling techniques used by plant explorers to collect germplasm, the status of germplasm maintained at USDA Plant Introduction Station at Griffin, Georgia, USA, the descriptors used for characterizing accessions and methodologies to develop core collection, the levels of variability discovered in core collection for seed quality and biotic stresses, the preservation and regeneration techniques to maintain cultivated and wild *Arachis* species, the difficulties associated with field collection of new germplasm as well for the exchange of those germplasm that were collected after adoption of Convention on Biological Diversity treaty, the memorandum of understanding signed between ICRISAT and USDA to facilitate germplasm exchange, and the needs to collect additional wild *Arachis* species in eastern Bolivia and northwestern Paraguay and cultivated groundnuts from Columbia, Venenzuela, Uruguay, and possibly from Bolivia, and the impact of use of genetic resources in cultivar development that benefited to USA peanut fanners more than US $ 200 million annually. In the following section we discuss the status of wild *Arachis* species and cultivated groundnut accessions maintained in ICRISAT gene bank, the core collection developed involving 15,000 accessions and its significance to the breeders, the variability reported for major abiotic and biotic stresses and seed quality traits in cultivated and wild *Arachis* germplasm, the successful crosses reported between wild *Arachis* species, the gene introgression from wild *Arachis* in to cultivated groundnut, and finally the impact of plant introductions in developing elite groundnut germplasm/cultivars at ICRISAT that were either released for cultivation or used as an improved source by breeders in national breeding programs around the world.

A. WILD ARACHIS SPECIES

A database of wild *Arachis* species, compiled at ICRISAT, is now available at http://www.icrisat.org/text/research/grep/homepage/groundnut/arachis/start.htm. Gregory and Gregory (1979) reported 296 successful cross combinations that resulted in 223 intrasectional hybrids in the then sections *Arachis, Erectoides, Rhizomatosae, Caulorrhizae, Extranervosae, Triseminalae,* and *Ambinervosae* and 73 inter-sectional hybrids involving *Arachis* with *Erectoides* and *Rhizomatosae; Erectoides* with *Rhizomatosae, Caulorrhizae,*

and *Ambinervosae;* and *Ambinervosae* with *Extranervosae.* Krapovikas and Gregory (1994) further report successful intra-sectional hybrids in 8 of the 9 sections in the genus *Arachis.* They could not produce hybrids involving species within section *Trierectoides.* They also reported intersectional hybrids involving *Trierectoides* with *Erectoides* and *Procumbentes; Erectoides* with *Heteranthae, Caulorrhizae, Procumbentes, Rhizomatosae,* and *Arachis; Extra-nervosae* with *Heteranthae; Caulorhizae* with *Procumbentes;* and *Rhizomatosae* with *Arachis* and *Procumbentes.* Hybrids involving section *Arachis* with *Rhizomatosae, Heteranthae, Procumbentes,* and *Erectoides* have also been successful at ICRISAT (Mallikarjuna and Bramel, 2001; Mallikarjuna, 2002). Both pre- and post-zygotic hybridization barriers have been shown to restrict crossing between *Arachis* species. These barriers are most severe when accessions from tertiary and quaternary gene pools are crossed with *A. hypogaea,* but such barriers may also be expressed in crosses with certain accessions of the secondary gene pool.

Wild *Arachis* species harbor a range of genes conferring resistance to pests and diseases (Table IV), oil and protein contents, and oleic (O)/linoleic (L) fatty acid ratios (Table V). Some genotypes show very high levels of resistance to rust, ELS, LLS, nematodes, GRD, PBNV, thrips, jassids, leaf miner, *Spodoptera,* and aphids. Accessions belonging to 13 species in section *Arachis* show wide variation for most of the morphological traits reported (Chandran and Pandya, 2000).

B. CULTIVATED GROUNDNUT

Over 15,000 accessions of cultivated groundnut, including 6351 landraces, from 92 countries are housed at ICRISAT (India). They differ for many vegetative, reproductive, physiological, and biochemical traits including their reactions to abiotic and biotic stresses (Singh and Nigam, 1997; Rajgopal *et al.,* 1997; Upadhyaya *et al.,* 2001e; 2003). The *Arachis* genepool includes sources of resistance to rust, ELS, LLS, GRD, PBNV, *A. flavus,* bacterial wilt, leaf miner, *Spodoptera,* jassids, thrips, and iron chlorosis, and tolerance to low and high temperature and drought as well as sources of photoperiod insensitivity (Table IV), and variation in total sugars, oil and protein contents, O/L ratio, and for flavor attributes (Table V). Genotypic differences in root hair density and/or root growth in groundnut have been associated with high phosphorus (P) acquisition in P deficient soils (Wissuwa and Ae, 2001). However, much of this variability remains poorly understood and under-utilized in genetic enhancement efforts mainly because of the large number of accessions in the *ex situ* collections, lack of data on the extent of the diversity present in them for specific characteristics, and high geno-type (G) X environment (E) interactions for traits of economic importance

Table IV
Sources of Resistance to Abiotic and Biotic Stresses Reported in *A. hypogaea* and Wild *Arachis* Species in Groundnut

Trait	Resistance in *A. hypogaea* germplasm		Resistance in Wild *Arachis* species	
	Reaction to abiotic and biotic stresses	Reference	Reaction to abiotic and biotic stresses	Reference
Rust	1.7–5.0[a]	Singh *et al.*, 1997	I[b]-HR[c]	Subrahmanyam *et al.*, 1983b; Stalker and Simpson, 1995; Pande and Rao, 2001
Early leaf spot	3.6–6.3[a]	Singh *et al.*, 1997; Stalker *et al.*, 2002a,b; Stalker and Lynch, 2002	I-HR	Subrahmanyam *et al.*, 1985b; Stalker and Simpson, 1995; Upadhyaya *et al.*, 2001f
Late leaf spot	2.9–5.0[a]	Singh *et al.*, 1997; Stalker *et al.*, 2002b	I-HR	Subrahmanyam *et al.*, 1985a,b; Stalker and Simpson, 1995; Pande and Rao, 2001
Peanut bud necrosis disease	13.6–23.7%	Dwivedi *et al.*, 1995b	< 20%	Reddy *et al.*, 2000a
Groundnut Rosette disease	1.0–12.0%	Subrahmanyam *et al.*, 1998; Olorunju *et al.*, 2001	HR	Stalker and Simpson, 1995; Subrahmanyam *et al.*, 2001
Nematode	MR[e]	Holbrook and Noe, 1992; Holbrook *et al.*, 1996; 1998; Timper *et al.*, 2000; Stalker *et al.*, 2002a	R[d]	Baltensperger *et al.*, 1986; Holbrook and Noe, 1990; Nelson *et al.*, 1989; Sharma *et al.*, 1999
A. flavus Seed infection	< 15.0%	Mehan, 1989	≤5%	Thakur *et al.*, 2000
Aflatoxin contamination	< 10 $\mu g\ g^{-1}$ seed	Mehan *et al.*, 1986	22–110 $\mu g\ g^{-1}$ seed	Mehan *et al.*, 1992; Thakur *et al.*, 2000
Bacterial wilt	1–25%	Singh *et al.*, 1997; Pande *et al.*, 1998	Resistance not reported in wild *Arachis* species	

Table IV (*continued*)

Trait	Resistance in *A. hypogaea* germplasm		Resistance in Wild *Arachis* species	
	Reaction to abiotic and biotic stresses	Reference	Reaction to abiotic and biotic stresses	Reference
Thrips	R–MR	Lynch, 1990; Wightman *et al.*, 1990; Campbell and Wynne, 1980; Dwivedi *et al.*, 1996b; Rao and Wightman, 1999; Amin *et al.*, 1985; Upadhyaya *et al.*, 2001e	R	Stalker and Campbell, 1983; Stalker and Simpson, 1995; Lynch and Mack, 1995; Amin, 1985
Jassids	R–MR	Lynch, 1990; Wightman *et al.*, 1990; Campbell and Wynne, 1980; Campbell *et al.*, 1971; Rao and Wightman 1999; Amin *et al.*, 1985; Dwivedi *et al.*, 1995a; Dwivedi *et al.*, 1993b; Stalker *et al.*, 2002a; Stalker and Lynch, 2002; Upadhyaya *et al.*, 2001e	R	Stalker and Campbell, 1983; Stalker and Simpson, 1995; Lynch and Mack, 1995; Amin, 1985
Leaf miner	MR	Wightman and Rao 1994; Anderson *et al.*, 1990b; Dwivedi *et al.*, 1993b; Rao and Wightman, 1999	R–HR	Wightman and Rao, 1994; Lynch and Mack, 1995
Spodoptera	MR	Dwivedi *et al.*, 1993b; Campbell and Wynne, 1980; Rao and Wightman, 1999; Stalker and Lynch, 2002	R–HR	Wightman and Rao, 1994; Lynch and Mack, 1995
Aphids	MR-HR	Padagham *et al.*, 1990; Wightman and Rao 1994; Minja *et al.*, 1999; Rao and Wightman, 1999	R–HR	Wightman and Rao, 1994; Stalker and Simpson, 1995; Lynch and Mack, 1995; Amin, 1985
Southern corn rootworm	R	Stalker *et al.*, 2002a; Stalker and Lynch, 2002		

(*continued on next page*)

Table IV (*continued*)

Trait	Resistance in *A. hypogaea* germplasm		Resistance in Wild *Arachis* species	
	Reaction to abiotic and biotic stresses	Reference	Reaction to abiotic and biotic stresses	Reference
Corn earworm	R	Stalker *et al.*, 2002a; Stalker and Lynch 2002		
Temperature	Tolerance to high temperature	Nageshwar Rao *et al.*, 1989; Greenberg *et al.*, 1992; Chauhan and Senboku, 1997; Wheeler *et al.*, 1997; Talwar *et al.*, 1999; Craufurd *et al.*, 1999, 2002; Prasad *et al.*, 1999	Wild *Arachis* species not evaluated for high temperature	
	Tolerance to low temperature	Upadhyaya *et al.*, 2001d	Wild *Arachis* species not evaluated for low temperature	
Photoperiod	Insensitive	Nigam *et al.*, 1997	Wild *Arachis* species not evaluated for photoperiod sensitivity	

[a]Scored on 1–9 scale where 1, no disease; 2 = <5% disease severity; 3, 6–10% disease severity; 4, 11–20% disease severity; 5, 21–30% disease severity; 6, 31–40% disease severity; 7, 41–60% disease severity; 8, 61–80% disease severity; 9, 81–100% disease severity.

[b]I, Immune.

[c]HR, Highly resistant.

[d]R, Resistant.

[e]MR, Moderately resistant.

