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Accomplishments and challenges of pigeonpea breeding research in India

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Abstract

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is a protein-rich pulse crop which can grow well under soil moisture limited environments. The crop can play a significant role in meeting the challenges of global food security under the looming threats of climate change, soil degradation and rising production costs. This would be possible through fast-track breeding of new cultivars with high and stable performances. This paper reviews the achievements of pigeonpea breeding research and suggests the growth trajectory for future programmes related to breeding of high yielding pure line and hybrid cultivars. In the past few decades, three pigeonpea breeding milestones have made their mark. These include development of (i) medium maturing disease resistant pigeonpea cultivars for greater yield and stability, (ii) high yielding early maturing pigeonpea cultivars for area expansion involving new production niches, and (iii) a trend setting hybrid breeding technology for breaking the decades-old low yield plateau. These innovations are showing their positive impact on pigeonpea production and productivity and hold promise for achieving nutritional security of masses in the country.

Key words: Pigeonpea, production constraints, variety, hybrids, production strategies

Introduction

Estimates of Alexandratos and Bruinsma (2012) revealed that the global population is likely to reach the nine billion mark by the middle of this century; and most of the increase would be in the semi-arid tropical regions, where poverty and malnutrition already have their foot prints.The shortage of protein, especially has led to malnutrition among the under-privileged children and women. For nutritional security of the growing population in India, a quantum jump in pulse production would be essential. In fact, enhancing the pulse production on a substantial scale in the backdrop of climate change, degrading soils and escalating production costs will be a Herculean task; and to achieve this goal, vigourous efforts at state, national and international levels would be required. The recognition of 2016 as the "International Year of Pulses" by the United Nations General Assembly is a right step towards generating global awareness and revisiting the pledges to overcome this issue. In this context, pigeonpea [*Cajanus cajan* (L.) Millsp.] can play a significant role because of its ability to grow well under diverse cropping systems/environments and marginal soils at subsistence level. Pigeonpea commands a high place among rainfed farming communities due to its abilities to fix atmospheric nitrogen, release of soil-bound phosphorus, and recovery from drought and other stresses (Saxena 2008). The estimated globally-sown pigeonpea area now stands at over 6.23 m ha, with a production of 4.74 m t, and average yield of 762 kg/ha (FAO 2015). The crop is well adapted to rainfed areas of India (5.06 m ha), Myanmar (0.5 m ha) and Africa (0.5 m ha). India is the largest (3.29 m tons) producer of pigeonpea; but this produce is insufficient to meet the domestic needs and about 500,000 tonnes of pigeonpea are imported annually. To increase production of the crop, the Indian Council of Agricultural Research (ICAR) launched a country-wide pigeonpea improvement

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programme with a positive impact in terms of area enhancement and production. Also, to achieve a quantum jump in yield, a cytoplasmic nuclear male sterility (CMS) based hybrid technology has recently been developed (Saxena 2015) and it is being promoted aggressively by International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and Indian Council of Agricultural Research (ICAR). This paper highlights the milestones achieved through various plant breeding research initiatives in pigeonpea.

Productivity constraints in pigeonpea

The issue of yield plateau

The food production balance at individual farmer level is always in favour of cereals. This relegates the cultivation of pulses to risk-prone marginal lands with limited inputs. Among the rainy season pulses, pigeonpea has established itself as the most reliable crop across a range of environments and soil types. However, the major constraint that still persists with the crop is its low on-farm productivity which, in the last six decades has remained low and stagnant between 700-800 kg/ha. In fact, there may be a number of crop production limitations for the low productivity, but lack of high yielding cultivars with stable performance under adverse growing conditions, is considered the key factor. In this context, the release of 87pigeonpea varieties at the national level also did not make any difference and the issue of plateauing yield still haunts both the scientists as well as policy makers. To meet the deficit of pulses in the country, the National Food Security Mission of India has launched a number of short- and long-term schemes including breeding new-generation inbred and hybrid cultivars. This would perhaps help in shattering the bar of yield plateau in pigeonpea.

Physiological constraints

For some reasons, crop physiology is the least researched area in pigeonpea; and the dismal on-farm productivity of the crop could partly be attributed to poor understanding of physiology of various stresses, pathways related to the survival of plants, and genetic control of key traits responsible for yield formation. It is important that in future high priority be given to research programmes in the field of crop physiology using both empirical as well as modern technologies.

Photo-sensitivity

Pigeonpea is a quantitative short-day plant and its flowering is delayed as the daylight durations extend beyond 13 h. Warm weather combined with long photo-periods promote longer vegetative phase, while short photo-periods and milder mean ambient temperatures (>18 and <25^o C) promote flowering. According to Silim et al. (2007), the optimum temperature for rapid flowering in pigeonpea is 24.7^o C for extra-early, 23^o C for early, 22.2^o C for medium and 18.3^o C for long duration varieties. Chauhan et al. (2002) showed that changes in photo-period influenced the dry matter partitioning. Also, it was observed that flowering under inductive short days of post-rainy season is more synchronous. In contrast, the long photo-periods lead asynchrony flowering and continuous accumulation of dry matter into vegetative structures. It is related to its genetic indeterminate nature, which creates unequal competition among developing pods and vegetative plant parts. This situation leads to reduced partitioning of dry matter in this crop.

Harvest index

Harvest index in the traditional pigeonpea cultivars is low and breeding of determinate cultivars was attempted earlier with the expectation of achieving better harvest index. However, Sheldrake and Naraynan (1979) showed that both determinate and indeterminate types had similar inefficiencies with respect to partitioning. However, the indeterminate types had greater advantage over determinates in the environments where growing period was longer, and less so in shorter growing environments (Chauhan et al. 1998). The yields in shorter growing season are often similar to that obtained in the longer season even with half the dry matter production in the former. However, the strong negative relationship between dry matter production and yield in pigeonpea makes it difficult to increase the harvest index component of yield without reducing biomass production and *vice-a-versa* (Chauhan et al. 1995).

