Pigeonpea

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Abstract

Pigeonpea was labeled as an orphan crop but is now a trendy and pacesetter, with ample genetic and genomic information becoming available in recent times. It is now possible to cross wild relatives not only from the *Cajanus* group placed in the secondary and tertiary gene pool but also the related genera placed in the quaternary gene pool. This is no small achievement for a legume which is an important crop of Asia and Africa and plays a major role in the diet of majority of the people of this region. The need of the hour is further committed research on wide crosses in pigeonpea.

7.1 Introduction

In a time of resource constraint, 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 rely on a rich source of genetic diversity. Although there is no shortage of genetic variation in nature, a process of genetic erosion due to various reasons, including 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 made them more susceptible to disease epidemics, but it also reduced 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 including India. 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. The germplasm of crop plants represents a precious source of genetic variation that can potentially insure more rapid and sustained crop

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plant improvement for many years to come (Tanksley and McCouch 1997).

7.2 Origin and Potential

Pigeonpea [*Cajanus cajan* (L.) Millspaugh] is an important crop providing protein 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 the vast majority of Indians, who consume pigeonpea in one form or the other daily. 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 Orissa, where the closest wild relatives (*Cajanus cajanifolius*) occur in tropical deciduous woodlands (van der Maeson 1995). Archaeological finds of pigeonpea include those from two Neolithic sites in Orissa, Gopalpur and Golbai Sassan, 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 they contain high levels of protein and the important amino acids like methionine, lysine, and tryptophan (Saxena et al. 2010). In combination with cereals, pigeonpea makes a well-balanced human diet. Pigeonpea is grown in low-input and risk-prone marginal environments. There is a large gap between potential yield (2,500 Kg/ha) and actual yield on farmer's fields which is 866.2 kg/ha in Asia and 736.2 kg/ha in Africa (Mula and Saxena 2010). It is a drought-tolerant and hardy crop of India, assuring sustainable returns from marginal lands with minimal inputs. Hence it 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. Pigeonpea is the first seed legume plant to have its genome sequenced. The first draft was done by a group of more than 30 ICRISAT and other institution scientists belonging to different organizations across the world (Varshney et al. 2012a).

7.3 Diversity in Crop Cultivars

Ample morphological diversity is exhibited by pigeonpea as a crop but the same is not true at the molecular level (Yang et al. 2006; Odeny et al. 2007). A low level of genetic diversity has led to a narrow genetic base, and this is reflected in the absence of resistance to various biotic and abiotic constraints. The reason for the low level of genetic diversity is 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 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, b). 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 and agronomic traits such as high protein content, identification and diversification of the cytoplasmic base of CMS system, and more recently introgression of pod borer (*Helicoverpa armigera*), pod fly, bruchid resistance, and other agronomic traits (Mallikarjuna et al. 2011a).

7.4 Production-Related Problems

Pigeonpea is an important crop of Asia and especially in India, where it forms an important source of protein in the vegetarian diet. Despite its immense importance in sustainable agriculture and continued breeding efforts directed toward genetic improvement, the global production per hectare of pigeonpea has remained static over the last three decades. The yield gap between the potential yield and on-farm yield is mainly due to the prevalence of various abiotic and biotic stresses in pigeonpea-growing areas together with its cultivation in marginal lands with low input supply and lack of efficient management practices (Varshney et al. 2012b). Among the various diseases, fusarium wilt, caused by *Fusarium udum* Butler, is the most important disease in the Indian subcontinent and East Africa (Saxena 2008). Occurrence of wilting during the pod-filling stage causes infection to pigeonpea seeds and yield losses up to 50–70 % (Marley and Hillocks 1996). Another disease severely affecting pigeonpea yield is sterility mosaic disease (SMD) caused by the pigeonpea sterility mosaic virus (PPSMV) causing losses up to 95–100 % with infection occurring early at <45-day-old plants (Kannaiyan et al. 1984). Apart from wilt and mosaic, *Phytophthora* blight caused by the fungus *Phytophthora drechsleri* Tucker f. sp. *cajani* is another important disease that has got the status of an economic concern. However, the disease is limited in distribution and witnesses more severity in short-duration cultivars as compared to long- or medium-duration genotypes (Ratnaparkhe and Gupta 2007). Among the variety of insects feeding on pigeonpea, the pod borer, *Helicoverpa armigera* (Hubner), is the most damaging pest worldwide, and its frequent occurrence often results in complete crop failure. Besides *Helicoverpa*, other pests like *Maruca* (*Maruca vitrata* Geyer), pod-sucking bugs (*Clavigralla horrida* Germar), and pod fly (*Melanagromyza chalcosoma* Spencer) pose a big threat to pigeonpea production. Moreover, infestations from storage pests like bruchids (*Callosobruchus chinensis*) intensify the situation and result in profound seed damage during storage. Among the abiotic constraints, salinity and waterlogging severely affect the pigeonpea production (Saxena 2008; Choudhary et al. 2011). The limited success achieved so far in addressing the problem of production constraints is mainly due to the complex mechanism underlying these stresses together with the lack of precise and efficient screening techniques. Genetic diversity and resistance to many of the constraints are not up to the desired level in the cultivated germplasm. Low use of germplasm which is 0.4 % of the total 13,771 accessions to develop advanced breeding lines may have also contributed to the lack of good sources of resistance. Factors responsible for the low use of germplasm might be the large size of germplasm collections and lack of presence of useful traits present in them, thus emphasizing the importance of wild relatives with extensive genetic diversity.

