Chapter 2
Cajanus

Nalini Mallikarjuna, K.B. Saxena, and D.R. Jadhav

2.1 Introduction

The cultivation of the pigeonpea goes back to at least 3,000 years. Its center of origin is India (Vavilov 1928; van der Maesen 1980), from where it traveled to East Africa and, by means of the slave trade, to the American continent. Pigeonpea is an ancient crop as there is a mention of pigeonpea in Sanskrit and Buddhist literature dating back to 400 BC to 300 AD (Krishnamurthy 1991). Today, pigeonpea is widely cultivated in all tropical and semi-tropical regions of both the old and the new world.

Pigeonpea is an important grain legume crop of rain-fed agriculture in the semi-arid tropics. The Indian subcontinent, eastern Africa and Central America are the world's three main pigeonpea-producing regions. Pigeonpea is cultivated in more than 25 tropical and subtropical countries, either as a sole crop or as an intercrop with cereals and other legumes. Being a legume, pigeonpea enriches soil through nitrogen fixation. Besides this, it also enriches the soil through the addition of other valuable organic matter and micronutrients. It has a special mechanism to release soil-bound phosphorus from vertisols by secreting pyssidic acid to meet its own as well as that of subsequent crop's phosphorous needs. Pigeonpea has an extensive root system that enables it to tolerate drought and improve soil structure by breaking plow pans. Besides its main use as dry dehulled splits, its tender green seeds and pods are used as vegetable. Its high protein (20–25%) containing leaves are used as fodder and dry crushed seeds as animal feed while the dry stems make quality fuel wood.

Pigeonpea is attacked by a range of biotic (diseases and insect pests) and abiotic (drought, salinity and water logging) factors, which are major constraints to the increased productivity of pigeonpea. Resistance to some of these constraints is not present in the cultivated genotypes, but the wild relatives have been found to be good sources of resistance. Besides this, wild *Cajanus* species have contributed desirable agronomic traits such as cytoplasmic male sterility (CMS) (Mallikarjuna and Saxena 2005; Saxena et al. 2005), dwarf growth habit (Saxena and Sharma 1995) and high protein content (Saxena et al. 2002).

Plant breeding continues to increase the productivity and ensure stable performance of crops in diverse environments. The adoption of genetically homogeneous cultivars has led to diminution of plant genetic diversity. This very process of crop improvement and narrowing of genetic variability is paving the way for epidemics of pests and diseases (genetic vulnerability), as seen in the case of the Phytophthora blight of potatoes in western Europe in 1845–1846 (Gregory 1983), the narrow cytoplasmic base of maize in the USA (Campbell and Madden 1990) and the coffee rust of the 1970s (Damania 2008). Therefore, there is a need of new allelic variation previously not encountered within a crop's domesticated gene pool. Such a situation may arise when attempting to introduce a crop into areas beyond its traditional eco-geographic range, or with the appearance of a new virulent pathogen race, as has been observed in race Ug 99, the stem rust of wheat.

Wild relatives of crop plants are important resources of variability with respect to resistance/tolerance to disease, insect pests and drought, and good agronomic traits; therefore, they could broaden the genetic base of variation of the crop. Whenever

Nalini Mallikarjuna (✉)
International Crops Research Institute for Semi Arid Tropics, Patancheru 502324, Andhra Pradesh, India
e-mail: N.Mallikarjuna@cgiar.org

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there is a major epidemic in a region, crop improvement scientists have found resistance to the constraint in the wild relatives of those crops. The recent stem rust of wheat and Phytophthora blight of potato are good examples where scientists have gone back to wild relatives for an integrated approach to tackle the constraints (New Delhi 2008).

It is often said that pigeonpea has reached its performance plateau (Saxena 2008). Although ample morphological diversity is exhibited by pigeonpea as a crop, the same is not true at the molecular level (Yang et al. 2006). The crop has a rich source of variability in the form of wild relatives, which have played a major role in the introduction of disease resistance, good agronomic traits such as high protein content, identification and diversification of cytoplasmic base of CMS system, to name a few.

2.2 Wild Relatives of Pigeonpea

The gene bank at ICRISAT conserves over 13,632 accessions of *Cajanus* species from 74 countries. This includes 555 accessions of wild relatives, which represent six genera and 57 species (Upadhyaya et al. 2007). The majority of the collection has been characterized for morpho-agronomic traits of importance in crop improvement.

Pigeonpea, *Cajanus cajan* L. belongs to the subtribe *Cajaninae*, which contains 13 genera. Earlier, the genus *Atylosia* and *Cajanus* were considered closely related, however, recently the genus *Atylosia* has been merged with the genus *Cajanus* (van der Maesen 1980). Subsequently, the genus *Cajanus* has 32 species, 18 of which are endemic to Asia and 13 to Australia and one to western Africa (van der Maesen 1986). Apart from these, there are other related genera, namely *Rhynchosia*, *Dunbaria*, *Flemingia*, *Paracalyx*, *Eriosema*, *Adenodolichos*, *Bolusafra*, *Carissoa*, *Chrysoscias* and *Baukea*. Figure 2.1 depicts the relationships among the wild species according to their crossability with cultivated species. *Cajanus* species, which are endemic to Australia, are *Cajanus lanceolatus*, *C. confertiflorus*, *C. viscidus*, *C. acutifolius*, *C. aromaticus*, *C. crassicaulis*, *C. lanuginosus*, *C. latisepalus*, *C. reticulates*, *C. pubescens*, *C. cinereus*, *C. marmoratus* and *C. mareebensis*, and *C. kerstingii* is endemic to Africa.