Breeding constraints

Limited genetic variability

Genus *Cajanus* contains large phenotypic variation within primary gene pool for most economically important traits. However, in contrast, the molecular genetic studies have shown limited genetic variability in the germplasm; and this may be responsible for limited genetic gains recorded in the productivity of pigeonpea. Shiv Kumar et al. (2003), while studying diversity among the parents used in breeding the released pigeonpea cultivars, concluded that 50% of cultivars had 10 parents in common. Singh et al. (2016)

also reported that more than one-third of the released cultivars originated directly from landraces. These examples revealed that in breeding for yield a limited parental diversity was used, and this could be the reason for the recovery of less productive recombinants. According to Yang et al. (2006) genetic diversity among the crossable wild relatives of pigeonpea is relatively high and this resource can be used to diversify genetic variability in the primary gene pool.

Genetic control of stresses

Under natural conditions, a number of stresses adversely affect pigeonpea growth, development and stability. Among biotic stresses, insects (mainly pod borers and podfly) and diseases (mainly wilt and sterility mosaic) are the common yield reducers. In general, genetic resistance against the insects is either lacking or too weak to make any impact with respect to genetic gains in breeding cultivars. Also, no information is available on the genetic control of the insect tolerance.

Genetic information on the resistance to wilt is well documented and inheritance patterns are quite clear. In different genotypes, 1or 2 genes with dominance and/or recessive action have been reported for controlling the wilt resistance (Saxena et al. 2014). However, more information needs to be generated in near future with respect to the biotypes of *Fusarium udum* and inheritance of their resistance. This will facilitate breeding of widely adapted wilt resistant cultivars. The resistance to sterility mosaic virus in controlled by recessive genes but their mode of inheritance is still unclear (Saxena and Sharma 1990). A number of cultivars with high levels of stable resistances to wilt and sterility mosaic diseases have been bred; and these occupy around 60-75% of the cropped area. Two cultivars, Maruti and Asha have played a major role in eradication of wilt and sterility mosaic in some districts of Karnataka, Maharashtra, Madhya Pradesh, and Telangana.

Drought is the most widely spread constraint in pigeonpea; but unfortunately, no conclusive information is available on the physiological parameters which directly or indirectly influence the incidence and intensity of drought under different environments and cropping systems. Temporary water-logging generally occurs in the fields with high water holding capacity and/or poor drainage. Generally, the risk of crop failure or yield reduction due to water-logging is greater in early types as compared to those taking 6-9 months to mature, due to possibility of the former group to recover from this stress. Water-logging tolerance involves metabolic adaptations and varies with species, plants and tissues. The formation of aerenchyma creates an internal gas exchange channel for air from the aerobic shoot to the hypoxic roots. Besides this, it also facilitates the counter-flow of volatile compounds accumulated in the anaerobic soil and plant tissue. Hingane et al. (2015) reported that in the water-logging tolerant genotypes some new morphological traits such as aerenchyma cells, lenticels, and/or adventitious roots were developed under water-logged conditions. These traits facilitated respiration in the stressed plants by supplying oxygen from stem to roots.

Genetic contamination of seed purity

Unlike most pulses, in pigeonpea the maintenance of genetic purity is rather difficult and resource-intensive, primarily due to occurrence of insect-aided natural out-crossing (Saxena et al. 2016a). Under these circumstances, the key traits for which a given variety was recognized are likely to be lost. This process of quality deterioration is quite rapid when recessive genes control the traits. There are examples where, in the absence of good seed management system, the out-standing disease resistant cultivars have become highly susceptible over a period of a few years. For instance, cv. 'Bahar', a high yielding widely adapted variety, known for its high degree of resistance to sterility mosaic virus became a mixture of resistant and susceptible plants within a few years and consequently, it lost its yield potential and adaptation. Another key point in this context is the strict maintenance of varietal maturity duration. This occurs due to enhanced indeterminateness of the plants which results in shifting their duration. For example, cultivar UPAS 120 used to mature in about 120 days now its maturity is extended by a month for the same reason, and thereby adversely affecting the prospects of pigeonpea - wheat rotation. Therefore, for sustaining high productivity of pigeonpea cultivars, an efficient seed chain with quality control needs to be established on priority basis.

Biological accessories for breeding pigeonpea

Genetic resources

Maintenance of genetic diversity within the working germplasm collection and its regular enrichment are important activities of any breeding programme. A large number of pigeonpea accessions have been collected from 52 Asian, African, and Latin American countries

(Table 1). Besides these, 47 wild species related to pigeonpea representing six genera of secondary and tertiary gene pools are also conserved for future use. This represents a good collection from Indian sub-continent (Upadhyaya et al. 2016), the primary centre of diversity. This primary gene pool of the crop offers an extensive range of variability for almost all the morphological and quality traits (Table 2). In pigeonpea the maturity plays a significant role in the adaptation of crop and the germplasm collection has almost continuous variation (<90 to >250 days) for this trait. To select appropriate materials with proper replacement of traits adaptation, this range has been divided into 11 maturity groups (Saxena 2008). In addition, a number of unique traits such as genetic male-sterility, cytoplasmic nuclear male-sterility, floral variants, dwarfs, decumbent, single-culm, etc. have also been conserved. To facilitate germplasm usage in breeding, representative subsets of germplasm in the form of 'core' and 'mini core' collections and 'reference sets' have been created at ICRISAT (Upadhyaya et al. 2016). The mini core collection contains accessions tolerant to water-logging (23), salinity (16), wilt (6), sterility mosaic (24), pod borer (14) etc.

Table 1. Global pigeonpea germplasm availability

Country	Organization	Cultivated	Wild spp.	Total
India	NBPGR	15127	41	15168
	ICRISAT	13216	355	13771
	IIPR	5195	-	5195
	IARI	1500	-	1500
Kenya	NGB	1288	92	1380
Australia	ATCFGRC	406	352	758
Columbia	CIAT	135	623	758
Ethiopia	ILRI	143	539	682
Others	#	1543	3	1546

Brazil, Nepal, Philippines, Thailand, Uganda

Table 2. Summary of germplasm variability and action in pigeonpea

Character	Pheno-typic variation	Gene action		
		Addi-tive	non-addi-tive	Addi-tive+ non-addi-tive
Plant height (cm)	39-310	*	*	*
Plant width(cm)	-	*		*
50% flower (days)	45-237	*		
75% maturity (days)	85-249	*	*	*
Pods/plant	16-1819		*	*
Seeds/pod	2 -9	*		*
100-seed weight (g)	2.7-25.8	*	*	*
Seed yield	-	*	*	
Protein (%)	13-32		*	*

