



Interspecific hybridization to introduce useful genetic variability for pigeonpea improvement

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Abstract

Pigeonpea (*Cajanus cajan* (L.) Millspaugh) is an important grain legume grown in tropical and subtropical regions of the world. Narrow genetic base coupled with low levels of resistance against important biotic/abiotic stresses in cultivated pigeonpea is the major constraint affecting its production and productivity globally. Wild *Cajanus* species are the reservoir of many important genes including resistance/tolerance to diseases, insect-pests and drought, and good agronomic traits and can be utilized to improve the crop cultivars, enrich variability, and broaden the genetic base. Utilization of wild *Cajanus* species has contributed for the development of cytoplasmic male sterility (CMS) systems for pigeonpea improvement. Pre-breeding populations involving promising wild *Cajanus* accessions belonging to secondary and tertiary gene pools as donors and popular pigeonpea cultivars as recipients were developed for enriching variability for pigeonpea improvement. Considerable variability was observed in these populations for morpho-agronomic traits and for biotic stresses. Two advanced backcross populations derived from wild *Cajanus* species are being genotyped to identify QTLs associated with agronomic traits for further deployment in pigeonpea improvement programs. Agronomically desirable and disease resistant introgression lines have been identified and shared with breeding programs for developing new high-yielding and climate-resilient pigeonpea cultivars with a broad genetic base.

Key words: *Cajanus*, pre-breeding, cytoplasmic male sterility (CMS), wild species, interspecific hybridization

Introduction

Pigeonpea [*Cajanus cajan* (L.) Millspaugh], an important grain legume crop, is cultivated in tropical and subtropical regions of the world between 30°N and 30°S latitude. It is mostly grown in Asia, Africa, and

Americas on 7.03 million hectares (m ha) area with an annual production of 4.89 million metric tons, and productivity of 695 kg ha⁻¹ (FAO 2014). The pigeonpea is widely grown in Asia which accounts for about 89% of the global pigeonpea area and ~80% of global pigeonpea production (Fig. 1). Major growing countries in this region are India (5.60mha), Myanmar (611,600 ha) and Nepal (17,006 ha). India alone contributes for about 80% area and over 67% global pigeonpea production. Africa, including major pigeonpea growing countries such as Kenya (276,124 ha), United Republic of Tanzania (250,509 ha), and Malawi (81,753 ha) accounts for over 9% of the global area and about 18% of the global production. The Americas produce over 2% of the total pigeonpea of the world (Fig. 1). It is primarily grown as a food crop and is consumed in a variety of forms such as the dry whole seed and dehulled, and split seed (dal) are used for cooking various dishes whereas immature tender green seeds and pods are also consumed fresh as a green vegetable. Besides food crop, it can also be used as forage, fodder, fuel and medicine. Besides pods and leaves, dry stems of pigeonpea are used for fuel, thatching and baskets making, etc. The plants are also used to culture the lac-producing insect. Pigeonpea has a deep root system which helps to withstand drought, and is grown on mountain slopes to bind the soil to reduce soil erosion. The plant has the ability to fix atmospheric nitrogen and in a cropping season, the plants fix about 40 kg ha⁻¹ atmospheric nitrogen. It also adds valuable organic matter to the soil through fallen leaves (up to 3.1 t ha⁻¹ of leaf dry matter) (Rupela et al. 2004). Its roots help in releasing soil-bound phosphorus to make it available for plant growth. Pigeonpea seed protein content (on average

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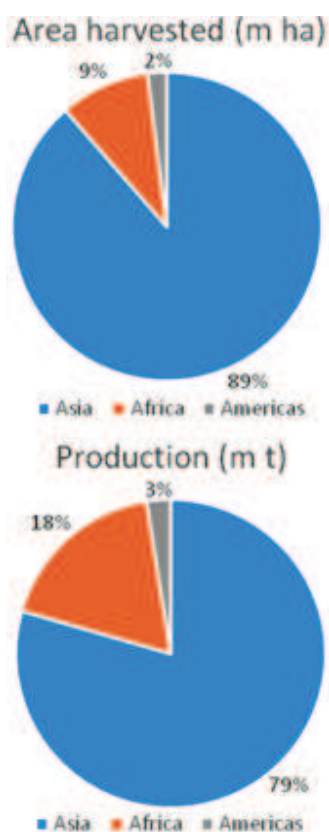


Fig. 1. Per cent contribution of different regions towards global pigeonpea area and production in 2014

approximately 21%) compares well with that of other important grain legumes. Owing to several unique characteristics and benefits, pigeonpea has become an ideal crop for sustainable agriculture systems in rainfed areas.