2.2.1 *Gene Pools of* Cajanus

Harlan and de Wet (1971) proposed a systematic means of grouping the germplasm of a crop species

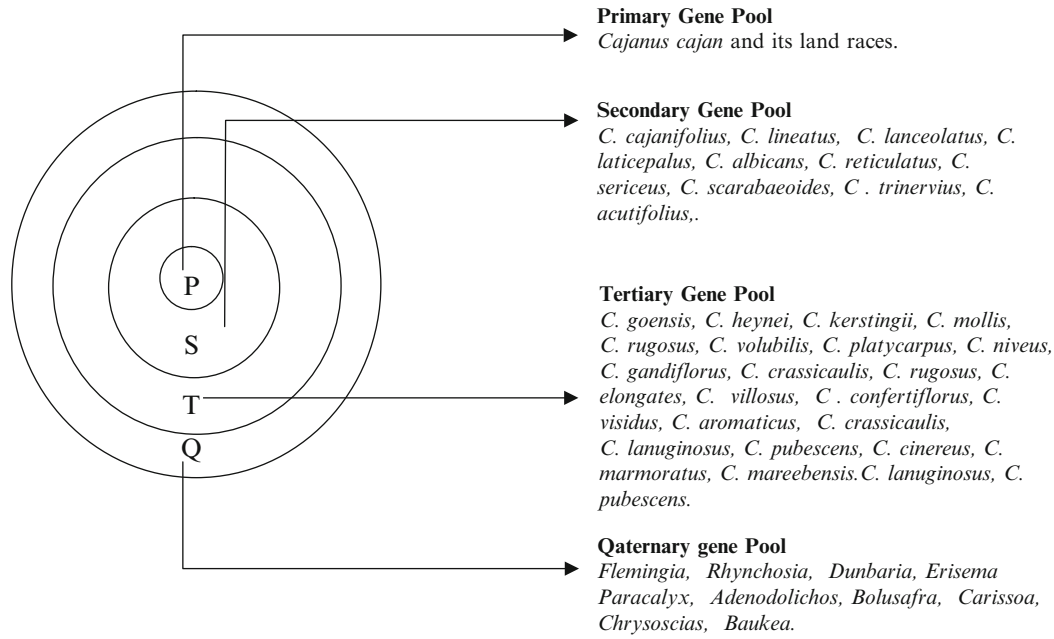

Fig. 2.1 Gene pools of the genus *Cajanus*

and their wild relatives. They constituted three basic gene pools and divided them as primary gene pool (GP1), secondary gene pool (GP2) and tertiary gene pool (GP3) and the quaternary gene pool (GP4).

2.2.2 Primary Gene Pool

The primary gene pool consists of cultivated species and its landraces. The germplasm in the primary gene pool are fairly easy to use; however, a perusal of the utilization pattern of *Cajanus* germplasm indicates that a very small proportion of germplasm has been used so far in pigeonpea improvement programs, globally. In pigeonpea, 57 ancestors were used to develop 47 varieties. The top ten ancestors contributed 48% to the genetic base of the released varieties (Kumar et al. 2003). One of the reasons for such poor utilization may be that in spite of the vast number of lines available in the primary gene pool, there is a lack of characterization, evaluation and genetic diversity data.

As the accessibility and utilization of a collection is inversely related to its size (Frankel and Soule 1981), a core collection of pigeonpea, which represents the genetic spectrum that is representative of >85% of the diversity of the entire collection, was developed (Reddy et al. 2005). This core collection has been characterized for phenotypic traits (Upadhyaya et al. 2007). The information generated in the development of core collection has shown that it is possible to further reduce the size of the collection into a mini core, which would have 1% of the collection. This will provide options to breeders to use the germplasm as parents, which will enhance the trait(s), besides broadening the genetic base of variation in the cultivars without hindering the progress of breeding programs.

To capture maximum diversity, a composite collection of *Cajanus* that consists of 1,000 accessions has also been developed through a well-directed Generation Challenge Program. This composite collection consists of a few accessions from wild species, the core collection and accessions with traits of economic importance and resistance to major biotic and abiotoic stresses. This composite collection will be genotyped using 20 polymorphic simple sequence repeat (SSR) markers to know the structure of the population. The genotyping data will be used to select a 300-accession reference collection for use by the global scientific community (*http://www.generationcp.org/sccv10/sccv10_upload/2005_annual_report.pdf*).

Many pigeonpea cultivars have shown important characters such as resistance to Alternaria blight, wilt, sterility mosaic disease (SMD) and Phytophthora blight (Sharma et al. 1987). Germplasm lines from different parts of India have contributed dwarfing genes with a recessive mode of gene action (Saxena et al. 1989). ICP 7035, a popular vegetable-type pigeonpea, with high sugar content and SMD resistance, is a line collected from Madhya Pradesh, India.

2.2.3 Secondary Gene Pool

The greatest contribution to the utilization of wild species for pigeonpea improvement is from this group as the species are cross-compatible, which means there would be chromosome recombination and transfer of useful traits/genes from wild *Cajanus* species. There are ten wild species in the secondary gene pool (Fig. 2.1), and each wild species has several collections. The accessions of a species are important sources of genetic diversity with the presence of useful traits (Saxena et al. 1996; Upadhyaya 2006; Sujana et al. 2008). The introgression of useful genes/traits from secondary gene pool species is carried out through conventional hybridization techniques. In general, the techniques such as hormone-aided pollinations and embryo rescue are not essential, but sometimes these techniques are necessary to obtain more hybrid seeds, as was done in the case of a cross involving *C. acutifolius* and *C. cajan* (Mallikarjuna and Saxena 2002). A number of wild species of this group have been used in the genetic improvement of pigeonpea, including development of unique cytoplasmic nuclear male sterile systems (CMS), high protein lines, dwarf plant stature, disease and pest-resistant lines.

