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Abstract Pigeonpea (*Cajanus cajan* L.) is the sixth most important grain legume in the world and second most important pulse crop after chickpea in India. It is a major source of protein for several resource poor rural and urban families of Asia, Africa, the Caribbean, and Latin America and can be cultivated successfully under limited inputs as well as rainfed conditions. Although enormous breeding efforts have been put to the improvement of pigeonpea during the last few decades, the progress in terms of increasing production and quality improvement has not been up to the desired level. One of the major reasons behind this is susceptibility of this crop to many biotic and abiotic stresses, as well as a narrow genetic base of cultivated germplasm thereby offering limited chances of genetic recombination and consequently slower rates of genetic improvement. On the other hand, wild relatives of pigeonpea have evolved naturally to survive environmental extremities including droughts, floods, excess heat, and cold and also have the capability to withstand damage by insect pests and diseases. Owing to these properties, these species have invoked interest of breeders in utilizing them for the improvement of their cultivated counterparts. Consequently, over the past many years, tremendous improvements of practical importance have taken place in pigeonpea utilizing wild genetic resources. This chapter summarizes such significant achievements and highlights the utilization status of wild species in genetic improvement of pigeonpea.

Keywords AB-QTL • Alien gene transfer • *C. platycarpus* • *C. scarabaeoides* • Distant hybridization • Gene pool • Pigeonpea

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7.1 Introduction

In a time of resource constraints, land pressure, environmental concerns, and population explosion, genetic improvement of crops becomes the most promising approach by which food production can meet the demand. For genetic improvement to succeed, plant breeders largely rely on available genetic variability on which they can make selection of desired plant types. Although there is no shortage of genetic variation in nature, a process of genetic erosion due to various reasons, including directed plant breeding, threatens modern varieties. All crop species were originally domesticated from wild plants by humans; the very process of domestication inherently reduced genetic variation (Ladizinsky 1985). The limited genetic variation among modern crop varieties not only makes them more vulnerable to disease and pest epidemics, but it also reduces the chance for plant breeders to identify new and useful combinations of genes, thus causing a slower rate of crop improvement in the long term.

There is renewed interest in the utilization of wild relatives for the improvement of crop plants worldwide. Wild ancestors of most crop plants can still be found in their natural habitats, but their numbers are slowly dwindling. There is an urgent need to conserve all the available germplasm under long-term storage. Germplasm of the crop plants represents a precious source of genetic variation that can potentially insure more rapid and sustained crop plant improvement for many years to come (Tanksley and McCouch 1997).

Pigeonpea [*Cajanus cajan* (L.) Millspaugh] is an important food legume providing protein nitrogen in the human diet to a large population of Asia, Africa, the Caribbean, and Latin America. It has a special place in the diet of vast majority of the Indians who consume pigeonpea in one form or the other in their daily cuisine. It also has wide applications in traditional medicine (van der Maesen 2006). Cultivation of the pigeonpea dates back to at least 3,500 years. The center of origin is the eastern part of peninsular India, including the state of Odisha, where the closest wild relatives (*Cajanus cajanifolia*) occur in tropical deciduous woodlands (van der Maesen 1995). Archaeological finds of pigeonpea include those from two Neolithic sites in Odisha, Gopalpur, and Golabai Sasan dating between 3,400 and 3,000 years ago and sites in South India, Sanganakallu, and Tuljapur Garhi, also dating back to 3,400 years ago. From India it traveled to East Africa and West Africa (Fuller and Harvey 2006). There, it was first encountered by Europeans, so it obtained the name Congo pea. By means of the slave trade, it came to the American continent, probably in the seventeenth century.

Nutritionally, pigeonpea contains high levels of protein and the important amino acids, namely, methionine, lysine, and tryptophan (Saxena et al. 2010). In combination with cereals, pigeonpea makes a well-balanced human diet. Pigeonpea is mostly grown in low-input and risk-prone marginal environments; therefore, there is a large gap between potential yield (2,500 Kg/ha) and actual yields on farmer's fields being 866.2 kg/ha in Asia and 736.2 kg/ha in Africa (Mula and Saxena 2010). Nevertheless, it is a drought-tolerant and a hardy crop, assuring sustainable returns from marginal lands with minimal inputs, hence is considered as a very suitable crop for subsistence agriculture.

