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Potential of wild species for genetic enhancement of some semi-arid food crops

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Abstract

Discovery and incorporation of genes from wild species provide means to sustain crop improvement, particularly when levels of resistance in the cultigens are low and virulent strains of pests and pathogens overcome the host plant resistance. The extent of utilization and the potential of the wild genepool for genetic enhancement were reviewed in five important food crops viz. sorghum, pearl millet, chickpea, pigeonpea and groundnut grown in the semi-arid tropics. Introgression from compatible wild germplasm in the primary gene pool resulted in transfer of new cytoplasmic male sterility systems in pearl millet and pigeonpea, development of high protein, cleistogamous flower and dwarf pigeonpea lines and foliar disease resistant groundnut cultivars. Utilization of wild species in secondary and tertiary gene pools has been generally limited due to sterility, restricted recombination or cross incompatibility. Nevertheless, these species are extremely important as they contain high levels of resistance to several important biotic and abiotic stresses. Several of them, like those belonging to the *Parasorghum* section and the rhizomatous *Arachis* species are sources of multiple resistances and hold great promise to sustain crop productivity.

Introduction

The genetic potential of wild relatives in crop improvement is well documented, particularly for crops like wheat, maize, potato, tomato, cotton, tobacco and sugar cane (Hawkes 1977; Stalker 1980; Plucknett et al. 1987). Not surprisingly, the greatest contribution of wild species has been in resistance breeding. When the level of resistance to various biotic and abiotic stresses in cultivated germplasm is low or the range of genetic variability is narrow and selection pressure results in virulent biotypes of the pests and diseases, the discovery and incorporation of additional genes for resistance from wild species becomes key to sustain crop productivity. Despite their importance, wild species have not received due attention from germplasm collectors. They remain underrepresented and account for less than two percent of the global germplasm collections of major food crops. The genebank at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at Patancheru, India holds over 104,000 accessions of germplasm of five important food crops namely, sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* R. Br.), chickpea (*Cicer arietinum* L.), pigeonpea (*Cajanus cajan* (L.) Millsp.) and groundnut (*Arachis hypogaea* L.). The assembled germplasm includes a total of about 2500 accessions of the wild and weedy relatives. Harlan and de Wet (1971) proposed a systematic means of categorizing wild species as to their usefulness for improving the cultigens. According to this concept, species that readily intercross with the cultigen and produce progenies that are fully or nearly fertile are grouped in primary gene pool. Consequently, geneflow between the species within this group can be accomplished by convention-

al breeding methods. Any partial sterility that appears in progenies is easily overcome by selection. The secondary gene pool includes species, which are somewhat distant from the cultigen. Hybridization is more difficult and the progenies have substantial degree of sterility usually because of chromosomal rearrangements and imbalance. The tertiary gene pool contains species that are related to the cultigen but where hybridization with the cultigen has not been possible or where hybrids have been completely sterile. The potential and extent of use of the wild species germplasm to overcome constraints in productivity in the five ICRISAT mandated crops (sorghum, pearl millet, chickpea, pigeonpea and groundnut) are described in this paper.

Sorghum

The genus sorghum is subdivided into five sections *Chaetosorghum*, *Heterosorghum*, *Parasorghum*, *Stiposorghum* and *Sorghum* (de Wet 1978). The section *Sorghum* includes two rhizomatous species, *S. halepense* ($2n = 40$) and *S. propinquum* ($2n = 20$) along with the annual *S. bicolor* ($2n = 20$), which is divided into three subspecies. Subspecies *bicolor* includes all domesticated grain sorghums, subsp. *drummondii* includes the stabilized derivatives of hybridization among grain sorghums and their closest wild relatives and subsp. *arundinaceum* consists of the wild progenitor of grain sorghums (de Wet 1978). The sorghum genetic resources collection held at ICRISAT genebank includes 461 wild germplasm accessions representing 26 species and subspecies (Table 1), besides 35,238 accessions of cultivated sorghums and eight accessions of *Sorghastrum* spp. Sizable collections of wild species are also maintained at the Australian Tropical Crops and Forages Genetic Resources Centre, Biloela, Australia (over 370 accessions of 23 species) (AusPGRIS 2002) and the USDA-ARS Southern Regional Plant Introduction Station, Griffin, Georgia, USA (about 250 accessions of over 10 species) (ICRISAT 2002a).

Sorghum is attacked by a wide range of pathogens and pests that cause significant economic losses.

Table 1. Wild species of sorghum maintained at ICRISAT.

Section	Species/Subspecies	Race	Number of accessions
Sorghum	*S. bicolor*/*S. arundinaceum*	*arundinaceum* (Desv.) de Wet & Harlan	33
		aethiopicum (Hack.) Rupr. ex Stapf	16
		verticilliflorum (Steud.) Piper.	102
		virgatum (Hack.) Stapf	18
	S. bicolor/*S. drummondii*	*drummondii* (Steud.) de Wet	157
	S. halepense	*halepense* (L.) Pers.	27
		controversum (Stued.) Snowden	4
		miliaceum (Roxb.) Snowden	6
	S. propinquum (Kunth.) Hitchc.		2
Chaetosorghum	*S. macrospermum* Garber		2
Heterosorghum	*S. laxiflorum* Bailey		14
Parasorghum	*S. australiense* Garber & Snyder		3
	S. brevicallosum Garber		2
	S. matarankense Garber & Snyder		3
	S. nitidum (Vahl) Pers.		2
	S. purpureosericeum (Hochst.) ex A. Rich) Aschers. & Schweinf.		9
	S. timorense (Kunth) Buse		17
	S. versicolor Garber		6
Stiposorghum	*S. angustum* S. T. Blake		10
	S. bulbosum Lazarides		1
	S. ecarinatum Lazarides		1
	S. extans Lazarides		1
	S. interjectum Lazarides		2
	S. intrans F. Muell. ex Benth.		2
	S. plumosum (R. Br.) *P. Beauv.*		3
	S. stipoideum (Ewart & J. White) Gardner & Hubb.		2
Unidentified			16
Total			461

Frederiksen and Duncan (1982) listed over 40 diseases in sorghum, but the most damaging among these are downy mildew [*Peronosclerospora sorghi* (Weston & Uppal) C.G. Shaw], grain moulds (*Fusarium*, *Curvularia* and Phoma sp.), anthracnose [*Colletotrichum graminicola* (Ces.) G.W. Wills] and ergot (*Sphacelia sorghi* McRae). Although sources of resistance were found in cultivated germplasm, pathogen virulence and lack of genetic diversity for resistance among cultigens necessitate the discovery and incorporation of new and durable sources of resistance from wild species.