2.2.3.1 Cytoplasmic Nuclear Male Sterile Systems

Five unique CMS systems have been developed for pigeonpea. These are A_1 cytoplasm derived from *C. sericeus* (Ariyanayagam et al. 1995). The CMS lines derived from this source are sensitive to temperature

changes. The male sterile plants change to male fertile under low-temperature conditions (Saxena 2005). Although the A_1 source produces good yield, the presence of fertile plants in the progeny prevents it from becoming a desirable source for the development of CMS system. The A_2 cytoplasm derived from *C. scarabaeoides* (Tikka et al. 1997; Saxena and Kumar 2003) is a stable source of CMS. The drawback of this system is that fertility restorers are inconsistent across environments. Hybrids derived from A_2 showed high heterosis for yield (IIPR 2007). Unstable seed set across environments is an undesirable character of this source. A_3 cytoplasm derived from *C. volubilis* (Wanjari et al. 2001) does not have quality fertility restoration system. Hence, this source is not popular as a cytoplasm to develop CMS system. The A_4 cytoplasm was derived using *C. cajanifolius* (Saxena et al. 2005). The system is stable across environments with very good fertility restoration system. The A_4 system is used at ICRISAT and by other pigeonpea breeders of India to exploit heterosis in pigeonpea. Crosses between *C. cajan* and *C. acutifolius* gave rise to CMS on cultivated pigeonpea cytoplasm, which was named as A_5 (Mallikarjuna and Saxena 2005). It is fully maintained by its male parent *C. acutifolius,* and most of the cultivated types restore fertility. The A_5 cytoplasm is still under development. Recently, crosses between *C. platycarpus* and cultivated pigeonpea gave rise to open flower (cleistogamous) segregants (Mallikarjuna et al. 2006). Some of the progeny were completely male sterile with white anthers. In the semi-fertile progeny, pollen shedding was not observed as the anthers had a thick cell wall. Self-pollination did not set seeds but seed set was observed when pollinated with a range of other cultivars. This may be another source of CMS in pigeonpea (Mallikarjuna unpublished results).

2.2.3.2 Cleistogamy

Pigeonpea is partially out crossing and insects mediate the process. The process of out-crossing is important in the development of CMS systems in pigeonpea but can lead to genetic deterioration. A partially cleistogamous line, which showed less than 1% cross-pollination, was purified from the cross *C. cajan* × *C. lineatus*, which was governed by a single recessive gene (Saxena et al. 1992). Partial cleistogamous lines developed from the above cross were found to be stable in India as well as in Sri Lanka. Cleistogamous trait can be utilized in pigeonpea to obtain pure seeds from genetic stocks.

2.2.3.3 High Protein and Seed Weight

High protein line, ICPL 87162, was developed from the cross *C. cajan* × *C. scarabaeoides* (Reddy et al. 1997). Dhal protein content of ICPL 87162 ranged from 30 to 34% compared to 23% in the control cultivar. ICPL 87162 is resistant to sterility mosaic disease but is susceptible to wilt. High protein breeding lines were developed from *C. sericeus*, *C. albicans* and *C. scarabaeoides*. Significant positive correlation between seed size and protein content was observed in lines derived from *C. scarabaeoides*. Lines HPL 2, HPL 7, HPL 40 and HPL 51 were some of the high protein and high seed weight lines derived from wild species (Saxena et al. 1987). More recently, crosses between pigeonpea and *C. acutifolius* yielded progeny with high seed weight. High seed weight accompanied by beige seed color is a desirable trait. The material is under multilocational testing (Mallikarjuna unpublished results).

2.2.3.4 *Helicoverpa armigera* Resistance

Cajanus scarabaeoides, *C. acutifolious*, *C. sericeus* and *C. albicans* are some of the wild *Cajanus* species with resistance to pigeonpea pod borer *H. armigera* (Sujana et al. 2008). *C. scarabaeoides*, a wild species of Indian origin, has multiple disease resistance (Kulkarni et al. 2003; Upadhyaya 2006). Pods of *C. scarabaeoides* have a dense covering of non-glandular and low density of glandular trichomes (Shanower et al. 1997). Since *C. scarabaeoides* had least damage compared to cultivated pigeonpea, it was concluded that non-glandular trichomes form a preventive layer for insect lodging and feeding on the pod surface. Further research is necessary to know the differences between different glandular and non-glandular trichomes to assign clear-cut influences of these trichomes. As large number of glandular trichomes are present on *C. cajan* pods, they may be playing a role in the high damage due to pod borers. *C. scarabaeoides* was used as a wild species to introgress resistance to sterility mosaic disease (Patancheru isolate) and

H. armigera insect (Mallikarjuna unpublished results). *C. acutifolius*, a wild species native of Australia, can be crossed with pigeonpea as a one-way cross. The reciprocal cross, using *C. acutifolius* as the female parent, aborts to give rise to immature seeds. In vitro interventions are necessary to obtain hybrid plants (Mallikarjuna and Saxena 2002). Advanced generation population from cross utilizing *C. acutifolius* as the pollen parent has shown resistance to pod borer damage (Mallikarjuna et al. 2007), variation in seed color and high seed weight (Fig. 2.2). Some lines have shown high level of resistance to pod borers, pod fly and bruchids under unprotected field conditions (Table 2.2).

Some of the other important traits identified in wild *Cajanus* are nematode resistance, Alternaria blight resistance (Sharma et al. 1987) and salinity tolerance (Subbarao 1988; Srivastava et al. 2006).