Pigeonpea is a cross-pollinated (20–70 %) species with a diploid number of $2n=2x=22$ and genome size of 858 Mbp. Among seed legumes, it is the first plant to have its genome sequenced. The first draft was done by a group of more than 30 scientists from ICRISAT and other institutions as well as ICAR (Singh et al. 2012).

Ample morphological diversity is exhibited by pigeonpea as a crop; however, the same is not true at the molecular level (Yang et al. 2006; Odeny et al. 2007). Low level of genetic diversity has led to a narrow genetic base, and this is reflected by the absence of resistance in this crop to various biotic and abiotic constraints. One of the reasons for low level of genetic diversity is due to the evolutionary bottleneck. There is some evidence that pigeonpea has a monophyletic evolution and has evolved from wild relative *Cajanus cajanifolius* (Kassa et al. 2012). There are 5–6 traits that differentiate *C. cajanifolius* from pigeonpea, such as flower morphology, pod color and morphology, pod constriction, seed color and strophiole, and 100-seed weight (Mallikarjuna et al. 2012a). Molecular studies revealed that a genetic dissimilarity index value ranging from 0.81 to 0.94 exists between the two species (Mallikarjuna et al. 2012a). But the crop has a rich source of variability in the form of wild relatives in different gene pools, 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, and more recently introgression of resistance to pod borer (*Helicoverpa armigera*), pod fly, and bruchid (Mallikarjuna et al. 2011a). The classification of Harlan and de Wet (1971) of grouping the germplasm of a crop is followed to group the genetic resources of pigeonpea including 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 related genera in the quaternary gene pool (GP4) (Table 7.1, Fig. 7.1).

Table 7.1 Different gene pools of pigeonpea

Primary gene pool	Secondary gene pool	Tertiary gene pool	References
<i>Cajanus cajan</i> , <i>C. cajanifolius</i>	<i>C. acutifolius</i> , <i>C. albicans</i> , <i>C. confertiflorus</i> , <i>C. lanceolatus</i> , <i>C. latisepalous</i> , <i>C. lineatus</i> , <i>C. reticulatus</i> , <i>C. scarabaeoides</i> , <i>C. sericeus</i> , <i>C. trinervius</i>	<i>C. goensis</i> , <i>C. heynei</i> , <i>C. kerstingii</i> , <i>C. mollis</i> , <i>C. platycarpus</i> , <i>C. rugosus</i> , <i>C. volubilis</i> , and other species	Smartt (1990), Singh et al. (2006), Kumar et al. (2011)



Fig. 7.1 Some wild relatives of pigeonpea. (a) *C. scarabaeoides*, (b) *C. lineatus*, (c) *Rhynchosia* spp.

In the genus *Cajanus* with 32 species and 11 related genera, *Cajanus cajan* is the only species cultivated throughout Asia and Africa for its protein-rich grains. The gene bank at ICRISAT conserves over 13,632 accessions of *Cajanus* species from 74 countries. This includes 555 accessions of wild relatives representing 6 genera and 57 species (Upadhyaya et al. 2007). Pigeonpea (*C. cajan* L.) belongs to the subtribe *Cajaninae* and contains 13 genera. Earlier the genera *Atylosia* and *Cajanus* were considered closely related, and later genus *Atylosia* was 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 1 to West Africa (van der Maesen 1986). Apart from these, there are other related genera, namely, *Rhynchosia*, *Dunbaria*, *Flemingia*, *Paracalyx*, *Eriosema*, *Adenodolichos*, *Bolusafr*, *Carissoa*, *Chrysoscias*, and *Baukea*. For details of the gene pools, please refer to the publication of Mallikarjuna et al. (2011a, b).

