

# Genetic Improvement of Pigeon Pea — A Review

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## Introduction

Pigeon pea [*Cajanus cajan* (L.) Millspaugh] is a short-lived perennial shrub that is traditionally cultivated as an annual crop in developing countries. It is an important legume crop mostly produced in Asia, Africa, Latin America, and the Caribbean region. Based on the vast natural genetic variability in local germplasm and the presence of numerous wild relatives, van der Maesen [139] concluded that India is probably its primary center of origin. Pigeon pea is a hardy, widely adapted and drought tolerant crop with a large temporal variation (90–300 days) for maturity. These traits allow its cultivation in a range of environments and cropping systems. Globally, pigeon pea is cultivated on 4.92 million hectares (Mha) with an annual production of 3.65 metric tons and productivity of 898 kg ha<sup>-1</sup> (<http://faostat.fao.org/>). In Asia, India (3.58 Mha), Myanmar (560,000 ha), China (150,000 ha), and Nepal (20,703 ha) are major pigeon pea growing countries. On the African continent, Kenya (196,261 ha), Malawi (123,000 ha), Uganda (86,000 ha), Mozambique (85,000 ha), and Tanzania (68,000 ha) grow considerable pigeon pea. The Caribbean islands and some South American countries also have considerable area devoted to growing pigeon pea. The traditional pigeon pea cultivars and landraces are long duration types grown as an intercrop with other more early maturing cereals and legumes. In addition to its main use as de-hulled split peas, its

immature green seeds and pods are also consumed fresh as a green vegetable. The crushed dry seeds are fed to animals while the green leaves form a quality fodder. In rural areas, dry stems of pigeon pea are used for fuel. In a cropping season, pigeon pea plants fix 40 kg ha<sup>-1</sup> atmospheric nitrogen [50] and add valuable organic matter to the soil through fallen leaves. Its roots help in releasing soil-bound phosphorus to make it available for plant growth [2]. With so many benefits at low cost, pigeon pea has become an ideal crop for sustainable agriculture systems in rain-dependent areas.

## Overview of Genetic Improvement Programs in Different Countries

### Asia

In comparison to other pigeon pea growing countries the research and development programs in India are extensive. The first scientific pigeon pea breeding effort in India was made by Shaw [125] who described morphological and agronomic traits of 86 elite field collections. Of these, some accessions were found to have high levels of resistance to *Fusarium* wilt disease. Similar efforts were made by Mahata and Dave [54] who identified a few elite early and late maturing high yielding types. Such crop improvement activities involving field collections and their evaluation continued for more than two decades without having a significant impact on productivity. Considering the high importance of pigeon pea in India, the Indian Council of Agricultural Research (ICAR) started an All India Coordinated Pigeon Pea Improvement Project in 1965. Under this mega program, crop improvement activities were launched simultaneously at 31 research centers in diverse agro-ecological zones [76]. The major objectives of this project were to assemble pigeon pea germplasm, identify sources of disease and insect resistances and to develop high

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yielding varieties in early, medium, and long maturity groups. To achieve these goals, most major breeding methods recommended for breeding self-pollinated crops were used. The most successful method turned out to be the pure lines selection from germplasm and segregating populations derived from hybridization. Thus far, 64 pure line varieties have been released from this project. Among these, 29 were selections from germplasm collected from farmers' fields, 30 varieties were bred from single or double crosses, and five were mutants [130]. The impact of these breeding efforts has been impressive with a 56% increase in area and 54% increase in total grain production, however, these efforts failed to enhance productivity of the crop.

Pigeon pea was introduced in China about 1,500 years ago [147]. In Yunnan and other southern provinces pigeon pea was grown for rearing lac insect (*Kerria lacca* Kerr.) to produce lac resin. By 1989, commercial cultivation of pigeon pea ceased due to the arrival of synthetic resins in the market. Cultivation was revived in 1999 with the introduction of new breeding materials from ICRISAT to control soil erosion and provide nutritive fodder during dry periods. Recently, Chinese scientists have started producing CMS-based hybrid pigeon pea seeds for export to India (Li Zenghong, personal communication). Although pigeon pea is an important crop in Nepal, their breeding program is mainly based on selection from landraces and introductions from ICRISAT. Long-duration varieties such as Bahar and Rampur Rahar are commonly grown. In Myanmar, pigeon pea area has increased exponentially and this crop is grown exclusively for export. Local landraces are generally grown and selections from these have been released for cultivation. In the Philippines, long-duration types are grown as a back yard crop as a vegetable. Recently an early maturing variety ICPL 88039 has become popular for sowing in rice-fallow. The potential of this variety for the Philippines is high (Heraldo Layaoen, personal communication).

#### *Southern and Eastern Africa*

The first pigeon pea breeding program in south and east African region began in 1968 at Makerere University in Uganda. The main objective of this program was to breed grain type varieties with short maturity [43]. The crop improvement activities at this station started by evaluating 5,400 germplasm collected from India, the Caribbean, the Philippines and identifying promising single plants for progeny row evaluation and selection. The progenies were primarily grouped on the basis of plant type and spreading and compact types were selected for low and high density cropping systems. In Uganda the pigeon pea research program was adversely affected by civil strife between 1973 and 1986.

In Kenya, pigeon pea research was initiated at the University of Nairobi in 1975 and National Dryland

Farming Centre, Katumani in 1979. Like in Uganda, most breeding activities were centered on collection, evaluation, and selection from germplasm. The first early variety released in Kenya was NPP670 that was developed through hybridization. In Tanzania, Ethiopia, Rwanda, Sudan, Somalia, and Burundi the pigeon pea improvement program started with germplasm introduction from ICRISAT and neighboring countries. Pure lines such as NPP610, RK101, TRT201 were identified for cultivation [68]. Scientists in Kenya also initiated research on population improvement by using the partially out-crossing nature of the crop with moderate success.

Considering the importance of pigeon pea in African agriculture, ICRISAT recently started a regional pigeon pea improvement program with assistance from the African Development Bank and NARS. In this program, emphasis was given to breeding high yielding, disease resistant, long duration varieties for deep soils and short maturing types for drought prone areas. The first early maturing variety ICPL 87091 was released simultaneously in Kenya, Malawi, Uganda, and Tanzania. A total of nine varieties were released under this program. The releases included four varieties in Malawi, three in Kenya, three in Tanzania, two in Uganda, and one in Mozambique. In eastern Kenya, about 20% of the farmers have adopted new pigeon pea varieties. Farmers also adopted new medium maturing pigeon pea varieties like ICEAP 00554 and 00557 both for grain and green vegetable purposes. In Tanzania, about 50% of the farmers in the Babi district adopted new varieties and the pigeon pea production area expanded to reach the neighboring districts of Karatu and Mbulu (SN Silim, personal communication). In some areas, farmers are adopting the long duration compact growth habit variety ICEAP 0053 to be grown in a maize intercropping system. The adoption of the long duration, *Fusarium* wilt resistant and consumer/ market preferred variety ICEAP 00040 in northern and central Tanzania, Kenya, and Malawi has resulted in increased grain yields and lowered production costs compared to local genotypes. These initiatives have been very effective; between 1976 and 2006 pigeon pea in southern and eastern Africa has recorded 133% increase in area (0.24 to 0.56 Mha) and 178% increase in production (0.14 to 0.3 metric ton).

#### *Southern and Central America and the Caribbean Region*

The Caribbean region constitutes a chain of island countries extending from Trinidad in the south to Jamaica in the north. In this region Dominican Republic is the highest pigeon pea growing country (17,000 ha) with an average yield of 945 kg ha<sup>-1</sup> [31]. The other pigeon pea growing countries are Panama (4,800 ha), Venezuela (3,344 ha), Jamaica 1,100 ha), Trinidad and Tobago (400 ha), Puerto

Rico (272 ha), and Grenada (520 ha). Pigeon pea in these areas is essentially a small farmer's enterprise but it is an important crop at the national level. Pigeon pea is generally grown as intercrop for consumption as fresh peas.

Research on pigeon pea in the Caribbean started in 1934 at the Imperial College of Tropical Agriculture to develop high yielding varieties with resistance to rust and jassids. The first variety released from this program, 'Prensado', was early in maturity and determinate in growth habit. This variety did not become popular among farmers [11]. Subsequently, three additional varieties 'Tobago', St. Augustine', and 'Lasiba', which were similar to traditional types in their phenology, were released and are still grown by farmers. In the mid-sixties selections from breeding populations were made which produced varieties having good quality grain and high yield under intercrop situations [11]. In addition to routine research on diseases, insects, and agronomic traits, the important breeding objective for the Caribbean region was to develop varieties that can provide year-round fresh pods for marketing. To achieve this, a photo-insensitive lines was partially successful. Spence and Williams [133] developed a cropping system for sowing pigeon pea around the shortest day of the year that not only induced agronomic dwarfing and early flowering, but also ensured availability of fresh pods for extended periods. In spite of extensive research conducted in the Caribbean, the prominent commercial cultivars include those developed in 1934 and 1956 [10].