7.5 Crop Gene Pools and Alien Introgressions

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 constitute three basic gene pools and are divided as primary gene pool (GP1), secondary gene pool (GP2), and tertiary gene pool (GP3) and the related genera in the quaternary gene pool (GP4). In the genus *Cajanus* with 32 species and 11 related genera, *Cajanus cajan* is the only species cultivated throughout Asia and Africa for its leguminous proteins. The gene bank at ICRISAT conserves over 13,632 accessions of *Cajanus* species from 74 countries. This includes 555 accessions of wild relatives representing six genera and 57 species (Upadhyaya et al. 2007). Pigeonpea belongs to the subtribe *Cajaninae* which contains 13 genera. Earlier the genera *Atylosia* and *Cajanus* were considered closely related; 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 one to West 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*. For details of the gene pools, please refer to the publication of Mallikarjuna et al. (2011a).

7.5.1 Primary Gene Pool

Considerable progress has been made in pigeonpea improvement by using variability within the cultivated species, and globally pigeonpea is grown on

4.5 million ha with a production of 3.5 million metric tons and productivity of 863 kg ha^{-1} (FAO 2009). The gene bank at ICRISAT, Patancheru, India, conserves the 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 the primary gene pool, it is not widely used (Wright 1997) as information on the presence of useful traits is not easily available and necessitating an 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 with the primary gene pool is of importance as they are easy to use with quicker gains and can be directly released as cultivars. Progress has been made in the utilization of material from the primary gene pool (Saxena 2000). 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 the 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 detailed characterization, evaluation, and genetic diversity data. In spite of the above constraints, 10 pigeonpea germplasm have been released as cultivars with two in Nepal, one in the Philippines, two in India, one in China, one in Fiji, and one each in Malawi and Venezuela between 1985 and 2005.

7.5.2 Secondary Gene Pool

The pigeonpea wild species collection at the ICRISAT gene bank has not been characterized and evaluated systematically, although the data is beginning to emerge. 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. 2010; Mallikarjuna et al. 2011a; Jadhav et al. 2012a, b). 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. 2011a). Cytoplasmic male sterile 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 the secondary gene pool as the female parent. One system has cultivated pigeonpea cytoplasm with the utilization of wild species as the male parent (Mallikarjuna and Saxena 2005). More recently, CMS trait was observed utilizing *C. lanceolatus*, which is a wild relative in the secondary gene pool (Sandhya S and Mallikarjuna N, unpublished data). Efforts are underway to identify their restorers. Once developed, this will be named as A_9 CMS system.

The process of outcrossing is important in the development of CMS systems, 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. The cleistogamous trait can be utilized in pigeonpea to obtain pure seeds from genetic stocks. Cleistogamous lines were identified utilizing *C. platycarpus* (Cherian et al. 2006), a wild relative in the tertiary gene pool of pigeonpea. These lines had open flowers. When CMS is developed on such lines, it will help better cross-pollination and thus better yield. High-protein breeding lines were developed from *C. sericeus*, *C. albicans*, and *C. scarabaeoides*. A 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. 2012a, b). *C. acutifolius*, a wild relative from the 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; Jadhav et al. 2012a), 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. 2012a). Bruchid resistance (Jadhav et al. 2012a) 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 the 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 may survive under waterlogged conditions (Aneesha Begum and Mallikarjuna N, unpublished data). Another species from the secondary gene pool, namely, *C. lanceolatus*, was crossed successfully with cultivated pigeonpea at ICRISAT and progeny lines developed (Srikanth et al. 2013). F_1 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. Bruchid growth and survival was inhibited in the lines derived from *C. lanceolatus*. 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 inhibitor activity in some of the lines (Sandhya Srikanth and Mallikarjuna, N, unpublished data). A new source of CMS was identified in the progeny lines and experiments are underway to identify maintainers and restorers (Sandhya Srikanth and Mallikarjuna N, unpublished data). Previously, Sateesh Kumar (1985) attempted crossing pigeonpea with *C. lanceolatus* but obtained sterile hybrids which did not flower and remained in the vegetative stage.