Table V
Variability for Oil and Protein Contents and O/L Ratio in *Arachis hypogaea* and Wild *Arachis* Groundnut Germplasm

	A. hypogaea		Wild *Arachis*	
Trait	Variability reported	Reference	Variability reported	Reference
Oil (%)	45–56	Ahmed and Young, 1982; Dwivedi *et al.*, 1993a	42–63	Cherry, 1977; Stalker *et al.*, 1989; Jambunathan *et al.*, 1993; Grosso *et al.*, 2000
Protein (%)	23–29	Young and Hamons, 1973; Dwivedi *et al.*, 1993a	17–31	Cherry, 1977; Jambumnathan *et al.*, 1993; Grosso *et al.*, 2000
O/L ratio	0.95–40.0	Norden *et al.*, 1987; Dwivedi *et al.*, 1993a, 1998b; Gorbet and Knauft, 1997; Harch *et al.*, 1995	0.35–0.23	Stalker *et al.*, 1989; Grosso *et al.*, 2000
Total sugars	23169–44795	Pattee *et al.*, 2000		
Sweet flavor	2.33–4.12 ifu	Pattee *et al.*, 1998		
Bitter flavor	2.43–4.46 ifu			
Roasted flavor	3.75–5.22 ifu			

(Tai and Hammons, 1978; Wynne and Isleib, 1978; Shorter and Hammons, 1985; Dwivedi *et al,* 1993a; Coffelt *et al,* 1993). Upadhyaya *et al.* (2001e) developed a core collection of 1704 groundnut accessions consisting of 584 (34.3%) accessions from subsp. *fastigiata* var. *vulgaris,* 299 (17.5%) from subsp. *fastigiata* var. *fastigiata,* 27 (1.6%) from subsp. *fastigiata* var. *peruviana,* 6 (0.4%) from subsp. *fastigiata* var. *aequitoriana,* 784 (46.0%) from subsp. *hypogaea* var. *hypogaea,* and 4 (0.2%) from subsp. *hypogaea* var. *hirsuta,* and arrayed these accessions in 23 clusters. When this core collection is evaluated for traits of economic importance including resistance to abiotic and biotic stresses, it should provide breeders with opportunities to further broaden the genetic base of the crop by integrating diverse germplasm into their breeding programs. In some countries particularly in India and Vietnam, tolerance to cold temperature is required as the low temperature prevailing during the planting time results in delayed germination and a reduced growth rate thus delaying the harvest. When Upadyaya *et al.* (2001d) evaluated their core collection for tolerance to low temperature (12°C), they identified 343 accessions with 81-100% germination compared to 43% germination in control cultivar ICGS 44 (ICGV 87128). Botanically these accessions represented subsp. *aequatoriana, fastigiata, peruviana, vulgaris,* and *hypogaea.*

The oil content of dried groundnut seeds is reported to vary from 44 to 56%, while protein content ranges from 22 to 30%. Groundnuts are also a rich source of minerals (phosphorus, calcium, magnesium, and potassium) and vitamins (E, K, and B group) (Savage and Keenan, 1994). Seed size, shape, color, oil and protein contents, fatty acid and amino acid composition, taste, and flavor are important quality traits in groundnut. Oleic (O), linoleic (L), and palmitic fatty acids, together, account for over 80% of the total fat in groundnut seeds (Dwivedi *et al.,* 1993a). Considerable genetic variation has been reported for pod size and shape, seed size and shape, seed color, oil content, and fatty acid composition (Norden *et al.,* 1987; Dwivedi *et al.,* 1989; 1998b; Branch *et al.,* 1990; Singh *et al.,* 1998; Upadhyaya *et al.,* 2001f).

Plant breeders in the USA have registered 62 *Arachis* germplasm lines possessing genes for resistance to biotic and abiotic stresses, and for seed quality traits for use in breeding programs (Isleib and Wynne, 1992, Table VI). Of these, 27 were introduced germplasm. However, because of stringent industry and market demands, US plant breeders use only those accessions that conform to market and industry standards. This has resulted in a narrowing of the genetic base of released cultivars there. ICRISAT breeders have used 78 plant introductions to develop 73 elite germplasm lines. Of these, 41 have been released for cultivation in 19 countries, and the remainder possesses genes for early maturity, seed dormancy, seed quality, photoperiod insensitivity, and resistance to rust, ELS, LLS, thrips, jassids, leaf miner, *Spodoptera,* PBNV, iron chlorosis, aflatoxin, and tolerance to drought (Table VI), and these elite

Table VI
List of Cultivars and Elite Germplasm with Specific Characteristics Developed by Conventional Breeding in Groundnut

Trait incorporated	Identity	Area of adaptation and other useful traits identified	Reference
Resistance to rust and/or LLS	ICGV 87160	Released in India and Myanmar; tolerant to leaf miner, peanut bud necrosis disease (PBND), and drought	Reddy *et al.*, 1992
	ICGV 86590	Released in India; tolerant to PBND, stem and pod rots, and *Spodoptera*	Reddy *et al.*, 1993
	ICGV-SM 85048	Released in Mauritius; resistant to web blotch (*Phoma arachidicola*)	Niagm *et al.*, 1998b
	ICGV-SM 86715	Released in Mauritius; resistant to pepper spot (*Leptosphaerulina crassiasca*)	Moss *et al.*, 1998
	ICGV 87165	Resistant to bacterial wilt, leaf miner, and *Spodoptera*	Moss *et al.*, 1997
	ICGV 86699	Resistant to stem and pod rots, tolerant to PBND and *Spodoptera*	Reddy *et al.*, 1996
	ICGV 87157	Tolerant to PBND, stem and pod rots, leaf minor, and mid-season drought	Niagm *et al.*, 1992b
	Southern runner	Released in USA	Gorbet *et al.*, 1987
	Yue You 223	Released in China	Liang *et al.*, 1999b
	TxAG 6 and TxAG 7	Resistant to ELS and nematodes	Simpson *et al.*, 1993
	GP-NCWS 1, GP-NCWS 2, GP-NCWS 3, and GP-NCWS 4	Interspecific derivatives resistant to late leaf spot	Stalker and Beute, 1993
	Zhonghua 117	Released in China, moderate resistance to rust and bacterial wilt and tolerant to acid soils	Guiying *et al.*, 1995

(*continued on next page*)

Table VI (*continued*)

Trait incorporated	Identity	Area of adaptation and other useful traits identified	Reference
	VRI Gn 5	Released in India, resistant to rust and late leaf spot	Vindhiyavarman and Mohammed, 2001
	Sylvia (ICGV 93207)	Released in Mauritius	Reddy *et al.*, 2001a
	Venus (ICGV 87853)	Released in Mauritius	Reddy *et al.*, 2000
Bacterial wilt	E Hua 5, Lu Hua 3, Yue You 5, Yue You 79, Yue You 92, Yue You 200, Yue You 202–35, Yue You 256, Yue You 589, Gui You 28, Wu You 4, Zhong Hua 2, and 93–81	Released in China; resistant to rust and root rot in You 202–35 and Yue You 79 and to rust in Yue You 256	Liang, 1998; Liao *et al.*, 1998; Liang *et al.*, 1999a
	Badak, Biawak, Jepara, Komodo, Landak, Mahesa, Simpai, Trenggiling, and Zebra	Released in Indonesia	Machmud and Rais, 1994
Soil born diseases	VG P9	Resistant to *Sclerotinia minor*, *Sclerotinia blight*, and *Cylindrocladium crotalariae*	Coffelt *et al.*, 1994a
	Tamrun 98	Released in USA, resistant to *Sclerotinia minor*	Simpson *et al.*, 2000
	Southwest Runner	Released in USA, resistant to *Sclerotinia minor*	Kirby *et al.*, 1998
Resistant to thrips, jassids, leaf miner, and *Spodoptera*	ICGV 86031	Photoperiod insensitive and resistance to PBNV and iron chlorosis	Dwivedi *et al.*, 1993b
Resistant to jassids	ICGV# 86252, 86393, 86455, and 86462	High density of trichomes on leaves	Dwivedi *et al.*, 1995a
Resistant to peanut bud necrosis virus	ICGV 86388	Resistant to jassids and thrips	Dwivedi *et al.*, 1996b
	Georgia Green	Released in USA, resistant to Tomato Spotted Wilt Virus	Branch, 1996

Table VI (*continued*)

Trait incorporated	Identity	Area of adaptation and other useful traits identified	Reference
Resistant to rosette virus	RG 1, KH 149A, KH 241D, 69–101, RMP 12, RMP 91, 28–206, and ICGV-SM 90704	28–206 and 69–101 released in Senegal and KH 149A, KH 241D, RMP 12 and RMP 91 in Burkina Faso	Bockelee-Morvan, 1983; Mauboussin *et al.*, 1970; van der Merwe *et al.*, 2001
Resistant to thrips and jassids	ALR 2	Released in India; resistant to stem rot and tolerant to rust and LLS	Varman *et al.*, 1998
Resistant to seed infection by *A. flavus*	ICGV# 88145 and 89104	Support low aflatoxin production	Rao *et al.*, 1995
	Streeton	Released in Australia; support low aflatoxin production	Cruickshank *et al.*, 2000
	ICGV# 91278, 91283, and 91284	Resistant to natural seed infection and in vitro seed colonization by *A. flavus*	Upadhyaya *et al.*, 2001c
Tolerant to drought	ICGV 87354	Resistant to rust	Reddy *et al.*, 2001b
	55–437, 73–30, 47–10, T3.3, TS 32–1, and 73–33	47–10, 55–437, 73–30, and 73–33 released in Senegal and T3.3 and TS 32–1 in Burkina Faso	Bockelee-Morvan, 1983
High yield per se	ICGS 1	Released in India; tolerant to mid-season drought and PBND	Nigam *et al.*, 1991b
	ICGV 87121	Released in India; tolerant to mid-season drought	Nigam *et al.*, 1992
	ICGV 87141	Released in India; tolerant to mid-season drought and PBND	Nigam *et al.*, 1991a
	ICGV 86325	Released in India; tolerant to PBND	Dwivedi *et al.*, 1996a
	Sinkarzei	Released in India; tolerant to mid-season drought and PBND	Nigam *et al.*, 1993

(*continued on next page*)

Table VI (*continued*)

Trait incorporated	Identity	Area of adaptation and other useful traits identified	Reference
	CG 7 (ICGV-SM 83708)	Released in Malawi, Uganda, and Zambia; superior oil quality and large seed size	Nigam *et al.*, 1995a
	ICGV-SM 83005	Released in Zambia	Nigam *et al.*, 1998a
	ICGS 11	Released in India and Srilanka; Tolerant to PBND and end-of-season drought, insensitive to photoperiod	Nigam *et al.*, 1990b
	ICGV 87128	Released in India; wide adaptability; tolerant to PBND, and mid- and end-of-seasons drought	Nigam *et al.*, 1990a
	ICGV 87187	Released in India; tolerant to end-of-season drought and PBND; insensitive to photoperiod	Nigam *et al.*, 1992a
	ICGS 35	Released in Korea	Nigam *et al.*, 1994a
	Jeokwantangkong	Released in Korea, resistant to pod rot	Youn-Sup *et al.*, 2000
	Luhua 15	Released in China; resistant to web blotch	Zhengchao *et al.*, 1997
Early maturity	ICGV 86143	Released in India and Vietnam	Upadhyaya *et al.*, 1997b
	ICGV 86015	Released in Pakistan, Nepal, and Vietnam	Nigam *et al.*, 1995b
	ICGV# 92196, 92206, 92234, and 92243		Upadhyaya *et al.*, 1998
	VA 93B	Released in USA for early maturity	Coffelt *et al.*, 1994b
	ICGV 94361	Early maturity and moderate resistance to rust	Upadhyaya *et al.*, 2001b
	Andru 93	Released in USA, early maturing into Virginia market type	Gorbet and Knauft, 1995
	Kadiri 4	Released in India	Reddy *et al.*, 1998
	Nonghua 22	Released in China, resistant to leaf spots and tolerant to drought	Gao *et al.*, 1996

Table VI (*continued*)

Trait incorporated	Identity	Area of adaptation and other useful traits identified	Reference
Fresh seed dormancy	ICGV# 86155, 86156, 86158, 87378, and 87921	Early maturity	Upadhyaya *et al.*, 1997a
	ICGV 93470	Early maturity with fresh seed dormancy	Upadhyaya *et al.*, 2001a
Large seed size	ICGV 86564	Released in Srilanka; high oil content and O/L ratio	Dwivedi *et al.*, 1994
	ICGV# 88438, 89214, and 91098	Released in Cyprus; high oil content, tolerant to lime induced iron chlorosis	Hadjichristodoulou *et al.*, 1997
	ICGV# 96230 and 96234	High O/L ratio	Dwivedi *et al.*, 1998b
	Huayu 16	High oil and protein contents, and resistant to root rot (*Macrophomina phaseolina*) and tolerant to peanut stripe virus	Zhengchao and Qingshu, 2000
	Huayu 17	Low oil	Shanlin *et al.*, 2000
	Georgia Browne	Released in USA for confectionery or candy use	Branch, 1994
	VA-C 92R	Released in USA, high seed calcium content	Mozingo *et al.*, 1994
	VA 98R	Released in USA, bright pod color and pink seed	Mozingo *et al.*, 2000
	Gregory	Released in USA	Isleib *et al.*, 1999
	Georgia Bold	Released in USA, resistant to TSWV	Branch, 1998
	Georgia Valencia	Released in USA, 3–4 seeded large pods	Branch, 2001
	BRS 151 Amendoim L7	Released in northeast region in Brazil, early maturing type	dos Santos, 1998
High O/L ratio	SunOleic 95 R	Released in USA	Gorbet and Knauft, 1997
	VG P 10	Released in USA, early maturity with large seed size	Coffelt and Mozingo, 1998
	Georgia Hi-O/L peanut	Large seed size and resistant to TSWV	Branch, 2000
	SunOleic 97R	Released in USA	Gorbet and Knauft, 2000

germplasm are widely used by NARS breeding programs to transfer these traits into locally adapted cultivars.