A large temporal variation for maturity (90-300 days) exists in pigeonpea, and is broadly categorized into different maturity groups: super-early (matures in < 100 days), extra-early (mature in 100-120 days), early (120-140 days), mid-early (matures in 140-160 days), medium (160-180 days) and long duration (>180 days). Each group is suited to a particular agro-ecosystem, which is defined by altitude, temperatures, latitude and day length. Due to short cropping seasons, extra-short and short duration varieties have potential for their inclusion as sole crop into rotation as an alternative to rice within the rice-wheat systems of the Indo-Gangetic Plains in Asia, especially during periods of water shortages, price incentives and problems of soil fertility.

Pigeonpea production is affected by several biotic

and abiotic constraints and their severity varies across geographic regions. For example, diseases such as sterility mosaic, fusarium wilt, *Phytophthora blight*, *Macrophomina* root rot and stem canker, and alternaria blight cause considerable yield losses in the Indian sub-continent; wilt and *Cercospora* leaf spot in eastern Africa; and witches' broom in the Caribbean and Central America. Besides diseases, several insect-pests also cause significant yield losses in pigeonpea. The pod damaging insects (pod borers and pod fly) cause significant yield losses in pigeonpea and therefore, are the most important pests on this crop. Among abiotic stresses, water logging, salinity and frost/cold are important constraint limiting pigeonpea production and productivity globally.

Like other grain legumes, pigeonpea also has a narrow genetic base and high levels of resistance/tolerance to important biotic/abiotic stresses are not available in the cultivated gene pool. This necessitates the exploitation of new sources of variability available in wild type germplasm to develop new cultivars with a broad genetic base.

Diversity in genus *Cajanus*

Pigeonpea is a diploid ($2n=2x=22$), often-cross pollinated crop with an insect-aided natural out-crossing ranging from 20 to 70% (Saxena et al. 1990) with. It belongs to the family *Leguminosae*, sub-family *Papilionoideae*, tribe *Phaseoleae*, and the subtribe *Cajaninae*. Currently, 11 genera are grouped under the subtribe *Cajaninae*, including *Cajanus*, *Rhynchosia* Lour., *Eriosema* (DC.), G. Don, *Dunbaria*, W. & A. and *Flemingia* Roxb. ex Aiton and the cultivated pigeonpea, *C. cajan* is the only domesticated species in *Cajaninae*. Sufficient genetic variability is present in the genus *Cajanus* for pigeonpea improvement as it comprised of 18 species from Asia, 15 species from Australia, and one species from West Africa. Of these, 13 are found only in Australia, 8 in the Indian subcontinent, 1 in West Africa, and remaining occurring in more than one country.

Based on the crossability relationships between cultivated pigeonpea and its wild relatives, van der Maesen (1990) placed cultivated pigeonpea and its landraces in primary genepool; all 10 cross-compatible species *C. acutifolius*, *C. albicans*, *C. cajanifolius*, *C. lanceolatus*, *C. latisepalus*, *C. lineatus*, *C. reticulatus*, *C. scarabaeoides*, *C. sericeus* and *C. trinervius* in secondary genepool; and the cross-incompatible species *C. goensis*, *C. heynei*, *C. kerstingii*, *C. mollis*,

C. platycarpus, *C. rugosus*, *C. volubilis*, and other *Cajaniinae* such as *Rhynchosia* Lour., *Dunbaria* W. and A., *Eriosema* (DC.) Reichenb in the tertiary genepool.