Evaluation of wild species for resistance to downy mildew received greater attention than other diseases. Karunakar et al. (1994) screened over 300 accessions and identified seven accessions of *S. purpureosericeum*, two accessions each of *S. bicolor* subsp. *drummondii*, *S. stipoideum*, *S. matarankense* and *S. nitidum*, and one each of *S. australiense*, *S. brevicallosum*, *S. plumosum* and *S. laxiflorum*, along with eight other unidentified *Parasorghum* species to be free from the disease. Significantly, all the accessions belonging to the section *Parasorghum* were either free from disease or highly resistant. In a recent study, *S. macrospermum* (*Chaetosorghum*), *S. timorense*, *S. versicolor* (*Parasorghum*), *S. angustum*, *S. ecarinatum*, *S. extans*, *S. interjectum* and *S. intrans* (*Stiposorghum*) were also found to be immune to downy mildew along with the two accessions (IS 21575 and IS 10983) of *S. bicolor* subsp. *drummondii* identified by Karunakar et al. (1994) (V. Kamala, personal communication). Identification of resistance in subspecies *S. drummondii* is of particular interest because of its cross compatibility with cultivated sorghums.

Young and Teetes (1977) described over 30 insects damaging sorghum. Among these, stem borer (*Chilo partellus* Swinhoe), shoot fly (*Atherigona soccata* Rondani) and midge (*Contarinia sorghicola* Coquillett) account for significant yield losses. Franzmann and Hardy (1996) tested 13 species of Australian indigenous sorghums for resistance to sorghum midge. They observed no oviposition on 11 species (*S. brachypodum*, *S. extans*, *S. interjectum*, *S. intrans*, *S. laxiflorum*, *S. leiocladum*, *S. macrospermum*, *S. matarankense*, *S. nitidum*, *S. stipoideum* and *S. timorense*), compared to 0.85% on other two species (*S. bulbosum* and *S. plumosum*) and 29.6% on *S. halepense*. Recently, Sharma and Franzmann (2001) evaluated eight species (*S. stipoideum*, *S. brachypodum*, *S. bulbosum*, *S. angustum*, *S. macrospermum*, *S. nitidum*, *S. laxiflorum* and *S. amplum*) for resistance to sorghum midge and reported that the wild relatives were less attractive and they were not preferred for oviposition by sorghum midge females.

Three species viz., *S. versicolor*, *S. purpureosericeum* and an unidentified wild species were reported to be immune to shoot fly infestation (Bapat and Mote 1983). High levels of resistance were found for shoot fly and spotted stem borer in *S. laxiflorum*, *S. australiense*, *S. brevicallosum*, *S. matarankense*, *S. nitidum*, *S. purpureosericeum*, *S. timorense*, *S. versicolor*, *S. angustum*, *S. ecarinatum*, *S. extans*, *S. interjectum* and *S. intrans* when evaluated under field conditions (V. Kamala, personal communication). On the other hand, *S. halepense* and races *aethiopicum*, *arundinaceum*, *verticilliflorum*, and *virgatum* of *S. bicolor* subsp. *arundinaceum* were highly susceptible to both the insects.

Based on crossability and fertility, species in the *S. bicolor* complex and *S. propinquum* are placed in the primary gene pool. The secondary gene pool includes *S. halepense*, which is an autotetraploid species that probably arose from a cross between *S. propinquum* and race *verticilliflorum* of subsp. *S. arundinaceum*. The tertiary gene pool includes all other sections of sorghum (Stenhouse et al. 1997). Bramel-Cox and Cox (1988) showed the possibility of increasing sorghum yields through transfer of genes from races *virgatum*, *arundinaceum* and *verticilliflorum*, all belonging to subspecies *S. arundinaceum* in section *Sorghum*. Most of the greenbug (Biotype C) resistant hybrids grown in U.S. were derived from race *virgatum* and best levels of antibiosis to Biotype E was found in *S. halepense* (see Duncan et al. 1991). However, efforts to cross members of section *Sorghum* with those in other sections have been unproductive. For example, Huelgas et al. (1996) attempted hybridization using *S. bicolor* female parents with 4 wild species: *S. macrospermum*, *S. timorense*, *S. matarankense* and *S. stipoideum* without success due to pre-fertilization cross barriers like lack of pollen germination or very slow and irregular pollen tube growth.

Pearl millet

The genus *Pennisetum* has been divided into five sections: *Gymnothrix*, *Eu-pennisetum*, *Penicillaria*, *Heterostachya* and *Brevivalvula* (Stapf and Hubbard 1934). Cultivated pearl millet belongs to the Section *Penicillaria* that includes both annual and perennial

species. The ICRISAT genebank holds 739 accessions of 23 wild species, besides the 21,392 accessions of the cultivated species and 11 accessions of *Cenchrus ciliaris* L. Among the wild species, *P. glaucum* subsp. *P. monodii* (syn. *P. violaceum*) constitutes the bulk of germplasm followed by *P. pedicellatum* and *P. polystachion* (Table 2). The USDA-ARS Southern Regional Plant Introduction Station, Griffin, Georgia, USA also maintains over 90 accessions of 21 *Pennisetum* species (USDA-ARS 2002a).

Downy mildew (*Sclerospora graminicola* (Sacc.) J. Schröt), smut [*Moesziomyces penicillariae* (Bref.) K. Vánky], ergot (*Claviceps fusiformis* Loveless) and rust [*Puccinia substriata* var. *indica* (Ellis & Barth.) Ramachar & Cummins] are the four major diseases of pearl millet. Although sources of resistance were identified in cultivated germplasm, their resistance could be overcome when the inoculum levels are high.