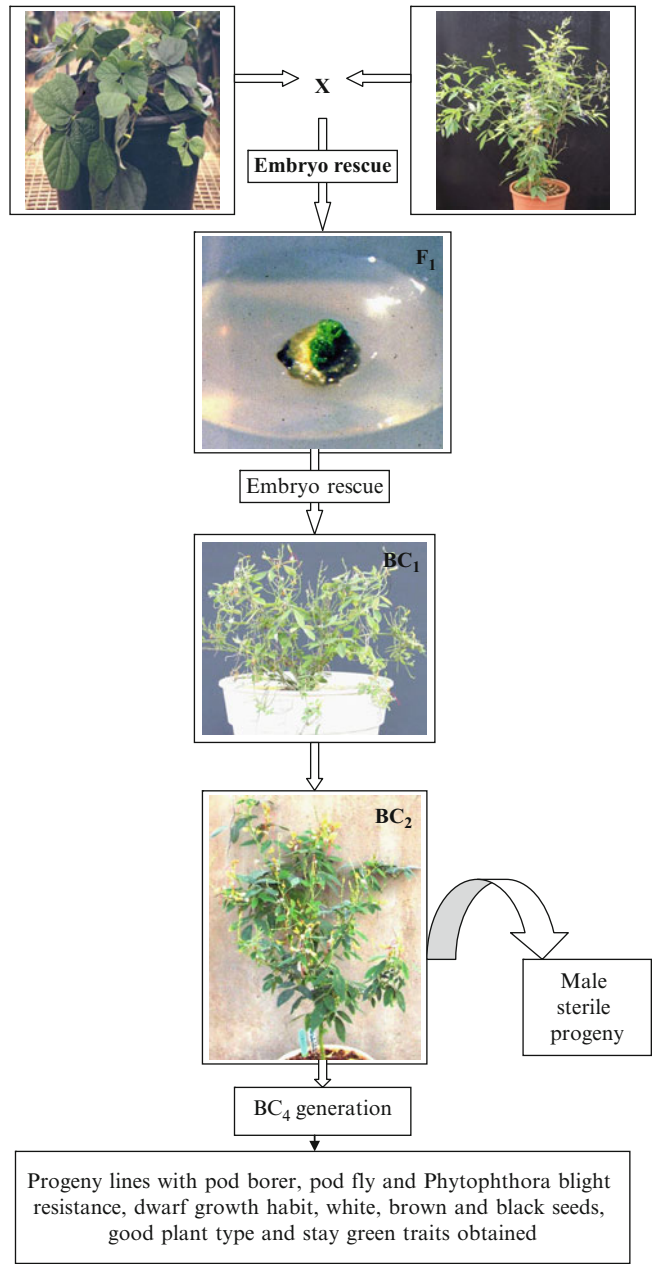

Fig. 2.2 Tapping useful genetic variation from *Cajanus platycarpus*

2.2.3.5 Sterility Mosaic Disease Resistance

Sterility mosaic disease (SMD) of pigeonpea is transmitted by eriophyid mites, *Aceria cajani*, the smallest arthropods, transmitting the virus called tenui-like virus (PPSMV). Infected pigeonpea plants show mosaic symptoms on the leaves and cease flowering, rendering the plants sterile with no pod formation. Until recently, the causal agent of SMD was not identified, but it was possible to identify resistant plants as well as segregating populations based on disease symptoms. There are three major isolates of this virus and amongst these the Bangalore isolate has been identified as the most virulent virus and sources of resistance are few. Lava Kumar et al. (2005) have shown that many of the wild *Cajanus* species are resistant to all the isolates of the SMD virus, and this resistance to SMD is monogenic and recessive (Kulkarni 2002). *C. scarabaeoides* (ICPW 94), which is resistant to all the isolates of SMD, was used in the crossing program, and the progeny were tested for resistance. Many of the plants were found to be disease-free and were classified as resistant. Some of the plants showed relatively mild disease symptoms, called as ring spots, and these were classified as moderately resistant. These plants flowered and set seeds. The susceptible plants had disease mosaic symptoms with crinkled leaves and did not flower and set seeds (Mallikarjuna and Wesley unpublished results). Lines derived from crosses with *C. acutifolius* and *C. platycarpus* have shown resistance to Patancheru isolate of SMD under field conditions (Saxena and Mallikarjuna unpublished results).

2.2.4 Tertiary Gene Pool

There are 20 wild species in the tertiary gene pool of pigeonpea (Fig. 2.1). Till date, only one wild *Cajanus* species from this gene pool is amenable to interspecific hybridization and gene transfer (Mallikarjuna and Moss 1995; Mallikarjuna et al. 2006). An important prerequisite for successful cross-pollinations using incompatible species is the application of growth regulators to pollinated pistils (Mallikarjuna 2003) followed by embryo rescue of aborting hybrid embryos (Mallikarjuna 1998). Embryo rescue technique is used to save aborting hybrid embryos in vitro. The immature aborting embryo is removed from seeds and cultured in vitro to produce hybrid plants. Hormone-aided pollinations and embryo culture have been valuable tools for the transfer of Phytophthora blight resistance from *C. platycarpus*, a wild species from the tertiary gene pool of pigeonpea, into pigeonpea (Mallikarjuna et al. 2006).

Wide crosses with distantly related species give rise to novel variation, not observed in either of the parents used in the crossing program (Hoisington et al. 1999). In the BC_2 plants, the flower color varied from yellow to orange-colored petals. Pollen fertility varied from 27 to 46% (Table 2.1). Some plants had open flowers, unlike those observed in pigeonpea or *C. platycarpus* (Cherian et al. 2006). Open flowers of pigeonpea is likely to play an important role in the development of hybrid pigeonpea as this trait will facilitate cross-pollination. Seed color ranged from white to black.

A selection was made in the BC_2 generation for open flower morphology and low pollen fertility, and this line was called F_1BC_2-E (Fig. 2.3). They were backcrossed with the recurrent parent pigeonpea cv. ICPL 85010. Two lines were observed to have total pollen sterility. Their progeny were also completely male sterile. Seeds from self-pollinations were not obtained, and forced self-pollinations did not set seeds. The flowers had white anthers with open flower morphology (Fig. 2.3: E15 and E4). Anthers had shrunken pollen sacs with no pollen. Some of the anther sacs had some pollen (Fig. 2.3: E15), but the anthers never dehisced to release the pollen grains.