In the Dominican Republic, pigeon pea is mainly grown by small farmers and about 80% of the annual harvest is exported in the form of canned or frozen green peas. Growth of pigeon pea cultivation in the Dominican Republic has been mainly due to the relocation of canning plants from Puerto Rico. According to Mansfield [59] information about pigeon pea cultivars in the Dominican Republic is unclear; farmers generally grow a mixture of varieties such as, 'Kaki' and 'Saragateado' which have been used for a long time for the canning industry in Puerto Rico. In general, four pigeon pea varieties are recognized in Dominican Republic. These are 'Kaki', 'Pinto Villalba', 'UASD', and 'Year-round'. These varieties are all long podded, large and white seeded.

In Puerto Rico, pigeon pea is predominantly cultivated for canning and for the local fresh pod market. The annual farm value of the crop is over \$3 million. The main breeding objectives are to develop high yielding varieties for different maturities and suitable dwarf lines for mechanical harvesting [1]. 'Kaki' is the most popular variety in Puerto Rico [9]. 2B Bushy is another popular early maturing semi-dwarf variety. The pigeon pea breeding programs in Puerto Rico and Venezuela made fairly good progress and released a few vegetable type varieties such as 'Panameno', 'Amarillo', 'Kaki', 'Saragateado', and

'Totiempo' [85]. There have been recent releases of pigeon peas in Puerto Rico and the Dominican Republic. 'Guerrero' and 'Cortada' were released in Puerto Rico in 2000 and 'Navideño' was released in the Dominican Republic in 2005. In Guadeloupe, several lines were introduced and suitable lines were identified [28]. In Venezuela, a cultivar called 'Panameno' was released in 1972 [85].

#### *Other Countries*

In the USA, a selection from an introduction from Pakistan was grown as cultivar called 'Norman' in North Carolina and Florida [46]. This was followed by a well directed program to breed varieties for fodder purposes that was started at the University of Hawaii in 1920 and a cultivar named 'New Era' was released [62]. In 1927, the local interest in pigeon pea declined due to the introduction of new forage legumes and the expansion of sugarcane. Today, pigeon pea is seldom seen in Hawaii [48]. Three early maturing determinate pigeon pea varieties MN1, MN5, and MN8 were bred at Minnesota (45°N) for the areas having a short warm season [26]. These lines were selected from breeding materials supplied by ICRISAT. These varieties are not currently in use in the country but they served as source for earliness in the breeding program at ICRISAT (KB Saxena, unpublished data). Recently, USA interest in pigeon pea has revived for fodder purposes and considerable research is being carried out at El Reno, Oklahoma where pigeon pea is used as a summer legume having excellent fodder yields [77–79].

In Australia, pigeon pea research started in early seventies for its use as a fodder crop [3, 14]. They found that pigeon pea to be a good annual fodder but when it was used as perennial there was considerable plant mortality. In 1978, research for grain product was initiated at the University of Queensland, Brisbane. Four pigeon pea varieties, Royes, Hunt, Quantum, and Quest, were released from this program, but none of the varieties is in cultivation due to their high susceptibility to pod borers. In Fiji, where traditionally long duration pigeon pea are grown, an ICRISAT germplasm (ICP 7035) was released as 'Kamika' which is popular for both vegetable and dry seed production.

### **Special Traits of Pigeon Pea**

#### *Genetic Studies*

Relatively few genetic studies of pigeon pea agronomic traits have been conducted. Basic information on the genetics of yield and related traits such as maturity, pods per plant, and seed size, which are essential to determine the most efficient breeding approaches for genetically

improving the yield potential of the crop, have not been widely reported. A summary of pigeon pea qualitative traits and their inheritance was compiled by Saxena and Sharma [99]. Data on yield and yield related traits were limited and researches in these areas have only recently received attention. Various genetic studies on quantitative traits of pigeon pea reported are abstracted in Table 1. Sharma and Green [119] concluded that the important agronomic characters are controlled primarily by genes with additive effects. Dominance and non-additive effects were also detected for yield, plant height, and protein content. Saxena et al. [90] studied the genetic nature of yield and its components in short-duration pigeon pea. They suggested that in quantitative breeding of any crop in which phenology is sensitive to environmental influences, the interpretation of results from experiments comparing mating designs is complicated by physiological changes associated with phenological differences. They further concluded that inheritance of yield and associated characters is confounded with the pleiotropic effects of genes influencing phenology.

#### Breeding Behavior

Highest consideration in any crop improvement program is given to its natural breeding system which will determine the mating designs and selection schemes. In contrast to most legumes, pigeon pea flowers are genetically structured to promote both cross and self-pollination. The nectar present within the large bright colored flowers of pigeon pea attracts a variety of pollinating insects. While these insects are foraging on the flowers a load of fresh pollen grains becomes attached to various body parts of the insects to facilitate natural outcrossing [144]. The extent of natural outcrossing in pigeon pea varies from place to place because it is directly dependent on the population of pollinating vectors. However, on average, natural outcrossing is around 20% [97] which is large enough

to cause genetic contamination of parental lines and selections. Sharma and Green [119] estimated that with 20% effective outcrossing, the heterozygosity expected at equilibrium is approximately 15.75%, which produces progenies less homozygous than an  $F_4$  population with complete selfing. Pigeon pea breeders always encounter difficulties in pedigree selection due to natural outcrossing. To overcome the negative effects of outcrossing, breeders often resort to artificial means to self plants by using muslin cloth bags or nylon nets to exclude pollinating insects. The other important consequence of natural outcrossing is that most landraces are heterogeneous and/or heterozygous and exhibit considerable variation. The high level of outcrossing necessitates selfing of parental lines for at least two to three generations before using them in hybridization programs. Pigeon pea breeders at ICRISAT, however, utilized the limited natural outcrossing to enhance yield potential of pigeon pea by developing an efficient hybrid breeding technology (see [Breaking Yield Plateau Through Hybrid Breeding](#)).

#### Maturity Range

Pigeon pea germplasm possesses a wide temporal range (90–300 days) for maturity and this variation is almost continuous in nature. Based on days to 50% flowering, Green et al. [34] classified pigeon pea types into ten maturity groups. Since maturity plays an important role in pigeon pea adaptation, this classification helps in selecting parents in crop breeding programs. This classification of maturity groups may not hold true at every location since the phenology of pigeon pea plants is highly influenced by photoperiod, temperature, and their interactions. Therefore, local breeders need to know the flowering behavior of parental lines before selecting them for hybridization and implementation of appropriate selection schemes [20].

#### Photoperiod Sensitivity and Specificity of Adaptation

Pigeon pea is a quantitative short day plant with the late maturing types having a strict day-length requirement for induction of flowering. The phenological responses in pigeon pea are influenced by photoperiod and temperature that have played a major role in the evolution of the various crop production systems that have been established. The photoperiod sensitive reaction in pigeon pea germplasm is not only linked to days to flowering but also to the amount of biomass produced [142]. Sowing of photoperiod sensitive types near to the shortest day of the year generally leads to physiological dwarfing of plants so that increased plant populations are required to optimize yields [133]. In early maturing genetic materials under natural day lengths at Patancheru (17°N), up to four seed-to-seed generations can be achieved within a calendar year [103]. This contrasts with late maturing types

**Table 1** Summary of gene action for various economic traits in pigeon pea as reported in literature

Character	Gene action		
	Additive	Non-additive	Additive+ non-additive
Plant height	*	*	*
Plant width	*		*
Days to mature	*	*	*
Pods/plant		*	*
Seeds/pod	*		*
Days to flower	*		
100-seed weight	*	*	*
Seed yield	*	*	
Protein %		*	*

that would require use of an environment control facility to provide shorter daylength and high temperatures for achieving a similar rapid generation turn over.

Sensitivity of pigeon pea to photoperiod has played an important role in determining its growth and development. The traditional pigeon pea cultivars and landraces are highly sensitive to photoperiod which limit their adaptation up to 30°N and S. In pigeon pea the photoperiod response is strictly linked to its flowering. Turnbull et al. [138] studied the influence of temperature and photoperiod on floral development of pigeon pea. They identified a few day-neutral cultivars under the 24/16°C temperature regime. They also reported a significant interaction between photoperiod and temperature in determining flowering responses. The time from floral initiation to flower opening (rate of floral primordia development) varied from 40 d under an 8 h photoperiod at 24/16°C to 22 days under 16 h photoperiod at 32/34°C. Saxena [92] reported that under extended photoperiod of 16 h, three major genes PS<sub>1</sub>, PS<sub>2</sub>, and PS<sub>3</sub> control flowering in the photoperiod sensitive parent MS<sub>4</sub>A. Hierarchically, PS<sub>3</sub> over-rides the expression of PS<sub>2</sub> and PS<sub>2</sub> over-ride PS<sub>1</sub>. These studies suggest that there is a need to fully understand the influences of photoperiod and temperature on flowering in the genotypes of different maturity groups. This might help breeders to manipulate flowering of the sensitive types by adjusting pre- and post-floral initiation temperature and photoperiod conditions.