The primary gene pool includes cultivated pearl millet *P. glaucum* subsp. *glaucum*, the wild progenitor *P. glaucum* subsp. *monodii* and the weedy form *P. glaucum* subsp. *stenostachyum*. Dominant genes for resistance to rust and leaf spot (caused by *Pyricularia grisea* (Cke.) Sarc.) were found in *P. glaucum* subsp. *monodii* (Hammons 1970). Transfer of genes controlling resistance to these diseases made possible the development of Tift 85, a disease resistant inbred (Hanna 1992). Hanna (1989) also reported the development of a stable male sterile cytoplasm A_4 from the subsp. *monodii*. The cytoplasm from *monodii* influences dry matter yields, providing a unique opportunity to increase productivity of commercial forage hybrids (Hanna 1997).

P. purpureum (napiergrass) is the only known species in the secondary gene pool. It is a rhizomatous perennial, with desirable characters like resistance to most pests, vigorous growth and outstanding forage yield potential. Napiergrass readily crosses with pearl millet, but produces triploid hybrids that are sterile (Hanna 1992). Nevertheless, they produce high yields of good quality fodder, therefore, commercial seed production potential is under investigation (Osgood et al. 1997). Genes for controlling earliness, long inflorescence, leaf size and male fertility restoration for improving pearl millet have also been transferred from *P. purpureum* (Dujardin and Hanna 1989).

The tertiary gene pool consists of the remainder of the wild *Pennisetum* species. The group includes both sexual and apomictic species that are diploid and polyploid, annual and perennial, and rhizomatous and nonrhizomatous. Wilson and Hanna (1992) evaluated

Table 2. Wild *Pennisetum* species maintained at ICRISAT.

Section	Species	Number of accessions
Brevivalvula	*P. cenchroides* Rich.	5
	P. pedicellatum Trin.	134
	P. polystachion subsp. *polystachion* L. Schult.	87
	P. polystachion subsp. *setosum* L. Schult.	1
	P. hordeoides (Lam.) Steud.	1
Eu -pennisetum	*P. clandestinum* Hochst. ex Chiov.	1
	P. setaceum (Forssk.) Chiov.	11
	P. villosum Fresen.	2
Gymnothrix	*P. divisum* (Forssk. ex Gmel.)	7
	P. hohenackeri Hochst. ex Stued.	7
	P. mezianum Leeke	4
	P. ramosum (Hochst.) Schweinf.	7
	P. thunbergii Kunth.	3
	P. flaccidum Griseb.	6
Heterostachya	*P. macrourum* Trin.	1
	P. orientale L.C. Rich.	34
	P. schweinfurthii Pilger.	5
	P. squamulatum Fresen.	2
Penicillaria	*P. alopecuroides* (L.) Spreng.	1
	P. macrostachyum (Brongn.) Trin.	1
	P. mollissimum Hochst.	48
	P. purpureum Schum.	35
	P. glaucum subsp. *monodii* (Lam.) L. Rich.	335
Unidentified		1
Total		739

the tertiary gene pool species for resistance to six fungal species. All species including several accessions of *P. pedicellatum*, *P. polystachion* and *P. subangustum* were resistant to rust, and all species except *P. squamulatum* were resistant to leaf spot. Recently, Singh and Navi (2000) screened 539 wild relatives of 12 species for resistance to downy mildew. All but two accessions each of *P. pedicellatum* and *P. polystachion* and four of the five accessions of *P. schweinfurthii* were immune to the disease, whereas other species showed both susceptible and highly resistant reactions. Some other useful characteristics found in this gene pool include apomictic reproduction, perennial growth habit, drought tolerance, cold tolerance, pest resistance and cytoplasm diversity (Hanna 1992). Apomictic but highly sterile hybrids were reported between pearl millet and *P. setaceum* (triploid) and *P. orientale* (tetraploid). The hexaploid obligate apomictic species, *P. squamulatum* was crossed successfully to a tetraploid pearl millet and several partially male sterile, obligate apomictic interspecific derivatives were produced (Hanna 1992). Interspecific hybrids were also obtained with *P. schweinfurthii* (Hanna and Dujardin 1986), which were male sterile, but partially female fertile. Attempts to produce interspecific hybrids between pearl millet and *P. ramosum* and *P. mezianum* using conventional techniques were not successful. Pollen of *P. pedicellatum* and *P. polystachion* germinated on the stigmas of pearl millet, but resulted in shriveled and immature seeds that did not germinate (Dujardin and Hanna 1989).

Chickpea

The genus *Cicer* L. comprises of 43 species – 33 perennials (all wild) and 9 annuals (one cultivated and 8 wild) and one unclassified species, grouped under four sections (van der Maesen 1987). ICRISAT genebank holds 148 accessions of eight annual wild *Cicer* species, besides 17,150 accessions of the cultivated chickpea (*Cicer arietinum* L.) (Table 3). Large collections of wild *Cicer* species are also maintained at the International Center for Agricultural Resort in Dry Areas (ICARDA), Aleppo, Syria (263 accessions, 8 annual species) (Singh et al. 1997b), and at the USDA-ARS Western Regional Plant Introduction Station, Pullman, Washington, USA (169 accessions, 21 species) (USDA-ARS 2002b).

Of the 47 diseases affecting chickpea, fusarium wilt [*Fusarium oxysporum* Schlecht. emnd Snyd. & Hans f.sp. *ciceri* (Padwick) Snyd. & Hans.)] and ascochyta blight [*Aschochyta rabiei* (Pass.) Lab.] (sexual sp. *Mycosphaerella rabiei* Kovachevski) are the most destructive. Among other diseases, botrytis gray mold (*Botrytis cinerea* Pers. ex Fr.), dry root rot [*Rhizoctonia bataticola* (Taub) Butler] and phytophthora root rot (*Phytophthora megasperma* Drechs.) are of regional importance. One of the major difficulties in breeding cultivars with durable resistance to wilt and blight is the presence of many races of pathogens. With phytophthora root rot, even the most resistant accessions show reduced yields under high inoculum levels (Brinsmead et al. 1985). Among many insect pests attacking chickpea, pod borer (*Helicoverpa armigera* Hübner), leaf miner (*Liriomyza cicerina* Rond.) and aphids (*Aphis craccivora* Koch.) in the field and bruchid beetles (*Callosobruchus chinensis* L.) in the store are important. Cyst (*Heterodera ciceri* Vovlas, Greco et Di Vito) and root-knot nematodes (*Meloidogyne* spp.) also attack chickpea, and among abiotic stresses, cold and drought are most important.

