

Nectarivore-aided Hybridization and its Exploitation for Productivity Enhancement in Pigeonpea

KB Saxena, AN Tikle, RV Kumar, AK Choudhary, and Bir Bahadur

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT),
Patancheru, 502 324, Telangana, India

¹Former Principal Scientist, ICRISAT, Patancheru, India,

Present address: 17- NMC Housing, Al Ain, Abu Dhabi, U.A.E. kbsaxena1949@gmail.com

²Sr Pulse Breeder, RAK Agricultural College, Sehore, MP, India. antiklepb@gmail.com

³Senior Manager, ICRISAT Patancheru, India, rvku3ar@gmail.com

⁴Principal Scientist, ICAR Research Complex, Darbhanga, India, akicar1968@gmail.com

⁵Department of Botany, Kakatiya University, Warangal, India. birbahadur5april@gmail.com

Abstract- A record of out-crossing in pigeonpea (*Cajanus cajan* (L.) Millsp.) from 32 locations indicated a large variation within and across 12 countries of Asia, Africa, and Americas. Pigeonpea breeders have exploited the natural hybrids within landraces for developing high yielding inbred cultivars in different countries. Similarly, natural hybrids selected from wild relatives of pigeonpea have been used to breed male sterility systems. During the last 40 years the importance of natural out-crossing in genetic enhancement of yield in pigeonpea has been well recognized, particularly in developing commercial hybrid technology; and it has allowed thousands of Indian farmers to harvest 30-40% more grains. This review provides an update on various aspects of natural out-crossing such as pollinating agents, extent of out-crossing, factors influencing out-crossing; besides this, the successful role of out-crossing in the genetic enhancement of yield in pigeonpea has also been discussed.

Index Terms- *Cajanus cajan*, hybrid seed production, cytoplasmic nuclear male sterility, natural hybrids, natural out-crossing.

I. INTRODUCTION

Food legumes are considered a group of highly self-pollinating crops which maintain their genetic purity under natural growing conditions; but it is not entirely true and certain level of natural out-crossing has been recorded in faba bean (*Vicia faba* L.), pigeonpea (*Cajanus cajan* L.), grass pea (*Lathyrus sativus* L.), soybean (*Glycine max* L.), mung bean (*Vigna radiata* L.), and common bean (*Phaseolus vulgaris* L.). In spite of knowing the ill effects of out-crossing on the genetic contamination of breeding materials and cultivars (Howard et al., 1919; Wilsie and Takahashi, 1934; Kadam et al., 1945; Gupta et al., 1981a), the legume breeders always resorted to breeding pure line cultivars. Some efforts to use the out-crossing in the genetic enhancement of yield were also made through hybrid breeding in crops like faba bean (Bishnoi et al., 2012), soybean (Palmer et al., 2001), and pigeonpea (Saxena, 2015). Among these, the constraint of out-crossing was converted into an opportunity in pigeonpea only with three commercial hybrids being available for cultivation in southern and central India (Saxena and Tikle, 2015). In this paper

an attempt has been made to review various aspects of natural out-crossing and the ways in which this natural phenomenon has been exploited in genetic enhancement of productivity in pigeonpea.