7.2 Primary Gene Pool

Considerable progress has been made in pigeonpea improvement by using variability within the cultivated species, and consequently, pigeonpea is grown on 4.5 million ha globally with a production of 3.5 million metric tons and productivity of 863 kg/ha (FAO 2009). The gene bank at ICRISAT, Patancheru, India, conserves 13,632 accessions of pigeonpea from 74 countries. This is the single largest collection of pigeonpea germplasm assembled in the world. The germplasm collection includes 8,215 landraces, 4,795 breeding lines, and 67 improved cultivars (Upadhyaya et al. 2012). In spite of the large germplasm collection in primary gene pool, it is not widely used (Wright 1997) as information on the presence of useful traits is not easily available and extended period of research whenever utilized (Goodman 1990). To overcome these issues, core and mini core collections have been developed (Upadhyaya et al. 2006). Variation within the primary gene pool is of utmost importance as accessions belonging to primary gene pool are easy to use with quicker gains and can be directly released as cultivars. Progress has been made in the utilization of material from primary gene pool (Saxena 2000). Pigeonpea varieties BDN-1 and Maruthi released in 1989 are selections from pure line breeding which are popular even today (Bantilan and Joshi 1996). Development of high-yielding varieties such as ICPL 87, ICPL 151, Prabhat, T 21, Pusa Ageti, CO 5, and JA 3 has also been reported (Singh et al. 2005).

In spite of the above successes, a perusal of utilization pattern of *Cajanus* germplasm indicates that so far a very small proportion of germplasm has been used in pigeonpea improvement programs globally. In pigeonpea, 57 ancestors were used to develop 47 varieties. The top 10 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 the vast number of lines available in the primary gene pool which lack characterization, evaluation, and genetic diversity data.

7.3 Secondary Gene Pool

The pigeonpea wild relatives' collection at ICRISAT gene bank has not been characterized and evaluated systematically, although the data is beginning to emerge (Upadhyaya et al. 2012). Main reasons could be low seed quantity, lack of resources, difficulties in phenology and growth habit, and lower priority than the cultivated species (Upadhyaya et al. 2012). However, limited evaluation of different species by researchers across the world indicated that the wild gene pool of pigeonpea, particularly the secondary gene pool, is a promising source for various biotic and abiotic stresses (Bohra et al. 2011; Jadhav et al. 2012).

Compatible wild relatives of pigeonpea which are placed in the secondary gene pool do not need specialized techniques in the crossability experiments in majority of the cases with a few exceptions (Mallikarjuna et al. 2011b). Cytoplasmic male sterility (CMS) systems were developed for pigeonpea exploiting the cross-pollination mechanism and utilizing wild *Cajanus* species. So far eight CMS systems have been reported utilizing wild relatives of pigeonpea (Mallikarjuna et al. 2012b). Of these, seven have been developed utilizing wild relatives from secondary gene pool. One system has cultivated pigeonpea cytoplasm (Mallikarjuna and Saxena 2005). More recently, CMS trait has been observed utilizing *C. lanceolatus*, which is a wild relative in the secondary gene pool (Sandhya and Mallikarjuna, unpublished data). Efforts are underway to identify their restorers. Once developed, this will be named as A₉ CMS system.

The process of outcrossing is important in the development of CMS systems in pigeonpea, but this 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.

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 are 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 (Jadhav et al. 2012).

C. acutifolius, a wild relative from secondary gene pool and 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 the cross utilizing *C. acutifolius* as the pollen parent has shown resistance for pod borer damage (Mallikarjuna et al. 2007), variation for seed color, and high seed weight. Some of the lines showed high level of resistance to pod borers, pod fly, and bruchid under unprotected field conditions

(Jadhav et al. 2012). Bruchid resistance (Jadhav et al. 2012) is an important trait for pigeonpea seeds under storage as resistance to the pest has not been observed in cultivated pigeonpea. These lines are available in pigeonpea breeding and Legume Cell Biology Units of Grain Legumes Program (CGIAR project on Grain Legumes).