### Ratooning

Botanically, pigeon pea is a perennial plant that has excellent capacity to regenerate itself from stubble under favorable environmental conditions following harvest. The success of a ratooned or regenerated crop depends on soil moisture, temperature, genetic potential of the cultivar to regenerate, and its maturity group [91]. In properly managed early and medium maturing cultivars the flowers regenerated after first grain harvest usually set pods with potential for producing a good second grain crop, whereas in late maturing cultivars the ratooned crop does not. Under good management practices, pigeon pea scientists harvested 5,200 kg ha<sup>-1</sup> grain yield from variety ICPL 87 in three harvests [21]. The ability of varieties to ratoon is also being exploited in developing breeding populations involving parents of very diverse maturity groups. The pod set on the ratooned plants is much higher than those of non-ratooned plants due to relatively greater flower retention in the former [89].

### Nitrogen Fixation

Nitrogen fixing nodules are produced in pigeon pea by a number of rhizobial strains belonging to the ‘cowpea miscellomy’ group [8]. Nodule formation and their develop-

ment in pigeon pea are affected by various biotic and abiotic factors such as moisture, soil type, daylength, crop duration, salinity, insect damage, nutritional factors, and temperature. Most nodules are formed on the secondary roots and the majority of these are located in the top 30 cm of the soil profile. Small nodules are frequent in the 120–150 cm soil zone and may occur at even greater depths [49]. Quantification of nitrogen fixation by pigeon pea is difficult due to its long duration and deep root system. Sen [117] used the nitrogen balance method to report that long duration crops could fix up to 200 kg N ha<sup>-1</sup> over a period of 40 weeks. Studies conducted with an early maturing variety revealed that a subsequent crop of wheat received 40 kg N ha<sup>-1</sup> from the previous pigeon pea crop [49]. They also observed an inadequacy of symbiotic N fixation for pigeon pea production suggesting scope for nitrogen application in yield improvement. Since considerable variability exists among rhizobium strains and pigeon pea genotypes for fixing atmospheric nitrogen, it will be useful to conduct experiments to study their effects and interactions before breeding for genetic improvement of nitrogen fixation in pigeon pea [49]. The author is not aware of any such research program.

### Implications of Special Traits

Breeding research and development of pigeon pea is considered more difficult than for some other food legumes due to various crop-specific traits. The most important pigeon pea specific trait is its natural partial outcrossing that directly impacts its breeding and selection efficiency. The presence of both additive and non-additive genetic variation allows breeders to breed both high yielding pure line cultivars and hybrids. Although the natural outcrossing provides opportunity to maintain a large amount of genetic variability within and among populations, breeders have to be extra careful while involved in breeding pure line cultivars. If the selected individual plants from segregating breeding populations are not protected from pollinating insects it may result in outcrossing. This will result in a certain proportion of hybrid plants in the subsequent single plant progenies of the selections to adversely affect the genetic advance. Similarly, sufficient care must be taken to avoid genetic contamination when multiplying nucleus and breeders' seed. The recommended isolation distance for seed multiplication is 500 m. Therefore, before launching a pigeon pea improvement program one must understand the nature and potential effects of special traits on breeding outputs.

### Breeding Methods

Pigeon pea is unique in having both self- and cross-pollination systems operating simultaneously under natural

conditions. Historically, pigeon pea breeders ignored the consequences of out-crossing on selection efficiency and used breeding procedures outlined for self-pollinated crops. This has limited breeding success towards enhancing quantitative traits such as seed yield.

#### Genetic Resources and their Utilization

Genetic variation within a species is a primary asset required for crop genetic improvement. Varieties having the desired genetic variation can be used as parental lines for hybridization or direct release as cultivars. The heterogeneous landraces can also be improved by pedigree selection for use in breeding programs.

ICRISAT has responsibility for collection, evaluation, preservation, and distribution of pigeon pea germplasm. At present the ICRISAT pigeon pea gene bank holds 13,632 accessions from 74 countries. Of these, 13,077 accessions belong to the primary gene pool [36]. This collection has vast genetic variation (Table 2) for important agronomic traits [84]. Pigeon pea breeders have effectively utilized both inter and intra accessions variability of the primary gene pool for developing high yielding varieties and useful genetic stocks [108].

More than 555 accessions representing 57 wild species are preserved in the secondary and tertiary gene pools of pigeon pea. Important traits available in the secondary gene pool can be transferred to cultivated types through traditional breeding methods. The secondary gene pool of the genus *Cajanus* also has useful genetic variation that could be exploited in pigeon pea breeding programs. For example *C. albicans*, *C. lineatus*, *C. scarabaeoides*, and *C. sericeus* have genes for high seed protein. In addition, *C. sericeus* also has resistance to sterility mosaic virus and P<sub>2</sub> race of *Phytophthora* blight disease. To date, no study has

been conducted on the relationship among the resistant sources originating from the primary and secondary gene pools of genus *Cajanus*.

The tertiary gene pool is also considered a genetic resource of importance as it contains many useful traits such as resistance to insects, diseases, and drought. Within the tertiary gene pool, *C. platycarpus* is the most useful species with a high level of resistance to the P<sub>3</sub> race of *Phytophthora* blight disease. This is the only source of resistance to the P<sub>3</sub> race in the entire pigeon pea germplasm pool. However, this species cannot be crossed to cultivated types using normal hybridization procedures. Some success has been achieved by applying hormones to pollinated buds and rescuing the developing embryo [55]. The derivatives of this cross show high levels of resistance to *Phytophthora* blight disease (N. Mallikarjuna, personal communication). In addition to diseases, moderate levels of resistance to insects like pod borers (*Helicoverpa armigera* and *Maruca testulalis*) and pod fly (*Melanagromyza obtusa*) have also been identified in the secondary gene pool and these have been transferred, with some degree of success, to the cultivated types [122].

#### Pure Line Breeding

Pigeon pea breeders knew as early as 1914 about natural outcrossing in this crop that made its landraces highly variable for most agronomic traits. Using naturally outcrossed lines as a base, they identified individual plants with promising traits to develop good pure line varieties through pedigree selection. Some of the released varieties, e. g. BDN-1 and Maruti, remain popular among farmers even 15–20 years after release. Variety Maruti, released in 1989, is still the leading variety, with over 90% adoption, in the wilt-prone districts of central India [13].

Pure line varieties have also been developed from breeding populations derived from single, double, and three-way crosses [129]. The parents for hybridization were chosen based on the breeding objectives and market traits such as seed size and color, potential yield, disease resistance, and genetic diversity. Mostly, diallel and lines × tester designs were used for determining the combining ability of parents in single cross combinations. One or two backcrosses to the adapted parents have been proved useful in breeding for locally adapted varieties [35]. The parental lines with a proven record of their stability of resistance in diverse environments should be selected for hybridization for developing disease resistant varieties. Further, if one is not sure about genetic purity of the parental lines, then it is always good to self them for one or two generations before crossing.

The cross combinations for developing breeding populations in pigeon pea are made by hand emasculation and pollination. Sharma and Green [118] and Saxena [114] have

**Table 2** Phenotypic variation for important economic traits in pigeon pea germplasm conserved at ICRISAT gene bank

Trait	Range	
	Minimum	Maximum
Days to 50% flowering	55.0	237.0
Days to 75% maturity	97.0	299.0
Plant height (cm)	39.0	385.0
Primary branches (no.)	2.0	66.0
Secondary branches (no.)	0.3	145.0
Recemes (no.)	6.0	915.0
Seeds per pod (no.)	1.6	7.6
100-seed mass (g)	2.8	25.8
Harvest index (%)	0.6	62.7
Shelling ratio (%)	5.7	87.5
Seed protein (%)	12.4	29.5

Source: [84]

outlined the finer details of hybridization techniques. Pod set following artificial hybridization is influenced by both genetic factors, such as genotype differences in pollen germination, and environmental factors, such as temperature, and day light conditions. For example, hybridizations made during cloudy days invariably lead to poor seed production. Saxena et al. [89] reported 19.5% mean pod set with a range of 5–40% from 283,560 hand pollinations made in a single cropping season.

Information at an early stage of a breeding program on the potential of particular crosses to produce promising segregants ensures efficient use of resources. However, the results of experiments on different crops to determine the value of potential crosses in breeding programs are not consistent. According to Allard [7], early generation selection for yield among crosses can be made but only with limited success. Lupton [53] also concluded that the value of early generation testing in plant breeding is rather limited. In pigeon pea, Saxena and Sharma [93] evaluated the potential of eight pigeon pea crosses involving diverse parents. They concluded that low-yielding crosses can be rejected on the basis of their  $F_1$  performance. The crosses recording high yield in the  $F_1$  generation should be tested again in the  $F_2$  generation for confirmation because  $F_2$  bulk performance was found to be consistently correlated with the cross performance in successive generations. They also suggested that  $F_2$  multi-location testing would help to reduce bias caused by genotype  $\times$  environment interactions when selecting crosses for additional selections.