Table 3. Annual Cicer species maintained at ICRISAT.

Section	Species	Number of accessions
Monocicer	*Cicer bijugum* Rech.	30
	C. cuneatum Hochat. ex Rich.	3
	C. echinospermum P.H. Davis	3
	C. judaicum Boiss.	47
	C. pinnatifidum Jaub. & Sp.	27
	C. reticulatum Ladiz.	32
	C. yamashitae Kitamura	5
Chamaecicer	*C. chorassanicum* (Bge.) M. Pop.	1
Total		148

The annual wild *Cicer* species have been extensively screened and several of them were identified as promising sources of resistance to major biotic and abiotic stresses (Table 4). Thus, Singh et al. (1981) identified high levels of resistance to ascochyta blight in *C. pinnatifidum*, *C. montbretii* Jaub. & Sp. and *C. judaicum* after evaluation of seven *Cicer* species. Nene and Haware (1980) reported resistance to *Fusarium oxysporum* f. sp. *ciceri* in *C. judaicum* after evaluating nine species, while Kaiser et al. (1994) reported resistance to race 5 in *C. bijugum*, *C. cuneatum* and *C. judaicum* and race 0 in *C. bijugum*, *C. canariense* Santos Guerra & Lewis, *C. chorassanicum*, *C. cuneatum*, *C. judaicum* and *C. pinnatifidum*. Infantino et al. (1996) screened 102 accessions of six annual *Cicer* species to fusarium wilt (isolate No. 526 II) and identified resistance in all

accessions of *C. bijugum* and some of *C. echinospermum*, *C. judaicum*, *C. pinnatifidum* and *C. reticulatum*. Singh et al. (1982) reported resistance to botrytis gray mold in C. *pinnatifidum*. Resistance to botrytis gray mold and ascochyta blight was identified in two accessions of *C. bijugum* (Haware et al. 1992) and resistance to cyst nematode in *C. bijugum*, *C. pinnatifidum* and *C. reticulatum* (Di Vito et al. 1996).

Singh and Weigand (1994) found resistance to leaf miner in *C. cuneatum*, *C. judaicum* and *C. reticulatum* after evaluation of 200 accessions of eight wild species. Two accessions (ILWC 39 and ILWC 181) of *C. echinospermum* had 0% infection among 137 accessions of eight wild *Cicer* species evaluated for reaction to *Callosobruchus chinensis*. ILCW 39 was also resistant to leaf miner (Singh and Ocampo 1997). Search for cold tolerance in 137 accessions of eight wild annual *Cicer* species identified high levels of tolerance in *C. bijugum*, C. *reticulatum* and *C. echinospermum* (Singh et al. 1990). An analysis of protein content in seven wild species showed that *C. bijugum* and *C. reticulatum* had highest protein content (32.7% and 30.6%) compared with the control value of 25.2% (Umaid Singh and Pundir 1991).

The perennial *Cicer* species are extremely difficult to grow, their potential value was not fully assessed, except in *C. montbretii* reported to be resistant to ascochyta blight (Singh et al. 1981) and *C. canariense* resistant to wilt (Kaiser et al. 1994).

Singh et al. (1998) analyzed the data on 228 accessions of eight annual wild *Cicer* species for diversity in response to six most serious biotic and abiotic stresses, namely ascochyta blight, fusarium wilt, leaf miner, bruchid, cyst nematode and cold. *C. bijugum*, *C. pinnatifidum* and *C. echinospermum* had accessions with at least one source of resistance to each stress. *C. bijugum* had the highest frequencies of the highest categories of resistance, followed by *C. pinnatifidum*, *C. judaicum*, *C. reticulatum* and *C. echinospermum*. *C. bijugum* also had the highest number of accessions with multiple resistance, two accessions had resistance to at least five stresses and 16 others to four.

Ladizinsky and Adler (1976) included *C. reticulatum* in primary gene pool because of its ability to readily cross and produce fertile hybrids with chickpea. *C. echinospermum* was placed under secondary gene pool, because gene exchange of this species with chickpea was impaired by high sterility of their F_1 hybrids due to reciprocal translocation (Ladizinsky et al. 1988). Singh and Ocampo (1997) developed lines superior in yield than the cultigen parent by introgression with *C. reticulatum* and *C. echinospermum*. Recently, through embryo rescue and tissue culture techniques, hybrids have been obtained between cultivated chickpea and *C. pinnatifidum*, which has strong resistance to ascochyta blight (Mallikarjuna 1999). The rest of annual and 33 perennial species show no possibility of gene exchange with cultivated chickpea, hence they were placed in tertiary gene pool. Because of their cross-compatibility to the cultigen, *C. reticulatum* and *C. echinospermum* will be the most valuable for immediate exploitation. However, use of genes present in other *Cicer* species requires novel means of gene transfer to the cultigen.

Pigeonpea

The revised genus *Cajanus* consists of 32 species. Only one of the species, *Cajanus cajan* (pigeonpea) is under cultivation and is pantropical in its distribution.

Table 4. Resistance to pathogens and pests or other useful traits (+) identified in Cicer species.

Species	Constraint or trait							
	FW	BGM	AB	CN	LM	CC	CO	HSP
C. bijugum	+	+	+	+			+	+
C. canariense (P)	+							
C. chorassanicum	+							
C. cuneatum	+				+			
C. echinospermum	+				+	+	+	
C. judaicum	+		+		+			
C. montbretii (P)			+					
C. pinnatifidum	+	+	+	+				
C. reticulatum	+			+	+		+	+

P = Perennial, FW = Fusarium wilt, BGM = Botrytis gary mold, AB = Ascochyta blight, CN = Cyst nematode, LM = Leaf miner, CC = Bruchid, CO = Cold, HSP = High seed protein.