Table 2.1 Analysis of morphological traits in progeny lines derived from *C. platycarpus*

Identity	Plant habit	Flower color	Flower morphology	Seed color	Pollen fertility
F1BC2-A	Erect	Orange keel	Closed	Brown	46
F1BC2-B	Semi-erect	Orange keel	Closed	Brown	30
F1BC2-C	Erect	Orange keel	Closed	Brown	33
F1BC2-D	Erect	Red keel	Open	Brown	33
F1BC2-E	Erect	Red keel	Open	Black	27

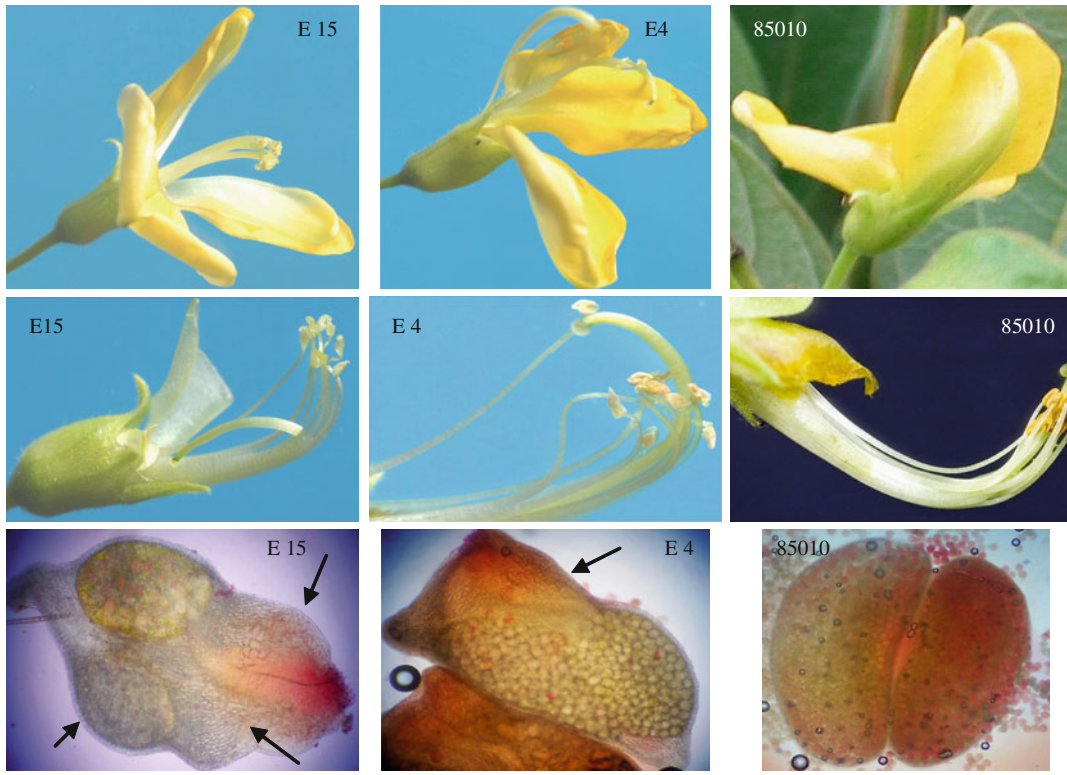

Fig. 2.3 Male sterility in the progeny from the cross *C. platycarpus* × *C. cajan*. E15: Flower, anther bundle and single anther. E 4: Flower, anther bundle and anther. 85010: Flower, anther bundle and single anther

Male sterility coupled with open flowers are traits important for the development of CMS systems as open flowers would favor cross-pollinations. None of the CMS systems available for pigeonpea have open flowers. Experiments are underway to identify restorers of fertility and maintainers of male sterility.

The progeny lines derived from F_1BC_2-A was backcrossed to cultivated recurrent parent ICPL 85010 and F_1BC_4-A lines were developed. Progeny lines were screened for days to flower, which varied from 60 to 92 days. In the parental lines, *C. platycarpus* flowered at 50 days and the cultivar ICPL 85010 flowered at 83 days. There was improvement in 100-seed weight compared to *C. platycarpus* (6.1 g/100 seeds). Three lines F_1BC4-A10-7, F_1BC4-A17-8 and F_1BC4-A14-6 had higher 100-seed weight than both the parents (Table 2.2). These might be good sources of bold seeds in pigeonpea. Protein content in all the hybrid lines was more than that in *C. platycarpus*, and F_1BC_4-A4 and F_1BC_4-A19-14 showed marginally more than that in the cultivated parent. Some of the lines (F_1BC_4-A8-4 and F_1BC4-A14-6) had a tendency towards male sterility with pollen fertility not exceeding 30% with open flowers and non-dehiscent anthers. Non-dehiscent anthers in open flowers coupled with high pollen sterility are desirable traits of a CMS source.