The effectiveness of pedigree selection mainly depends upon closeness of a phenotypic value to its genotype with minimum influence from the environment. Therefore, pedigree selection is more powerful for traits with high heritability. In addition to the environmental influence, non-additive gene effects in the heterozygotes and large genotype  $\times$  environment interactions contribute to low heritability and slower genetic advance for quantitative characters, particularly in early generations. Selections based on individual plant yields in early segregating generations have been ineffective both in cereals [61] and legumes [20]. Green et al. [35] observed in single crosses of pigeon pea that the phenotypic variance of individual plant yield was similar in the selfed parents and their  $F_2$ s, indicating high environmental influence on the expression of single plant yield. In spite of these limitations pedigree selection has resulted in the development of high yielding varieties such as ICPL 87, ICPL 151, Prabhat, T.21, Pusa Ageti, CO 5, and JA 3 [130].

#### Population Breeding

In self-pollinated crops, various conventional breeding procedures may restrict recombination and retain undesir-

able linkages. Reduced recombination reduces the chances of accumulating desirable alleles in pure line selections. Pigeon pea, as predominantly self-pollinated, has natural populations exhibiting a homozygous and heterozygous balance [119]. Few attempts have been made in the past to utilize natural outcrossing of pigeon pea for genetic enhancement of yield. Khan [44] recommended formation of composite lines in pigeon pea for maintaining genetic variability, recombination breeding, and selection of high yielding inbred lines. He also emphasized that these composites can be further improved through random mating for three or four generations for release as open-pollinated varieties. Onim [68] compared two mass selection schemes in marginal rainfall areas of Kenya and reported 2% yield gains per cycle under stratified mass selection and 4% yield gains per cycle mass selection with progeny testing.

A population breeding program based on dual population system [75] was initiated in pigeon pea to enhance recombination frequency through inter-mating of genotypes. In this method, an  $F_2$  population of a cross involving parents with known dominant and recessive traits was grown in isolation under open pollination and single plants with the recessive marker were bulk harvested at maturity. In contrast in  $F_3$  open pollinated generation, the plants with the dominant marker gene were harvested and again in the  $F_4$  generation plants with the recessive marker were selected. This alteration in selection ensures that in each cycle only cross-pollinated plants are advanced to the next generation. This method, however, failed produce any significant gain in the yield over the controls [34]. Byth et al. [20] studied various pigeon pea population improvement schemes and concluded that although mean and genetic variation within the populations can be increased through these out-breeding methods, no cultivar was ever released.

#### Utilization of Mutagenic and Somaclonal Variation

Initial induced mutation studies in pigeon pea were targeted to identify effective doses of different mutagens and to study their effects on inducing genetic variation for agronomically important traits. Use of mutagenesis for pigeon pea improvement has been limited thus far to the release of only five varieties. Ethyl methane sulfonate (EMS) treatment, 0.6% solution, was effective for producing high-yielding pigeon pea variety CO 3 while 16 Kr of gamma rays resulted in the development of another high yielding variety CO 5. Two high yielding varieties, TT 5 and TT 6, were developed for rainfed areas of central zone using fast neutrons [71]. Variety TT 6 has 25% larger seed and higher yield than its parent T-21. Subsequently, another variety TAT 10 was developed by mating two mutant

inbreds derived from fast neutrons. TAT 10 is high yielding and matures about a month earlier than its control. Bhatia [15] reviewed the topic of mutagenic breeding and postulated that future use of mutagens will be restricted for improvement of difficult-to-breed traits such as increased root development, nodulation, resistant host-pathogen interactions, photo-insensitivity, and apomixis.

Chintapalli et al. [24] attempted to exploit somaclonal variations in pigeon pea tissue cultures for crop improvement by producing an R<sub>2</sub> population from regenerated cotyledon explants. The R<sub>2</sub> population exhibited wide variation in floral morphology, plant height, seed size, and seed color. The tissue culture induced mutation events yielded both dominant and recessive alleles in the progenies. A pedigree selection scheme was exercised within single plant progenies grown under field conditions to fix the genes responsible for the variation. Field evaluation of R<sub>6</sub> somaclonal lines continued to exhibit significant variation for yield, seed size, and seed color. Rated superior among these lines was ICPL 99073 with white attractive seeds that were 25% larger to confer a 15% increase in seed yield (K.B. Saxena, unpublished). This result highlights the potential utility of somaclonal mutations for pigeon pea improvement.

#### Utilization of Wild Relatives of Pigeon Pea

The wild relatives of cultivated species can be an important source of genetic variability for desired agronomic traits including resistance to various biotic and abiotic stresses and seed quality. Utilization of wild species in pigeon pea improvement is generally envisaged as coming from the secondary gene pool since normal chromosome recombination, which helps in the transfer of useful genes to cultivars, takes place at this level [29].

The genus *Cajanus* has 32 species, 18 of which are endemic to Asia, 13 to Australia, and one to Africa [140]. ICRISAT conserves 555 *Cajanus* accessions. Considerable genetic diversity has been reported within each species [98, 104, 105]. Introgression from the secondary gene pool can be accomplished through conventional hybridization but sometimes, as has been demonstrated in crossing *C. acutifolius* with *C. cajan*, one or two applications of growth hormones to pollinated buds improves fertilization and embryo development [56]. Successful examples of using crossable wild species in pigeon pea breeding include the development of (1) a highly cleistogamous line [100], (2) genetic dwarfs [102], (3) high protein lines [109], (4) cytoplasmic male sterile (CMS) lines [116], (5) cyst nematode (*Heterodera cajani* Koshy.) resistance [98], (6) soil salinity resistance [135], (7) *Phytophthora* blight resistance [56], and (8) *Helicoverpa* tolerance [83].

The tertiary gene pool of pigeon pea consists of 20 wild species. Thus far only one species, *C. platycarpus*, has been used to transfer *Phytophthora* blight resistance into cultivated types. This was achieved by pollinating emasculated *C. platycarpus* flowers with fresh pigeon pea pollen. Growth regulators were applied to the pollinated flowers to obtain viable hybrid embryos that were excised and cultured in artificial media [57]. *C. platycarpus* is the only species in the germplasm pool having a high level of resistance to the P<sub>3</sub> race of *Phytophthora*. Inbred lines with high levels of *Phytophthora* blight resistance have been selected from this breeding program (N. Mallikarjuna, personal communication).

#### Genetic Transformation

Genetic alleviation of major biotic and abiotic stresses through insertion of known alien gene(s) or specific DNA sequence(s) into the genome of cultivated types is an alternative way of enhancing crop yield and stability. The most important biotic stress of pigeon pea that has never been addressed adequately through traditional plant breeding [83] is susceptibility to the *Helicoverpa armigera* pod borer. Research has been initiated for genetic transformation of pigeon pea by perfecting a tissue regeneration protocol that produced normal plants from this material [51]. Transformation in pigeon pea is possible through either *Agrobacterium* or biolistics, but thus far only the *Agrobacterium* approach has succeeded in producing transgenic plants targeting specific traits. Recently, Sharma et al. [124] reported recovery of pigeon pea transgenics for *Helicoverpa* pod borer resistance through direct organogenesis from axillary buds following 72 h cocultivation with *A. tumefaciens* strain C 58 harboring the binary plasmid pHS 72 having a codon-optimized for the *cryI Ab* and fused *npt 11* and *uid A* genes. Insect resistant varieties of other food crops have been produced using  $\delta$ -endotoxins of *Bacillus thuringiensis* (Bt). Protease inhibitor genes and insecticidal chitinase genes might also help in controlling *Helicoverpa* pod borer damage [123]. Bt and cowpea inhibitor genes are available in transgenic pigeon pea plants [124]. In spite of these preliminary successes, more positive events having a greater impact need to be produced for controlling pod borers under field conditions (K.K. Sharma, personal communication). Genetic transformation might also be used to introduce other beneficial genes not available in the primary and secondary gene pools.

#### Molecular Breeding

Gepts [33] discussed use of molecular markers for improving the efficiency of plant breeding programs because at the molecular level recognizing the presence or absence of a particular gene is independent of plant part or



plant age. Also, in contrast to morphological traits, molecular markers are not influenced by various pleiotropic and epistatic interactions. The first step in molecular breeding, therefore, is to establish linkage between a gene and its marker locus. Subsequently specific DNA diagnostic tests can be applied to assist plant breeders in selection. The identification of useful breeding lines with the help of linked molecular markers is popularly known as marker-assisted selection (MAS). MAS is particularly useful for traits having low heritability where phenotypic selection would be poorly effective.

In contrast to the situation with cereals, the development and use of molecular markers in legumes have been limited to a few crops. Kelly et al. [42] developed molecular maps for bean (*Phaseolus vulgaris* L.) and cowpea (*Vigna unguiculata* L. Walp). They were able to locate genes for important economic traits such as disease and insect resistance, seed size, pod size etc. In bean breeding, marker-assisted selection for disease resistance has been a success.