Genetic information

Phenotypic expression of a given trait is the consequence of direct and indirect effects of numerous biological events and environment factors and their interactions. Therefore, to enhance the selection efficiency, it is important to understand the inheritance pattern of key traits and their mode of expression under different environments. This will help breeders in creating new variability and designing efficient selection and testing schemes. In pigeonpea, limitation of reliable information on the aspects such as number of genes, their mode of action, heritability, and genotype-environment interactions perhaps has slowed the process of genetic gain for quantitative traits. The heterozygosity of the parental lines, caused by natural out-crossing, also adversely affects the genetic gains in pedigree breeding programmes. Green et al. (1981) and Saxena and Sharma (1990) while reviewing this subject, concluded that important agronomic characters were primarily controlled by genes with additive and non-additive effects (Table 2). They also stated that the inheritance of yield and yield related traits is also further affected by some major genes (e.g. photo-sensitivity and indeterminateness) with strong pleiotropic effects on plant phenology.

Screening technologies for key stresses

Since fusarium wilt and sterility mosaic virus are common diseases of most pigeonpea growing areas, an effective field screening technology was developed at ICRISAT by Nene et al. (1981). Besides this, pot culture technologies for screening against Alternaria blight and Phytophthora bight diseases have also been developed (Mamta Sharma pers. com.). For water-logging, separate methodologies were developed for screening at seed germination and early seedling stages (Chauhan et al. 1997, Sultana et al. 2013). Similarly for salinity also, a pot screening technology was developed by Subbarao et al. (1991). Srivastava et al. (2006) found that a NaCl treatment @ 1.01 g/kg was suitable for salinity screening in pigeonpea. For drought, pod borers, and podfly so far no reliable screening technology is available for pigeonpea. Improving drought tolerance is urgently needed in medium and long duration types; and since they exploit residual moisture, giving attention to root traits could be valuable.

Cytoplasmic nuclear male sterility systems

Cytoplasmic-nuclear male-sterility (CMS) is being used on a large scale across various genera and species for commercial exploitation of hybrid vigour. The expression of CMS is determined by interaction between specific nuclear and cytoplasmic genetic factors. In pigeonpea, Tikka et al. (1997) reported the development of CMS lines by combining the cytoplasm of *Cajanus scarabaeoides* with nuclear genome of cultivated type. The A_2 CMS system exhibited high stability across diverse environments and was used in breeding hybrids. Saxena et al. (2005) crossed a wild species (*Cajanus cajanifolius*) as a female parent with cultivar ICP 28 to develop A_4 CMS system. In this system both the male sterility and its fertility restoration were highly stable across diverse environments. This CMS system proved to be a success and now it is being used in breeding commercial pigeonpea hybrids in India (Saxena 2015). Subsequently seven more CMS systems were bred in pigeonpea (Saxena et al. 2010, Saxena 2013).

Natural cross-pollination

Pigeonpea flowers produce sufficient amounts of nectar to attract a variety of insects which cause cross-pollination. These nectarivore insects visit open flowers and collect nectar from the nectaries present at the base of the flowers to affect cross-pollination. The degree of natural out-crossing depends on a number of factors and hence, its extent varies considerably from place to place. In a recent review, Saxena et al. (2016a) reported that in pigeonpea the out-crossing ranged from 0 to 48% in India, 14 to 19.64% in Sri Lanka, 13 to 70% in Kenya, and 8 to 22% in Uganda. The natural out-crossing in pigeonpea is considered both boon – for hybrid seed production and bane - for maintaining genetic purity of cultivars.

Traditional breeding technologies and accomplishments

Breeding high yielding varieties

Pedigree breeding: In spite of the known potential dangers of natural out-crossing of the selections, most pigeonpea breeders resorted to pedigree breeding without pollination control. Out of 87 cultivars released in India, 82 were bred through pedigree breeding (Table 3). Interestingly 55% of these were developed through selections from the populations derived through bi-parent matings, and the remaining were selections from heterogeneous landraces. Shiva Kumar et al. (2003) reported that the genetic variability among parental lines used in breeding pigeonpea varieties was limited. Similar views were also expressed by Upadhyaya et al. (2016). Since genetic variability is the prime source of harvesting new recombinants, pigeonpea breeders should have a serious look at this vital breeding pre-requisite.

Table 3. Pigeonpea cultivars developed through different breeding methods

Maturity	Total releases	Germplasm selection	Hybridization & selection	Mutation breeding
Early	34	6	24	4
Medium	37	17	19	1
Late	16	9	7	0
Total	87	32	50	5

Mutations: It is a useful breeding tool for creating genetic variability for both qualitative as well as quantitative traits for exercising selections. In pigeonpea only five released varieties originated through mutagenesis. The successful mutagens include EMS (0.6%), gamma rays (16 Kr), and fast neutrons. The popular varieties developed through this approach are Co 3, Co 5, TT 5 and TT 6. In addition, cultivar TAT 10 was developed through pedigree breeding within the populations derived from the matings of two mutant genotypes. Bhatia (2000) while reviewing this subject postulated that in future the use of traditional mutagens in breeding cultivars will be restricted. However, considering its potential in creating new variability, the future mutation research in legumes should be directed towards improving more difficult traits such as photo-insensitivity and the development of roots, nodulation, etc.

Breeding cultivars with resistance to biotic stresses

In pigeonpea, huge losses occur year-after-year due to the damage caused by two pod borers- *Helicoverpa* *armigera* and *Maruca vitrata*; and so far no reliable genetic solution is available. The resistance breeding for *Helicoverpa* is a complex issue, and in spite of diverting huge resources to identify effective host-plant resistances, so far the success has been elusive. Extensive field screening of >7000 germplasm at ICRISAT for tolerance to *Helicoverpa* did not yield useful results, except identifying a few accessions with relatively less pod damage, but their stability over seasons, location, and years could not be established. In addition, large intra-accession variability for pest damage, its recovery and variation in insect population in different years further added to the low heritability for pod borer tolerance. In spite of these limitations, ICRISAT and ICAR released a medium maturing *Helicoverpa* tolerant pigeonpea line (ICPL 332) as 'Abhaya'. In the trials conducted under insecticide-free conditions for three years ICPL 332 recorded 35% pod borer damage as compared to 65% damage in the control cultivar. In these experiments ICPL 332 yielded 49.6% more yield over the control (1250 kg/ha).