III. HIGHLIGHTS AND CONSTRAINTS OF CONVENTIONAL GENETIC IMPROVEMENT IN GROUNDNUT

A. BREEDING METHODS AND CULTIVARS

The most commonly used breeding methods in groundnut are (1) pedigree selection, (2) bulk-pedigree selection, and (3) single-seed descent. Backcross breeding has not been used extensively as most of the economically important traits in groundnut are quantitatively inherited (Wynne and Gregory, 1981; Knauft and Wynne, 1995). Often, breeders make single crosses to generate variability. However, with increased emphasis on multiple resistance breeding, emphasis is now focused on complex crosses followed by intercrossing of segregants to bring the desired improvement into breeding populations. While selection for resistance to insect pests and diseases is practiced in early generations, selection for yield and yield component traits is delayed to later generations. Recurrent selection has also been used for continued genetic enhancement in groundnut (Guok *et al.,* 1986; Halward *et al.,* 1991b).

Over 276 groundnut cultivars were released between 1920 and 2000 for cultivation in various countries in Asia, Africa, and the Americas. Each has specific adaptation to its respective region of production and cropping system (Isleib *et al.,* 1994; Godoy and Giandana, 1992; Table VI). Breeding for high seed yield has caused changes in dry matter allocation. More recently developed cultivars have reduced vegetative mass, shorter main stem length, and greater reproductive allocation (partition more of their daily assimilate to fruit) than those developed previously (as predicted by Duncan *et al.,* 1978). Further studies on reproductive efficiency (RE) revealed that high yield in more recently released cultivars appears to be related more to total flower production than to RE, and therefore, future increases in seed yield might be accomplished by developing cultivars with a combination of high RE, harvest index, and total flower count (Coffelt *et al.,* 1989). A yearly genetic gain of nearly 15 kg per hectare has been reported for large-seeded Virginia type cultivars released from the 1950s to the 1970s in the USA (Mozingo *et al.,* 1987). The highest yielding cultivars developed during the 1950s, 1960s, and 1970s had an average yield increase of 3.4%, 10.2%, and 18.5%, respectively, over the standard NC 4. However, since the 1970s there has been increased emphasis on improving pest resistance and quality traits so that the yield potential of cultivars released since that time has not surpassed those of the highest yielding cultivars released during the 1970s.

B. SUCCESSES AND LIMITATIONS TO CONVENTIONAL BREEDING

1. Disease Resistance

Cultivars resistant to rust, bacterial wilt, and groundnut rosette disease (GRD) have been developed (Table VI). Bacterial wilt resistant cultivars are grown in South East Asia and the Far East and GRD resistant cultivars are grown in Africa on large acreage. However, many cultivars continue to be susceptible to rust, early leaf spot (ELS) and/or late leaf spot (LLS). A few cultivars with moderate resistance to rust and LLS have been released in China, India, Mauritius, and the USA. The adoption of rust and LLS resistant cultivars among SAT farmers has been low mainly because of their relatively long duration and low shelling outturn (proportion of seeds to pods; also referred to as shelling percentage or meat content). Progress in ELS and LLS resistance breeding has been limited by the absence of high levels of resistance in cultivated groundnut and the linkage of resistance with long duration, lower partitioning and with undesirable pod (highly reticulated, constricted, prominently ridged and conspicuously beaked pods with thick shells) and seed (purple or blotched seed color) characteristics (Wynne *et al.,* 1991; Singh *et al.,* 1997). In contrast, several wild *Arachis* species show a very high level of resistance to ELS and LLS. They also possess very small and catenate pods. The success in transferring ELS and LLS resistance from wild *Arachis* species to cultivated groundnut has been limited mainly because of cross compatibility barriers, the linkage of resistance with many undesirable pod characteristics, and the long periods of time required for developing stable tetraploid interspecific derivatives. Despite these obstacles, a few interspecifc derivatives possessing high levels of resistance to ELS, LLS, and nematodes have been developed (Table VI). A nematode resistant cultivar, Coan, derived from an interspecific cross, has been released for cultivation in the USA. There has been some progress toward developing elite groundnut germplasm resistant to seed infection and/or aflatoxin production by *A. flavus,* and tolerance to peanut bud necrosis virus (Table VI). "Streeton" has been released for commercial cultivation in Australia because of its excellent yield, grade stability, and lower susceptible to aflatoxin contamination under drought conditions. There are only a few examples of multiple resistances incorporated into elite groundnut germplasm (Table VI).

2. Insect Pest Resistance

Resistance to thrips and jassids and tolerance to leaf miner and *Spodoptera* has been successfully transferred into improved genetic backgrounds (Table VI). A few interspecific derivatives possessing high levels of resistance to southern corn rootworm, corn earworm, *Spodoptera,* and jassids have been developed from interspecifc crosses in the USA (Table VI). However, reduced vulnerability to one or more of these pests has not been the primary criterion for release of any

improved groundnut cultivar in SAT regions to date. Lack of a high level of resistance to leafminer and *Spodoptera* in cultivated groundnut, and difficulties in conducting reliable resistance screens under field conditions are the main reasons for the slow progress in developing improved germplasm with resistance to these pests. Many of the wild *Arachis* species, in contrast, possess a high degree of resistance to leafminer and *Spodoptera* (Table IV). However, these are not readily cross compatible with cultivated groundnut. A transgenic approach might be the best option to incorporate genes for resistance to leafminer and *Spodoptera* into cultivated groundnut, provided that genes conferring reasonable levels of resistance can be identified and isolated.

3. Abiotic Stress Tolerance

Success in breeding drought tolerant groundnut genotypes using conventional plant breeding methodologies has been limited. However, recent studies revealed that genotypic variation for physiological traits (specific leaf area, water use efficiency, amount of water transpired, transpiration efficiency, and harvest index) under drought stress conditions are associated with drought tolerance (Nageswara Rao *et al.,* 1993; Nageswara Rao and Wright, 1994; Wright *et al.,* 1994; Craufurd *et al.,* 1999; Nageswara Rao and Nigam, 2001). These traits are, now, being used to select for drought tolerance in groundnut. A few drought tolerant cultivars have been released in West Africa (Table VI). Elite groundnut germplasm with tolerance to mid-season and/or end-of-season drought stress has been developed at ICRISAT (Table VI).

4. Quality Traits

Seed size, oil content, and oil quality as measured by variation in the O/L ratio are important seed quality traits in groundnut. For confectionery and Other means of direct consumption, groundnuts with large seed size, low oil content, and a high O/L ratio are preferred. Oils with high O/L ratios are less prone to oxidation and the development of unfavorable flavors. Groundnut seeds with high O/L ratios have long product stability and shelf-life (James and Young, 1983; Branch *et al.,* 1990). Oil content and O/L ratio are highly influenced by G x E interaction (Dwivedi *et al.,* 1993a). Seed size is not an important trait for oil types but varieties with high oil content and a high O/L ratio are preferred. Excellent progress has been made in developing high-yielding breeding lines with large 100-seed mass (>80 g) (Table VI), However, these are late-maturing types and many have high oil contents-a trait not preferred for edible groundnut. Success in combining large-seed size, high O/L ratio, and early maturity in genotypes belonging to subsp. *fastigiata* has been very limited. Although in the late 1990s,

US-based researchers reported large genetic variability for O/L ratio (Table V), success in improving the chemistry of oil quality has been limited. This is partly due to the inaccessibility of germplasm with unique oil profiles (such as F435). Recently, improved groundnut cultivars with high O/L ratios have been released in the USA (Table VI).

5. Adaptation and Yield

Photoperiod, temperature, and photoperiod by temperature interactions influence the partitioning (also known as harvest index) and therefore the adaptation of groundnut genotypes to new environments (Nigam *et al.,* 1994b; 1998c). The breeding environment under which selection is conducted among segregating populations strongly influences the yield adaptability of the selected groundnut genotypes (Branch and Hildebrand, 1989). Genotypes with large seeds and/or resistance to pests and diseases are, in general, sensitive to photoperiod whereas early maturing types are least affected by variation in photoperiod (Flohr *et al.,* 1990; Nigam *et al.,* 1997). Groundnut is grown on a wide range of soils, and strong soil type X genotype interaction suggests specific varietal adaptation for soil types (Nageswara Rao *et al.,* 1992).

Crop duration also plays an important role in yield and adaptation of genotypes. Early maturing cultivars are suitable for areas where the growing season is short, end-of-season droughts or early frosts are common, low temperature at sowing resulted delayed germination and slow growth, and the crop is grown in after rice with residual moisture. Many breeding programs including ICRISAT's developed several cultivars with a potential yield of 3 t ha^{-1} and a 90 day maturity (Table VI). However, most of the early maturing cultivars have small seeds (30-40 g 100^{-1} seeds), possess no seed dormancy, and are highly susceptible to pests and diseases. Some progress has been made in efforts to combine early maturity with relatively large seed size (50 g 100^{-1} seeds), 2-3 weeks of fresh seed dormancy, tolerance to cold temperature, and moderate resistance to rust and late leaf spot (Table VI). A short period of seed dormancy is beneficial as it helps to reduce losses associated with low germination if there is rain at harvest and proper care has not been taken to fast dry the groundnut pods. Substantial progress has been made towards developing medium- and late-maturing cultivars adapted to rainfed and/or post-rainy irrigated high input situations. In Zimbabwe and China, some of these varieties produced over 9.0 t ha^{-1} pod yield (Smart, 1978; Yanhao and Caibin, 1990). However, there is a wide gap between realized yields at the farm level (world average yield 1.0 t ha^{-1}) in SAT regions when compared to the average yields (3.0 t ha^{-1}) in China, the USA and the highest yields reported from China and Zimbabwe. There is therefore a need to incorporate multiple stress resistance into improved genetic backgrounds, even if it requires some sacrifice in yield

IV. OVERVIEW OF BIOTECHNOLOGY APPLICATIONS IN GROUNDNUT

A. MOLECULAR GENETIC DIVERSITY ANALYSIS

Assessment of genetic diversity and development of genetic linkage maps are important steps in the development of molecular breeding programs. Only very low levels of molecular genetic polymorphism have been detected among cultivated groundnut accessions using isozymes, restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), DNA amplification fingerprinting (DAF), and amplified fragment length polymorphism (AFLP) markers (Grieshammer and Wynne, 1990; Kochert *et al.,* 1991; Bhagwat *et al.,* 1997; He and Prakash, 1997; Subramanian *et al.,* 2000). Similarly, Hopkins *et al.* (1999) have found only six simple sequence repeat (SSR) markers that detected polymorphisms amongst cultivated groundnut. However, Dwivedi *et al.* (2001) detected upto 41% genetic dissimilarity in RAPD profiles among 26 cultivated groundnut accessions. In contrast, abundant DNA marker polymorphisms have been detected between wild species in section *Arachis* (Halward *et al.,* 1991a; 1992; Paik-Ro *et al.,* 1992; Lanham *et al.,* 1992). This supports the hypothesis that *A. hypogaea* may have originated from a single hybridization event followed by chromosome doubling, with very little subsequent introgression from related diploid species (Young *et al.,* 1996).