Nadimpalli et al. [64] used restricted fragment length polymorphism (RFLP) DNA as the specific nuclear probes to study genetic diversity among wild species of the pigeon pea genus *Cajanus*. Ratnaparkhe et al. [80] reported that the level of DNA polymorphism among wild species was extremely high. However, the DNA polymorphism among pigeon pea cultivars was very low [132]. Punguluri et al. [74] used amplified fragment length polymorphism (AFLP) analysis of six cultivars and two of its wild relatives (*C. volubilis* and *Rhynchosia bracteata*) and reported that the wild species shared only 7% of the amplified DNA bands with the cultivars, whereas among the cultivars 87% of the amplified bands were shared in common. Diversity array technology (DArT) markers [146] analyses also revealed low polymorphism among pigeon pea cultivars and high polymorphism between cultivated pigeon pea and its wild relatives. At present, only ten simple sequence repeat (SSR) markers are available in the public domain for pigeon pea [18]. To develop a resource of microsatellite markers for pigeon pea, the primer pairs were generated for 39 microsatellite loci. These markers (19 polymorphic loci) yielded an average of 4.9 alleles per locus while the observed heterozygosity ranged from 0.17–0.80 with a mean of 0.42 per locus [66]. In one recent study, randomly amplified polymorphic DNA (RAPD) markers were used with bulk segregation analysis to report an association of two loci for *Fusarium* wilt resistance [47]. This preliminary report of an association between a molecular marker and a phenotype is the first of its type for pigeon pea and remains to be confirmed. The high level of intra-accession heterogeneity and the narrow genetic variation among cultivars has hindered the construction of molecular maps and marker trait association analysis in pigeon pea.

## Trait-specific Breeding

### Earliness

In every pigeon pea growing country the traditional production systems have evolved around long duration photo-sensitive types. Due to their long vegetative phase, extending from 120 to 150 days, the traditional cultivars are intercropped with some short duration (90–100 days) cereals and legumes. Due to slow initial growth of pigeon pea the accompanying cereal crops exert tremendous competition on the growth and development of inherently slow growing pigeon pea plants resulting in poor canopy development and low yields. Considering the increasing demand for this protein-rich legume, breeders found it essential to breed high yielding early maturing varieties that would help in diversifying legume-based cropping systems. The first early maturing variety T-21 was developed from a cross (T- $\times$ T-190) in 1961. Subsequently, Pusa Ageti was developed at Indian Agriculture Research Institute (IARI) in 1971. This variety was determinate in growth and suffered from heavy pod borer damage. Another early maturing variety BS- 1 was selected from a population of T-21 [76]. Although these varieties were early (150–160 days), they could not fit well in cereal-legume cropping system. Therefore breeding for extra early (90–120 days) type began and the first such variety released was Prabhat. Almost at the same time, the variety UPAS 120 was developed at Pantnagar University [127].

Among the first six early maturing varieties released in India during 1972–1976, only UPAS 120 was accepted by farmers. Subsequently, a few more early maturing varieties were released and among these Manak for northern India and Pragati for peninsular India were outstanding. These varieties are cultivated as pure stands and under good crop management they produce about 2,000 kg ha<sup>-1</sup> yield. This has been achieved by developing a unique high density production package for maximizing yield [20]. In pigeon pea both determinate as well as non-determinate varieties are available. The determinate type plants, with flowers borne in clusters on the top of canopy, are generally short in height, uniform in growth, pod setting, and maturity. The determinate varieties released in India, Trinidad and Puerto Rico are suitable for mechanized harvesting of dry and vegetable pods. The first large seeded, high yielding, short-duration pigeon pea variety Pragati was developed by pedigree selection from a single cross involving a long duration, large seeded line and a short duration, small seeded cultivar. In multi-location testing, this pure line variety produced 20% higher yield with 28% larger seed size than control. The success of this breeding approach resulted in the world wide release of a number of varieties such as ICPL 151, ICPL 2 (in India); ICPL 87091 (in

Kenya, Malawi, and Uganda); Hunt, Quantam, and Quest (in Australia); Prasad (in Sri Lanka); Megha (in Indonesia); and MN 1, MN 5, and MN 8 (in USA). Since early maturity is associated with photo-insensitivity in pigeon pea [142], these varieties exhibited relatively wide adaptation. In the International Nurseries of ICRISAT, such lines produced 1,500–3,000 kg ha<sup>-1</sup> yield at latitudes ranging from 0 to 42°N [108]. One of the most recent short duration cultivar ICPL 88039, which matures in 85–90 days at 17°N latitudes and 130–140 days at 30°N latitudes, has proved to be very productive in extending pigeon pea cultivation into nontraditional areas.

### Dwarfness

Traditional pigeon pea cultivars grow 2 to 3 m in height and are susceptible to insect damage. Lacking genetic resistance to insects necessitates the use of control chemicals for achieving high yields. The height of pigeon pea plants is, however, a major problem in achieving effective sprayings. Agronomic dwarfing, which can be induced by sowing pigeon pea under reducing daylengths [133], is one way to restrict plant height, but such plantings fail to produce the biomass that is essential for realizing high yields. In addition, since pigeon pea is cultivated as rainfed crop, sowings it in the shorter photo-periods of the post-rainy season invariably result in poor root and canopy establishment. Such crops suffer from both intermittent and terminal droughts. Under the circumstance of not having insect resistance, the introduction of dwarfing genes into productive genetic backgrounds is the best approach to enable control of insect damage. Saxena and Sharma [102] reported 12 types of genetic dwarfs in pigeon pea. Among these, the D<sub>1</sub> dwarf, which is characterized by single recessive gene control of shortened internodes and a high number of primary and secondary branches Saxena et al. [96], was used to breed high yielding dwarf varieties. The dwarf lines bred under this program, were on average 30% to 50% shorter in height than the control cultivar and had productivity comparable to those of the tall control varieties [112].

### Disease Resistance

Although over 50 diseases have been reported in pigeon pea, only a few of them are of economic importance. Reddy et al. [82] reviewed pigeon pea diseases and concluded that wilt, caused by *Fusarium udum* Butler, is the most important disease in the Indian sub-continent and eastern Africa. Considering the extent of economic losses due to these diseases, disease resistance breeding takes priority at ICRISAT and this program is mainly centered on wilt and sterility mosaic diseases. Primarily, *Fusarium udum* is a soil borne fungus [19] but if wilting occurs during pod-filling

stage it can also result in seed infection [37]. The most characteristic symptom of wilt is a purple/brown color band extending upwards from the base of the main stem. Most symptoms appear at flowering and podding stages. Field losses due to wilt are total and the use of resistant cultivars is the best strategy to overcome this disease. A number of resistant sources have been identified at ICRISAT [82]. Since in many pigeon pea growing areas both the diseases occur on a large-scale, the breeding program are designed to develop varieties with combined resistance, besides high yield.

Sterility mosaic disease is important in India and Nepal. The causal agent of the disease has remained elusive to identification and characterization over many decades. Jones et al. [40] identified the causal agent as a virus resembling tenuivirus in appearance. It was named as pigeon pea sterility mosaic virus (PPSMV). This virus is transmitted through an eriophyid mite (*Aceria cajani*). After infection the pigeon pea plants become bushy with pale green leaves. Generally such plants do not produce flowers and pods. Sometimes variation in symptom expression caused by environment and genotypes are also observed [82]. An early infection of sterility mosaic disease leads to total yield losses. A number of genotypes with high level of resistance have been identified.

*Phytophthora blight* disease caused by *Phytophthora drachsleri* cajani has a limited distribution. Etiology of *Phytophthora blight* is not fully understood. The infected plants have water-soaked lesions on leaves and brown slightly sunken lesions on stems and petioles [81]. The stem and branches break at the point of infection. A persistent humid and cloudy weather helps in spread of this disease. High levels of resistance to this disease are not available in pigeon pea germplasm.

Witches broom is an important pigeon pea disease of the Caribbean and South America. This disease is characterized by excessive proliferation and clustering of branches and small pale green leaves [17]. Some phytoplasma-like-organism and rhabdovirus particles have been isolated from the infected plants but their role is not fully understood [60]. Cercospora leaf spot disease (*Cercospora cajani*) occurs in eastern and southern Africa, Asia, Latin America, the Caribbean and Pacific [65]. It causes huge losses if the infection occurs at flowering stage or before podding [67]. Powdery mildew (*Leveillula taurica*) is an important foliar disease of Africa. Anthracnose, caused by *Colletotrichum cajani* Rangel., is another important foliar disease of Puerto Rico [137]. It infects pods and leaves leading to destruction of young seeds. Infection on young pods results in their abortion and death. The other pigeon pea diseases recorded in different parts of the world are collar rot (*Rhizoctonia rolfsii*) in India, Philippines, Puerto Rico; macrophomina stem canker (*Macrophomina phaseolina*) or phoma stem canker in Africa; *Alternaria* leaf spot (*Alternaria tenuis-*

*sima*) in India, Puerto Rico, Brazil, and USA; powdery mildew (*Leveillula taurica*) in Africa, and dry root rot (*Rhizoctonia bataticola* Taub) in India [82].

Recent unpublished data from the Indian Institute of Pulses Research (IIPR), Kanpur showed the prevalence of five races of *Fusarium udum*. Three races have also been identified for sterility mosaic virus (Vishwadhhar, personal communication). These races are presently being characterized at the molecular level and their sources of resistance are being identified.