This variety, in spite of good yield and tolerance to pod borer, could not make any impact due to its high susceptibility to fusarium wilt disease. Recently, this weakness of ICPL 332 was overcome through selection under disease sick plots; and it was renamed as ICPL 332WR (Sharma 2016). This variety is likely to contribute significantly towards sustainable production of pigeonpea. The other pod borer, *Maruca vitrata* (Geyer) causes serious losses to early maturing genotypes, especially under humid conditions. Some pigeonpea genotypes with moderate levels of resistance to this pest were identified in Sri Lanka (Saxena et al. 2002); but no targeted resistance breeding programme was ever followed. Blister beetles also cause serious damage in some areas, but so far there is no genetic solution to overcome this constraint.

Since fusarium wilt and sterility mosaic diseases are prevalent in most pigeonpea growing areas, strategy to breed cultivars with genetic resistance to both the diseases was adopted and a number of cultivars and hybrid parents were bred. Also, for breeding resistant cultivars, using pedigree selection and selfing within the landraces had been very effective. In India for example, variety Maruti, a selection from ICP 8863 is proving a boon to the farmers of wilt-prone areas of north Karnataka and southern Maharashtra, with adoption rate in some districts as high as 60%. Similarly, in eastern and southern Africa, the most popular pigeonpea variety "Nandolo wanswana" a wilt resistant selection from a Tanzanian landrace (ICP 9145) has shown a big impact. In Malawi, it occupies > 60% area. Such genotypes have also been used extensively as donor parents in the breeding programmes. In 1992, ICRISAT developed a widely adapted variety ICPL 87119 (Asha). This variety, besides recording 20% high yield, exhibit high level of resistance to wilt and sterility mosaic diseases.

Breeding cultivars with resistance to abiotic stresses

Abiotic stresses often lead to productivity fluctuations in pigeonpea. The magnitude of damage to the crop depends on the frequency, intensity, and periodicity of the stresses. Therefore, breeding of tolerant cultivars is important for sustainable production across environments and years. To quantify the ill-effects of the stresses and to develop breeding strategies, various parameters such as stress tolerance index, stress susceptibility index, and geometric mean productivity were proposed to select tolerant genotypes. Besides this, information on the genetic basis of tolerance and identification of the tolerance-related traits is essential to formulate the selection strategy. The key abiotic stresses affecting pigeonpea are drought, temperature, salinity, and water-logging (Araujo et al. 2015).

Drought: Pigeonpea enjoys the reputation of being most drought tolerant pulse primarily due to its deep root system; hence, it grows well under most rainfed situations. In light soils, however, the crop often suffers from intermittent and terminal moisture stress and it responds positively to irrigation (Chauhan et al. 1987). Overall, the research towards understanding this stress in pigeonpea has been meager and inconclusive. Some physiological studies conducted in Australia by Lawn and Troedson (1987) revealed that drought situation in pigeonpea adversely affects light interception and production and partitioning of dry matter. The extent of yield losses, however, depends on the severity, timing, and duration of the drought. Terminal drought generally leads to leaf and flower drop and thereby results in reduced pod set and nitrogen accumulation (Muchow 1985, Chapman and Muchow 1985). It is clear that under the present scenario of scientific knowledge, the breeding for drought tolerance is not a possibility in near future. The best strategy to tackle this stress is to seek to escape the effects of drought by using cultivars whose maturity duration matches with the soil moisture.

Temperature: Traditionally, long duration (200-300 days) pigeonpea cultivars are sensitive to low temperature (<10^{o} C) during reproductive stage and affects both the development of floral buds and pollen dehiscence/fertilization. The effected plants produce a second flush of flowers and when the temperatures increase to 20^{o} C and beyond. Under these situations, plant maturity is delayed leading to significant yield losses. Sandhu et al. (2007) reported identification of 32 pigeonpea genotypes which exhibited tolerance to as low as 0° C temperature at Ludhiana and produced normal flowering and podding under the low temperature environment. So far no breeding activity has been initiated to address this abiotic stress.

Soil salinity: It is an ever-increasing production constrain in many parts of the world. Dua and Sharma (1996) reported that late maturing pigeonpea genotypes show better salinity tolerance than early types. Salinity also delays flowering by 10-15 days and it prolongs the peak period of flower production, and reduces pod number and seed weight (Promila and Kumar 1982). Singh et al. (2016) screened 120 diverse genotypes for salinity tolerance under laboratory and five genotypes were found be highly tolerant. Among wild species, *C. platycarpus, C. scarabaeoides* and *C. sericeus* were good sources of tolerance. According to Subbarao et al. (1991) and Wahid et al. (2006) the salt tolerance in pigeonpea was attributed to high concentrations of K^{+}, proline, free amino acids, and soluble sugars.

Water-logging: Sultana et al. (2013) reported that pigeonpea seedlings are most susceptible for water-logging. Hingane et al. (2015) observed emergence of aerenchyma and lenticels under water-logged situations and these facilitated oxygen supply to the plants for their survival. Both, Singh et al. (2016) and Sultana et al. (2013) recorded significant genetic variation for in vitro water logging in pigeonpea. They identified several water-logging tolerant genotypes in pigeonpea and among these ICP 8859, AL 1843, PAU 881, AH-06-8, AH-07-74 and ICPL 332 were prominent (Table 4). Among these, (Table 4) five genotypes exhibited tolerance to both water-logging and salinity (Singh et al. 2016). The inheritance studies showed that both water-logging (Perera et al. 2001) and salinity (Subbarao et al. 1991) tolerance were controlled by non-allelic single dominant gene. This implies that such genes could be transferred, singly or together, to the adapted cultivars for reducing losses caused by two key abiotic stresses. Once identified, MAS could speed up development of water-logging and salinity tolerant genotypes.