Assessment of molecular diversity should facilitate the identification of agronomically valuable and diverse germplasm for use in linkage mapping and genetic enhancement of specific traits in groundnut. Agronomically superior germplasm lines with relatively high level of DNA marker polymorphism have been identified at ICRISAT. This should facilitate the mapping of many important agronomic traits including ICG 405, ICG 1705, ICG 6284, and TMV 2 for early leaf spot (ELS); ICGV 99001, ICGV 99004, and TMV 2 for late leaf spot (LLS); ICGV 99003, ICGV 99005, and TMV 2 for rust; ICG 6323, ICG 6466, ICG 11044, and JL 24 for groundnut rosette disease (GRD); CSMG 84-1, TAG 24, ICGV 86031, ICGV 87128, TMV 2 NLM, and Chico for drought; ICG 7893, ICG 15222, and Chico for bacterial wilt; and U 4-7-5, 55-437, and J 11 for resistance to seed infection and/or aflatoxin production by *A. flavus.* ICG 405, ICG 1705, ICG 6284, ICG 7893, ICG 11044, and 55-437 originated from South America, ICG 6323, ICG 6466, and J 11 from Africa, ICG 15222 from China, and U4-7-5 from North America. ICGV 99001, ICGV 99003, ICGV 99004, and ICGV 99005 are derivatives from interspecific hybridization made at ICRISAT. The

highly susceptible accessions included are TMV 2 for rust, ELS, and LLS; JL 24 for GRD; and Chico for bacterial wilt. The drought tolerant accessions show wide variation in specific leaf area, partitioning, and water-use efficiency.

B. MOLECULAR GENETIC LINKAGE MAPPING

The groundnut genome is nearly 20 times larger than *Arabidopsis thaliana,* and 2-6 times larger than *Oryza sativa, Medicago truncatula, M. sativa, Phaseolus vulgaris, Sorghum bicolor, Lycopersicon esculentum, Solatium tuberosum, Ipomoea batata,* and *Glycine max.* However, the groundnut genome is of a size similar to *Gossypium hirsutum, Zea mays,* and *Helianthus annuus,* and smaller than *Pisum sativum, Lensculinaris esculenta, Hordeum vulgare, Avena sativa,* and *Triticum aestivum* (Table VII). Variation in genome size among accessions of *A. hypogaea (2n = 4x =* 40) and *A. duranensis* (*2n = 2x =* 20) (Singh *et al.,* 1996), and between *A. hypogaea* and *A. monticola* (Temsch and Greilhuber, 2000) has also been reported. Genome size variation in groundnut has not been related to ecological or evolutionary factors. Variation in genome size is generally the result of differences in the amount of repetitive DNA and ploidy level (Flavell *et al.,* 1974).

The first RFLP-based genetic linkage map of groundnut, with a total map distance of approximately 1063 cM, was constructed using an F_2 population derived from an interspecifc cross between two related diploid species (*A. stenosperma* and *A. cardenasii)* in section *Arachis* (Halward *et al.,* 1993). Burow *et al.* (2001) subsequently reported the RFLP-based tetraploid genetic linkage map of groundnut derived from a BC_1 population of TxAG 6 with Florunner. TxAG 6 was derived by crossing the A-genome diploid hybrid from *A. cardenasii* (GKP-10017, PI 262141) X *A. chacoensis* (GKP-10602, PI 276235) as male parent on to the B-genome species *A. batizocoi* (K-9484, PI 298639) as female parent. The resulting tri-species hybrid was chromosome doubled to produce fertile amphiploids. Three hundered and seventy RFLP loci were ultimately mapped to 23 linkage groups with a total map distance of approximately 2210 cM. This map is unique in that the donor parent is a synthetic polyploid created by crossing three diploid species. These RFLP loci will detect alleles in populations involving crosses between wild *Arachis* species or between *A. hypogaea* X wild *Arachis* species crosses. They are unlikely to detect alleles in *A. hypogaea* X *A. hypogaea* crosses. Holbrook and Stalker (2003) reviewed the progress achieved in (1) identifying RAPD and RFLP markers linked with root-knot nematode and southern corn rootworm damage and for components of resistance to leaf spots in interspecific hybrid with *A. cardenasii* in the pedigree, (2) markers associated with cylindrocladium black rot resistance and sporulation to *C. arachidicola* in a *hypogaea* cross, and (3) utility of these markers to monitor

Table VII
Chromosome Number (2n = 2x) and Genome Size Variation Among Major Cereals, Legumes, Oilseeds, and Tuber Crops (http://www.nalusda.gov/pgdic/tables/nucdna.html)

Ploidy	Crop		Chromosome number (2n = 2x)	Genome size (Mbp/lC)
	Common name	Scientific name		
Diploid	Arabidopsis	*Arabidopsis thaliana*	10	145
	Medicago	*Medicago truncatula*	16	454-526
	Rice	*Oryza sativa* sps. *Indica*	24	419-463
	Rice	*Oryza sativa* sps. *japonica*	24	415-439
	Black mustard	*Brassica nigra*	16	468
	Turnip rape	*Brassica compestris* sps. *oleifera*	20	468-516
	Turnip	*Brassica compestris* sps *rapifera*	20	511
	Pakchoi	*Brassica compestris* sps. *chinensis*	20	507
	White mustard	*Brassica hirta*	24	492
	Urdbean	*Vigna mungo*	22	574
	Moongbean	*Vigna radiata*	22	579
	Cowpea	*Vigna unguiculata*	22	613
	Lima bean	*Phaseolus lunatus*	22	622
	French bean	*Phaseolus vulgaris*	22	637
	Runner bean	*Phaseolus coccineus*	22	709
	Chickpea	*Cicer aerietinum*	16	738
	Jowar	*Sorghum bicolor*	20	748, 772
	Brown mustard	*Brassica juncea*	36	1105
	Tepary bean	*Phaseolus acutifolius*	22	647
	Sunflower	*Helianthus annuus*	34	2871-3189
	Garedn pea	*Pisum sativum*	14	3947, 4397
	Lentil	*Lensculinaris esculenta*	14	4063
	Barley	*Hordeum vulgare*	14	4873
	Tomato	*Lycopersicon esculentum*	24	907-1000
	Soybean	*Glycine max*	40	1115
	Rapseed	*Brassica napus*	38	1129-1235
	Tobacco	*Nicotiana tabaccum*	48	4221-4646
	Oat	*Avena sativa*	42	11315
Tetrapolid	Groundnut	*Arachis hypogaea*	40	2813
	Cotton	*Gossypium hirsutum*	52	2118,2374
	Alfalfa	*Medicago sativa*	32, 16	1510
	Potato	*Solanum tuberosum*	48, 24, 72	1597-1862
	Maize	*Zea mays*	20	2292-2716
Hexaploid	Wheat	*Triticum aestivum*	42	15966
	Sweetpotato	*Ipomoea batatas*	90	1597

Table VIII
Total Map Distance (cM), Number of Markers Mapped, and Average Marker Distance of Groundnut DNA Marker vis a vis Those Reported in Cereals, Legumes, and Oilseeds Crops

Crop	Mapping population	Total map distance (cM) and # markers mapped	Average marker distance (cM)	Reference
Oryza sativa	An F_2 population of the cross between sub sps *japonoca* and *indica*	1521.6 cM and 2275 markers	0.67	Harushima *et al.*, 1998
Phaseolus vulgaris	RILs from a cross between BAT93 × Jalo EEP 558 (BJ)	1226 cM and 563 markers	2.18	Freyre *et al.*, 1998
Sorghum bicolor	RILs from a cross between BT_x623 and IS620C	1406 cM and 470 markers	2.99	Bhattramakki *et al.*, 2000b
Helianthus annuus	An F_2 population of the cross between HA370 and HA372	1326 cM and 400 markers	3.31	Gedil *et al.*, 2001
Glycine max	RILs from a cross between BSR-101 and PI437.654	3441 cM and 840 markers	2.90	Cregan *et al.*, 1999
Vigna unguiculata	RILs from a cross between IT84S-2049 and 524B	972 cM and 181 markers	5.37	Menendez *et al.*, 1997
Arachis hypogaea	BC_1 population of a cross between synthetic amphidiploid (TxAG-6) {[*A. batizocoi* × (*A. cardenasii* × *A. digoi*)]^{4x}} and Florunner	2210 cM and 370 markers	5.97	Burow *et al.*, 2001
Cicer arietinum	RILs from an interspecific cross between *Cicer arietinum* (FLIP84-92C) and *Cicer reticulatum*	981.6 cM and 116 markers	8.46	Santra *et al.*, 2000

the introgression of nematode resistance in wild species chromosome segments from *A. cardenasii* in *A. hypogaea.*

High-density genetic linkage maps are theoretically useful to detect markers tightly linked to quantitative trait loci (QTL) with economically important traits (Paterson *et al.,* 1988; Lander and Botstein, 1989), to clone gene(s) by chromosome walking (Wicking and Williamson, 1991), and to facilitate marker-assisted selection of desirable genes in breeding programs (Burr *et al.,* 1983; Tanksley *et al.,* 1989). The average marker distance in the current RFLP based tetraploid genetic linkage map of cultivated groundnut is greater than those reported for *Oryza sativa, Phaseolus vulgaris, Sorghum bicolor, Helianthus annuus, Glycine max,* and *Vigna unguiculata* but smaller than *Cicer arietinum* (Table VIII). There is a need to saturate the groundnut genetic linkage map with PCR-based co-dominant markers, preferably SSRs, in order to provide sufficient markers for routine marker-assisted breeding.

C. PROGRESS IN MODEL SYSTEMS AND COMPARATIVE MAPPING AMONGST LEGUMES

1. Marker Systems and Linkage Mapping in Soybean

Among the legumes, soybean has been the most widely studied crop for development of suitable marker assays for assessment of genetic diversity, marker-trait relationships, identifying genes/quantitative trait loci (QTL) associated with useful traits, and constructing genetic linkage maps for map-based cloning of genes for the targeted genetic enhancement in soybean. Since 1990, a large number of reports have been published on the use of DNA markers in assessing genetic diversity for identifying diverse germplasm in soybean yield improvement (Narvel *et al.,* 2000; Brown-Guedira *et al.,* 2000; Concibido *et al.,* 2003). There are also a considerable number of publications using the full range of available types of marker assay to map the genes underlying a wide range of biotic constraints (Concibido *et al.,* 2003; www.gsfgg.uiuc.edu/invited/2_1_01.pdf) and agronomic traits (Lee *et al.,* 1996a,b; *Orf et al.,* 1999; Sebolt *et al.,* 2000; Concibido *et al.,* 2003), and the use of such maps for marker-assisted selection to map-based cloning of genes for the genetic enhancement in soybean (Polzin *et al.,* 1994; Keim *et al.,* 1997; Cregan *et al.,* 1999).