7.5.3 Tertiary Gene Pool

There are 20 wild species in the tertiary gene pool of pigeonpea (Mallikarjuna et al. 2011a). Until now, only one wild *Cajanus* species from this gene pool has been successfully crossed and traits of interest transferred (Mallikarjuna et al. 2011b). *Cajanus platycarpus* was successfully crossed utilizing hormone-aided pollinations and in vitro interventions (Mallikarjuna 1998) to obtain hybrids. Progeny lines showed variation for days to flower, growth habit, seed weight and number, seed color, and resistance to pod borer, pod fly, bruchids, *Fusarium*, and sterility mosaic disease (Mallikarjuna N unpublished data). Some cleistogamous lines were identified in CMS lines (Cherian et al. 2006), 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 Arrays 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 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. 2011b). Diversity Arrays Technology (DArT) analysis showed the presence of *C. platycarpus* genome ranging from 2.0 to 4.8 %. The presence of nonparental DNA sequences was presumably because of recombination, ranging from 2.6 to 10.4 % (Mallikarjuna et al. 2011b).

More recently, another species from the tertiary gene pool, namely, *C. volubilis*, was crossed with pigeonpea. In F_2 generation, extra short duration lines were recovered in 2011. 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 Season of 2012 and were found to retain the trait. Dwarf growth habit coupled with determinate and semi-determinate plants was observed. In the determinate types, the number of pods per inflorescence and the number of inflorescence were more than that observed in the extra early and determinate cultivar MN5 (Sandhya Srikanth and Mallikarjuna N, unpublished data).

7.5.4 Quaternary Gene Pool

There are 11 related genera, namely, *Rhynchosia*, *Flemingia*, *Dunbaria*, *Eriosema*, *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 (Drabu et al. 2011), 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 in 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 to get rid of unwanted constituents (Murthy and Emmannuel 2011). 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), RBC, and WBC counts 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 until now. 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 (Mallikarjuna N and Varshney R unpublished data). Although the initial process of crossing *Rhynchosia* with pigeonpea 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

Advanced backcross quantitative trait locus detection method abbreviated as AB-QTL increases the efficiency of identifying and transferring beneficial alleles from exotic germplasm (Tanksley and Nelson 1996). In this method, instead of using traditional F_2 or RIL mapping populations, it 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 BC_2 or BC_3 generations, it may be possible to detect dominant, partially dominant, overdominant, 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 selfing. 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) and groundnut (Chap. 8, this volume). Initial screening efforts have shown that AB-QTL lines have resistance to pod borers, *Phytophthora* blight, high yield, and a few other desirable traits.

7.7 Diversity in Expression of Traits Due to Alien Introgression

7.7.1 Segregation of Traits Following Classical Inheritance Pattern

Wild relatives from the secondary gene pool cross with cultigen following the Mendelian pattern of inheritance. This meant the F_1 produced broadly showed the expression of both the parental species in the ratio of 1:1. When the F_1 was selfed, the progeny lines segregated to traits in the ratio of 3:1, again following the Mendelian pattern of segregation. Similar results were observed when a tertiary gene pool species *C. platycarpus* was crossed with the cultigen (Mallikarjuna et al. 2011b). DArT analysis of the BC_4F_1 lines, where the recurrent parent was the cultigen, showed that it followed the Mendelian pattern of inheritance having approximately 94 % percent C. *Cajan* genome and the remaining of C. *platycarpus* (Mallikarjuna et al. 2011b).