Of the 31 wild species, 13 are endemic to Australia, eight to Indian subcontinent and Myanmar, one to west Africa and rest of the species occur in more than one country (van der Maesen 1990). The ICRISAT genebank currently holds 213 accessions representing 20 species, besides about 13,300 accessions of cultivated pigeonpea (Table 5). The wild gene pool assembled at ICRISAT also includes other related genera like *Rhynchosia* (35 species, 303 accessions), *Flemingia* (8 species, 18 accessions), *Eriosema* (4 species and 7 accessions) and *Dunbaria* (2 species, 12 accessions). Besides ICRISAT, the Australian Tropical Crops and Forages Genetic Resources Centre at Biloela holds about 150 accessions of 13 *Cajanus* wild species (AusGRIS 2002).

The major constraints to pigeonpea production among the insect pests are pod borer (*Helicoverpa armigera* Hübner) and pod fly (*Melanagromyza obtusa* (Malloch). While pod fly damage is common in long-duration cultivars in central and northern India, damage due to pod borer can be often extensive in all the maturity groups and yield losses of up to 100% were reported. Other lepidopteran pod borers including larvae of plume moth (*Exelastis atomosa* Wals.) and the blue butterfly (*Lampides boeticus* L.) are locally damaging. Bruchid beetles are commonly found damaging seeds in the ripe pods and stored seeds. Among diseases, fusarium wilt (*Fusarium udum* Butler), sterility mosaic and phytophthora blight [*Phytophthora drechsleri* Tucker f. sp. *cajani* (Pal, Grewal & Sarbhoy) Kannaiyan, Riberio, Erwin & Nene] are economically important. Several species of nematodes also attack pigeonpea and very low levels of resistance is reported in cultivated germplasm.

The wild relatives of pigeonpea possess many agronomically desirable traits, including resistance to major diseases and pests (Table 6). An evaluation of 166 accessions of 16 species for insect resistance showed that wild relatives are rarely damaged, though the insects feed on the plants under no choice conditions (ICRISAT 1996). Shanower et al. (1997) studied the survival, growth and fecundity of *H. armigera* on pods of *C. cajan* and two wild species and reported that larval survival on *C. scarabaeoides* was 21%, compared to 57% on *C. platycarpus* and 78% on *C. cajan*. The dense covering of non-glandular trichomes on *C. scarabaeoides* acts as physical barrier and prevents small larvae reaching the surface of the pods. It is suggested that resistance to *H. armigera* in cultivated pigeonpea could be improved by transferring genes regulating the production of non-glandular trichomes on pods from *C. scarabaeoides*. *C. reticulatus* has also been reported to be resistant to pod borer (Dodia et al. 1996), besides being hardy and fire tolerant (Akinola et al. 1975). In a recent study at ICRISAT, accessions of *Rhynchosia aurea* DC., *R. bracteata* Benth. ex Bak.,

Table 5. Cajanus species maintained at ICRISAT.

Section	Species	Number of accessions
Cajanus	*C. cajanifolius* (Haines) van der Maesen	5
Atylia	*C. cinereus* (F. v. Muell)F.v. Muell	1
	C. confertiflorus F.v. Muell	1
	C. grandiflorus (Benth. ex Bak.) van der Maesen	5
	C. lineatus (W. & A.) van der Maesen	10
	C. reticulatus (Dryander) F.v. Muell	3
	C. sericeus (Benth. ex Bak.) van der Maesen	4
	C. trinervius (DC.) van der Maesen	3
Fruticosa	*C. acutifolius* (F.v. Muell) van der Maesen	12
	C. lanceolatus (W.V. Fitzg.) van der Maesen	1
	C. latisepalus (Reynolds & Padley) van der Maesen	1
Cantharospermum	*C. albicans* (W. & A.) van der Maesen	20
	C. elongats (Benth.) van der Maesen	1
	C. goensis Dalz.	1
	C. rugosus (W. & A.) van der Maesen	6
	C. scarabaeoides (L.) Thouars	102
Volubilis	*C. crassus* (Prain ex King) van der Maesen	10
	C. mollis (Benth.) van der Maesen	8
Rhynchosoides	*C. platycarpus* (Ewart & Morrison) van der Maesen	17
	C. marmoratus (R. Br. ex Benth.) van der Maesen	2
Total		213

C. scarabaeoides, *C. sericeus*, *C. acutifolius*, *C. albicans* and *Flemingia bracteata* (Roxb.) Wight were found to have high levels of resistance to *H. armigera* (Sharma et al. 2001). In another study, significant inter- and intra-specific differences were found in relative susceptibility to pod fly and pod wasp (*Tanaostigmodes cajaninae* LaSalle). Resistance to pod fly damage was found in *C. scarabaeoides*, *C. sericeus*, *C. acutifolius*, *C. lineatus*, *C. albicans* and *R. bracteata*. Accessions of *C. scarabaeoides*, *C. albicans*, *F. stricta* Roxb. and *R. bracteata* showed resistant reaction to pod wasp (H.C. Sharma, personal communication).

In an evaluation for phytophthora blight resistance, *C. platycarpus* and *C. sericeus* were identified as immune (Kannaiyan et al. 1981). *C. albicans*, *C. lineatus*, *C. sericeus* and *C. crassus* are resistant to sterility mosaic (see Ramanandan 1980). Recently, resistance for sterility mosaic disease was also identified in three of the 33 accessions of *C. scarabaeoides* and *C. albicans* screened after artificial inoculation (ICRISAT 2000). Most species of *Cajanus*, especially *C. mollis*, *C. scarabaeoides* and *C. albicans* have higher protein concentrations (28–30%) compared with cultivated pigeonpea. A high protein line (ICPL 87162) with $>$ 27% seed protein and good seed size was developed by crossing with *C. scarabaeoides* (Reddy et al. 1997). The closely related species, *F. bracteata* showed high percentage of the essential aminoacids, methionine and cystine, which are limiting in pigeonpea (Remanandan 1980). Cytoplasmic male sterility, an important trait, which could not be easily found in pigeonpea, was obtained by exploiting wild *Cajanus* species. Thus, cytoplasmic genetic male sterile lines were obtained from pigeonpea crosses with *C. scarabaeoides* (Reddy and Faris 1981) and *C. sericeus* (Ariyanayagam et al. 1995). Wanjari et al. (2000) reported that cytoplasmic male sterility from *C. sericeus* was actually a single dominant gene possibly acting in concert with a single recessive gene to mimic cytoplasmic male sterility.