II. PIGEONPEA FLOWER AND NECTARIES

Reddy (1990) studied floral morphology of pigeonpea and reported that its typical flower has zygomorphic corolla with petals. Corolla handedness in respect of contortion of wing petals either to the left or right hand side in different flowers on the same raceme a unique feature was first reported in *Papilionaceae* by Bahadur and Rao (1981). In the past aestivation of *Papilionaceous* flower was reported to be typically vexillary, i.e. descending imbricate (see Jackson, 1940). However, based on a critical study of 29 genera comprising 52 species, Rao et al. (1986) brought to notice that the vexillary aestivation shows considerable variation and recognized various types viz., *Butea* type (handedness present in both wings and vexillum; *Cajanus* type (handedness present only in vexillum only; *Phaseolus* type (handedness present in wing petals only and handedness present both in vexillum and wing petals with sub-types called as *Gliricida* type and *Crotalaria* types, respectively. This aestivation mechanism, the authors believed, is to compact the floral bud and ensure self-pollination initially as well as entomophily at later stage. Standard petal is clawed at base, 14-22 mm long and 14-20 mm width. The wing petals of pigeonpea are asymmetrically biauriculate, 15-20 mm long and 6-7 mm wide, obovate with a straight upper margin and clawed base. The keel petals are boat-shaped, 14-17 mm long, 5-7 mm wide, clawed, dorsally split and cover both androecium and gynoecium. Pigeonpea flower has 10 stamens, oriented in a diadelphous (9 +1) format. The odd stamen has a groove that provides passage for nectar that is secreted at the base of filaments. The anthers of pigeonpea are ellipsoid, about 1-2 mm long, yellow, and tapering towards the top and flattening at the base. The style is long, filiform, glabrous and attached to a thickened and capitate (swollen) stigma. The ovary is superior, sessile with marginal placenta and 2-9 ovules (Reddy, 1990).

In spite of representing leguminous family the pigeonpea flowers are not truly cleistogamous; and only for the first 2-3

days the buds remain cleistopetalous (closed); and during this period 70-80% of them get self-pollinated. Subsequently, both pollinated as well as un-pollinated buds open and they remain in this condition for the next 24-48 hours. During this period the pollinating insects visit the flowers in search of nectar and affect cross-pollination. Thus pigeonpea flowers with a peculiar floral morphology, as described above, encourage both self- as well as cross-pollination on the same branch of the plant. Lord (1981) described such floral configuration as "pre-anthesis cleistogamy". Rao and Bahadur (1981) attempted to understand the dimorphic nature of stamens in pigeonpea and classified various developmental stages of the flower into seven groups starting with young bud to mature flower. They noted that in early stages the 10 stamens are clearly dimorphic in height and also differ slightly in anther shape and with diadelphous configuration. Of these, four have short filament and the remaining six, including the odd posterior (free) stamen that is grooved at base for insects to access nectar, have long filaments. They cohere and form a staminal column to remain free from the keel petals. The filaments of short anther tier grow rapidly during the final stage in such a way that all the stamens come to the same level at maturity. Anthers of pigeonpea are connivent; dehiscing by longitudinal slits; latrorse/introrse. Anthesis of short stamens precedes that of the longer stamens. Pollen grains of both stamens are monads/single, yellow, powdery, binucelate and equally viable and show reticulate exine as seen under scanning electron microscope, being slightly larger in size (34.5 microns) from short stamen tier than those of the longer tier measuring 32.8 microns. Pollen grains from both the stamen tiers shed almost synchronously and accumulate in keel till the corolla unfolds enabling the slender style with globose stigma to emerge through the centre of the staminal column picking up the stored pollen from the keel affecting self-pollination. As the flowers are cleistogamous and the life of the flowers stretches for few days only, nectar secretion continues and the foragers effectively bring about cross-pollination as well by depressing the keel and exposing the wet receptive stigma to the pollinators' body.

To date there is no comprehensive information on nectary, nectar chemistry, nectar dynamics and the mechanism of nectar robbing by various insect visitors and potential pollinators of pigeonpea. Gulyas and Kinscesek (1982) investigated the floral nectarines of 26 genera and 46 species of *Papilionaceae* and recognized various types of nectaries of which three are staminal. Due to non-availability of this rare publication, pigeonpea breeders were unaware of this information which is so vital for flower-insect visitation for nectar and consequently pollination and breeding. However, it is necessary to mention that in *Lathyrus* and *Trifolium* the nectary is epimorphic, opposite the free stamens and form a ring; while in *Phaseolus* the nectary is pipe-like on either sides of the stamens and ring-shaped opposite to the 10th free stamen as in *Vicia faba* (Gulyas and Kinscesek, 1982). Details of *Cajanus* nectaries are not available but look similar to *Vicia*.