7.7.2 Segregation Pattern of Genomic Dominance

C. volubilis, a wild relative in the tertiary gene pool of pigeonpea, produced F_1 hybrids when crossed with the cultigen. The F_1 hybrid showed traits of both the parental species of both *C. volubilis* and the cultigen, and the hybridity was further confirmed by SSR analysis (Sandhya Srikanth and Mallikarjuna N, unpublished data). F_1 hybrid was selfed to produce F_2 progeny lines. All the plants from F_2 onward showed genomic disequilibrium by resembling the cultigen with respect to morphological traits. None of the plants had any morphological traits or characters of *C. volubilis*. Molecular analysis of F_2 plants confirmed that they resembled the cultigen. Such a phenomenon has not been observed in pigeonpea wide crosses using compatible wild relatives from the secondary gene pool (Mallikarjuna and Saxena 2002; Saxena et al. 2010). Genomic asymmetry was observed in the present cross as distantly related genomes of *Cajanus*, i.e., of cultigen and of *C. volubilis*, were brought together for the first time through hybridization. Bringing together distantly related genomes involves radical and rapid mode of speciation by means of interspecific hybridization. It has been observed in wheat that, when different genomes were brought together, there was predominance of one genome over the others (Flagel et al. 2009; Rapp et al. 2009). In wheat A and B genome hybrids, B genome exhibited more or higher marker polymorphism than the A genome (Chao et al. 1989). Genome-wide transcriptome analysis in synthetic *Arabidopsis* allotetraploid showed that expression patterns from one genome could be dominant over the other (Wang et al. 2006a, b). Pumphrey et al. (2009) observed that some of the genes were similar to one of the parental genomes in synthetic hexaploid wheat. In the present investigation too, predominant expression of one of the parental genomes over the other was observed, and this can be explained taking examples of wheat, *Arabidopsis*, etc., that when distantly related genomes are brought together, there is silencing of the expression of the other genome completely or partially, although the DNA from the other parent is present, at least for many of the morphological traits female parental genome expression is obvious. Genome asymmetry has been observed not only for the expression of morphological traits but for other important traits in a few crops when different genomes are brought together by hybridization. Genome asymmetry in the control of storage proteins has been observed in wheat (Levy et al. 1988). In *Gossypium hirsutum*, genome asymmetry was found in the accumulation of seed storage proteins (Hu et al. 2011). Genome asymmetry in the control of agronomic, disease, and pest resistance traits has also been observed in wheat (Feldman et al. 2012). There were unsuccessful attempts in the past to cross pigeonpea with *C. volubilis* pollen (Pundir and Singh 1985). This is the first report of successful interspecific hybridization between pigeonpea and *C. volubilis*. Morphological traits of the F_1 hybrid were more skewed toward the female parent, and such phenomenon is not new when distant genomes are made to come together through wide hybridization. *C. volubilis* is a wild relative of pigeonpea placed in its tertiary gene pool (Mallikarjuna et al. 2011a; Bohra et al. 2010). Genomic studies have also shown its distant relationship with cultivated pigeonpea (Punguluri et al. 2007). Genome-wide transcription analysis in synthetic *Arabidopsis* allotetraploid showed that expression patterns from one genome could be dominant over the other genome (Wang et al. 2006a, b). Pumphrey et al. (2009) found that a small percentage of hybrids between wheat and synthetic hexaploids were similar to one of the parents. We report for the first time in pigeonpea that such a phenomenon is taking place in the hybrid between *C. cajan* (cultivated pigeonpea) and *C. volubilis* with the morphology of the F_2 hybrids skewed toward the female parent. Genetic control in storage proteins has been observed in allopolyploid wheat. Galili and Feldman (1984) showed that inactivation of an endosperm protein is brought about by an intergenomic suppression. Wheat genome-driven control of some agronomic, pest, and disease resistance was observed in wheat. Peng et al. (2000) observed that the R-gene cluster in the B genome of wheat and high marker clustering in the B genome than the A genome are the result of the expression of genome asymmetry. The ability of one genome to suppress the activity of genes in another in newly formed hybrids with different genomes may be to prevent defective organ formation/phenotype.

7.8 Conclusions

The synthesis of the review article shows the state-of-the-art information on experiments to broaden the genetic base of pigeonpea, elevating the crop to a trendsetting legume. Firstly, its genome sequence became available and now with interspecific and intergeneric hybrids utilizing wild relatives from secondary, tertiary, and quaternary gene pools is a path-breaking research. Concerted efforts might yield many more intergeneric crosses utilizing many more not only *Rhynchosia* species but with other genera such as *Flemingia*, *Dunbaria*, etc. At present there are 230 *Rhynchosia* species reported, and many of them have useful traits of interest. The need of the time is the committed research to exploit this vast gene pool with a major effort to cross many more species of *Cajanus* and utilize other related genera too. The results of the present investigation open new vistas in wide crosses research in pigeonpea. No other food legume crop has been investigated for alien introgression and succeeded in crossing wild relatives from all the gene pools, namely, secondary, tertiary, and quaternary. 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, 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 trendsetter. 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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