The inheritance of resistance to either *Fusarium* wilt or sterility mosaic diseases is not fully understood. Pal [69] reported that resistance to pigeon pea wilt was controlled by multiple factors while Shaw [126] suggested that wilt resistance was conditioned by two complementary genes. Joshi [41] indicated that resistance to wilt was controlled by a single dominant gene. In support of the Shaw's suggestion, Pathak [70] identified two complementary genes in determining the resistance to *Fusarium* wilt. Resistance to sterility mosaic virus in pigeon pea appears complex. Singh et al. [128] reported that the resistance was controlled by four independent non-allelic genes. Of these, two were dominant and the remaining two recessive; the presence of at least one dominant and one recessive gene was essential for imparting resistance to this disease. Sharma et al. [120] reported that sterility mosaic reaction was controlled by four alleles at two loci. Two alleles control immunity, one of which is dominant and the other recessive to the allele for tolerance. The allele responsible for tolerance is dominant over the other three alleles.

ICRISAT has an excellent open field technique for simultaneous screening against both the diseases. For this purpose, a field with heavy *Fusarium* inoculation has been established and in this sick plot the 'spread row technology' [82] is used to create high level of sterility mosaic disease inoculums. Each growing season, susceptible cultivars are grown at regular intervals in the sick plot to monitor disease build-up. A number of genetic stocks with high levels of resistance to one or both diseases have been identified [82]. These primary sources of resistance are being used to develop high yielding varieties with resistance to both diseases. Varieties including ICP 7035, ICPL 87119, ICPL 98063 etc., which occupy a substantial area in India, Nepal, and China, were bred by this program.

### Insect Resistance

Vegetative and reproductive organs of pigeon pea plants attract over 200 species of insects. Pigeon pea plants have the ability to recover from damage caused to the vegetative organs due to their perennial growth habit, long life cycle, and deep roots. However, recovery to the reproductive organs is uncertain, slow and dependent on genotype, soil

moisture, and climatic conditions. Under certain situations the economic losses caused by major pod and seed boring insects can approach 100%. The insects such as pod borers *Helicoverpa armigera* and *Maruca vitrata*, and pod fly (*Melanagromyza obtusa*) are most damaging. Since *Helicoverpa armigera* is the global pest of pigeon pea, crop improvement efforts at ICRISAT were targeted to develop cultivars with resistant to this pest.

Screening of pigeon pea germplasm for *Helicoverpa* resistance under open field conditions identified those accessions with relatively less pod damage [83]. These accessions were found to have pod borer resistance greater than the released cultivars. Under non-sprayed conditions, these selections produced 860 kg ha<sup>-1</sup> grain yield with only 40–50% pod damage. On the contrary, the released susceptible cultivar recorded 90% pod damage and yield of only 110 kg ha<sup>-1</sup> of grain [83]. The increased resistance was attributed to differences in ovi-position preference. Considering the heavy losses caused by this insect, these results were considered important, but soon it was realized that under heavy infestations or no-choice field conditions, these resistant selections also experienced extensive pod borer damage. Even pyramiding of resistant genes from different germplasm did not enhance the level of resistance [122]. Subsequently, research on pure line breeding for pod borer resistance was abandoned to currently explore such alternative approaches as utilization of wild species and incorporation of insecticidal genes. Pod wall trichomes and their exudates are known to be important in insect defense by effecting insect ovi-positional behavior and host selection process. Aruna et al. [12] reported that various trichome traits of wild species such as their orientation, density, type, and length were dominant over the trichome features of cultivated types and each trichome trait was governed by single gene.

*Maruca vitrata* is another serious insect of tropical legumes. In Sri Lanka, pigeon pea yield losses due to *Maruca* range up to 100%. Field screening of 271 germplasm accessions revealed a large variation for *Maruca* damage to flowers and pods. On average, *Maruca* damage in determinate accessions was higher (66–75%) than in non-determinate (41–50%) types [106]. To purify these genetic stocks a pedigree selection for *Maruca* resistance breeding was practiced for four generations under non-sprayed field conditions. Some determinate as well as non-determinate selections showed significant yield advantage over controls. Yield losses in the resistant selections under non-sprayed conditions were 15–17% in contrast to 70% yield losses in the control cultivar [110]. Resistance to *Maruca* damage was conditioned through yield compensation mechanisms. Poor larval growth and any other interference in larvae feeding on the resistant lines possibly contributed to the resistance [121]. Saxena et

al. [110] showed it was also possible to reduce the number of insecticide sprays on these *Maruca* resistant selections from five to only two.

#### Abiotic Stress Resistance

Drought, soil salinity, and water-logging are major abiotic stresses in areas that produce pigeon pea. However, due to complex nature of these stresses and lack of appropriate screening technologies no systematic breeding program has been undertaken to breed varieties with high levels of resistances to these stresses. Although pigeon pea has deep roots, yield losses due to drought are large and widespread, especially when it occurs during critical seedling and reproductive stages. Lopez et al. [52] reported genotypic differences for drought resistance in pigeon pea. Such variation was associated with the ability of resistant genotypes to maintain efficient production and partitioning of dry matter during periods of drought. Chauhan et al. [22] identified a promising short duration cultivar ICPL 88039 that showed a moderate level of drought resistance. This cultivar is now being grown as a second crop after harvest of a rainy season paddy rice crop when post-rainy season droughts prevent economic cultivation of other food crops. Under these circumstances, ICPL 88039 has produced up to 1,500 kg ha<sup>-1</sup> grain yield in Sri Lanka [107] and the Philippines (K.B. Saxena, unpublished data).

Globally, over 100 Mha of arable land suffer from high soil salinity, especially in irrigated areas. Salinity stress adversely affects plant growth at all stages, but as with drought, the most sensitive periods are seedling and reproductive stages [63]. In spite of its high potential damage, little effort has been made to develop lines with genetic resistance against salinity stress in legumes. A pigeon pea mini-core collection along with some wild species and field collections from predominantly saline areas was evaluated for resistance to irrigation with 75 mM NaCl solution [134]. Results showed that the collections originating from Bangladesh, Indonesia, and coastal areas of India had relatively high levels of salinity resistance. The resistant pigeon pea genotypes had greater biomass and less Na content in their shoots. Among the wild species, *C. sericeus*, *C. acutifolius*, *C. platycarpus*, and *C. scarabaeoides* showed resistance to salinity, but in contrast to what was found in the pigeon pea cultivars, there was no relationship between salinity tolerance and Na accumulation [134]. In another study (N. Srivastava, unpublished data) the pigeon pea hybrids, as a group, were more resistant to salinity than their pure line parents.

Short periods of water-logging is a persistent problem in several pigeon pea growing areas. Water-logging is on increase due to unpredictable climatic changes and deforestation. Water-logging is now included as one of the major abiotic stresses that

needs to be overcome for stabilizing the productivity of rainy season crops including pigeon pea. Water-logging can cause reduced biomass and yield or total crop loss. Chauhan et al. [23] developed a pot culture screening procedure to identify a few resistant genotypes among the advanced breeding lines. Genetic resistance in these cases was directly associated with the ability of plants to produce lenticels under water-logged conditions. This trait was controlled by single dominant gene [72]. So far, no effort has been made to incorporate water-logging resistance into high yielding cultivars.

#### High Protein

Pigeon pea seed is highly nutritive with an average protein content of 20–22%. Some wild relatives of pigeon pea, such as *C. scarabaeoides*, *C. sericeus*, and *C. albicans*, have protein content as high as 32–34% [109]. Considering the lower protein content within the primary gene pool, a breeding program to transfer high protein into pigeon pea from its wild relatives was undertaken. However, these wild species have a number of agronomically undesirable traits such as bushy or trailing plant type, small dark colored seeds, hard seed coat, pod shattering, and low yield, which make the development of high yielding, high protein cultivars challenging. The wild species were first crossed with popular cultivars and tested for hybridity by comparing agronomic traits. The F<sub>1</sub> plants were then selfed to grow a large (2,500–3,000) F<sub>2</sub> population and a pedigree selection scheme was implemented to identify plants with high protein and good agronomic traits. Since seed size was independent of seed protein in these populations [95], selection for seed size and protein content was done simultaneously. These high protein lines have shown stability across environments and years [109]. After eight generations of plant-to-progeny selection, several inbred lines with protein content up to 28% and grain yield and seed size equal to the check variety were developed [109]. It was estimated that 350–450 kg protein can be harvested by growing these high protein selections on a one hectare plot. These lines on average yielded 100 kg ha<sup>-1</sup> additional protein. The increased nutritive value of this material [131] is important since pigeon pea is predominantly cultivated and consumed locally by resource poor farmers. Limited rat feeding trials to evaluate the nutritive value of cooked and raw pigeon pea samples of high and low protein genotypes showed that the high protein genotypes were superior to controls by providing more utilizable protein [129].

#### Vegetable Types

Pigeon pea pods used as a vegetable are normally picked when their seeds have reached physiological maturity, that is, when they are fully grown and start losing green color.