All the lines were screened for *H. armigera* (pod borer), *Melanagromyza obtusa* (pod fly) and *Callosobruchus chinensis* (bruchids) under unprotected field conditions. Damage due to *H. armigera*, in the wild parent *C. platycarpus*, was less than 1%. Damage in cultivated parent ICPL 87 was 69%. Damage in F_1BC_4-A derivatives ranged from 2 to 37% with majority of the lines with less than 15% damage (Table 2.2). It was observed that there were significant differences between the lines for pod borer and bruchid resistance and 100-seed weight (Table 2.2). The results show that there is good scope to transfer *H. armigera* resistance from *C. platycarpus*. Line F_1BC_4-A19-14 has pod borer and bruchid resistance (Table 2.2), and marginally high protein was an additional desirable trait present in the line. Line F_2BC_4-A22 plants consistently showed short stature

Table 2.2 *Cajanus platycarpus* progeny showing insect resistance and seed weight

Line no.	Yield components		Biotic stresses			
	Healthy pods pl^{-1} (no.)	100-seed wt (g)	Pod borer damage (%)	Pod fly damage (%)	Bruchid damage (%)	
F1BC4-A4 10-7-1	81.3 ± 35.81 gh	10.29 ± 1.15 bc	9.91 + 7.11 ijklm	14.54 defgh	1.03	jkl
F1BC4A4 10-12-1	99.5 ± 90.42 cde	9.82 ± 0.76 ef	16.61 + 7.77 ef	12.05 hij	2.12	fghj
F1BC4A4 13-2-1	91.25 ± 27.35 g	9.44 ± 1.40 ghi	11.12 + 9.09 ghijklm	15.84 de	2.74	fgh
F1BC4A4 13-2-1	63.2 ± 26.19 hij	8.64 ± 0.61 l	10.14 + 7.55 ijklm	10.24 ijk	0.04	l
F1BC4A4 13-5-1	79.27 ± 31.12 h	9.52 ± 0.85 ghi	12.59 + 6.81 fghijkl	12.85 fghi	6.28	cde
F1BC4A4 13-5-1	70.55 ± 27.29 hi	9.11 ± 0.73 jk	6.85 + 4.45 m	12.52 ghi	0.23	kl
F1BC4A4 14-16-1	95.94 ± 63.37 cdef	9.22 ± 0.92 ij	14.67 efghi	14.52 efgh	1.55	hjk
F1BC4A4 14-21-1	74.33 ± 47.75 hi	8.56 ± 6.59 l	10.26 ijklm	7.68 k	7.44	bcd
F1BC4A4 14-18-1	118.22 ± 76.41 a	10.27 ± 0.72 bcd	9.71 jklm	12.94 fghi	1.38	hjkl
F1BC4A4 14-4-1	72.05 ± 41.13 hi	9.70 ± 0.82 efg	18.56 cde	9.48 jk	1.98	ghj
F1BC4A4 14-6-1	106.93 ± 84.15 abc	9.92 ± 0.96 e	15.89 + 7.71 b	10.80 ij	1.01	jkl
F1BC4A4 14-6-1	54.50 ± 30.17 jk	9.85 ± 0.82 ef	24.12 + 15.07 efg	10.64 ijk	0.47	kl
F1BC4A4 14-9-1	111.35 ± 79.42 ab	8.64 ± 0.87 l	13.18 fghijkl	14.96 defg	3.50	f
F1BC4A4 15-14-1	73.52 ± 35.28 hi	9.60 ± 0.88 fghi	13.42 fghijk	3.73 l	2.01	ghj
F1BC4A4 17-1-1	50.15 ± 25.25 jk	8.82 ± 0.69 kl	9.43 jklm	16.68 de	0.13	kl
F1BC4A4 17-5-1	67.6 ± 39.04 hi	9.14 ± 0.73 ij	13.28 fghijkl	14.61 defgh	0.00	l
F1BC4A4 17-8-1	73.11 ± 41.36 hi	11.02 ± 1.62 a	11.42 ghijklm	10.98 ij	14.33	a
F1BC4A4 19-1-1	76.00 ± 49.35 h	9.61 ± 0.89 fghi	9.46 jklm	7.74 k	7.69	bc
F1BC4A4 19-12-1	77.95 ± 36.69 h	9.42 ± 1.10 ghi	7.23 m	15.71 def	8.65	b
F1BC4A4 19-14-1	8.54 ± 7.29 m	9.36 ± 0.43 ij	15.25 efgh	41.75 a	0.00	l
F1BC4A4 19-20-1	22.82 ± 7.59 cdef	10.46 ± 0.99 b	22.85 bc	16.57 de	2.52	fgh
F1BC4A4 19-8-1	99.7 ± 71.36 cd	9.28 ± 1.08 ij	14.18 efghij	11.48 ij	1.06	jkl
F1BC4A4 20-10-1	34.17 ± 24.76 l	9.98 ± 1.66 de	21.52 bcd	21.65 b	0.33	kl
F1BC4A4 20-5-1	10.54 ± 7.42 hi	9.82 ± 0.63 ef	10.55 ijklm	20.19 bc	0.00	l
ICPL 85010 (S)	12.00 ± 0.93 m	7.66 ± 0.93 m	68.00 a	17.41 cd	3.10	fg
Mean ± SE	74.26 ± 5.48	9.48 ± 0.14	15.61 ± 2.36	14.30 ± 1.39	2.78 ± 0.70	
CD (0.05)	11.31	0.29	4.88	2.87	1.45	

Means within the same row with same letter are not significantly different ($P < 0.05$)

with bushy growth habit, a trait not observed in the rest of the progeny.

Screening thousands of germplasm lines for Phytophthora blight, especially for race P_3, has failed to identify lines with resistance. Race P_3 is the most virulent race. Screening wild *Cajanus* for Phytophthora blight disease has resulted in the identification of *C. platycarpus*, which has shown resistance to all isolates of Phytophthora blight fungi. Although *C. platycarpus* belongs to the tertiary gene pool of pigeonpea, it has been successfully crossed, and progeny have been generated at ICRISAT (Mallikarjuna et al. 2006). Screening interspecific derivatives to Phytophthora blight disease under glasshouse conditions has shown that it is possible to transfer resistance from *C. platycarpus* (Mallikarjuna et al. 2005). Tetraploid progeny from F_1 hybrid *C. platycarpus* × *C. cajan* showed high level of resistance to Phytophthora blight disease, under both field and glasshouse-simulated conditions. As it was not possible to backcross them to pigeonpea, the progeny is best suited as a ground cover due to its semi-trailing growth habit. These results show that there is ample scope to transfer resistance from wild *Cajanus* into the cultivated *Cajanus* species.