Table 4. List of water-logging and salinity tolerant genotypes identified at PAU, Ludhiana

Group	Water-logging	Salinity
Highly tolerant	AL 1843, PAU 881, AH-06-8, AH-07-74, ICPL 332	ICP 8859, AL 1843, PAU 881, AH-06-8, AH-07-74, ICPL 332
Tolerant	AL 1702, AL 1744, AL 1811, AL 1849, AL 1856, AH-06-3, AH-06-7, H-05-71, Pusa 2012-1, ICP 14085, ICPL 20241, ICPL 99051, ICPA 2039, BS 8	H-2000-14, H-2001-25, ICPL 20128, ICPL 20237, SGBS 6
Susceptible	ICP 8859, JBP 36B	AL 1758, AL 1760, AL 1778, AL 1843,

Modified from Singh et al. (2016)

Breeding cultivars for special niches

Rice-wheat rotation

A key development in pigeonpea agronomy occurred when it was realized that pigeonpea could be grown in rotation with wheat. Initially, an early variety UPAS 120 was used in this system but often it delayed the wheat sowings due to delayed maturity of pigeonpea caused by excess moisture or early winter rains. Although pigeonpea- wheat is less profitable than rice-wheat rotation but certain production constraints such as reducing productivity, increasing soil salinity and poor response to added fertilizers are forcing researchers to look for some alternatives; and the option of pigeonpea-wheat rotation has been found to be a viable option (Dahiya et al. 2002).

With the development of extra early maturing cultivars such as Manak, AL 15, and ICPL 88039, the adoption of this legume-cereal crop rotation has increased in Punjab, Haryana and Indo-Gangetic plains were bred and provided greater turn-around time for wheat sowings. The introduction of pigeonpea has provided farmers an option to replace the heavy water-demanding rice with pigeonpea that required only two irrigations for crop establishment. In this cropping sequence, the wheat crop also recorded additional yields around 1000 kg/ha. These increases were attributed to increased residual benefits, return of organic material rich in nitrogen, and other nutrients to the soil, besides permitting timely sowing of wheat crop (Dahiya et al. 2002). Although, the pigeonpea-wheat rotation has demonstrated a way forward for sustainability in the cereal dominated agriculture system, some challenges to achieve greater yields still need attention. These include availability of quality seed, managing insects, breeding of high yielding cultivars, and appropriate cultural practices.

Pigeonpea on slopping hills

In the slopping lands of Uttarakhand, repeated soil erosion and landslides are common events. This leads to the erosion of top soils leading to deficiency of organic matter and important micro and major nutrients. To overcome this problem, an extra early pigeonpea cultivar ICPL 88039 was introduced; and it exhibited an extra ordinary adaptation in the low and mid hills up to 1500 m elevation. This cultivar on average produced about 1000 kg/ha yields, with a maximum of 1878 kg/ha (Saxena et al. 2011). Besides this, it also arrested soil erosion. This cultivar was released as VL Arhar 1 for general cultivation in Uttarakhand.

Breeding of varieties for post-rainy season

The cultivation of pigeonpea during the post rainy season is popular in the areas where extended flooding is a common event during monsoon season. The farmers wait for water to clear and then start field operations for post rainy season sowings. Systemic research of cultivating pigeonpea in such areas was started at Dholi (Bihar). Due to strong photo-sensitivity of pigeonpea, the phenology of plants is drastically modified and this results in agronomic dwarfing, reduced biomass, increased harvest index, and synchronous flowering. Since pigeonpea is a short day plant, the flowering is induced in less time (around the shortest day) and consequently, the biomass production is also reduced; and it is directly related to the time of planting. The September-sown crop will have relatively more biomass than that of October-sown crop. The temperature also plays an important role in plant growth and development, and hence this production system is suited to the areas where winter is mild and there is no incidence of frost. These include the states of Bihar, Bengal, and coastal areas of Andhra Pradesh, Tamil Nadu and Odisha. Varieties such as Bahar, WB 20(105), AS 71-31, DA 11, Pusa 9 and NDA 3 have been found to adapt well in this cropping system. The post-rainy season pigeonpea crop is highly suited to mechanized culture. In Dholi yields up to 2-3 t/ha have been recorded repeatedly. The major challenge the crop often faces is the incidence of Alternaria blight (*Alternaria tenuissim*) disease. One of the germplasm collections ICPL 366 has been found to be highly resistant to this disease.

Breeding cultivars with special traits

Harvest index

Yield improvement by manipulating harvest indices has been a matter of speculation in pigeonpea due to its adaptation in diverse production systems and multiple traditional uses. The biomass production in pigeonpea has been reported to be positively associated with seed yield. According to Chauhan et al. (1995) while breeding high yielding cultivars the biomass has never been used as selection criteria and it appears that the breeders have unconsciously selected for greater biomass production capacity as the main determinant of yield. In most cases yield is positively linked to longer growing duration and very little of it from the ability for better partitioning. Even the enhanced capacity of hybrids is also linked to greater biomass production without altering their harvest index. Ideally, if greater biomass production could be combined with greater partitioning, it will lead to a greater potential and homeostasis in yield. To achieve this, it would be prudent if breeders/ physiologists start routinely measuring harvest indices in their materials through a well-established relationship between dry matter and yield. The improvement in harvest indices through reduced biomass production will compromise the use of pigeonpea for many of the other purposes for which the crop is traditionally cultivated. These include fuel wood, improvement of soil nutrition (through tremendous leaf fall) and soil structure (through extensive deep root system), and more importantly, the capacity of the plants to regenerate from ill effects of various biotic and abiotic stresses. In fact, so far no concerted effort has been made in this direction in any maturity group and the situation is not likely to change in the near future.

Temperature sensitive male sterility

Effect of various environmental factors on the expression of genes controlling male sterility or fertility has been well documented in different plant species (Kaul 1988). Recent success in breeding a temperature sensitive male sterility system in pigeonpea (Saxena 2014) has opened up new options (technology) for breeding hybrids. Such male sterile lines when exposed to low (< 24^{o} C) temperature regimes, become fully fertile and produce self-pollinated seeds; hence, unlike normal CMS lines, it will not require any maintainer (B-) line for seed multiplication. The same A-line when sown under high (>25^{o} C) temperature regime, will remain male sterile. Adoption of this hybrid technology would require identification and use of seperate seed production sites with strict temperature reqirements for the seed production of the A-lines and hybrids.