The pods are an excellent vegetable and are an important food commodity in the Caribbean, Africa, and some parts of India. It is a good substitute for the green pea (*Pisum sativum*) when it is unavailable. Although vegetable pigeon pea is not normally as sweet as green pea, it is preferred by some consumers and is usually less expensive. The traditional vegetable pigeon pea genotypes are late maturing and produce fresh pods for a limited period only. ICRISAT has bred a number of early maturing vegetable types from which fresh green pods are harvested over longer periods, which helps to increase grower returns. One such variety, ICPL 87091, has become very popular in India, southern and eastern Africa, and China. In a normal season it produces 5,000–6,000 kg ha<sup>-1</sup> of fresh pods in three or four pickings. Similarly, the perennial vegetable type pigeon pea line ICP 7035 is very popular in Fiji, China, and the Philippines. According to Faris et al. [32] the vegetable pigeon pea seed is more nutritious as a green vegetable than when it is consumed as a mature seed. On a fresh weight basis, vegetable pigeon pea has a greater edible portion, more protein, carbohydrates, crude fiber, and fat than does the green pea. In addition, its protein is easily digestible. Although there is less starch in green seed than in the mature seed, it is more digestible [32]. Vegetable pigeon pea also has more minerals and generally greater vitamin content than does the green pea (*Pisum sativum*). Particularly noteworthy is their high level of vitamin A.

#### Fodder Types

Pigeon pea plants have been used as fodder by farmers for centuries. After harvesting the pod bearing branches, farmers leave plant stubble in the field for regeneration of a new crop for browsing by domesticated animals in the dry summer months. Stubble regrowth provides fresh fodder at a time of the year when there is a deficit of carbohydrate, fiber, and protein for animals [143]. According to Embong and Ravoof [30] pigeon pea leaves is a good substitute for alfalfa in animal feed formulations, particularly in areas that are not suitable for growing alfalfa.

In 1978, the USA National Technical Information Service prepared a report for the US National Science Foundation, in which the need to introduce pigeon pea into the USA was stressed. Out of 60 breeding lines evaluated, six were selected which produced >4,000 kg ha<sup>-1</sup> grain in three months. Subsequently a series of pigeon pea trials were conducted at Grazing Lands Research Laboratory, El Remo, Oklahoma for its use as fodder. Rao and Coleman [77] demonstrated that pigeon pea provided abundant forage of high quality when fodder deficit often occur with other pasture systems. Its forage quality approaches that of alfalfa and soybean. Pigeon pea also provided 30 kg N ha<sup>-1</sup> to the subsequent wheat crop [78, 79].

Past genetic improvement of pigeon pea has focused on increasing and stabilizing seed yield and relatively few attempts were made to improve the crop for fodder. According to Blümmel and Saxena [16] considerable differences exist among pigeon pea cultivars in fodder traits such as leaf protein content and *in vitro* digestibility. Cultivar differences exist also when fodder was harvested around flowering time, for example the nitrogen retention in sheep fed forages from five different cultivars of pigeon pea varied threefold [4]. Assessment of pigeon pea forage quality by the conventional laboratory measures of protein content, fiber constituents, *in vitro* digestibility, and metabolizable energy content failed to rank the cultivars for fodder quality as accurately as when the assessment was made on actual livestock productivity trials using sheep [45]. These findings have important implications for crop improvement because pigeon pea forage contains a variety of secondary plant components such as condensed tannins that enhance the quality of forage but are not measured in the laboratory. On the other hand, the hydrolysable tannins and alkaloids deteriorate the forage quality [5, 6]. Therefore, breeding of pigeon pea for forage quality and quantity needs to address such issues to make a positive impact [16].

#### Breaking Yield Plateau through Hybrid Breeding

Indian archival records show that the first pigeon pea variety was developed by selecting a wilt resistant genotype from landraces [126]. Subsequently, more than 100 pure line pigeon pea varieties were released for cultivation over the last 70 years [130] resulting in substantial increases in pigeon pea production areas [87], but productivity from these crop improvement endeavors has not increased.

To achieve a breakthrough in yield, pigeon pea breeders unsuccessfully tried various breeding methods such as pure line breeding, population breeding, mutation breeding, and inter-specific crosses. ICRISAT scientists also developed a hybrid breeding system using partial natural outcrossing of the crop coupled with genetic male-sterility [81, 94]. Combining these two components, Saxena et al. [101] developed the world's first pigeon pea hybrid ICPH 8, which was released for cultivation in 1991. Performance of ICPH 8 in 100 multi-location trials, under diverse agro-ecological conditions, conducted over a period of 6 years recorded an average 30.5% yield gain over the best available pure line variety UPAS 120. Such yield gains of the hybrid were confirmed in a series of on farm trials [101]. These results revealed substantial levels of hybrid vigor that could be exploited commercially. This hybrid, in spite of high yields, failed to be adopted due to the high cost of seed production and this necessitated breeding for a more efficient cytoplasmic-nuclear male-sterility (CMS) system.

## Development of Cytoplasm-Nuclear Male-Sterility (CMS) Systems

An intensive search in the pigeon pea germplasm collection failed to identify any CMS genotype. Consequently, ICRISAT scientists designed to synthesize CMS genotypes by combining the cytoplasmic genome of wild relatives with the nuclear genome of pigeon pea cultivars. This breeding approach has so far yielded the following five CMS cytoplasm (A<sub>1</sub> through A<sub>5</sub>).

1. *C. sericeus* (A<sub>1</sub>) cytoplasm: *C. sericeus* is an erect shrub of Indian origin which can easily be crossed with pigeon pea cultivated types. The CMS lines derived from this species are sensitive to environment so that male-sterile plants revert back to male-fertility under low (around 10°C) temperatures [112]. This is particularly true of early maturing A<sub>1</sub> CMS lines. In long duration A<sub>1</sub> CMS lines such sex reversion events were relatively low. The reasons for this difference between the early maturing and late maturing lines are not fully understood. The hybrid combinations produced by using A<sub>1</sub> CMS produced good yields, but due to the presence of pollen shedders in female parent it was not further developed by commercial seed producers.
2. *C. scarabaeoides* (A<sub>2</sub>) cytoplasm: *C. scarabaeoides* is the most common wild relative of pigeon pea and it is endemic to the dry areas of India, Sri Lanka, Australia, Africa, China and elsewhere. The A<sub>2</sub> CMS system derived from this species [111, 136] is very stable, but the fertility restoration of its hybrid plants is inconsistent across environments. Hybrids derived from this source also showed significant heterosis for yield [38]. However, poor seed set in the hybrids in some environments restricts its full scale commercialization.
3. *C. volubilis* (A<sub>3</sub>) cytoplasm: *C. volubilis* is a perennial wild relative of pigeon pea but is difficult to cross with cultivated types. The A<sub>3</sub> CMS line developed from this species [141] could not be utilized in hybrid breeding due to lack of quality fertility restoration.
4. *C. cajanifolius* (A<sub>4</sub>) cytoplasm: Unlike other wild relatives of pigeon pea, plants of *C. cajanifolius* resemble the cultivated types. This wild species, considered as progenitor of cultivated type [27], is endemic to the forests of central India. The A<sub>4</sub> CMS system derived from this species [113] is the best due to its stability across environments and years and it has perfect fertility restoration in the F<sub>1</sub> hybrid plants. A<sub>4</sub> CMS is now extensively used by breeders to develop commercial pigeon pea hybrids.
5. *C. cajan* (A<sub>5</sub>) cytoplasm: This is a unique CMS system because in this case the wild species *C. acutifolius* was used as the male parent and the cultivated pigeon pea

(*C. cajan*) was used as the female parent [58]. Unfortunately, the A<sub>5</sub> CMS system is maintained only by its wild relative male parent and almost all the cultivated types used so far restored the male fertility. Attempts are now being made to find male sterility maintainers among the cultivated types.

## Pigeon Pea Hybrids

To produce heterotic hybrids adapted to diverse environments it is essential to have genetic diversity among the hybrid parents. Advanced generation (F<sub>6</sub>, F<sub>7</sub>) breeding lines having diverse parentage, popular cultivars, and elite germplasm were crossed with CMS lines and screened for maintainer and restorer lines. Considerable variation among maintainers and restorers has been incorporated for important agronomic traits. Among maintainers the variation for flowering (57–112 days), maturity (90–192 days), plant height (62–262 cm), and 100-seed mass (7.4–19.2 g) is high. Similarly, male-fertility restorers exhibited considerable diversity for flowering (59–142 days), maturity (96–193 days), plant height (39–190 cm), and 100-seed mass (6.3–13.0 g). The genetic diversity observed in the male sterility maintainers and fertility restorers will allow pigeon pea breeders to develop hybrids adapted to different agro-ecological areas and cropping systems such as short duration pure cropping, long duration intercropping, and specific disease-prone areas.

Among medium maturing hybrids, ICPH 2671 is most outstanding. It matures in 165–175 days, has high levels of resistance to both wilt and sterility mosaic diseases, and produces over 30% more biomass than the best pure line control. Over three years of testing ICPH 2671 produced 2,937 kg ha<sup>-1</sup> grain and exhibited 61% heterosis over the best control cultivar. Several short- and medium-duration high-yielding hybrids with significant heterosis have also been identified from multi-location trials. Hybrids such as ICPH 3371, ICPH 3491, and ICPH 3497 demonstrated both high yield and high levels of resistance to wilt and sterility mosaic diseases.