It is hoped that the techniques developed for the cross *C. platycarpus* × *C. cajan* will be useful to cross other wild *Cajanus* species from the tertiary gene pool with cultivated *C. cajan*.

2.2.5 Quaternary Gene Pool

Wild species placed in the quaternary gene pool of *Cajanus* belong to different genera, such as *Flemingia*, *Rhynchosia*, *Dunbaria* and *Eriosema*, to name a few (Fig. 2.1). Results of an exhaustive crossing experiment have shown that some of the species in

this group may be amenable to hybridization with pigeonpea; however, these results need to be confirmed (Mallikarjuna unpublizhed results). Until more cross-ability studies are carried out using species from this gene pool, it may not be possible to access genes/traits from this gene pool for pigeonpea improvement. Isolation of genes from wild species, especially from the quaternary gene pool, may be an important strategy to introduce genes through genetic transformation, which are not amenable to wide crosses research. Alternatively, protoplast fusion may be an important technique to introduce genes/traits from this gene pool.

2.3 Genetic Diversity in the Genus *Cajanus*

Biochemical markers have been effectively used to detect polymorphism. Krishna and Reddy (1982) used esterase isozymes to study species affinity between pigeonpea and a few of the wild relatives. Esterase isozymes studies showed affinity between wild species *C. scarabaeoides*, *C. albicans*, *C. scarabaeoides*, *C. sericeus* and *C. volubilis* with closer affinity between *C. albican* and *C. scarabaeoides*. *C. platycarpus* had distinct band and did not show affinity with any of the wild species used in the study or with pigeonpea. *C. cajanifolius* showed a closer affinity to *C. cajan*. Panigrahi et al. (2007) carried sodium dedocyl sulfate–polyacrylamide gel electrophoresis (SDS-PAGE) analysis of seed albumins and globulins of 11 *Cajanus* species including cultivated species *C. cajan*. Banding patterns revealed *C. cajanifolius* to be the closest to *C. cajan*, with *C. platycarpus* as an outgroup species justifying its status as a tertiary gene pool species (van der Maesen 1986). The study also showed *C. cajan* sharing homology with *C. cajanifolius* and also with *C. scarabaeoides*, *C. albicans*, *C. volubilis* and *C. sericeus*. These results indicate that pigeonpea is a product of multigenomic interaction involving *C. cajanifolius*, *C. scarabaeoides* and other species.

Boehringer et al. (1991) used allozymes and were able to detect polymorphism between Indian and Zambian genotypes of pigeonpea. Nadimpalli et al. (1994) used restriction fragment length polymorphism (RFLP) markers to determine phylogenetic relationships among 12 species belonging to four related genera. Two closely related *Cajanus* species, *C. scarabaeoides* and *C. cajanifolius*, showed a close relationship with each other; amongst the two, *C. cajanifolius* was closer to *C. cajan*. Interestingly, species belonging to different genera grouped together and were away from the above group. Species belonging to *C. lineatus*, *C. albicans* and *C. sericeus* formed a group that had a closer relationship with the first group. Utilizing random amplified polymorphic DNA (RAPD) markers, it was possible to distinguish pigeonpea cultivars, albeit with low levels of polymorphism (Ratnaparkhe et al. 1995). High level of polymorphism was observed between different species of *Cajanus* with *C. albicans*, *C. sericeus* and *C. lineatus*, which are of Indian origin, showing closer relationship to *C. cajan* than to *C. acutifolius*, *C. grandifolius* and *C. reticulates*, which are of Australian origin. *Rhynchosia* species grouped together, with *Flemingia stricta* being distinct from rest of the species used in the study. Punguluri et al. (2006) used amplified fragment length polymorphism (AFLP) markers to study genetic diversity in pigeonpea cultivars that were found to have low level of diversity (87% common bands), but they were able to distinguish Pusa cultivars from others. Genetic distance between wild relatives *C. volubilis* and *Rhynchosia bracteata* was high, and also from the cultivated pigeonpea. Ribosomal genes from wheat and *Vicia faba* were used to distinguish pigeonpea cultures and some wild relatives. The probes were not able to distinguish cultivars, but polymorphism was observed between species but not within species. The study showed a close relationship between *C. cajan* and *C. scarabaeoides*, and they, in turn, were related to *C. mollis* and *C. albicans*. *C. reticulates* showed 95% similarity with *C. platycarpus*. This study concluded that *C. Scarabaeoides* is closer to *C. cajan* than *C. cajanifolius* (Parani et al. 2000). In conclusion, genetic diversity studies show that two wild relatives, *C. cajanifolius* and *C. scarabaeoides*, are closely related to pigeonpea than any of the compatible wild species of the genus.

The merger of genus *Cajanus* with *Atylosia* has strong cytological support with the same chromosome number in all the species being $2n = 22$ (Deodikar and Thakar 1956; Dundas 1990). Chromosome number analysis of 20 species belonging to five genera namely *Cajanus*, *Rhynchosia*, *Dunbaria*, *Flemingia* and *Paracalyx* showed $2n = 22$ chromosome number (Ohri and Singh 2002).

There is further evidence from cytology that *C. cajanifolius* is the progenitor species of *C. cajan* as the two have similar karyotype, and the hybrids between the two species show normal meiosis with high pollen fertility and high seed set (Pundir and Singh 1985). Hybrids between *C. cajan* and wild species *C. scarabaeoides*, *C. albicans*, *C. sericeus* and *C. acutifolius* showed 0–2 univalents with mature seed set (Pundir and Singh 1985). The presence of univalents shows that the genomes of *C. cajan* and the above-mentioned wild *Cajanus* species are more divergent than *C. cajanifolius*. The reciprocal crosses involving *C. lineatus* (Mallikarjuna unpublished results) and *C. acutifolius* did not set mature seeds. The aborting F_1 embryos from the cross *C. acutifolius* × *C. cajan* were germinated in vitro and hybrid plants obtained. In spite of normal chromosome segregation at metaphase in 96% of the meiocytes, pollen fertility was only 12–16% (Mallikarjuna and Saxena 2002).