Screening of the wild species for salinity tolerance identified *C. albicans* and *C. platycarpus* as more tolerant than the cultivated pigeonpea. Both these species survived in sand culture system at 12 dS m^{-1} (Subbarao et al. 1991). In another study, resistance to root-knot nematode was identified in *C. reticulatus*, *C. scarabaeoides*, *Flemingia macrophylla* (Willd.) Prain. ex Merrill, *F. stricta* and *F. strobilifera* (L.) Aiton and *Rhynchosia rothii* Benth. ex Aitch. (ICRISAT 1990).

Six of the Indian wild species; *C. cajanifolius*, *C. scarabaeoides*, *C. trinervius*, *C. albicans*, *C. lineatus* and *C. sericeus* were successfully crossed with pigeonpea (Pundir and Singh 1987). Hence, it should be possible for incorporation of desirable traits from these species through normal recombination. Interspecific hybrids have also been obtained with the Australian species; *C. acutifolius*, *C. confertiflorus*, *C. lanceolatus*, *C. latisepalus* and *C. reticulatus*. However, the hybrids had higher levels of meiotic abnormalities than reported in hybrids between pigeonpea and Indian species (Dundas 1990). Recently, *C. platycarpus* which carries genes for photoperiod insensitivity, earliness and resistance to phytophthora blight and salinity has been successfully crossed with pigeonpea using embryo rescue (Mallikarjuna and Moss 1995).

Novel plant types were identified from interspecific crosses involving the species in the primary gene

Table 6. Resistance to pathogens and pests or other useful traits (+) identified in wild species of pigeonpea.

Species	Constraint or trait									
	SMV	PhB	RN	PB	PF	PW	PI	SA	DT	HSP
C. acutifolius				+	+					
C. albicans	+			+	+	+		+		+
C. cajanifolius										
C. crassus	+									
C. lineatus	+				+					
C. mollis										+
C. platycarpus		+		+			+	+		
C. reticulatus			+	+					+	
C. scarabaeoides	+		+	+	+	+				+
C. sericeus	+	+		+	+		+			

SMV = Sterility mosaic virus, PhB = Phytophthora blight, RN = Root-knot nematode, PB = Pod borer, PF = Pod fly, PW = Pod wasp, PI = Photoperiod insensitive, SA = Salinity, DT = Drought resistance, HSP = High seed protein.

pool. For example, a partially cleistogamous line which shows less than one percent cross pollination was produced from an interspecific population of *C. cajan* × *C. lineatus*, using which three agronomically superior lines with very low crossing levels (0.15–1.33%) were developed (Saxena et al. 1998). A shortest genetic dwarf with height ranging from 25–40 cm (D_0 type) was isolated and purified from a cross between *C. cajan* and *C. scarabaeoides* (Reddy 1990). Using this source, agronomically superior dwarf varieties were developed.

Groundnut

The genus *Arachis* comprises 69 species placed in nine sections. Section *Arachis* includes the cultivated groundnut *Arachis hypogaea* L (Gregory et al. 1973). The groundnut germplasm collection held at ICRISAT genebank includes 414 accessions, representing eight sections and 41 wild species, besides some 14,800 accessions of the cultigen (Table 7). The Southern Regional Plant Introduction Station, USDA-ARS at Griffin, Georgia, USA maintains over 700 accessions of 60 wild *Arachis* species (USDA-ARS 2002a).

Early leaf spot (*Cercospora arachidicola* Hori), late leaf spot (*Cercosporidium personata* (Berk. & Curt.) Deighton], rust (*Puccinia arachidis* Speg.), stem and pod rot caused by *Sclerotium rolfsii* Sacc., peanut mottle virus and bud necrosis diseases are some of the important diseases of groundnut. Major pests include leaf miner (*Aproaerema modicella* Deventer), tobacco armyworm (*Spodoptera litura* Fab.), hairy caterpillars (*Amsacta albistriga* Walk. and *A. moori* Butler) and sucking insects like aphids (*Aphis craccivora* Koch.), thrips (*Thrips palmi* Karny.) and jassids (*Empoasca kerri* Pruthi). In addition, invasion during harvest and post harvest operations by *Aspergillus* spp. and production of aflatoxins are of major concern.

The sources of resistance reported so far in cultivated groundnut represent a narrow range of variability and wild species have been used to broaden the genetic base (see Ker and Mess 1987). *Arachis* species have been extensively screened and several of them were reported to have high levels of resistance to diseases caused by various fungi, viruses and nematodes (Table 8). Abdou et al. (1974) identified *A. diogoi* (Syn. *A. chacoense*) as highly resistance to early leaf spot and *A. cardenasii* immune to late leaf spot caused by *C. personatum*. Subrahmanyam et al. (1985a) identified *A. chacoense*, *A. cardenasii*, *A. stenosperma*, *A. repens*, *A. appressipila*, *A. paraguariensis*, *A. villosulicarpa*, *A. hagenbeckii*, and *A. glabrata* as resistant to late leaf spot. Subrahmanyam et al. (1983) also reported that most accessions of *A. batizocoi*, *A. duranensis*, *A. correntina*, *A. stenosperma*, *A. cardenasii*, *A. chacoense*, *A. villosa*, *A. appressipila*, *A. pusilla*, *A. villosulicarpa*, *A. hagenbeckii* and *A. glabrata* were immune to rust after screening 61 accessions of wild species under filed and laboratory conditions. Sources of resistance to peanut mottle virus were identified in six wild rhizomatous groundnut (probably *A. glabrata*) accessions (Demski and Sowell 1981) and in *A. pusilla*, *A. cardenasii*, *A. diogoi* and *A. correntina* (Subrahmanyam et al. 1985b). *A. glabrata* was also found to be immune to peanut web blotch [*Didymella arachidicola* (Choch.) Taber, Pettit & Philley] (Subrahmanyam et al. 1985c). Resistance to tomato spotted wilt virus was found in *A. diogoi*, and three other species *A. pusilla*, *A. correntina* and *A. cardenasii* though became infected in the greenhouse, expressed no symptoms in the field (Subrahmanyam et al. 1985b). Hebert and Stalker (1981) evaluated 90 accessions and found high levels of resistance to peanut stunt virus in species of sections *Arachis*, *Caulorhizae*, *Erectoides* and *Rhizomatosae*. Reddy et al. (2000) evaluated 83 wild *Arachis* germplasm accessions belonging to 24 species of five sections for resistance to peanut bud necrosis virus (PBNV). One accession each of *A. benensis* and *A. cardenasii*, and two accessions of *A. villosa* in the section *Arachis*, two accessions of *A. appressipila* in section *Procumbentes*, and one accession of *A. triseminata* in section *Triseminatae* were found to be resistant to the virus. Since both *A. cardenasii* and *A. villosa* hybridize with cultivated peanut, resistant to PBNV could be transferred through conventional breeding.