Some of the advance generation lines derived from *C. acutifolius* were screened for waterlogging by germinating them and later growing them under waterlogged conditions. A few lines grew under waterlogged conditions, and formation of lenticels was observed in the region above the water surface. The region gave rise to roots which entered the soil through the water surface. This shows that some of these lines that may survive were resistant to waterlogged conditions (Aneesha Begum and Nalini Mallikarjuna, unpublished data).

Another species from secondary gene pool, namely, *C. lanceolatus*, was crossed successfully with cultivated pigeonpea at ICRISAT and progeny lines developed. F₁ hybrids flowered, but some of the hybrids were pollen sterile, and in the rest of the hybrids, pollen fertility varied from 25 to 55 %. All the hybrids were female fertile. Progeny lines developed from the cross were screened for bruchid resistance. *C. lanceolatus* inhibited bruchid growth and survival. Some of the lines showed delayed bruchid growth and delayed life cycle, thus showing antibiosis mechanism of resistance to bruchids. Lines were screened for protein content, and some of the lines showed higher protein content than both their parents. Further biochemical analysis showed higher content of proteinase inhibitors activity in some of the lines (Sandhya Srikanth and Nalini Mallikarjuna, unpublished data). A new source of CMS was identified in the progeny lines, and experiments are underway to identify maintainers and restorers. Sateeshkumar (1985) attempted crossing pigeonpea with *C. lanceolatus* but obtained hybrids which did not flower and remained in the vegetative stage.

7.4 Tertiary Gene Pool

There are 20 wild species in the tertiary gene pool of pigeonpea (Mallikarjuna et al. 2011a, b.). Until now, only one wild *Cajanus* species from this gene pool was amenable to interspecific hybridization and gene transfer (Mallikarjuna et al. 2011b). *C. platycarpus* was successfully crossed utilizing hormone-aided pollinations and in vitro interventions to obtain hybrids. Progeny lines showed variation for days to flower; growth habit; seed weight and number; seed color; resistance to pod borer, pod fly, and bruchids; and cytoplasmic male sterility. Some chasmogamous lines were identified in CMS lines, a trait favoring total cross-pollination. Hence utilizing *C. platycarpus* not only broadened the genetic base of pigeonpea, but it was possible to introgress useful traits. Diversity Array Technology (DArT), a genome-wide marker technology, was used to genotype the parents and advance generation hybrids after four backcrosses. A total of 1,225 markers were found polymorphic among the parents and the progeny. The results of the study showed that apart from DNA stretches from the female and male parent, there was some novel DNA polymorphism observed in the progeny not seen in both the parental species. It was

interesting to observe that as per theoretical calculations, there should be 3.12 % of *C. platycarpus* genome after four backcrosses with cultivated parent *C. cajan* (Mallikarjuna et al. 2011a). Diversity Array Technology analysis showed the presence of *C. platycarpus* genome ranging from 2.0 to 4.8 %. The presence of non-parental DNA sequences was presumably because of recombination, ranging from 2.6 to 10.4 % (Mallikarjuna et al. 2011a).

More recently another species from tertiary gene pool, namely, *C. volubilis*, was crossed with pigeonpea. In F₂ generation, extra short-duration lines were recovered. These lines flowered earlier than the short-duration cultivar ICPL 85010 which was the female parent of the cross. The lines were again screened for the short-duration trait in rabi 2012 and were found to retain the trait. Dwarf growth habit and determinate and semi-determinate plants were observed. In the determinate types, the number of pods per inflorescence and the number of inflorescence was more than that observed in the extra-early and determinate cultivar MN5 (Sandhya Srikanth and Nalini Mallikarjuna, unpublished data).

7.5 Quaternary Gene Pool

There are 11 related genera, namely, *Rhynchosia*, *Flemingia*, *Dunbaria*, *Erisema*, *Paracalyx*, *Adenodolichos*, *Bolusafra*, *Carissoa*, *Chrysoscias*, and *Baukea* including *Cajanus* under the subtribe Cajaninae.