Importance of wild *Cajanus* species

In RS Paroda gene bank at ICRISAT, Patancheru, India, about 13,220 accessions of cultivated pigeonpea and 562 accessions of wild species originated/collected from 60 countries are conserved for use in pigeonpea improvement programs. Compared to cultivated pigeonpea, wild species are the reservoir of many useful genes/alleles as they have evolved under natural selection to survive climate extremes. Evaluation of wild *Cajanus* species have identified accessions having very high level of resistance/tolerance to various stresses such as wild *Cajanus* species especially, *C. scarabaeoides*, *C. acutifolius*, *C. platycarpus*, *C. reticulatus*, *C. sericeus*, and *C. albicans* having resistance to pod borer, *Helicoverpa armigera* (Rao et al. 2003; Sujana et al. 2008; Sharma et al. 2009) and wild *Cajanus* accessions as new sources of resistance to *Alternaria* blight (Sharma et al. 1987), phytophthora blight (Reddy et al. 1996; Rao et al. 2003; Mallikarjuna et al. 2005), sterility mosaic disease (SMD; Kulkarni et al. 2003; Rao et al. 2003; Kumar et al. 2005), pod fly (Saxena et al. 1990; Rao et al. 2003) pod fly and wasps (Sharma et al. 2003), root-knot, and nematodes (Sharma et al. 1993a, b; Sharma, 1995; Rao et al. 2003), and tolerance to salinity (Subbarao 1988; Subbarao et al. 1991; Rao et al. 2003; Srivastava et al. 2006), drought (Rao et al. 2003), and photoperiod insensitivity (Rao et al. 2003). Potential sources of resistance for bruchids (*Callosobrochus maculatus*) have also been identified in *C. scarabaeoides*, *C. acutifolius*, and *C. platycarpus* (Jadhav et al. 2012). Besides resistance/tolerance to important biotic/abiotic stresses, wild *Cajanus* species with agronomically desirable traits such as early flowering, high seed number per pod, and high seed protein content (Upadhyaya et al. 2013) have also been identified. These wild species hold a great potential for the genetic amelioration of pigeonpea.

Utilization of wild *Cajanus* species for pigeonpea improvement

It is well known that wild species harbor high levels of genetic diversity to survive against various biotic/abiotic stresses, especially under changing climatic conditions and thus hold a great potential for crop improvement. Though the potential of wild *Cajanus* species for pigeonpea improvement is well known, their frequent utilization in breeding programs is hindered

due to the linkage drag and different incompatibility barriers between cultivated pigeonpea and wild *Cajanus* species. For enriching the variability in primary genepool, pre-breeding provides a unique opportunity by exploiting wild species and cultivated germplasm, and will ensure continuous supply of new and useful genetic variability into the breeding pipelines to develop new cultivars having high levels of resistance and broad genetic base (Sharma et al. 2013). At ICRISAT, systematic pre-breeding efforts have been made which have contributed significantly for pigeonpea improvement. The major achievements include:

Development of cytoplasmic-nuclear male sterility (CMS) system

The most significant achievement of utilizing wild *Cajanus* species in hybridization program is the development of unique cytoplasmic-nuclear male sterility system (CMS). Eight unique CMS systems have been developed with cytoplasm derived from wild *Cajanus* species belonging to secondary and tertiary genepool species. These include A₁ cytoplasm derived from secondary genepool species, *C. sericeus* (Ariyanayagam et al. 1995), A₂ cytoplasm derived from secondary genepool species, *C. scarabaeoides* (Tikka et al. 1997; Saxena and Kumar 2003), A₃ cytoplasm derived from tertiary genepool species, *C. volubilis* (Wanjari et al. 2001), A₄ cytoplasm derived from secondary genepool species, *C. cajanifolius* (Saxena et al. 2005), A₅ cytoplasm derived from secondary genepool species, *C. acutifolius* (Mallikarjuna and Saxena 2005), A₆ cytoplasm derived from secondary genepool species *C. lineatus* (Saxena et al. 2010a), A₇ CMS system derived from tertiary genepool species *C. platycarpus*, and A₈ CMS system derived from *C. reticulatus*.

Introgression of useful traits

Efforts have been made to introgress useful traits from wild *Cajanus* species belonging to secondary and tertiary genepool into popular pigeonpea cultivars. The major objective of these activities is to develop new genepools with high frequency of useful genes, wider adaptability, and a broad genetic base for resistance/tolerance to important biotic/abiotic stresses as well as for agronomic and nutrition-related traits. Further, to minimize the linkage drag associated with utilizing wild species in crop improvement programs, efforts were made to develop advanced backcross populations. Using wild *Cajanus* species, viable hybrids have been produced between pigeonpea and *C. platycarpus* (Mallikarjuna and Moss 1995), *C.*

Table 1. Wild *Cajanus* species used as promising donors for creating new genetic variability for pigeonpea improvement at ICRISAT, Patancheru