III. THE FORAGERS AND THEIR ACTIVITIES

For mass cross-pollination it is essential that the transfer of pollen from male parent to female is performed easily; and in nature it is accomplished by certain external agencies such as

wind, water, and/or animals. Natural cross-pollination in pigeonpea was first reported in the early part of 20th century by Howard et al. (1919) but the definite information about pollinating agents was not available. To quantify the role of wind in cross-pollinating pigeonpea, Kumar and Saxena (2001) conducted an experiment under controlled conditions using a strong wind blower and concluded that in pigeonpea wind does not play any role in cross-pollination, implying that under field conditions some other external factors are responsible for pollen transfer. Howard et al. (1919) postulated that insects were responsible for cross-pollination in pigeonpea, but the first attempt to identify the insects was made by Sen and Sur (1964). They observed high activity of thrip (*Megalurothrips usitatus*) both inside and outside the buds and flowers, and opined that these might be responsible for cross-pollination in pigeonpea. Williams (1977) also reported that thrips were quite active in foraging pigeonpea flowers, but she but did not visualize their positive role in cross-pollination. Gupta et al. (1981b) observed that the thrips, although carried pollen and moved a lot in and around flowers but being tiny creatures they were unable to perform cross-pollination. The reasons for the inability of thrips to pollinate pigeonpea flowers are not clear and in this direction an elaborate study is warranted.

Pando et al. (2011) observed that during foraging, a load of pollen got stuck on proboscis, hairs, silk, legs, abdomen, thorax, and mouthparts of the insects and that each insect had 5500 to 107,333 pollen grains and >90% of this were from pigeonpea (Williams, 1977). Pathak (1970) recorded *Apis mellifera* and *A. dorsata* as the main pollinators in pigeonpea. Williams (1977) reported >24 insect species visiting pigeonpea flowers but only *Megachile bicolor* and *M. conjuncta* were involved in cross-pollination at Patancheru (India). *Xylocopa* (carpenter bee) and *Bombus* (bumble bee) species affected cross-pollination in Kenya (Onim, 1981). In Punjab (India), Brar et al. (1992) reported both *Megachile lanata* and *Apis dorsata* were the main pollinators, while Verma and Sidhu (1995) observed high activity of *M. lanata* and *Xylocopa* species on pigeonpea flowers. Zeng-Hong et al. (2011) found that in Kunming (China), insects belonging to *Megachile*, *Xylocopa*, and *Apineae* species were most frequent visitors to pigeonpea fields and they actively participated in cross-pollination. In Nepal, 13 insect species were recorded on pigeonpea but only *A. mellifera* was involved in cross-pollinating pigeonpea (Thapa, 2006). In Cameroon, Mazi et al. (2014) reported 19 insect species visiting pigeonpea fields in Dang, but *Chalicodoma rufipas* and *Megachilidae* were the main foragers and these species were active in sucking nectar and cross-pollination. Pando et al. (2011) reported that in Yaounde among the insects that visited pigeonpea flowers, 46.15% were from family *Apidae* and 42.14% from *Megachilidae*. Among these, *Chalicodoma cincta cincta* were most frequent (28.99%) visitors, followed by *Xylocopa* (22.04%) and *Apis mellifera* (11.41%).

Saxena and Kumar (2010) reported that at ICRISAT a number of insect species frequently visited flowers of both pigeonpea as well as its wild relatives and observed that on a clear sunny day the peak insect activity was between 1000 and 1600 h; while in Cameroon the insect activity in pigeonpea fields started at 0700 h and continued till 1600 h; and it peaked between 0009 -1000 h (Pando et al., 2011). Onim (1981) reported that each insect visit to pigeonpea flower lasted for 15-