High protein content

The problem of protein mal-nutrition among people living under subsistence level is growing with dangerous proportions, due to increasing population, limitation of arable land and low productivity. Hence, there is a need to produce more protein per unit area. The present day pigeonpea cultivars contain about 22% protein (Saxena et al. 2002) and breeding new cultivars with high protein would be a right step forward. Since the genetic variation for protein content is limited (Narsimha and Desikachar 1978; Manimekalai et al. 1979; Singh et al. 1984), the alternative sources of high protein germplasm were used from secondary gene pool to breed high protein pigeonpea cultivars.

Information on the genetic nature of protein content is essential for effective breeding results, but unfortunately, little research has been conducted on this aspect in pigeonpea. Dahiya and Brar (1977) and Durga (1989) recorded a strong maternal influence on the expression of protein content of an F_1 individual. Dahiya et al. (1977) reported that in pigeonpea at least 3-4 genes controlled its protein content. Durga (1989) reported that protein content in pigeonpea was controlled by additive and complementary gene action; and low protein was dominant or partially dominant over high protein. Saxena and Sharma (1990) while reviewing the subject concluded that in pigeonpea both additive and non-additive genetic variations were important for the expression of seed protein.

Three high protein (28.5-30.5%) wild species donors, *C. scarabaeoides*, *C. sericeous*, and *C. albicans* were used in breeding high protein lines. These species can be crossed easily with cultivated types but had undesirable agronomic traits such as small seeds (1.9-2.8 g/100 seeds), seed shape (flat, irregular), seed colour (grey, black), plant type (creeper, trailing) and perennial with long maturity duration. Therefore, the selection of desirable segregants combining high protein and good agronomic traits was difficult. In F_9 generation, a few selections with high (28-32%) protein content, acceptable seed size (9-10 g/100 seeds), and brown coloured round seeds were made. The agronomic evaluation of the lines derived from these selections revealed that inbreds HPL 40-5 and HPL 40-17 produced over two tonnes/ha grain yield with 27% protein (Saxena and Sawargaonkar 2015). This accounted for an additional protein harvest of about 100 kg/ha. These results also demonstrated that in pigeonpea seed yield, seed size and protein can be enhanced simultaneously. Biological evaluation of these lines showed that the high-protein selections were also significantly superior to the control cultivar in utilizable protein. These were nutritionally superior to control cultivar due to their greater sulfur-containing amino acids (Singh et al. 1990). Hence, their whole seeds or decorticated split peas (*dal*) have potential to address the issues related to protein mal-nutrition.

Modern breeding technologies and accomplishments

Breeding hybrid cultivars

To breed high yielding cultivars pigeonpea breeders in the past deployed pedigree selection and released dozens of varieties, but without any significant gains in their productivity. In this context, the recent success in evolving a hybrid pigeonpea breeding technology (Saxena 2015) holds promise. It has generated a lot of optimism and enthusiasm among the breeders to smash the decades-old yield plateau.

To develop this technology as a first step, the CMS lines, their maintainers and fertility restorers were bred. The natural out-crossing was used to produce hybrid seeds. The first set of hybrids was evaluated in multi-location trials in 2006. The range of standard heterosis (superiority of hybrid over control cultivar) was vey encouraging. GTH 1, was the first early maturing CMS-based hybrid with A_2 cytoplasm that was bred at Gujarat Agricultural University. In multi-location trials, this hybrid recorded > 50% yield advantage over the control. In the on-farm demonstrations also it recorded 25.3% standard heterosis, and soon it was identified for release but failed to restore male fertility under diverse environments. Since the largest area under pigeonpea cultivation is under medium maturing cultivars (161-200 days), this group received priority in breeding hybrids. In this group a number of hybrid parental lines were bred and over 5,000 hybrid combinations were tested. As expected, the hybrids demonstrated a large variation for standard heterosis, but interestingly, about 10% of them exhibited in excess of 30% heterosis. It is believed that some of the hybrids such as ICPH 3491 (57% heterosis), ICPH 3497 (44% heterosis), and ICPH 3481 (41% heterosis), which performed consistently well in diverse environments can benefit the farming communities in future. The traditional long duration (>250 days) pigeonpea cultivars have limited adaptation to the soils that are deep and have high moisture holding capacity. In this group, the potential of hybrids is also high but not much breeding research has been carried out. Some hybrids such as ICPH 2307 (53% heterosis), ICPH 2306 (39% heterosis), and ICPH 2896 (38% heterosis) hold promise.

The first CMS-based commercial pigeonpea hybrid ICPH 2671 was produced at ICRISAT. In the multi-location trials (2005 to 2008), it recorded 35% superiority over the control cultivar Maruti. In 1,829 pre-release on-farm trials, conducted in five provinces and using farmers' cultural practices, the hybrid ICPH 2671 (1400 kg/ha) produced 52% more yield (Table 5) than the local check (954 kg/ha). Considering its overall performance, ICPH 2671 was released for cultivation in 2010 in Madhya Pradesh (Saxena et al. 2013). After this breakthrough, hybrids ICPH 3762 (unpublished) and ICPH 2740 (Saxena et al. 2016) were also released in states of Odisha and Telangana, respectively. Both these hybrids recorded mean yield advantage of about 40% ove the popular cultivars in farmers' fields.

Table 5. Seed yield (kg/ha) of hybrid ICPH 2671 in the on-farm trials

State	Farmers (no.)	Hybrid yield	Control yield	Standard heterosis (%)
Maharashtra	782	969	717	35
Andhra Pradesh	399	1411	907	55
Jharkhand	288	1460	864	69
Madhya Pradesh	360	1940	1326	46
Total/mean	1829	1445	954	52

Source: Saxena et al. (2013)

After some initial setbacks, the hybrid pigeonpea seed technology was also perfected (Saxena 2015). The on-farm validation of hybrid seed production technology was done in diverse environments (Table 6). On average, the hybrid yields in Madhya Pradesh (2242 kg/ha) were greater than those recorded in Telangana state. Such harvests gave a healthy seed-to-seed ratio (1: 200 to 1: 300). The cost of producing of one hectare of pigeonpea hybrid seed, excluding the rental value of land, was Rs. 26,395. This seed plot produced hybrid yield of 1440 kg/ha and resulted in the net profit of Rs. 70,000/ha. Using these estimates, the farm gate price of hybrid seed was Rs.18.85/kg.