Soybean yields in the past 75 years in USA have more than tripled from 12 bushels per acre in 1924 to 40 bushels per acre in recent years, and at least half of it is attributable solely to genetic improvement through breeding. However, a greater emphasis have now been placed on use of genomics to bring rapid genetic enhancement in soybean yields (http://129.186.26.94/genomics/soybean_genomics.html) that should enable US growers to make the soybean production globally competitive and meet the ever increasing energy

(good quality oil and protein) demands of world population. The focused research priorities for soybean improvement in USA are use of DNA markers, transformation, structural genomics, functional genomics, and bio-informatics technologies for increasing the genetic potential of soybean crop. The US researchers have developed a time bound (in most of the cases 3-5 years) targeted action plan to provide large number of DNA markers (2000 SSR and 10,000 SNP markers in public domain); characterize allelic variation in major candidate genes; improve the efficiency of transformation by 5-10 folds and generate technology to precisely deliver DNA; develop transgenic screens to elucidate gene function; tag 80% of the genes; develop and integrate the genetic, physical, and transcript maps; assign biological function to identified genes; use comparative genomics to understand soybean interaction with pathogens and symbionts; and identify bioinformatics needs of the soybean genomic program (http://129.186.26.94/genomics/soybean_genomics.html). The successful application of biotechnology-assisted breeding of soybean provides considerable direct and indirect support for similar progress in other legume crops.

2. Model Systems and Comparative Mapping

The family Leguminoseae consists of three subfamilies: Caesalpinioideae, Mimosoideae, and Papilionoideae (Raven and Polhill, 1981; Herendeen *et al.,* 1992). Within the Papilionoideae, three evolutionary lineages are represented by the beans (common beans, cowpea, and soybean), the cool season legumes (lentil, pea, chickpea, and alfalfa), and groundnut (Stylosanthes). The close phylogenetic relationship between these species suggests that a comparative genomics approach will be useful to define the common attributes of this legume subfamily. Thus, knowledge of genome structure and gene function gained from the intensive study of model legume species such as *Glycine, Medicago* and *Lotus* should enable more effective research in other legumes. With this in mind, an international legume genomics initiative has been formed between USA Universities and the International Agricultural Research Centers of the Eco-Regional Alliance on legumes to translate the benefits of the "consensus legume genome" for rapid impacts on the genetic improvement of tropical legumes. For example, researchers will be able to determine if genes for drought resistance in two legume species share a common origin, or if they are derived from different genetic determinants. Alternatively, having intensively characterized the nature and location of genes for a given trait in a model species, it may then be easy to identify similar genes in another lesser studied crop. Such information will allow leap-frogging progress in the genetic improvement of lesser studied crops and may lead to rapid and cost effective means for breeders to carry out trait-based mining of large germplasm collections.

Comparative mapping studies in cereals have demonstrated that gene content and orders are highly conserved between different species. Integration of the genetic maps of rice, foxtail millet, sugarcane, sorghum, maize, the *triticeae* cereals, and oats into a single synthesis reveals that some chromosome arrangements characterize taxonomic groups, while others have arisen during or after speciation (Devos and Gale, 1997). The linear organization of genes among nine species in the grass family, differing in basic chromosome numbers (5-12) and nuclear DNA amount (400-6000 Mb), can be described in 25 "rice linkage blocks" (Gale and Davos, 1998). Elucidation of the organization of the economically important grasses with large genomes such as maize will to a greater or lesser extent be predicted from sequence analysis of smaller genomes such as rice. Synteny studies will be greatly aided by knowledge of the entire sequence of *Arabidopsis* and in due course *Medicago* and *Lotus.* Examples of conserved collinearity between *Arabidopsis* and *Brassica* (Kowalski *et al.,* 1994; Cavell *et al.,* 1998; Quiros *et al.,* 2001; Ryder *et al.,* 2001), between *Arabidopsis* and tomato (Ku *et al.,* 2000, 2001), between tomato and potato (Tanksley *et al.,* 1992), between *Arabidopsis* and soybean (Grant *et al.,* 2000), and between the dicot genome of *Arabidopsis* with monocots such as sorghum and rice has been reported (Paterson *et al.,* 1996; van Dodeweerd *et al.,* 1999; Mayer *et al.,* 2001). Lee *et al.,* (2001) have suggested the use of *Arabidopsis* as a "bridge species" to resolve the genome evolution among dicots. They not only reported conservation of large regions of the genomes in soybean, *Phaseolus vulgaris,* and *Vigna radiata* but these conserved regions were also relatively conserved in *Arabidopsis.* They also suggested that there is conservation of blocks of DNA between species as distantly related as legumes and brassicas, representing 90 million years of divergence. Cross-species, cross-genera, and cross-kingdom comparisons are, therefore, providing critical information for understanding how genes are structured, how gene structure relates to gene function, and how changes in DNA have given rise to the biological diversity on the planet (McCouch, 1998).

Preliminary comparative mapping studies have been conducted between soybean and cowpea (Maughan *et al.,* 1996), pea and lentil (Weeden *et al.,* 1992), pea and chickpea (Simon and Muehlbauer, 1997), mungbean and cowpea (Menancio-Hautea *et al.,* 1993; Fatokun *et al.,* 1993), mungbean, common bean, and soybean (Boutin *et al.,* 1995), azuki bean and rice bean (Kaga *et al.,* 2000), and mungbean and lablab (Humphry *et al.,* 2002). Localized synteny between *Arabidopsis* and distantly related dicot crops (Paterson *et al.,* 1996; Ku *et al.,* 2000) suggests that it may be possible to utilize progress in *Arabidopsis* and *Medicago* genomes to enhance molecular breeding efforts in groundnut. For example, the reported synteny between a segment of tomato chromosome 2 and *Arabidopsis* chromosome 4 has been used to identify several expressed sequence tags (ESTs) including TX680 that cosegregate with ovate fruit shape in tomato (Ku *et al.,* 2001). Conservation of the genome microstructure between

Arabidopsis and rice (22 of the 56 genes identified in the rice genome segement were also represented in the corresponding *Arabidopsis* genome segment, with at least five genes present, in conserved order, in each segment) can be identified even between monocot and dicot species (Mayers *et al.,* 2001). These reports clearly demonstrate that rich sources of new markers can be obtained at relatively low cost by mining public sequence databases (Ku *et al.,* 2001). Thus, using the identified position or known sequence of important genes in model species it may be possible to quickly locate genes of similar function in lesser- studied crops. Such approaches promise to dramatically enhance progress in molecular breeding of groundnut.

Researchers have recently adopted *Medicago truncatula* as a model legume particularly for the study of plant-microbe interactions (e.g., symbiotic nitrogen fixation, mycorrhizal and legume-pathogen interactions) that cannot be studied in *Arabidopsis.* It is the native to Mediterranean Basin, exhibits tolerance to drought and salinity, and can be grown in a wide range of soil and environmental conditions (Barker *et al.,* 1990; Cook *et al.,* 1997). The key attributes of this species include: a small diploid genome (haploid chromosome number 8 and genome size of about 5 x 108 bp/lC), self-fertility nature, prolific seed production, rapid generation cycling, and ease of transformation using *Agrobacterium tumefaciens* and regenerated to yield fertile transgenic plants (Cook, 1999). It has numerous ecotypes that exhibited wide diversity for growth habit, flowering time, and disease resistance. It has been recognized as a potential model crop for comparative mapping and syntenic relationships with *Arabidopsis* and other legume crops (Cook, 1999).

D. WIDE CROSSES

Wild *Arachis* species harbor genes for resistance to many abiotic and biotic stresses (Table IV), and for seed quality traits (Table V). Many of the wild species are not cross compatible with *A. hypogaea,* and the major barrier for gene introgression to *A. hypogaea* is post-zygotic failure of embryo development. However, diploid species of section *Arachis* and the cultivated tetraploid *A. hypogaea* can be crossed at the same ploidy level, reducing sterility in hybrids. Strategic approaches to introgress genes from wild diploid species to *A. hypogaea* include (1) interploidy crosses [between *A. hypogaea* (AABB genomes) and wild diploid species (AA or BB genomes)], (2) artificial polyploidization (crosses between *A. hypogaea* and autotetraploid wild species with either AA or BB genomes), and (3) resynthesis (crosses between *A. hypogaea* and amphidiploid wild species containing both AA and BB genomes or only the AA genome), followed by recurrent backcrossing to *A. hypogaea* genotypes (Stalker and Moss, 1987; Singh *et al.,* 1991; Simpson, 2001). These crossing schemes can be expected to facilitate interspecific chromosome pairing that can result in different

frequencies of inter- and intra-genomic recombinations. Using these techniques, several interspecific tetraploid derivatives have been developed with the aim of introgressing genes for resistance to rust, ELS, LLS, nematodes, southern corn rootworm, corn earworm, *Spodoptera,* and jassids (Gardner and Stalker, 1983; Moss, 1985; Singh, 1986a,b; Stalker and Moss, 1987; Singh *et al.,* 1991; Simpson *et al.,* 1993; Stalker and Lynch, 2002; Stalker *et al.,* 2002a,b). Simpson and Starr (2001) released the first root-knot nematode-resistant peanut cultivar (Coan) in USA that contains a pest resistant gene from *A. cardenasii.* However, this has allowed only slow progress in transferring resistance genes from wild *Arachis* to *A. hypogaea* in improved genetic backgrounds because of problems associated with linkage drag. Exploitation of alien germplasm in the genus *Arachis* has so far only in the primary and secondary gene pools. Use of an aneuploid series in cultivated groundnut improvement might enhance the utilization of diploid species of section *Arachis* from the secondary gene pool. The possibilities of alien gene transfer from the tertiary gene pool within the accessible limit of *A. hypogaea* also exist by using bridge species, *in vitro* fertilization and hormone treatment, protoplast fusion, and plant regeneration techniques (Singh *et al.,* 1991).

E. GENETIC TRANSFORMATION

Sharma *et al.* (2000) reviewed the prospects for transgenic resistance and concluded that with the advent of genetic transformation techniques, it has become possible to clone and insert genes (δ-endotoxins from *Bacillus thuringiensis* (Bt), protease inhibitors, and enzymes and plant lectins) into crop plants to confer resistance to insect pests. Holbrook and Stalker (2003) reviewed the progress achieved in development of an efficient tissue culture and transformation systems to introduce foreign DNA into groundnut, and the transgenic plants developed having genes for resistance to Tomato Spotted Wilt Virus and lesser cornstalk borer in USA. Transgenic groundnuts with *IPCVcp* or *IPCVreplicase, GRAVcp,* and rice chitenase genes have been produced at ICRISAT, and these are in various stages of characterization under containment glasshouse and/or controlled field conditions (ICRISAT, 2001). The first products of transgenic plants with *IPCVcp* gene are being evaluated for resistance to peanut clump virus (PCV) under field conditions during 2002 rainy season at Patancheru, India. A new initiative with Japan International Research Center for Agricultural Sciences has been taken up to use their constructs (rd29A:DREBlA) carrying drought responsive elements (DRE) of *Arabidopsis* into *Arachis* for inducing drought resistance in groundnut. The putative transformants obtained in *Agrobacterium-mediated* transformation are being characterized for presence and expression of the introduced genes, and the confirmed transgenic groundnut plants will be later on evaluated for their

response to drought stress conditions (Sharma and Lavanya, 2002). It is hoped that once favorable genes for resistance to leaf miner, *Spodoptera,* groundnut rosette assistor virus (GRAV), drought, and aflatoxin have been introduced into cultivated groundnut accessions through wide crosses and/or genetic transformation, these genes will become ideal candidates for marker-accelerated introgression in support of adaptive breeding across the world.