Recently, Subrahmanyam et al. (2001) evaluated 116 accessions representing 28 wild species for resistance to groundnut rosette disease. A total of 25 accessions belonging to *A. diogoi*, *A. hoehnei*, *A. kretschmeri*, *A. appressipila*, *A. cardenasaii*, *A. villosa*, *A. stenosperma*, *A. pintoi*, *A. kuhlmannii*, *A. triseminata*, and *A. decora* were identified with high levels ofresistance. High levels of resistance to early leaf spot, hitherto undiscovered in cultigens were also identified in wild *Arachis* species including *A. appressipila*, *A. triseminata*, *A. magna*, *A. sylvestris*, *A. pusilla*, *A. valida* and *A. dardani* (ICRISAT 2000).

Sources of resistance to most insect pests were

Table 7. Arachis species maintained at ICRISAT.

Section	Species	Number of accessions
Arachis	*A. batizocoi* Krapov. & W. C. Gregory	6
	A. benensis Krapov., W.C. Gregory & C.E. Simpson	3
	A. cardenasii Krapov. & Regoni	15
	A. correntina (Burkart) Krapov. & W.C. Gregory	2
	A. decora Krapov., W.C. Gregory & Valls	10
	A. diogoi Hoehne	2
	A. duranensis Krapov. & W.C. Gregory	61
	A. glandulifera Stalker	4
	A. helodes Martius ex Krapov. & Regoni	3
	A. hoehnei Krapov. & W.C. Gregory	5
	A. ipaensis Krapov. & W.C. Gregory	1
	A. kempff-mercadoi Krapov. W.C. Gregory & C.E. Simpson	3
	A. kuhlmannii Krapov. & W.C. Gregory	17
	A. magna Krapov., W.C. Gregory & C.E. Simpson	1
	A. monticola Krapov. & Rigoni	7
	A. palustris Krapov., W.C. Gregory & Valls	2
	A. stenosperma Krapov. & W.C. Gregory	29
	A. valida Krapov. & W.C. Gregory	4
	A. villosa Benth.	9
Caulorhizae	*A. pintoi* Krapov. & W.C. Gregory	21
	A. repens Handro	1
Erectoides	*A. archeri* Krapov. & W.C. Gregory	1
	A. hermannii Krapov. & W.C. Gregory	2
	A. major Krapov. & W.C. Gregory	2
	A. oteroi Krapov. & W.C. Gregory	1
	A. paraguariensis Chodat. & Hassl.	8
	A. stenophylla Krapov. & W.C. Gregory	2
Extranervosae	*A. retusa* Krapov., W.C. Gregory & Valls	1
	A. villosulicarpa Hoehne	2
Heteranthae	*A. dardani* Krapov. & W.C. Gregory	18
	A. pusilla Benth.	16
	A. sylvestris (A. Chev.) A. Chev.	27
Procumbentes	*A. appressipila* Krapov. & W.C. Gregory	7
	A. chiquitana Krapov., W.C. Gregory & C.E. Simpson	3
	A. kretschmeri Krapov. & W.C. Gregory	5
	A. matiensis Krapov., W.C. Gregory & C.E. Simpson	6
	A. rigonii Krapov. & W.C. Gregory	2
	A. subcoriacea Krapov. & W.C. Gregory	1
	A. vallsii Krapov. & W.C. Gregory	3
Rhizomatosae	*A. glabrata* Benth.	81
Triseminatae	*A. triseminata* Krapov. & W.C. Gregory	5
Unidentified		15
Total		414

identified in wild *Arachis* species (see Wightman and Ranga Rao 1994). Tolerance to plant-parasitic nematodes *Meloidogyne arenaria* Chitwood was identified in *A. batizocoi* and *A. cardenasii* (Nelson et al. 1988; Holbrook and Noe 1990). Green house evaluation of 184 accessions of 33 wild *Arachis* spp. for root-knot nematode (*Meloidogyne javanica* Chitwood) led to the identification of high levels of resistance in *A. helodes*, *A. sylvestris*, *A. kretschmeri*, *A. kuhlmannii*, *A. stenosperma* and an unidentified species. Seven of the accessions were highly resistant, 33 accessions were resistant and 14 were moderately resistant (Sharma et al. 1999).

Wild *Arachis* species are potentially valuable germplasm sources for traits other than diseases and insect resistance. For example, *A. villosulicarpa* was reported to have high tryptophan content (1.44–1.66%) (Amaya et al. 1977). Many of the *Arachis* species are extremely drought resistant (Stalker and Moss 1987).

Due to ploidy differences and genomic incompatibilities, attempts to introgress resistance form wild

Table 8. Resistance (+) to pathogens and pest identified in wild *Arachis* species.