Table 6. Hybrid seed production (kg/ha) recorded in six states

State	Locations	Mean yield	Highest yield
Andhra Pradesh	34	998	1750
Madhya Pradesh	9	1674	3040
Gujarat	4	1179	1669
Maharashtra	5	603	1017
Odisha	40	523	1040
Karnataka	2	1138	1900
Total/Mean	94	1019	3040

Source: ICRISAT reports

In the rainfed farmers' fields the hybrids often produced 1000-1500 kg/ha grain; these productivity levels were doubled and, sometimes, even crossed 4000-5000 kg/ha mark (Saxena 2015). Such productivity levels at commercial level are very encouraging and more farmers are adopting this technology. Therefore lately, the attention has shifted to expand the area under hybrid cultivation. In this context, the release of a disease resistant widely adapted medium duration hybrid ICPH 2740 has played a key role. In 2015, the hybrids occupied around 100,000 ha, and in 2016, it was increased to over 150,000 ha. At present the area expansion is receiving attention of central and various state Governments (Saxena et al. 2016b) and it is expected that soon the hybrid technology will benefit a large number of Indian farmers.

Genomics

In contrast to above mentioned advances the genomics research in pigeonpea geared up relatively recently with the development of 'Pigeonpea Genomics Initiative' and further expansion with "International Initiative for Pigeonpea Genomics" consortium. Several genomic enriched libraries, BAC clone libraries and transcriptome assemblies were established for the development of PCR-based simple sequence repeat markers (6,212 BES-SSRs and 8,137 EST-SSRs) and comparing genes and genomic structures with other species. Later, DArT arrays comprising of 15,360 loci, GoldenGate platform with 768 single nucleotide polymorphism and competitive allele-specific polymerase chain reaction (KASPar) assays for 1,616 SNPs were developed. In additionally, 5692 single feature polymorphisms and intron spanning region (ISR) markers have also been developed (RK Saxena et al. 2014). These markers have been used to construct a number of inter-specific and intra-specific genetic maps and for quantitative trait loci analysis. In the year 2012 pigeonpea genome sequence was decoded (Varshney et al. 2012), which further enriched the genomics resources with millions of markers. Genome sequence information has also provided details on genes, repetitive DNA and transposable elements and understanding the composition and organization of the pigeonpea genome. Comparison of pigeonpea genome with other crop species genomes revealed clusters of genes that were common and specific to the pigeonpea. Presently, this information from genomics is being used to identify the markers associated with the traits of importance deploy them in genomics assisted breeding, understanding the evolutionary aspects, bringing novel alleles to broaden the genetic base. The details on this subject including relevant literature are given in the article written by RK Saxena and Rajiv Varshney and available in this volume.

Transformations

Recent research in pigeonpea genetic transformation has resulted in development of transgenic plants resistant to various diseases and insect pests (Sharma et al. 2006). Genetic improvement through traditional breeding for pod borer resistance has been restricted due to non-availability of reliable genetic sources; and to overcome this constraint, recombinant DNA and genetic transformation technology are now being used. The genetic engineering approaches using both tissue culture as well as *in planta* methods of transformation have been attempted by various groups to incorporate resistance to *Helicoverpa* pod borer. The genes producing insecticidal proteins from *Bacillus thuringienses*, proteases and chitinase are being used (Bhatnagar-Mathur, pers. comm.). The expression of chimeric *cry1AcF* gene in transgenic pigeonpea has been demonstrated towards resistance to *Helicoverpa* (Ramu et al. 2011). A large number of transgenic events are currently being evaluated for their efficacy at ICRISAT and IIPR. Interestingly, these events not only showed high larval mortality but they also resisted the larval damage. Gene pyramiding with two different insecticidal genes and tissue-specific expression has been attractive options to for durable insect resistance. Besides this, ICRISAT is also involved in developing bio-fortified pigeonpea for enhanced beta-carotene levels (Bhatnagar-Mathur pers. comm.). Research has also been initiated to develop pigeonpea transgenics by using the phytoene synthase gene (*psy1*) that converts geranylgeranyl pyrophosphate to phyotene. Increase in the phyotene content during the biosynthetic pathway of carotenoids increases the â-caretone level, which is a precursor of Vitamin A and is likely to contribute towards the malnourished population.

Future research and development strategy

Environmental characterization

India is climatically very diverse and although the country has been divided into agro-ecological regions based on expert opinion; these may or may not be relevant to pigeonpea. In fact, the target production environments (TPEs) for pigeonpea will need to be re-defined for cultivating early, medium, and long duration types. Such regions will also need to be further characterized for yield potential, risk to production, yield gap and drought and thermal regimes as has been done by agro-climatologists for mung bean and chickpea in Australia (Chauhan pers. comm.) using a modeling approach. A major advantage of this approach is that besides prioritizing breeding objectives for drought and other abiotic constraints, it can help identify key locations representing individual agricultural eco-regions that can be used for conducting multi-location tests, and also give the likely idea of the adaptation zone of a variety. A variety identified to be superior in a particular agro-ecoregion may have better specific adaptation to that region and a variety found to be superior in more eco-regions could be more widely adapted.

Pre-breeding initiatives to enrich genetic variability

Pre-breeding is a futuristic research approach that deals with diversifying genetic base of breeding materials for selection. Since it is a long-term activity and involves utilization of distant relatives carrying useful genes/traits, the selection of parental lines should be done with utmost care.

Secondary and tertiary gene pools are very valuable resource for crop improvement. Pigeonpea has 32 wild relatives with very diverse genetic base. The tertiary gene pool cannot be crossed easily with cultivated types. The exception is *C. platycarpus,* which can be crossed with pigeonpea using tissue culture technology (Mallikarjuna and Moss 1995). The crossable wild relatives of pigeonpea (Table 7) carry a number of useful traits. These include high seed protein in *C. albicans* and *C. scarabaeoides*; resistance to sterility mosaic virus in *C. lineatus* and *C. sericeus*; resistance to *Phytophthora* blight in *C. platycarpus*, and tolerance to *Helicoverpa* pod borer in *C. scarabaeoides*. Interestingly, a considerable genetic variation has been reported among the accessions with in a wild species. The diverse crosses, generally suffer from unwanted linkage drag and hence, appropriate selection strategies should be made to utilize these species. The major accomplishments of wide hybridization in pigeonpea include development of (i) cytoplasmic nuclear male sterility systems (cytoplasm donor *C. cajanifolius*), (ii) high protein genotypes (donor species *C scarabaeoides*), (iii) extra early photo-insensitive lines (donor species *C. platycarpus*), and (iv) pod borer tolerant lines (donor species *C. platycarpus*).