V. OPPORTUNITIES FOR MOLECULAR BREEDING IN GROUNDNUT

A. CURRENT UNDERSTANDING AND GENETIC BASIS OF ECONOMICALLY IMPORTANT TRAITS

1. Rust

The characterized sources of resistance to rust in *A. hypogaea* exhibit component mechanisms that reduce the rate of disease development. Thus resistant lines have increased pathogen incubation periods, decreased infection frequencies, and reduced pustule sizes, spore production, and spore germinability (Subrahmanyam *et al.,* 1983a; Mehan *et al.,* 1994). In contrast, the characterized sources of resistance in wild *Arachis* species and their interspecific derivatives have more dramatic effects on the pathogen. In particular, uredosori on these accessions are observed to be small (containing very few uredospores), slightly depressed, and do not rupture to release their uredospores (Subrahmanyam *et al.,* 1983b). Resistance to rust in *A. hypogaea* is conferred either by a few recessive genes (Knauft, 1987; Kalekar *et al.,* 1984; Paramasivam *et al.,* 1990) or predominantly controlled by additive, dominance, and additive X additive and additive X dominance genetic effects (Reddy *et al.,* 1987; Varman *et al.,* 1991). In addition, partial dominance is reported in some diploid species (Singh *et al.,* 1984).

2. Early Leaf Spot (ELS)

Incubation period, infection frequency, lesion diameter, and defoliation are important components of resistance to ELS. The resistant germplasm accessions have longer incubation periods, reduced sporulation rates, lesion diameters, infection frequencies, and less defoliation (Nevill, 1981; Waliyar *et al.,* 1993; http://www.icrisat.org/text/research/grep/homepage/annualreport/annualreport.
htm). Resistance to ELS is quantitative and controlled by additive, dominance, and additive x additive genetic effects (Kornegay *et al.,* 1980; Hamid *et al.,* 1981;

Anderson *et al.,* 1986; Green and Wynne, 1987). Maternal effects and/or cytoplasmic factors have also been reported (Coffelt and Porter, 1986; Kornegay *et al.,* 1980; Sharief *et al.,* 1978).

3. Late Leaf Spot (LLS)

Resistance to LLS is partial and is similar to the "slow rusting" type of resistance. Sporulation rate, lesion size, lesion number, and latent period are important components that contribute to a desired field score for LLS (Chiteka *et al.,* 1988; Anderson *et al.,* 1990a). Resistant genotypes have longer incubation periods, fewer lesions, and lower sporulation rates than susceptible genotypes (Nevill, 1981). Both two-gene (Tiwari *et al.,* 1984) and five-locus recessive genetic models (Nevill, 1982) have been reported for resistance to LLS. Recessive genes for resistance have been reported in crosses involving cultivated groundnut and wild *Arachis* species (Sharief *et al.,* 1978). Other studies report predominantly additive genetic variance for most of the components of resistance to LLS (Kornegay *et al.,* 1980; Hamid *et al.,* 1981; Anderson *et al.,* 1986; Jogloy *et al.,* 1987).

4. Groundnut Rosette Disease (GRD)

All three agents [groundnut rosette virus (GRV), groundnut rosette assister virus (GRAV), and satellite RNA (sat RNA)] should be present in the plant on which the vector (*Aphis crassivora*) feeds for effective transmission of disease by the vector (Bock *et al.,* 1990). An efficient reverse transcription-polymerase chain reaction (RT-PCR) assay has been developed that allows the detection of each of the three components of the rosette virus syndrome (Naidu *et al.,* 1998). GRV resistance is controlled by two independent recessive genes in crosses between resistant (RG 1 and RMP 40) and susceptible (JL 24, ICGM 48, and Mani Pintar) germplasm in groundnut (Nigam and Bock, 1990). However, dominant monogenic resistance to rosette was also reported in a cross between RMP 12 and M 1204.781 (Olorunju *et al.,* 1992) while resistance to aphids in ICG 12991 appears to be recessive in nature (van der Merwa, pers. comm.). GRV resistance seems to be effective against both chlorotic and green rosette.

5. Bacterial Wilt

Resistance to bacterial wilt in groundnut is a function of the duration of the latent period, degree of vascular browning, hypersensitive reaction showing partial symptoms, and rate of wilting. The late-maturing Virginia runner

(subsp. *hypogaea* var. *hypogaea*) and Dragon (subsp. *hypogaea* var. *hirsuta*) types have longer latent periods than the early maturing Spanish (subsp. *fastigiata* var. *vulgaris*) and Valencia (subsp. *fastigiata* var. *fastigiata*) types. A large number of land races of Dragon types from south China are reported to be resistant to bacterial wilt (Duan *et al.,* 1993). Resistance has also been correlated with specific root characteristics in some genotypes. The susceptible genotypes tend to have a long and strong main root while the resistant genotypes tend to have long lateral roots (Liao *et al.,* 1992). Resistance to bacterial wilt has been reported to be recessive or partially dominant in crosses between resistant (Xiekangqing, Taishan Sanlirou, You 112, and Taishan Zhenzhu) and susceptible (Honghua No. 1, E Hua No. 3, Heyou No. 4, and Youguo) genotypes (Wang *et al.,* 1985; Liao *et al.,* 1986). Three major genes have been reported to confer resistance to bacterial wilt in groundnut accessions Xiekangqing, Taishan Sanlirou, Taishan Zhengzhu, and Hong Hua 1 (Liao *et al.,* 1990). However, both cytoplasmic and nuclear factors have been reported to confer resistance to bacterial wilt in some Dragon types.

6. Aflatoxin Contamination

Groundnuts are prone to aflatoxin contamination by *A. flavus.* Drought during pod formation substantially increases the level of aflatoxin contamination. It was reported that pre-harvest infection by *A. flavus* requires a drought period of 30-50 days and a mean soil temperature of 29-31°C in the podding zone (Cole *et al.,* 1989; 1995). The susceptibility of groundnut to aflatoxin contamination is related to lower water activity (0.80-0.95) in the kernel and favorable temperature (25-32°C) for growth of *A. flavus* (Schearer *et al.,* 1999). As the kernel moisture content decreases under end-of-season drought, protection from natural defense mechanisms is lost and the kernel becomes vulnerable to colonization by *A. flavus* and aflatoxin contamination. Because of the high correlation between seed moisture and pre-harvest aflatoxin contamination (Dorner *et al.,* 1989), there is the possibility to select for reduced pre-harvest aflatoxin contamination by identifying germplasm with the capacity to maintain high kernel water activity during severe drought stress. The drought tolerant lines, PI 145681 and Tifton 8, support less pre-harvest aflatoxin contamination than drought-intolerant line, Florunner (Holbrook *et al.,* 2000).

Resistance to *A. flavus* in groundnut is reported to operate independently in at least three tissues: pod, seed coat, and cotyledons (Mixon, 1986). Resistance to pod infection is confered by pod wall structure and the presence of a wax layer while resistance to seed invasion and colonization is correlated with thickness and density of palisade cell layers and absence of fissures and cavities. However, seed coat resistance is effective only in intact seed testa. Phenolics have also been implicated in imparting resistance to seed infection (Pettit *et al.,* 1989).

Resistance to seed colonization by *A. flavus,* aflatoxin production, and pre-harvest infection in crosses AR 4 X NC 7 and GFA 2 X NC 7 were controlled by different genes all with low heritabilities (Utomo *et al.,* 1990). However, Mixon (1976) reported a high broad-sense heritability for percentage seed colonization in cross PI 337409 x PI 331326.

Lipoxygenase (LOX) enzymes and their products could play a role in the *Aspergillus*- seed interaction. The C6-C12 products of the LOX pathway inhibit *Aspergillus* spore germination (Doehlert *et al.,* 1993; Zeringue *et al.,* 1996) and methyl jasmonate inhibits aflatoxin biosynthesis but not fungal growth (Goodrich-Tanrikulu *et al.,* 1995). The 9S- and 13S-hydroperoxides differentially affect *Aspergillus* mycotoxin biosynthesis (Burow *et al.,* 1997; Gardner *et al.,* 1998) and these same hydroperoxides act as *Aspergillus* sporulation factors (Calvo *et al.,* 1999), suggesting that LOX isozymes play a role in regulating *Aspergillus* infection and aflatoxin contamination in oil seeds crops. Burow *et al.* (2000) cloned and characterized a peanut seed lipoxygenase gene, *PnLOXl.* This gene encodes a 98 kDa protein highly similar in sequence and biochemical properties to soybean LOX2. The gene is highly induced by *Aspergillus* infection and the active protein produces a mixture of 9S- and 13S-hydroperoxides. PnLOXl is an organ-specific gene expressed in immature cotyledons but is highly induced by methyl jasmonate, wounding, and *Aspergillus* infection in mature cotyledons. Some of the cloned genes of aflatoxin biosynthetic pathway can be effectively utilized to induce resistance to aflatoxin production.

7. **Drought**

A number of physiological mechanisms have been correlated with genotypic differences in yield under drought stress including variation in transpiration, water-use efficiency (WUE), and partitioning under end-of-season drought stress (Nageswara Rao *et al.,* 1993). Variation in WUE arises mainly from genotypic differences in water use. Carbon isotope discrimination (A) can be used to select genotypes with improved WUE under field drought stress conditions. However, analysis of A is not economic particularly when to analyse a large number of plants in segregating generations. A strong relationship between WUE and specific leaf area (SLA) and between A and SLA revealed that genotypes with thicker leaves had greater WUE (Wright *et al.,* 1994). SLA could, therefore, be used as a rapid and inexpensive indirect selection criterion for WUE to facilitate selection for end-of-season drought tolerant genotypes (Nageswara Rao and Wright, 1994). However, there appears to be a negative relationship between WUE and partitioning under end-of-season drought stress conditions suggesting that selection for high WUE might enhance groundnut dry matter production under stress but not necessarily improve pod yield (Wright *et al.,* 1994; Nageswara Rao and Wright, 1994). SLA is also highly

influenced by G x E interaction. Additive genetic effect for A, and both additive and additive X additive epistasis effects for SLA (Jayalakshmi *et al.,* 1999; Nigam *et al.,* 2001) and partitioning (Dwivedi *et al.,* 1998a; Nigam *et al.,* 2001) are reported. Variation in root characteristics and the ability of roots to extract water from deeper layers of the soil profile have also been reported (Ketring, 1984).

Drought stress triggers a number of physiological and developmental changes associated with selective increase or decrease in the biosynthesis of a number of distinct proteins that alter enzyme activity. The changes in protein profile are due to changes in transcription rate, RNA stability, post-transcriptional control, and protein turnover (Smirhoff and Colombe, 1989). Several genes responding to dehydration at the transcriptional level have been reported in plant species (Skriver and Mundy, 1990; Shinozaki and Yamaguchi-Shinozaki, 1996; Bray, 1997; Oliver *et al.,* 1998; Tabaeizadeh, 1998). Using RT-PCR, Jain *et al.* (2001) reported 43 peanut transcripts (mRNA) responsive to drought (PTRD) and these show quantitative variation in their levels and duration of expression in tolerant (PI 145681) and susceptible (Florunner) groundnut genotypes. PTRD-1, -10, and -16 are completely suppressed due to prolonged drought in the tolerant genotype indicating these transcripts may be used as markers along with other morphological characters such as large root system and visual stress ratings for screening genotypes with drought tolerant characteristics in groundnut (Ketring, 1984; Rucker *et al.,* 1995; Holbrook *et al.,* 2000).