Species	Pathogen or pest													
	RUS	LLS	ELS	PSV	GRV	PMV	TSWV	PBNV	PBV	APH	MIT	THR	JAS	RN
A. appressipila	+	+	+		+			+						
A. batizocoi	+													
A. benthamii				+										
A. benensis								+						
A. cardenasii	+	+			+	+	+	+				+	+	
A. correntina	+					+	+			+	+	+	+	
A. diogoi	+	+			+	+	+			+		+		
A. dardani			+											
A. decora					+									
A. duranensis	+			+								+	+	
A. glabrata	+	+		+		+			+	+		+	+	
A. hagenbeckii	+	+											+	
A. helodes														+
A. hoehnei					+									
A. kuhlmannii					+									+
A. kretschmeri					+									+
A. magna			+											
A. paraguariensis		+										+		
A. pintoi					+									
A. pusilla	+		+			+	+					+	+	
A. repens		+		+								+	+	
A. rigonii												+	+	
A. stenosperma	+	+			+									+
A. sylvestris			+											+
A. triseminata			+		+			+						
A. valida			+											
A. villosa	+				+			+		+		+	+	
A. villosulicarpa	+	+												

RUS = Rust, LLS = late leaf spot, ELS = Early leaf spot, PSV = Peanut Stunt Virus, GRV = Groundnut rosette virus, PMV = Peanut Mottle virus, TSWV = Tomato spotted wilt virus, PBNV = Peanut Bud Necrosis Virus, PBV = Peanut web blotch, THR = Thrips, APH = Aphids, MIT = Mites, JAS = Jassids.

species to cultivated groundnut are fraught with difficulty. Based on cytogenetic affinities, *A. monticola*, and the wild tetraploid species of section *Arachis* that crosses freely with *A. hypogaea* are grouped in primary gene pool. A variety 'Spancross' developed in the USA from an interspecific cross involving *A. monticola* was released in Tanzania (Hammons 1970). The secondary gene pool is represented by diploid species of section *Arachis* that are cross compatible with tetraploid *A. hypogaea*. These species provide a reservoir of genes resistant to various diseases and pests that can be effectively used despite ploidy differences. For example, the diploid species *A. cardenasii* has been crossed to *A. hypogaea* and the sterile triploid was colchicine treated to restore fertility through doubling of chromosomes. The resulting hexaploid was backcrossed with the cultivar and stable tetraploid derivatives were obtained through selection. This strategy has resulted in release of two elite germplasm lines ICGV 86699 (Reddy et al. 1996) and ICGV 87165 (Moss et al. 1997) with multiple disease and insect resistance. Another interspecific derivative, ICGV-SM 86715 was released as 'Veronica' in Mauritius for general cultivation (Moss et al. 1998).

Recently, two root-knot nematode resistant germplasm lines (GP-NC WS 5 and GP-NC WS 6) derived from an *A. hypogaea* × *A. cardenasii* (PI 262141) interspecific cross were released in the USA by North Carolina Agricultural Research Services (Stalker et al. 2002). Four more lines (GP-NC WS 7, GP-NC WS 8, GP-NC WS 9 and GP-NC WS 10), derived form the same interspecific cross *A. hypogaea* × *A. cardenasii* (PI 262141), resistant to corn earworm (*Heliothis zea* (Bodie), potato leafhopper (*Empoasca fabae* Harris) and southern corn rootworm (*Diabrotica undecimpunctata howardi* Barber) were released by North Carolina Agricultural Research Services in the USA (Stalker and Lynch 2002).

The tertiary gene pool includes species of others

sections that cannot be hybridized with *A. hypogaea* by conventional means. The major barrier for introgression appears to be postzygotic failure of embryo development. Nevertheless, hybrids have been obtained with *A. paraguariensis* (section *Erectoides*) and *A. appressipila* (section *Procumbentes*), both resistant to early leaf spot, using embryo rescue and tissue culture techniques (ICRISAT 1995). However, fertility could not be restored in the intersectional hybrids, therefore, their potential could not be exploited.

Discussion

Screening wild species of sorghum, pearl millet, chickpea, pigeonpea and groundnut identified several sources of resistance to important pests and diseases. Transfer of new cytoplasmic male sterility to pigeonpea and pearl millet, development of chickpea with enhanced yield, pigeonpea with high protein, cleistogamous flowers and dwarfing genes, groundnut varieties resistant to foliar diseases were achieved through backcross followed by selection, the most common approach for gene introgression from compatible wild germplasm. Nevertheless, there has been only limited exploitation of wild species in secondary and tertiary gene pools due to cross incompatibility with the cultigens. These genepools include species that are sources of multiple resistance to important biotic and abiotic stresses, therefore of significant value. Recent advances in plant biotechnology provide new tools to exploit the genes locked up in these gene pools. The genetic linkage maps developed for most major crops based on molecular markers make it possible to scan the genomes of wild species for new and useful genes. Somatic hybridization by protoplast fusion and plant transformation could overcome many of the obstacles to interspecific hybridization among divergent species. Protoplasts have been successfully fused and by applying reliable plant regeneration protocols, the potentials of somatic fusions have been exploited for crop improvement in *Brasicca*, *Nicotiana*, *Solanum* and forage legumes (Cocking 1985).

Transformation involves the stable introduction of DNA sequences from unrelated organisms. However, lack of availability of efficient transformation methods to introduce foreign DNA could be a barrier to the application of recombinant DNA methods in some crop plants. While efficient tissue cultures and transformation methods have been developed in groundnut, pigeonpea and chickpea, tissue culture research is underway to develop transformation methods for both sorghum and pearl millet (Sharma and Ortiz 2000). Where amenable, molecular marker facilitated introgression is a fast emerging breeding tool, which can be effectively used for transfer of genes of interest breaking undesirable linkages or linkage drag. Molecular markers could be used to map resistance genes in crosses between wild species or accessions of the same species in the secondary and tertiary genepools and once resistance genes are located, they can be transformed into cultivated germplasm. In rice, Tanksley and McCouch (1997) reported molecular markers that looked for genes from the wild species in contrast to conventional methods that look for the phenotypes. Thus, two QTLs which could increase yield by approximately 17%, each were identified using advanced backcross method to examine alleles from the wild species *Oryza rufipogon* Griff in the genetic background of an elite Chinese hybrid.

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