55 seconds; while Pando et al. (2011) recorded a high foraging speed of 10.33 flowers/min. Mazi et al. (2014) reported that bees, on average, hovered and showed buzzing activity on a flower for 28 seconds to collect pollen, 43 seconds to collect nectar, and for 63 seconds to collect both nectar and pollen. They also mentioned that 54.45% of the visiting insects collected both pollen and nectar. Pando et al. (2011) reported that out of 19 insect species visiting pigeonpea flowers, 13 collected both pollen and nectar, 3 collected only nectar and the remaining 3 species were involved in collecting only pollen. In an experiment conducted at ICRISAT under net houses containing hives, it was observed that *Apis mellifera* did not visit plants with no pollen grains (M.I. Vales Pers. Comm.). In a significant study Zeng-Hong et al. (2011) reported that the pollinating insects were more frequent on male fertile plants with a mean of 4.8 visits /10 minutes as compared to male sterile counterparts which recorded only 2.8 visits /10 minutes. They attributed this differential behaviour to presence of chemicals (flavone and flavonol), nectar, and a specific scent that is produced by mature pollen grains to attract the insects.

IV. NATURAL CROSS-POLLINATION

Natural out-crossing in pigeonpea occurs at almost every place; its extent however, varies from place to place. The natural out-crossing in pigeonpea was first noticed in 1909, when Howard et al. (1919) observed incredible bee activity on pigeonpea flowers. They also reported a large variation for different traits in single plant progenies selected from farmers' fields. In 1912-13, they conducted the first ever field experiment to determine the extent of natural out-crossing in pigeonpea. Genotypes with yellow petals and white seed coat (both recessive traits) were used as female parent and those with red petals and brown seed coat (dominant traits) were used as contaminant. Based on the scoring of F₁ plants for flower and seed color, they estimated the extent of out-crossing among progenies from 2.25 to 12.0%. Based on these significant observations they concluded that "natural out-crossing was a common event in pigeonpea and insects were involved in this". Subsequently, a number of reports have appeared from different locations/countries showing a wide range (Table 1) in the extent of natural out-crossing in pigeonpea.

In India, reports from 16 locations were available which showed a wide range (0 to 48%) in the extent of out-crossing. A single study from China reported that in Guangxi province the natural out-crossing in pigeonpea ranged from 0 to 60% with a mean of 24.6% (Yang et al., 2003). In Sri Lanka, Saxena et al. (2004) reported 0.14 to 19.64% natural out-crossing. In Nepal (K.B. Saxena, Pers. Comm.) and Myanmar (Kyu Kin Lay, Pers. Comm.) the out-crossing was observed to be between 20-30%. In Kenya, Onim (1981) reported 12.6% (Kibos) to 70.0% (Kabete) out-crossing; while in Uganda 8-22% out-crossing was recorded by Khan (1973). In Cameroon, 15-39% out-crossing was recorded by Pando et al. (2011). In Puerto Rico, the levels of out-crossing were low; while in Trinidad (Ariyanayagam, 1976) and Australia (Byth et al., 1982) the out-crossing ranged from 2-40%.

In most cases the reasons for this variation were difficult to understand but in some cases the reasons were well defined. For

example in Sri Lanka and Australia, the observed differences in the out-crossing were attributed to the variation in floral morphology. In Sri Lanka, <1% out-crossing was recorded in the line with cleistogamous (Saxena et al., 1994) flowers; while 40% out-crossing was recorded in cv. ICPL 87, which had normal (pre-anthesis cleistogamous) flowers. Similarly in Australia, the low out-crossing in cv. Royes was due to its wrapped petals (Byth et al., 1982), but in cv. ICPL 87 the out-crossing was high (40%). Interestingly, at Patancheru, the out-crossing in cv. Royes was also high (Saxena et al., 1987). These observations suggested that both in Australia and India (Patancheru) the density of pollinators was high, but their constitution was different.

V. FACTORS ENCOURAGING NATURAL CROSS-POLLINATION

Pigeonpea flowers are borne in bunches on racemes of variable lengths and, unlike most legumes, their morphology and biology make them prone to both self- and out-crossing. Besides population density of pollinators, some other factors which encourage out-crossing directly or indirectly are discussed in the following text.