8. Seed Quality Traits

One hundred-seed mass, oil content, and oleic (O) and linoleic (L) fatty acid ratio are important seed quality traits in groundnut. Oil content is quantitatively inherited trait (Layrisse *et al.,* 1980; Makne and Bhale, 1987). Several studies involving high oleic acid groundnuts revealed that high oleic acid is controlled by two duplicate recessive genes, and one of the recessive alleles occurs with high frequency in US peanut breeding populations whereas the other allele is rare (Holbrook and Stalker, 2003). Oleic acid content is also reported to be influenced by additive and additive X additive genetic effects (Layrisse *et al.,* 1980; Moore and Knauft, 1989; Mercer *et al.,* 1990; Upadhyaya and Nigam, 1999b). Jung *et al.* (2000a) reported that high oleate groundnut resulted from reduction in the activity or transcript level of microsomal oleoyl-PC desaturase. They isolated two non-allelic but homoeologus genes, *ahFAD2A* and *ahFAD2B,* from the developing peanut seed with a normal oleate seeds. *ahFAD2A* is expressed in both normal and high oleate seeds. Reduction in *ahFAD2B* transcript levels in the developing seeds is correlated with high oleate trait. Further studies revealed that a mutation in *ahFAD2A* and a significant reduction in levels of the *ahFAD2B* transcript together cause the high oleate phenotype, and expression of one gene

encoding a functional enzyme appears to be sufficient for the normal oleate phenotype (Jung *et al.,* 2000b). Hundred seed mass is a quantitatively inherited trait controlled by additive, dominance, and epistatic effects (Wynne *et al.,* 1970; Garet, 1976; Sandhu and Khera, 1976; Layrisee *et al.,* 1980; Arunachalam *et al.,* 1985; Upadhyaya and Nigam, 1998).

9. Yield, Maturity, and Adaptation

Many agronomically important traits in groundnut appear to be quantitatively inherited (reviewed by Murthy and Reddy, 1993). Additive, non-additive, and epistatic genetic effects are reported for early maturity, pod yield, pods and seeds per plant, pod length and width, seed length and width, shelling outturn, and sound mature seeds (Parker *et al.,* 1970; Wynne *et al.,* 1970; 1975; Garet, 1976; Sandhu and Khera, 1976; Gibori *et al.,* 1978; Isleib *et al.,* 1978; Layrisse *et al.,* 1980; Sangha and Labana, 1982; Arunachalam *et al.,* 1985; Swe and Branch, 1986; Dwivedi *et al.,* 1989; Upadhyaya and Nigam, 1998). Response to photoperiod is controlled by additive gene action in some crosses and partial dominance to dominance in others (Nigam *et al.,* 1997). However, some agronomically important traits have been reported to have a simple genetic basis. For example, days to first flower is controlled by a single gene with additive gene action (Upadhyaya and Nigam, 1994). Although, three independent genes with complete dominance at each locus appear to control the number of days to the accumulation of 25 flowers. Similarly, fresh seed dormancy in a cross between dormant (ICGV 86158 and ICGV 87378) and non-dormant (JL 24) genotypes is conferred by the dominant allele of a single gene (Upadhyaya and Nigam, 1999a).

Heterosis is reported in crosses between the subspecific groups of groundnut for biomass, pod and seed yield, pod and seed size, pod and seed number per plant, shelling outturn, and 100-seed mass (Wynne *et al.,* 1970; Garet, 1976; Layrisee *et al.,* 1980; Isleib and Wynne, 1983; Swe and Branch, 1986; Dwivedi *et al.,* 1989), and its magnitude is linearly related to genetic divergence of the parents (Isleib and Wynne, 1983; Arunachalam *et al.,* 1982; 1984). Pod yield in groundnut is a function of crop growth rate, reproductive duration, and partitioning. However, the low heritability of these traits suggests that conventional selection for them during early segregating generations will not be very effective (Ntare and Williams, 1998).

B. DEVELOPING APPROPRIATE PCR-BASED MARKERS

Recent advances in the development of PCR-based marker protocols have revolutionized genetic analysis and opened new possibilities in the study of

complex traits in crop plants. The hybridization-based co-dominant markers (RFLP) and PCR-based dominant-markers (RAPD and AFLP) in many crops have been superseded by co-dominant PCR-based markers (SSR). However, when screening cultivated groundnut accessions with SSR markers (Hopkins *et al.,* 1999) polymorphisms were rarely found. In contrast, RAPD and RFLP markers associated with resistance to nematodes have been reported in interspecific crosses in groundnut (Burow *et al.,* 1996; Choi *et al.,* 1999). However, both RAPD and RFLP technologies have their own limitations for applications in large-scale marker-assisted breeding programs. The AFLP assay has been frequently used in diversity and mapping studies in many crop plants. However, effort to convert AFLP marker into simple co-dominant PCR markers has met with mixed success, is laborist, expensive and time consuming.

The low level of detectable molecular genetic variation among cultivated groundnut greatly constrains progress in molecular breeding of this crop. The RFLP-based tetraploid map developed by Burow *et al.* (2001), based on an interspecific cross, is likely to be useful in terms of locating specific genes of interest in this interspecific cross. However, the markers themselves may be of mixed value in molecular breeding programs as their linkage to loci of interest may be lost as a result of different recombination patterns in cultivated crosses. Clearly, there is a need to use assays that are more likely to reveal polymorphisms, such as microsatellitic markers (SSR) and single nucleotide polymorphisms (SNP). A collaborative project between ICRISAT and University of Georgia (USA) has recently generated 192 SSR primer pairs which produce scorable amplification products in cultivated groundnut from genomic libraries of the groundnut cultivar, Florunner. To date 110 SSR markers reveal genetic variation in a diverse array of 24 groundnut landraces (ME Ferguson, ICRISAT, pers. comm.). Recent developments in SNP technology indicate that in the near future, additional options may be available for rapid identification of large numbers of polymorphic markers (Kanazin *et al.,* 2002). SNPs comprise the largest set of sequence variants in most organisms (Kwok *et al.,* 1996; Kruglyak, 1997). SNPs are biallelic markers but occur very frequently within the genome, their mutation rate is low, capable of high throughput genotyping, and are often linked to genes (Kwok and Gu, 1999). For example a map containing 1.42 million SNPs distributed throughout the human genome have been constructed, with an average density of one SNP every 1.9 kb (The International SNP Map Working Group, 2001). SNPs have also been reported in crop plants such as *Arabidopsis* (Cho *et al.,* 1999; Drenkard *et al.,* 2000), barley (Schmitz *et al.,* 2000; Kota *et al.,* 2001a,b), common bean (Melotto and Kelly, 2001), groundnut (Lopez *et al.,* 2000), maize (Bhattramakki *et al.,* 2000a; Tenaillon *et al.,* 2001), rice (Ayres *et al.,* 1997; Larkin and Park, 1999), and soybean (Coryell *et al.,* 1999; Meksem *et al.,* 2001). SNPs map with a resolution of 3.5 cM have also been reported in *A. thaliana* that has been used to map *Eds*16 gene, located at 7 cM interval on the bottom of chromosome 1 between markers SNP 177 and SNP 231, involved in

the defence response to the fungal pathogen *Erysiphe orontii* (Cho *et al.,* 1999). The generation of denser biallelic maps should allow high-throughput indentification of both monogenic and polygenic traits and thus effectively removing the rate-limiting nature of high-resolution mapping from the study of biological processes (Cho *et al.,* 1999).

C. MAPPING AND GENETIC ENHANCEMENT STRATEGIES

Marker-assisted selection (MAS) offers great promise for improving the efficiency of conventional plant breeding. Molecular markers are especially advantageous for traits where conventional phenotypic selection is difficult, expensive or lacks accuracy or precision (Crouch, 2001). This includes resistance to certain pathogens and insect pests plus tolerance to abiotic stresses, quality parameters, and complex agronomic traits with low heritabilities. The essential requirements for developing marker-assisted selection systems are (1) availability of germplasm with substantially contrasting phenotypes for the traits of interest, (2) highly accurate and precise screening techniques for phenotyping mapping populations for the trait of interest, (3) identification of flanking marker(s) closely associated with the loci of interest and the flanking regions on either side, and (4) simple robust PCR-based marker technology to facilitate rapid and cost effective screening of large breeding populations.

Molecular marker studies using near-isogenic lines (NILs) (Muehlbauer *et al.,* 1988), bulked segregant analysis (Michelmore *et al.,* 1991), and recombinant inbred lines (RILs) (Burr *et al.,* 1988) have accelerated the mapping of many genes in different plant species. Advanced backcross QTL analysis has been proposed for the simultaneous discovery and transfer of valuable QTL from unadapted and wild germplasm into elite breeding lines (Tanksley and Nelson, 1996). This approach is effective for QTL from the donor line which have dominant, partially dominant or over-dominant gene action, and allows the generation of elite NIL for specific QTL for rapid variety development and reduced linkage drag around targeted QTL.

Trait heritability, the proportion of additive genetic variance explained by the marker loci affecting the trait, the selection method used, and the effective population size influence the selection efficiency of both conventional and marker-assisted breeding programs. MAS is equally effective for characters with low heritability when additive (Lande and Thompson, 1990) or non-additive (Gimelfarb and Lande, 1994) genetic variance are associated with the marker loci. The effectiveness of MAS decreases as the linkage distances between marker and target QTL increases. Linkage disequilibria between the marker loci and QTL, that condition trait expression, also influence the effectiveness of MAS (Lande and Thompson, 1990).

D. MARKER-ASSISTED GENE INTROGRESSION FROM WILD *ARACHIS* TO *ARACHIS HYPOGAEA*

Wild *Arachis* species and exotic germplasm are usually agronomically inferior to modern cultivars. However, reports in rice and tomato suggest that wild germplasm may contain alleles capable of improving both yield and seed quality of elite cultivars (Xiao *et al.,* 1996; Tanksley and McCouch, 1997). However, the effects of these alleles is often masked by the presence of deleterious genes at nearby loci. Advanced backcross populations and molecular genetic tools can be used to exploit the genetic potential of wild species for enhancing yield, seed quality, and resistance to diseases of elite genetic materials (Tanksley and Nelson, 1996). Whereas resistance to rust, ELS, LLS, and nematodes has been successfully transferred into *A. hypogaea* from wild *Arachis* species, only early attempts have been made to tap favorable genes from wild species for enhancing yield and seed quality in groundnut. There is a need to exploit these, along with disease resistance genes, to develop interspecific derivatives for enhanced yield, seed quality, and resistance to abiotic and biotic stresses in groundnut. MAS and marker-accelerated backcross breeding promise to dramatically improve the efficiency and success for rapid transfer of alien chromosome segments containing genes for yield, seed quality, and resistance to pests and diseases as it minimizes the deleterious linkage drag that often a problem while transferring genes from wild species or exotic germplasm by conventional breeding techniques.

E. MARKER-ASSISTED BACKCROSS BREEDING

Marker-assisted backcrosss breeding facilitates gene introgression from a "donor" line into the genomic background of a "recipient" line. Molecular markers can be used to assess the presence of the introgressed genes ("foreground selection") and to accelerate the return to the recipient parent genome ("background selection"). Over the past decade a number of important simulation studies have been conducted to ascertain conditions under which MAS could be competitive with conventional phenotypic selection. Frisch *et al.* (1999a) determined the optimal positioning of flanking markers and minimum number of individuals required to obtain, with a specific probability of success, at least one desired individual when backcrossing to transfer a target allele. Their study revealed that the length of the carrier chromosome, the chromosomal position of the target locus, its distance to the flanking marker loci, and the number of individuals evaluated influenced the efficiency of marker-assisted backcrossing. Frisch *et al.* (1999b) then compared various selection strategies with regard to the proportion of the recurrent parent genome (RPG) recovered and the number of marker data points (MDP) required in a backcross program designed for

introgression of one target allele from a donor line into a recipient line. They concluded that increasing population sizes from generation BC_1 to BC_3, in comparison to a constant population sizes across all generations, reduce the number of required MDP by as much as 50% without affecting the proportion of RPG. A four-stage selection approach, emphasizing in the first generations, selection for recombinants on the carrier chromosome of the target allele, reduced the required number of MDP by as much as 75% in comparison to a selection index taking into account all markers across the genome. Frisch and Melchinger (2001a) reported marker-assisted backcross strategy for the simultaneous introgression of two genes with respect to RPG recovered and the number of MDP required. Their simulation study, using data from published genetic linkage map consisting of 80 markers and assuming selection for dominant target genes in maize, revealed reduction in the number of back cross generations from six to three can be attained with 1000-1500 MDP for unlinked as well for linked target locus. Small population sizes in early generations and large population sizes in advanced generations require less MDP than constant or decreasing population sizes while attaining the same RPG content. Frisch and Melchinger (2001b) further demonstrated the use of marker-assisted backcross breeding for introgression of a recessive target gene from a donor into the genetic background of a recipient line by foreground selection combined with background selection for reducing the donor chromosome segment around the target gene.