Many of these genera are classified as underexploited legumes. *Rhynchosia* is one such example as it harbors important nutritional and therapeutic properties, with the presence of phytochemicals such as alkaloids, glycosides, anthraquinones, carotenoids, coumarins, dihydrochalcones, fatty acids, flavonoids, steroids, and triterpenoids (Bakshu and Venkataraju 2001). Some species of *Rhynchosia* are used as human and animal diet (Oke et al. 1995). Many of the tribal communities in India soak the seeds in water and consume the seeds after boiling and decanting many times (Murthy and Emmanuel 2011). Apart from this, many of the *Rhynchosia* species are known to exhibit antitumor and thus curative properties. Normally during cancer treatment iron deficiency and anemia are major issues. It was observed that treatment with *Rhynchosia* seeds restored hemoglobin (Hb) count and RBC and WBC count to normal levels. With the interest in dietary flavonoids and suppression of cancer, *Rhynchosia* species are surely going to attract more attention in the coming days.

None of the genera in the quaternary gene pool have been successfully crossed with pigeonpea. Among the genera in the quaternary gene pool, *Rhynchosia* was selected to initiate crossing/introgression/gene transfer experiments as it had many desirable properties, as listed above. It was possible to successfully cross *Rhynchosia* with pigeonpea through hormone-aided pollinations. The success rate of crossing *Rhynchosia* was low, not exceeding 1–2 %, but it was possible to obtain hybrids. Screening the hybrids with molecular markers confirmed the hybridity (Nalini Mallikarjuna and Rajeev Varshney, unpublished data). Although the initial processing

of crossing was challenging, nevertheless, hybrids were obtained. They were fertile and it was possible to obtain self and backcross progenies. Experiments to screen and study the progeny lines for different traits/constraints are in progress.

7.6 AB-QTL Mapping Populations Utilizing Wild *Cajanus* Species

Advance backcross quantitative trait loci detection method abbreviated as AB-QTL increases the efficiency of identifying and transferring beneficial alleles from exotic germplasm (Tanksley and Nelson 1996). This method instead of using traditional F₂ or RIL mapping populations, involves two or three backcrosses to the recurrent parent during population development, thus reducing the amount of donor introgressions in each individual. This method is especially advantageous where wild relatives are used to develop mapping populations. AB-QTL method is used for simultaneous discovery and transfer of valuable QTLs from wild relatives. Since QTL analysis is delayed till BC₂ or BC₃ generations, it may be possible to detect dominant, partially dominant, over dominant, additive, and epistatic QTLs to name a few.

Introgression of useful genes/traits accompanied by undesirable genomic fractions harboring deleterious alleles, collectively called linkage drag, can be overcome to identify favorable exotic quantitative trait locus (QTL) alleles for the improvement of agronomic traits. Two wild relatives, namely, *C. cajanifolius* (the progenitor species) and *C. acutifolius*, a wild species from the secondary gene pool and with many desirable traits (Mallikarjuna et al. 2011a), were used to develop AB-QTL mapping populations. The populations are ready for phenotyping and genotyping after two backcrosses and selfings. It is envisaged that such mapping populations will identify useful alleles present in the wild species as observed in other crops such as rice (Septiningsih et al. 2003).

7.7 Conclusions

No other leguminous crop has been investigated for alien introgression and succeeded in crossing wild relatives from all the gene pools, namely, secondary, tertiary, and quaternary gene pools. Pigeonpea is one crop where tremendous progress has been made to cross wild *Cajanus* species from different gene pools and introgress genes/traits successfully. With these successes it can no more have a narrow genetic base. With the advances in pigeonpea genomics, and a major effort in sequencing the crop, and success in wide crosses in pigeonpea, it has emerged from being labeled as an orphan crop to a trend setter. Recent successes in wide crosses show that it is possible to introduce desirable traits such as pod borer resistance, develop CMS systems, develop lines with multiple disease and pest resistance, change plant type, and increase seed weight and yield.

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