Commercial seed production for pigeon pea hybrids involves large scale seed production of a female line (A/B), restorer line (R), and hybrid combination (A×R). Each set of material is planted in fields separated from other pigeon pea crops by a distance of at least 500 m. For seed production of the A/B lines, the breeder seed of both A- and B-lines are planted simultaneously using a row ratio of 4:1. The trials conducted at Patancheru showed that this ratio produced 1,135 kg ha<sup>-1</sup> of A-line seed [115]. The row ratio of four female/one male also gave good (975 kg ha<sup>-1</sup>) yield for the hybrid (A×R) seed production.

Primary structure of CMS-based hybrid pigeon pea technology is now developed and is being adopted to suit specific environment as a continuing process. Evaluation of a range of lines has demonstrated that pigeon pea hybrids have greater potential for enhancing yield. It is now the responsibility of breeders to ensure that hybrid cultivars are made available to farmers. Also, since pigeon pea is predominantly cultivated by small resource poor farmers, there is a need to keep hybrid seed costs low. In India, both public and private seed industries are viable and it behooves breeders to make use of both. In 2007, the ICRISAT pigeon pea hybridization program shared parent seeds with 14 private and three public sector seed companies. It is believed that an excellent beginning has been made in hybrid breeding and now it is just a few steps away from commercialization.

## Development of Pigeon Pea Varieties for New Niches

### Breeding Varieties for Rice–wheat Cropping System

Cultivation of rice (*Oryza sativa* L.) in the rainy-season followed by a wheat (*Triticum aestivum* L.) crop in the post-rainy season is an important production system on over 10–12 Mha. This system produces staple grain for over 500 million people in south Asia. Cultivation of high yielding dwarf rice and wheat in irrigated areas has relegated the growing of nutritive legumes to marginal environments. Over the last 40 years, high input cultivation of rice and wheat has helped solve problems of food security in developing countries. However, there are now increasing concerns about the sustainability of yields in this cereal–cereal crop rotation system. Continuous cultivation of rice and wheat is lowering soil fertility and organic matter [145], depleting ground water resources, and exacerbating weed, disease and insect problems [73]. Soil salinity is also emerging a serious problem in such areas. It has been suggested that sustainability of food production could be enhanced and the process of land degradation reversed if these high input cropping systems were appropriately diversified, especially with rotation of legumes.

Among legumes, short duration pigeon pea varieties have been found beneficial in a rotational cropping system. At present, pigeon pea–wheat rotation is estimated to occupy about 0.25 Mha and this area could be increased significantly if suitable varieties existed. Introduction of pigeon pea not only provides nutritionally superior grain and fuel, but it also enhances stability of production by improving soil nutrition and structure. The most popular short duration variety UPAS 120 does not provide enough flexibility for wheat sowings. New pigeon pea varieties,

which mature about three weeks earlier than UPAS 120, would allow timely field preparation and sowing of the wheat crop. Variety ICPL 88039 appears promising for such a legume–cereal rotation. It is harvested by mid-November and produces 20–35% more grain yield [25]

### Breeding Varieties for Rice-fallows

Significant rainy season paddy areas of Asia are left fallow in the subsequent season due to unavailable irrigation water, inadequate rainfall, and non-availability of suitable crop varieties. In Sri Lanka alone, about 0.2 Mha land is left fallow annually after the rainy season paddy rice crop [107]. Among the legume crops tested for integration into this system, early maturing pigeon pea varieties have high potential because of their ability to survive and produce economic yields under residual moisture and fertility. Early maturing pigeon pea lines produced economic yields in an experiment conducted in Sri Lanka involving no tillage and no fertilizer. Among these lines, ICPL 179 and ICPL 88039 maturing in 85–90 days and producing 1.0–1.5 t ha<sup>-1</sup> grain yield were most promising. Introduction of pigeon pea in paddy fallows is not only likely to increase farmers' income but also to improve soil productivity [39, 107]. Recently ICPL 88039 has also been successfully introduced in the rice-fallows of northern provinces of the Philippines (K.B. Saxena, unpublished data).

### New Pigeon Pea Cultivars for High Latitudes

Traditional pigeon pea cultivars and landraces require a long growth period to flower because of their strict short day requirements. This has restricted their adoption beyond 30°North and South latitude. In recent years pigeon pea is assuming greater importance in crop diversification programs of Asia due to its role in enhancing sustainability of rainfed cropping systems. Breeders have developed varieties that mature in 90–120 days and are relatively insensitive to photoperiod. These cultivars have the ability to flower under long-day photoperiods of 20 h or more and mature before the onset of the cool season. Such photo-insensitive cultivars have shown adaptation to latitudes ranging from the equator (Kenya) to 46°N (Prosser, USA) and 45°S in New Zealand. Pigeon pea cultivars ICPLs 83105, 85010, and 85030 produced 1,500–2,500 kg ha<sup>-1</sup> grain yield at Prosser [108]. Suitability of such cultivars offers opportunities for extending pigeon pea cultivation into new niches.

### Breeding Varieties for Post-rainy Season

Traditionally, pigeon pea is a rainy season crop but its potential for production in post-rainy season has been

demonstrated by Roysharma et al. [86]. Plant phenology of the crop is drastically changed under the post-rainy season system due to sowings under declining photoperiods that results in small size plants. To realize high yields from such plantings high plant populations are essential. The yield potential of pigeon pea in post rainy season is substantially higher (3,400 kg ha<sup>-1</sup>) than that of rainy season (2,500 kg ha<sup>-1</sup>) under pure cropping. Satyanarayana and Rao [88] reported that post rainy season pigeon pea is more beneficial than is the rainy season crop in the coastal areas of south India because the post rainy season crop avoids pod borer and water-logging damage. Recently, variety ICPL 85063 has been released for cultivation in post-rainy season. This variety has produced up to 3,500 kg ha<sup>-1</sup> yield and farmers grow it as an intercrop with black gram (*Vigna mungo*), soybean (*Glycine max*) or groundnut (*Arachis hypogea*).

#### Breeding Varieties for High Altitudes

Pigeon pea is an essential ingredient in Indian cooking and for centuries in neighboring China, pigeon pea was used for rearing lac insects (*Laccifer lacca*). When China's lac industry collapsed, pigeon pea cultivation disappeared from Chinese farmlands until improved varieties from ICRISAT revived cultivation. Interestingly, the re-introduction of pigeon pea into China was not primarily for its value as a food legume but for conserving soils in sloping mountain regions so that after a few years other food crops could be cultivated. New pigeon pea varieties were tested for the first time in China in 1999. Two provinces were selected for research on the role of pigeon pea in various cropping systems, especially for controlling soil erosion and rehabilitation of degraded and eroded soils. In the last few years pigeon pea is being grown on a large scale in Yunnan and Guangxi provinces. In addition to organized seed distribution, there has been a lot of farmer-to-farmer spread of pigeon pea seed. According to informed sources (Zong Xuxiao, personal communication), the area currently under pigeon pea in China is around 150,000 ha.

The renewed development of pigeon pea cultivation in China signifies the success of ICRISAT's partnership based research in China. Strong pigeon pea research programs have also been established by the Institute of Resources Insects of the Chinese Academy of Forestry in Kunming (Yunnan) and at the Guangxi Academy of Agriculture Sciences, Nanning (Guangxi). The pigeon pea crop can be seen in China growing on the roadsides, hill slopes and riverbanks. At present, efforts are also being made to popularize pigeon pea for human food, especially as green peas. Chinese food technologists have developed a number of snacks, food items, and drinks using dry and green seeds of pigeon pea.

#### Summary

For centuries pigeon pea has been a prime source of protein to millions of resource poor farmers in the rainfed tropics and sub-tropics. In spite of its low productivity and profitability, the crop has survived due to its ability produce reasonable amounts of grain under rainfed conditions with low or no inputs. In recent years the importance of this crop has increased due to growing shortage of irrigation, erratic rainfall, and increased need for protein rich food. The multiple uses and its role in sustainable agriculture make pigeon pea a favorite crop of small land holders. Significant progress has been made over the last few decades through breeding for reducing crop duration, improving seed quality, and overcoming the constraints of major diseases like wilt and sterility mosaic. These milestones have helped to increase the production and area of pigeon pea, even though yield per unit of land area has remained as low as ever. Since the demand for pigeon pea is increasing and land area available for expansion is limited, research now needs to focus on the genetic enhancement of yield. Exploitation of heterosis for yield and restructuring plant type for increased harvest index are two possible ways for achieving a breakthrough in yielding ability. In tropical environments, where restricted biomass is the major production constraint, pigeon pea hybrids are expanding because they are capable of producing more than 30% additional biomass. Hybrid pigeon pea technology has conclusively demonstrated their feasibility, if the seed production constraints are addressed adequately. The recent development of the A<sub>4</sub> CMS system has provided the opportunity for the commercialization of pigeon pea hybrids. High levels (30–60%) of hybrid vigor observed over the standard cultivars and easy methods for producing hybrid seed have attracted a number of private and public seed companies in India. It appears that a renaissance in pigeon pea production has been made and soon farmers will reap the benefits of hybrid technology.

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