Analysis of the F_1 hybrid between *C. platycarpus* and *C. cajan* showed a mean of six univalents and eight bivalents. The presence of six univalents shows that the genomes of *C. platycarpus* and *C. cajan* are divergent with 2–3 non-pairing chromosomes. Pollen fertility in the hybrid was 0.05%, which again shows that the two genomes are not closely related (Mallikarjuna et al. 2006). The placement of *C. platycarpus* in the tertiary gene pool of pigeonpea is therefore justified.

2.4 Genomic Resources

Molecular markers are an important resource to study the geographical origin, genotype identification and genetic diversity, molecular linkage map, gene synteny, trait tagging and marker-assisted selection, association mapping, map-based cloning. RAPD technique was used to identify parents from hybrids of the cross *C. platycarpus* × *C. cajan* (Mallikarjuna 2003). Although RAPDs are not favored as compared to other markers, they can still be effectively used to distinguish parents and hybrids. Kotresh et al. (2006) used RAPDs to show association between markers and Fusarium wilt resistance. Until now, there were only ten SSR markers, which could be used to detect variation in pigeonpea (Burns et al. 2001). In the study by Odeny et al. (2007), 208 SSR loci were identified by screening a non-enriched partial genomic library. Primers were designed for 39 SSR loci, 20 of which amplified PCR products of the expected size. Nineteen of the primer pairs were polymorphic amongst 15 cultivated and nine wild *Cajanus* accessions. A community effort was undertaken (Dubey et al. 2009) to develop more SSR markers. Several SSR-enriched genomic DNA, cDNA and bacterial artificial chromosome (BAC) libraries were developed from leading varieties of pigeonpea. A total of 86,268 BAC-end sequences were generated that provided 9,956 pseudo-contigs and 42,285 singletons. A large number of SSR markers are being developed from BAC-end sequences and SSR-enriched libraries. By using 454/FLX sequencing on the normalized cDNA pool from 20 tissues representing different developmental stages, a total of 496,705 sequence reads have been generated to provide approximately 22,000 unigenes. Once SSR markers are developed from this study, the crop will be on par with other legumes such as chickpea, which has more than 400 SSR markers (Lichtenzveig et al. 2005).

Diversity array technology (DArT) is a novel genome-wide genotyping method. It offers low-cost, high-throughput and sequence-independent genotyping. Yang et al. (2006) reported the development and application of DArT for pigeonpea. DArT analysis showed no clear differentiation among cultivars from different regions, with cultivars from Africa showing some diversity. There was differentiation between wild and cultivated species. They inferred that morphological variation observed in cultivated pigeonpea accessions was much higher than that observed at the molecular level, whereas the wild species of pigeonpea and its related genera exhibited a higher degree of molecular diversity than that observed at the morphological level.

A beginning has been made to develop advanced backcross QTL (AB-QTL) analysis as proposed by Tanksley and Nelson (1996). In this approach, a wild species is crossed with the elite cultivar and backcrossed once or twice (sometimes more) with the elite cultivar, and selfed for one or two generations (sometimes more). The segregating BC_1F_2/BC_2F_2/BC_2F_3 lines are phenotyped for traits of interest and genotyped with polymorphic markers. This is a method for transferring agronomically important quantitative traits from wild species to the cultivated species. The approach has great potential to harness the wealth of wild relatives for pigeonpea improvement, where the cultivated species show low level of

polymorphism and susceptible to major diseases and insect pests.

2.5 Conclusion

Pigeonpea is an important protein rich food of vegetarian diet. It is a favorite crop of small holder farmers as the crop can tolerate and yield high under drought conditions when many other crops fail. Pigeonpea yield has reached a plateau and is susceptible to a range of diseases caused by virus, fungi and bacteria. Although high degree of morphological variability is seen, the same is not true at the molecular level. Crop improvement programs are looking for increased genetic diversity by tapping wild relatives from different gene pools. There is enough evidence to prove that *C. cajanifolius* is the progenitor species of pigeonpea. The secondary gene pool has contributed various traits for the improvement of the crop. In spite of the success obtained in the utilization of wild relatives from the secondary gene pool, there is scope to use others, which has not been attempted in the crossing program. Progress has been made to exploit and introgress useful traits including male sterility from *C. platycarpus*, a tertiary gene pool wild relative of pigeonpea. This has opened up avenues to tap other species in the tertiary gene pool. There are many species in the tertiary gene pool of the genus *Cajanus*. Many of them have not yet been crossed with pigeonpea. It is possible that some of the species placed in the tertiary gene pool may move to secondary gene pool, if they are cross-compatible with cultivated pigeonpea. Enhanced genomic resources may be available in the near future as there is international collaboration to develop them.

2.6 Future Prospects

Pigeonpea is a source of protein for vegetarian diet and resource poor farmers in the rainfed tropics. It has built in resilience to withstand drought and can yield even under very low input conditions. Efforts to broaden the genetic base and introduce traits for various biotic stresses and desirable abiotic traits have been significant. There is renewed interest to exploit more wild relatives from the secondary gene pool, and such efforts would have a big impact on broadening the genetic base of variation of pigeonpea and introduction of useful biotic, abiotic and agronomic traits. The possibility of exploiting wild relatives from the tertiary gene pool has opened up new vistas for the broadening of the genetic base of variation and for improvement in pigeonpea. Development of genomic resources has gained new impetus with community effort, and the development of genome-wide markers may open avenues for molecular marker-assisted gene introgressions and breeding.

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