Species	Useful traits
Secondary gene pool	
<i>C. cajanifolius</i>	Resistance for alternaria blight, and high seed protein (>30%)
<i>C. albicans</i>	Resistance/tolerance for alternaria blight, sterility mosaic disease, pod borer (<i>Helicoverpa armigera</i>), salinity, high seed number per pod (>6) and high seed protein (>30%)
<i>C. scarabaeoides</i>	Resistance/tolerance for alternaria blight, sterility mosaic disease, pod borer (<i>Helicoverpa armigera</i>), cyst nematode, salinity, early flowering (51-118 days) and high seed protein
<i>C. sericeus</i>	Resistance/tolerance for alternaria blight, phytophthora blight, pod borer (<i>Helicoverpa armigera</i>), and salinity
<i>C. acutifolius</i>	Resistance for pod borer (<i>Helicoverpa armigera</i>)
Tertiary gene pool	
<i>C. volubilis</i>	Resistance for Alternaria blight
<i>C. platycarpus</i>	Resistance/tolerance for alternaria blight, phytophthora blight, salinity, photoperiod insensitivity, super-early flowering (34-40 days) and high seed protein (>30%)

reticulatus var. *grandifolius* (Reddy et al. 2001), *C. acutifolius* (Mallikarjuna and Saxena 2002), and *C. albicans* (Subbarao et al. 1990). Using cross-compatible secondary genepool species, *C. cajanifolius* (ICPW 29), *C. acutifolius* (ICPW 12 and ICPW 004), *C. scarabaeoides* (ICPW 281), and cross-incompatible tertiary genepool species, *C. platycarpus* (ICPW 68), and *C. volubilis* (ICPW 173) having useful traits such as tolerance to salinity, pod borer resistance, phytophthora blight resistance, extra-early flowering and maturity and photoperiod-insensitivity, (Srivastava et al. 2006; Sujana et al. 2008; Mallikarjuna et al. 2005, 2011; Jadhav et al. 2012) (Table 1), and two pigeonpea cultivars (ICPL 87119 and ICPL 85010), pre-breeding populations have been generated at ICRISAT, Patancheru, India. ICPL 87119 (Asha) is a medium-duration and ICPL 85010 is an early-duration pigeonpea variety, both cultivated in India. Embryo rescue technique was used to generate population

using *C. platycarpus* (Mallikarjuna and Moss 1995, Mallikarjuna et al. 2006).

Enriching variability for agronomic traits

Preliminary evaluation of two advanced generation populations derived from a cross involving *C. acutifolius* (ICPL 85010 × ICPW 004) and *C. platycarpus* (ICPW 68 × ICPL 85010) consisting of 68 and 138 introgression lines (ILs), respectively for morpho-agronomic traits revealed considerable variability for days to flowering, number of branches per plant as well as for pod and seed traits (Table 2).

Table 2. Variability for different agronomic traits in advanced backcross populations derived from *C. acutifolius* and *C. platycarpus* evaluated during 2014 rainy season, ICRISAT, Patancheru

Traits	Range	
	<i>C. acutifolius</i> derived population	<i>C. platycarpus</i> derived population
Days to first flowering	88-132	71-121
Days to 50% flowering	91-137	74-127
Plant height (cm)	145.8-211.6	124.0-230.0
Primary br. (no.)	8-28	10-40
Secondary br. (no.)	3-30	4-52
Tertiary br. (no.)	0-7	0-22
Pods per plant (no.)	35-267	27-245
Pod weight/plant (g)	21-98	8-88
100-seed weight	6.2-21.1	6.2-13.2

In both populations, ILs having early maturity, and high pod number have been identified. Promising ILs having high number of pods per plant, seeds per pod and 100-seed weight (>20.0 g) have been identified from the population derived from ICPL 85010 × ICPW 004 cross (Fig. 2; Sharma and Upadhyaya, 2016).

Using *C. cajanifolius* accession, ICPW 29, and *C. acutifolius* accession, ICPW 12 as donors and pigeonpea variety ICPL 87119 as recipient, two advanced backcross populations consisting of 183 (derived from ICPL 87119 × ICPW 29) and 149 (derived from ICPL 87119 × ICPW 12) ILs were developed. Considerable variability for morpho-agronomic traits was observed in these two populations (data not given). Based on the overall plant aspect score, especially focusing on maturity duration, erect plant type, and high number of pods per plant, promising plants were selected from these two populations. The promising