5.1 Nectar production

Nectar is a thick sugary liquid secreted by floral nectaries to attract pollinating insects, and contains sugars (sucrose, glucose, and fructose), various amino acids, lipids and even alkaloids etc. (see reviews on nectar chemistry by Bahadur et al., 1986, 1998). The amount of nectar produced by plants determines the insect visitations, their foraging speed, and ultimately the extent of cross-pollination. Fischer and Leal (2006) reported that bigger flowers produced more nectar in *Passiflora coccinea*, while Heinrich (1979) observed that the amount of nectar secreted by an individual flower will be based on the balance between plant frugality and its requirement to attract pollinators. Radhika et al. (2010) reported that nectar production in *Brassica napus* starts with the opening of flowers, it peaks when the corolla is fully expanded, and continues until the corolla wither. They further reported that nectar production is regulated by a phyto-hormone called as "jasmonic acid", which is produced endogenously just before the release of nectar from floral nectaries. Severson and Erickson (1984) reported that in soybean floral structure was responsible for nectar production. They also observed significant genetic variation among soybean cultivars for various floral characteristics such as morphology, nectar production, and nectar quality. Hence, breeding for greater nectar content and attract more pollinating bees is a possibility (Palmer et al., 2001). Cunningham et al. (2006) reported blend of volatile benzoid and monoterpeneoid linalool odours from flowers in *Cajanus* that helps in relative preferences of foragers especially *Hymenoptera* insects.

In pigeonpea information on different aspects of nectar production is limited. Kumar et al. (2009) reported that nectaries in pigeonpea are located at the base of perianth and that the nectar production is consistent throughout the day across the entire flowering duration. The nectarivore insects extend their proboscis and while sucking the nectar they brush anthers to collect pollen grains or pistil for pollination. The insect activity in pigeonpea peaks in the second week of flowering, and during

this period, the flowers produce sufficient nectar to attract repeated visits of nectarivore, and once the pollination and fertilization are over, the nectar is gradually absorbed back into the plants system (Kumar et al., 2009). Yogesh et al. (2009) reported the nectar sugar production in two cultivars of pigeonpea. They noted nectar sugar content of flowers at different time intervals and noted no difference in dry nectar sugars content of flowers plucked at different hours of the day.

5.2 Extended stigma receptivity

Extended period of stigma receptivity is another key factor encouraging cross-pollination and fertilization in pigeonpea. Dalvi and Saxena (2009) reported that pigeonpea stigma becomes receptive a day prior to flower opening; and for the next three days, including the day of flower opening, it peaks. At this time the petals start unfolding with about 35% of the buds still containing receptive stigma and they remained so for the next two days and this period coincides with the visits of nectarivore insects, and while sucking nectar they collect pollen grains and transfer them on to stigmatic surface of other flowers. It is relevant to mention that the anatomy and cyto-chemical aspects of *C. cajan* shows that the style is hollow with few layers of boundary cells, while the stigma is wet and receptive with copious non-specific esterases and acid phosphatases (Sunanda and Shivanna, 1992).

5.3 Extended flowering duration

Perennial and non-determinate growth habit of pigeonpea allows plants to continue their vegetative and reproductive stages simultaneously. They remain in this condition for extended periods until the required pod set is attained or growing conditions become unfavourable. For a long time it has been observed that under conducive growing conditions, pigeonpea plants produce numerous flowers in more than one flush, but about 80% of them drop resulting in the production of limited number of pods at a given time. Sheldrake (1979) postulated that the factors leading to severe floral abscission in pigeonpea are primarily physiological in nature. He further hypothesized that pigeonpea plant produces a lot of assimilates, but its supply to the reproductive parts of the plants is regulated in such a way that at a given time only a limited number of pods is set than the plant is potentially capable of filling. Also, there seems to be a threshold level of nutrient supply below which pod set does not take place. It has also been observed that soon after floral abscission, the perennial nature of plant forces the emergence of a new flush of vegetation and flowers and produce some more pods, and this process continues until the capacity pod load on a plant is achieved. This extension of reproductive period therefore allows setting of more number of out-crossed pods on pigeonpea plants.