Hospital and Charcosset (1997) provided a general framework for the optimization of the use of molecular markers in backcross breeding programs aimed at introducing one to several superior QTL into a recipient line. Using at least three markers per QTL allows a good control of the donor chromosome segment over several generations. When several target alleles are monitored simultaneously, background selection among the limited number of individuals resulting from the foreground selection step accelerates the increase in genomic similarity with the recurrent parent with only limited increase in the cost. These flanking markers should cover ~10-20 cM around the estimated position of the gene to ensure that allele frequency does not decline in later generations (Visscher *et al.,* 1996). Hospital *et al.* (1997) found that the relative efficiency of MAS over purely phenotypic selection in the first generation increases with (1) larger population sizes, (2) lower trait heritabilities, and (3) higher type-I error risk. However, at low heritability the response to MAS is more variable than response to phenotypic selection. The MAS may become less efficient than phenotypic selection in long term as the rate of fixation of QTL with large effects in early generations is balanced by a higher rate of fixation of unfavourable alleles at QTL with small effects in later generations. MAS efficiency therefore depends on the genetic determinism of the trait. Alternating generations of MAS and conventional phenotypic selection appeared to offer the best improvement in genetic gain per unit time in applied breeding programs. Sen and Churchill

(2001) developed simple Monte Carlo algorithm to implement Bayesian QTL analysis for the genetic analysis of QTLs in an inbred line cross. This algorithm simulates multiple version of complete genotype information on a genomewide grid of locations using information in the marker genotype data. Weights are assigned to the simulated genotypes to capture information in the phenotype data, and the weighted genotypes are used to approximate quantities needed for statistical inference of QTL locations and effect sizes. In this approach only weights are recomputed as the analyst considers different candidate models. This approach allows the analyst to focus on modeling and model comparisons, and can accommodate multiple interacting QTL, non-normal and multivariate phenotypes, covariates, missing genotype data, and genotyping errors in any type of inbred line cross.

F. PRIORITIZING TRAITS FOR MARKER-ASSISTED SELECTION

The major constraints to groundnut productivity have been discussed in Section 1B. Table IX summarizes the traits of economic importance and the suggested conventional and non-conventional techniques for genetic enhancement in groundnut. For many traits, adequate and cost effective progress is being made through traditional approaches. Traits for which MAS is not justified include maturity, pod yield, pod size and shape (except in situations wherein resistance to pests and diseases is linked with undesirable traits), seeds per pod, seed color, shelling outturn, sound mature seeds, 100-seed weight, and seed dormancy as well resistance to rust and bacterial wilt. There is a large pool of genetic variation reported for these traits in cultivated groundnut gemplasm (Singh and Nigam, 1997; Rajgopal *et al.,* 1997; Upadhyaya *et al.,* 2001e; Table IV) that are easy to exploit through conventional breeding techniques. Several cultivars with these characteristics have been developed and are commercially grown in semi-arid tropics (Table VI).

In general, traits that justify the cost and time required to develop and apply MAS system, will include those that are difficult or expensive to score, traits that are associated with deleterious linkage drag, traits that are controlled by different genetic mechanisms such as GRD (GRV, GRAV, and sat RNA) or traits where the application of DNA markers will allow breeders to address new goals. For traits such as ELS, LLS, nematodes, leafminer, and *Spodoptera* there are only low to moderate levels of resistance (or tolerance) available in cultivated groundnut. In contrast, many wild *Arachis* species show a very high degree of resistance to these diseases and pests (Table IV). However, the resistant wild species are often sexually incompatible with cultivated groundnut. Efforts to overcome incompatibility in wide crosses for transferring resistance genes from the tertiary gene pool of genus *Arachis* by using non-conventional techniques have had limited success but are beginning to liberate useful interspecific

Table IX
Traits and Breeding Strategy Suggested for Rapid and Cost Effective Genetic Enhancement in Groundnut

Trait	Conventional Breeding	Marker-assisted Selection	Wide Crosses + Marker Assisted Backcross	Genetic transformation	Genetic basis
Maturity	•				Polygenic, refer page 192
Pod yield	•				Polygenic, refer page 192
Pod size and shape	•				Polygenic, refer page 192
100-seed weight	•				Polygenic, refer page 192
Shelling outturn	•				Polygenic, refer page 192
Sound mature seeds	•				Polygenic, refer page 192
Seed dormancy	•				Monogenic, refer page 192
O/L ratio[a]		•			Oligogenic, refer page 191–192
Aflatoxin				•	Polygenic, refer page 189–190
Drought		•		•	Polygenic, refer page 190–191
Leaf miner			•		Not known
Spodoptera			•		Not known
Rust	•				Oligogenic, refer page 187
ELS[b]			•		Polygenic, refer page 187–188
LLS[c]			•		Both oligo- and poly-genic, refer page 188
Bacterial wilt	•				Oligogenic, refer page 188–189
GRD[d]	•			•	Mono- and diagenic refer page 188
PBND[e]				•	Not known

[a]O/L, Oleic/Linoleic fatty acid ratio.
[b]ELS, Early leaf spot.
[c]LLS, Late leaf spot.
[d]GRD, Groundnut rosette disease.
[e]PBND, Peanut bud necrosis disease.

progenies (N Mallikarjuna, ICRISAT, pers. comm.). Marker-assisted back cross breeding is therefore suggested for rapid transfer of resistant gene(s) from wild *Arachis* to cultivated groundnut. Efforts to select for high levels of resistance to PBNV or TSWV have received with limited success by conventional breeding techniques. Similarly most of the GRD resistant accessions of cultivated groundnut germplasm are resistant to GRV with few exceptions that are resistant to aphids but susceptible to GRV, and none resistant to GRAV. Several wild *Arachis* species, on contrary, are reported to possess high level of resistance to GRAV, sat RNA, PBNV, and TSWV. An efficient tissue culture and transformation system has been reported in groundnut. Wide crosses and/or genetic transformation are therefore suggested to introduce genes for resistance to these diseases into cultivated groundnut. Wild *Arachis* species are no better than levels of resistance reported for aflatoxin in cultivated groundnut accessions. Thus, a transgenic approach may be the most effective option to introduce genes for resistance to aflatoxin in groundnut.

Traits associated with seed quality (as measured by O/L ratio: higher the ratio better the shelf-life of the groundnut products) and drought tolerance (specific leaf area, total transpiration, water use efficiency, and partitioning) are difficult and uneconomic to measure in large segregating generations. They are also substantially influenced by genotype-by-environment interaction. Thus, breeding progress in these traits by conventional techniques has had limited success. MAS may therefore be a highly justified option for indirect selection for high O/L ratio and drought tolerance in groundnut.

VI. CONCLUSION

Groundnut is extensively grown in the semi-arid tropics (SAT) by resource-poor farmers. Several abiotic and biotic stresses limit groundnut productivity and affect its seed quality. Drought and temperature among abiotic stresses and rust, early leaf spot (ELS), late leaf spot (LLS), and aflatoxin among biotic stresses are the global constraints to groundnut production and adversely influence seed quality. Regionally, groundnut rosette disease (GRD) in Africa; bacterial wilt, leafminer, *Spodoptera,* and peanut bud necrosis disease (PBND) in South and/or South East Asia; corn earworm, lesser corn stock borer, southern corn rootworm, *Sclerotium,* nematodes, and tomato spotted wilt virus (TSWV) in North America; and low calcium and phosphorus availability in acidic soils in Latin America and Caribbean are important constraints to groundnut production. These stresses together cause annual yield losses exceeding US $ 3.2 billion, and probably half of this could be recovered through genetic enhancement in groundnut (ICRISAT, 1994).

Researchers have made excellent progress toward developing elite groundnut germplasm/cultivars with specific traits. However, there has been only limited success in introgressing good seed quality and resistance to the above mentioned constraints into an elite genetic backgrounds. The major constraints to rapid genetic enhancement include (1) disease resistance genes are often closely linked with loci conferring undesirable pod and seed characteristics, (2) disease resistant germplasm are late maturing types, have lower partitioning, and are sensitive to photoperiod than agronomically elite susceptible materials, (3) large genotype-by-environment interactions for traits of economic importance, and (4) limited gene introgression from wild *Arachis* species to cultivated groundnut. The application of DNA markers will allow breeders to break non-pleiotropic associations and pyramid genes for resistance to abiotic and biotic stresses with improved productivity and seed quality of groundnut.

Assessment of genetic diversity and development of a saturated genetic linkage map are important steps in the development of molecular marker-assisted breeding programs. There are over 15,000 cultivated groundnut accessions maintained in ICRISAT gene bank. ICRISAT scientists have developed a core collection consisting of 1704 accessions, and this core when further evaluated could provide new sources of variation for use in breeding programs. The *Arachis* species harbor genes capable of improving both seed yield and quality in addition to high levels of resistance to ELS, LLS, nematodes, leafminer, and *Spodoptera.* Many of the wild *Arachis* species are not cross compatible with cultivated groundnut. However, efforts to overcome incompatibility in wide crosses, by using non-conventional techniques, have started to liberate interspecific progenies with high levels of resistance to leaf spots, nematodes, *Spodoptera,* and leafminer. Marker-assisted backcross breeding should minimize the linkage drag as it greatly facilitate monitoring of introgressed chromosome segments carrying beneficial genes from wild *Arachis* to cultivated groundnut. An efficient tissue culture and transformation system has been developed, and transgenic groundnut plants with *IPCVcp* or *replicase, GRAVcp,* and rice *chitenase* genes have been produced that are in various stages of characterization under containment glasshouse and/or field conditions at ICRISAT. Transgenic approach may be the best option to introduce genes for resistance to aflatoxin as conventional breeding has failed to enhance the level of resistance beyond that present in cultivated groundnut germplasm. For traits such as GRAV, PBNV, and TSWV the use of wide hybridization and/or genetic transformation may be the most efficient strategy to introduce resistance genes into cultivated groundnut. Once favorable genes are introduced into cultivated groundnut through wide crossing and/or genetic transformation techniques, these genes will become ideal candidates for marker-accelerated introgression.

DNA marker based genetic linkage map should enable breeders to effectively pyramid genes for good seed quality (high O/L ratio and resistance to aflatoxin) and resistance to ELS, LLS, aflatoxin, nematodes, leafminer, *Spodoptera* and

tolerance to drought into agronomically enhanced breeding populations in a much shorter time than would be possible by conventional techniques. Recombinant inbred lines (RILs) mapping populations are being developed to map the genes underlying most of these traits. Meanwhile, substantial efforts are still required to develop sufficient PCR-based markers (particularly SSR and SNP markers) for the construction of high-density genetic linkage map and for the routine application in the molecular breeding of abiotic stress tolerance, biotic stress resistance, yield, and seed quality in groundnut. The use of automated technologies will become increasingly important for large-scale germplasm characterization and realistic scale marker-assisted genetic enhancement in groundnut.

ACKNOWLEDGMENTS

The authors wish to thank C.T. Hash, D.V.R. Reddy, R.P. Thakur, K.K. Sharma, N. Mallikarjuna, P.J.A. ven der Merwe, E. Mace (ICRISAT), R.L. Jarret (USDA), and R. Ortiz (IITA) for their feedback and discussions during the development of this manuscript. Assistance provided by T. Ravindrakumar, D. Yadgiri, and K.D.V. Prasad for formatting the text and figures is gratefully acknowledged.

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