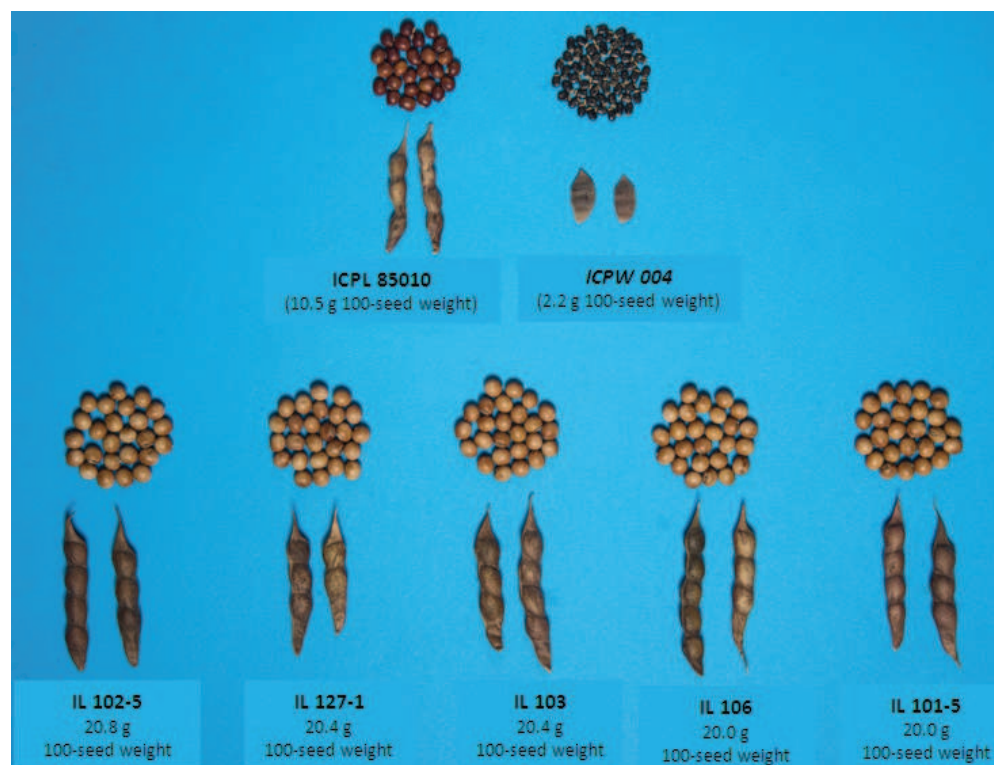


Fig. 2. Introgression lines (ILs) derived from *C. acutifolius* having variations for pod traits and high 100-seed weight

selected ILs were grouped into different maturity durations (early duration, mid-early duration and medium duration) and are being evaluated with the best available pigeonpea cultivars for yield-contributing traits to identify high-yielding ILs in different maturity groups.

In the advanced segregation population derived from *C. volubilis*, extra-early maturing ILs having dwarf plant height and determinate growth habit have been developed (Fig. 3). These ILs hold potential in developing extra-short and short-duration pigeonpea varieties, which fit well in various cropping systems, especially in pigeonpea-wheat rotation in the rice-wheat cropping system in North-west India as well as in rice-fallows in lower latitudes.

Nutrition-related traits

Utilization of wild *Cajanus* species has also contributed significantly towards the improvement of nutritional quality of cultivated pigeonpea. Some wild *Cajanus* species namely *C. scarabaeoides*, *C. sericeus*, *C. albicans*, *C. crassus*, *C. platycarpus*, and *C. cajanifolius* have higher seed protein content (average 28.3%) compared to pigeonpea cultivars (24.6%) (Singh and Jambunathan 1981). A high protein line, ICPL 87162

was developed from the cross *C. cajan* x *C. scarabaeoides* (Reddy et al. 1997). This line contains 30 to 34% protein content compared to control cultivar (23% protein). Breeding lines with high protein content have also been developed from *C. sericeus*, *C. albicans*, and *C. scarabaeoides*. Utilization of wild *Cajanus* species has resulted in the development of several lines such as HPL 2, HPL 7, HPL 40 and HPL 51 having high protein and high seed weight (Saxena et al. 1987).



Fig. 3. Extra-early maturing and dwarf introgression lines (ILs) derived from *C. volubilis* at ICRISAT, Patancheru

Disease resistance

Screening of two advanced backcross populations derived from *C. acutifolius* (ICPL 85010 x ICPW 004) and *C. platycarpus* (ICPW 68 x ICPL 85010) crosses

for sterility mosaic disease and wilt under field sick-plot at ICRISAT, Patancheru, India resulted in the identification of 15 ILs derived from *C. acutifolius* and two ILs from *C. platycarpus* having combined resistance against SMD and wilt. These ILs will provide new sources of SMD and wilt resistance derived from wild *Cajanus* species for utilization in breeding programs to develop new cultivars with broad genetic base.