Table 7. Crossable wild relatives of pigeonpea available for potential use in pre-breeding

Cajanus spp.	Pod borer	Alternaria blight	Sterility mosaic	Phytophthora blight	Soil salinity	Cyst nematode	High protein
acutifolius	*						
albicans	*	*	*		*		*
cajanifolius		*					
lineatus		*					
reticulatus	*						
scarabaeoides	*	*	*		*	*	*
sericeous	*	*		*	*		*
platycarpus		*		*	*		*

Diversification of CMS lines

In most crops the cytoplasmic diversity is limited and the commercial hybrids are based on one or two cytoplasm. In a dynamic hybrid breeding programme, it is essential that sufficient diversity is maintained among female parents. This will protect the hybrids from any potential genetic threat arising due to single cytoplasmic genome that may carry genes susceptible to certain biotic or abiotic stresses. In pigeonpea the male sterility systems have been diversified for both nuclear as well as cytoplasmic diversity. So far nine diverse cytoplasms representing nine *Cajanus* wild species have produced CMS systems (Saxena et al. 2010, Saxena 2013). Among these, the A_4 cytoplasm has been used in breeding commercial hybrid cultivars; and the A-lines carrying this cytoplasm have also been diversified at nuclear level to facilitate hybrids for different maturity groups and cropping systems (Saxena and Tikle 2015). In commercial hybrid programmes genetic diversity plays an important role in the expression of hybrid vigour. The mitochondrial genomic diversity can be ascertained using RFLP patterns. In rice, about 95% of the commercial hybrids have the same WA cytoplasm (Brar et al. 1998) and it is not a healthy situation. In pigeonpea also, the breeders should take a serious view of it and attempts should be made to diversify the cytoplasm base of A-lines. Hence, before launching the cytoplasmic and nuclear diversification programmes, it would be useful to assess the candidate genotypes for their nuclear/ cytoplasmic diversity at molecular level.

Identification of heterotic groups

Even though the genetic mechanisms that explain heterosis are not fully understood, the value of genetically distinct parents in hybrid breeding has been well established. Richey(1922) demonstrated the importance of geographic (=genetic) diversity in the manifestation of hybrid vigour. Subsequently, various concepts and processes of selecting elite hybrid parents were proposed and used from time to time; and lately, the concept of 'heterotic groups' emerged. It involved clustering and of parental lines on the basis of their combining ability, origin, or genetic diversity to identify hybrid parents and breed hybrids with greater performance. In recent times, the availability of improved statistical and genomics tools have made the formation of heterotic groups (Aguiar et al. 2008) more refined and meaningful.

In pigeonpea, Saxena and Sawargaonkar (2014) developed the first set of heterotic groups that were established using multi-location hybrid yield data. Based on specific combining ability data, they constituted seven heterotic groups and also demonstrated that the hybrid yield was much greater when the parental lines represented two diverse heterotic groups. Pandey et al. (2015) used multivariate analysis to develop heterotic groups in long duration pigeonpea. Aguiar et al. (2008) opined that use of SSR markers eliminated environmental and genotype x environment effects, and therefore, the results were not in full agreement with phenotypic data. Mudaraddi and Saxena (2015) used SSRs to classify 20 pigeonpea A-lines and 132 fertility restorers into different heterotic groups. They formed two heterotic groups of the male sterile lines, while the fertility restorers exhibited relatively more variability and formed three heterotic groups. In this study, the inter-specific derivatives formed a distinct and diverse group, but the hybrids involving these lines were unproductive due to linkage drag.

Increased public private partnerships

The profitability from hybrids needs to high enough to attract both seed producers and cultivators. The success in such an endeavour, however, depends in harnessing complementary skills of partners, specializing in different disciplines. At present, the hybrid pigeonpea programme is well knit with various ICAR institutions and state universities. The partnership of ICRISAT with the private seed sector has been fruitful in sharing breeding materials and resource mobilization under the umbrella of 'Hybrid Parents Research Consortium'. The mainactivities of this partnership are sharing of technology, training of pesonnel, and organizing field days, and formal/informal discussions. These partnerships helped in taking the hybrid technology to the door-steps of farmers.

Summary and conclusions

To overcome the global shortage of pigeonpea it is important that positive advances be made in both vertical and horizontal directions. In the last few decades a number of milestones have been achieved and the national pigeonpea area and production have recorded significant gains. On the research and development fronts, the following three pigeonpea breeding accomplishments have made a significant impact in the recent past.

- Breeding of extra and super early cultivars with wide adaptation,
- Broad-based disease resistant medium and long duration inbred cultivars, and
- Evolution of trend-breaking hybrid technology.

The extra early cultivars have revolutionized the traditional agriculture in new niches. These include introduction of pigeonpea on the slopping hills, low rainfall areas of Rajasthan, and diversification of rice-wheat system. This endeavour has not only increased the production but also has helped in rejuvenating soils with respect to its structure and nutrition. Breeding of broad-based disease resistant medium and long duration inbred cultivars has helped in reducing huge losses caused by wilt and sterility mosaic virus to provide greater stability of production. The hybrid pigeonpea technology has potential for additional productivity of 1000-1500 kg/ha. The development of a sustainable pigeonpea seed chain remains the key for success because of natural out-crossing. Pigeonpea is capable of fulfilling various social, nutritional, and economic needs of smallholder farming communities. The State Agricultural Universities, National Food Security Mission, State Departments of Agriculture, and public and private seed sector are supporting the crop for enhancing its productivity and production and this will pave the passage for the national food security and long-term agricultural sustainability. However, major challenges of enhancing on-farm productivity and genetic solution for managing insect pests still haunting the researchers and policy makers.

Declaration

The authors declare no conflict of interest.

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