Insect-pest resistance

Evaluation of wild *Cajanus* species has identified accessions/species having high levels of antixenosis for oviposition (*Cajanus acutifolius*, and *C. sericeus*), high expressions of antibiosis (*C. acutifolius*), high density of type 'C' and 'D' trichomes (*C. scarabaeoides*, and *C. sericeus*) and low amounts of sugars and high amounts of tannins and polyphenols (*C. albicans* and *C. acutifolius*) (Sharma et al. 2009). These species were used in the crossing program with an objective to combine these different components governing pod borer resistance into common genetic background. Using four wild species, *Cajanus acutifolius*, *C. sericeus*, *C. scarabaeoides*, and *C. albicans* and two pigeonpea cultivars, ICPL 87119, and ICP 8863, eight interspecific F_1 crosses were generated. The F_1 crosses generated using a common cultivar were further crossed amongst themselves to generate two 4-way F_1 crosses in order to combine different components of pod borer resistance from different species into a common genetic background. The 4-way F_1 crosses were further backcrossed with the respective cultivated recipient parent to recover the genetic background of cultivated types. At present, two 4-way BC_1F_1 populations are being advanced further to develop ILs with high levels of resistance against pod borer.

Identification of marker-trait associations

Effective use of wild *Cajanus* species in pigeonpea improvement requires systematic surveys of accessions at the genome level, identification of adaptive alleles to environmental extremes, and incorporation of wild alleles into cultivated backgrounds for trait analysis and breeding. Advanced backcross populations derived from ICPL 87119 × ICPW 12, and ICPL 87119 × ICPW 29 crosses having small segments introgressed from wild species into the genetic background of cultivated types provide valuable resource for such studies. At ICRISAT, these two mapping populations are being used for high density genotyping to identify QTLs introgressed from wild

Cajanus species, *C. acutifolius* and *C. cajanifolius* for important agronomic traits. Identification and utilization of these QTLs will accelerate pigeonpea improvement programs.

Impact of utilizing wild species for pigeonpea improvement

Utilization of wild *Cajanus* species has contributed significantly for pigeonpea improvement through the development of CMS system and introgression of useful variability for developing new cultivars with broad genetic base. Development of CMS systems derived from wild species have changed the scenario of pigeonpea cultivation in India and elsewhere. The A_4 sterility system, which is the only system having stability across environments with good fertility restoration, was used to develop the world's first commercial pigeonpea hybrid, ICPH 2671 (Saxena et al. 2013). Significant genetic variability for morpho-agronomic traits has been generated through interspecific hybridization and the promising ILs having high levels of disease resistance and good agronomic performance have been shared with breeders at ICRISAT and NARS partners for evaluation across locations to identify stable high yielding ILs and release the most promising ILs as variety/ies for specific regions as well as use as new sources of genetic variability in breeding programs for developing new cultivars with a broad genetic base. Based on the good agronomic performance, recently, three ILs, ICPL 15028 and ICPL 15036 (both derived from *C. acutifolius* ICPW 12) in mid-early duration group, and ICPL 15084 (derived from *C. cajanifolius* ICPW 29) in medium-duration group have been included in the Initial Varietal Testing (IVT) of AICRP on Pigeonpea across different locations in India during 2016 rainy season.

Overall, it can be concluded that utilization of wild *Cajanus* species have contributed significantly for pigeonpea improvement. The development of CMS systems derived from wild species has paved way for the development of hybrid pigeonpea, which has revolutionized pigeonpea cultivation in India and elsewhere. Besides this, the development of pre-breeding populations using pigeonpea cultivars as recipients and wild *Cajanus* species as donors have created new and diverse genetic variability through the introgression of useful traits into pigeonpea cultivars. ILs having good agronomic performance and high levels of resistance against important biotic stresses have been identified and shared with NARS partners to develop new cultivars with a broad genetic

base. Systematically developed advanced backcross populations derived from wild *Cajanus* species provide valuable resource for genomic studies. Genotyping of two advanced backcross populations is in progress to identify QTLs for important agronomic traits for further deployment in pigeonpea improvement programs. Besides this, the development of backcross populations derived from complex interspecific crosses will help to improve levels of pod borer resistance by combining different components of resistance from different wild *Cajanus* species into common genetic background and would assist in developing ILs having high levels of pod borer resistance.

Declaration

The authors declare no conflict of interest.

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