5.4 Ecology and alternate hosts for pollinating insects

Physical factors such as temperature, humidity, wind direction and its velocity, and natural habitat also influence natural out-crossing, directly or indirectly by supporting the build-up insect population (Bhatia et al., 1981). It has been observed at ICRISAT that the pigeonpea fields located near alternate host plants such as specific fruit trees, grasses, and legumes also help in harbouring critical mass of pollinating

insects and thereby encouraging cross-pollination. Besides this, small water bodies, natural (ponds, rivers etc.) or artificial (tanks, irrigation channels, bore wells etc.) or water-logged/muddy paddy fields were also helpful in maintaining high insect activity and cross-pollination. In certain genotypes high/low temperatures or short/long photoperiods can also induce male sterility/fertility in crop plants (Kaul, 1988). In pigeonpea the temperature-sensitive male sterility has already been reported (Saxena, 2014). Such pigeonpea genotypes remain male fertile under temperatures < 24°C, but when they are exposed to high (>25°C) temperatures they turn completely male sterile and thus become prone to natural out-crossing.

5.5 Defective male reproductive system

In plant system certain developmental defects may inhibit self-pollination and fertilization. These include self-incompatibility, male sterility, or any other morphological floral abnormality. Kolreuter (1763) was the first to record the existence of plants with impaired anthers in some natural populations. Since then numerous reports of such abnormal biological events have been published in most crop species (see reviews by Kaul, 1988 and Saxena and Hingane, 2015). Choudhary (2011) reported self-incompatibility in some pigeonpea genotypes. Such situations encourage natural cross-pollination in plants and produce hybrid seed under natural conditions.

VI. FACTORS INHIBITING CROSS-POLLINATION

6.1 Cross-incompatibility

Studies have shown that certain level of female sterility also exists in pigeonpea germplasm. Saxena et al. (1987) reported no pod set on artificial hybridization when two germplasm accessions ICP 102 and ICP 11947 were used as female parents in 54 cross combinations, while their reciprocal crosses produced good (>30%) pod set. It was also observed at ICRISAT that in a wild relative of pigeonpea (*C. sericeus*) some accessions had very poor (<1%) pod set with artificial cross-pollination, while in others the success was quite high >25%. In contrast to normal cultivars, such cross-incompatible genotypes were phenotypically more uniform under open-pollinated field conditions (KB Saxena Pers. Comm.) and did not require artificial selfing for maintaining their genetic purity.

6.2 Altered floral morphology

Byth et al. (1982) reported a floral modification, characterized by over-lapping of petals, enlacing each other, which did not allow native insects to forage and thus inhibited natural out-crossing. This trait initially looked very promising, but it was not able to cross-pollination in other environments; and it may be due to the presence of different pollinator species (Saxena et al., 1987). Besides this, Saxena et al. (1993) selected a mutant with abnormal floral morphology. In this mutant the anthers (Fig.1) are non-diadelphous (free at the base instead of normal 9+1) configuration. Its keel petals is partly surround standard petal enfolding the two wing petals giving it a cylindrical shape and this considerably delays the unfolding of petals and hence do not attract the pollinivore or nectarivore

insects. The natural out-crossing in this mutant varies from 0-2%.

6.3 Use of agro-chemicals

A critical mass of the pollinating insects is essential to reap the benefits of cross-pollination in hybrid seed production. Sometimes in a particular location, a significant decline in the density of pollinating insects is observed; and this could be due to loss of habitat, or consequence of any specific disease. Besides this, a non-judicious use of toxic pesticides (such as carbamates, organophosphates or synthetic pyrethroids) and herbicides (such as round up) can also result in a significant decline in the population of pollinators. In certain cases the levels of these agro-chemicals are low which does not eliminate useful insects, but adversely affects their performance due to impairment of neurological functions including memory, cognition or behaviour, foraging ability, reproduction, and ultimately weakening or loss of hives. These situations often lead to reduced cross-pollination under natural habitats.

VII. GENETIC ENHANCEMENT IN RELATION TO NATURAL OUT-CROSSING

7.1 Enriching genetic variability with natural gene flow

Darwin (1877) opined that natural gene flow across related and unrelated individuals through natural cross-pollination helps in the evolutionary processes through enhanced adaptation. In a crop like pigeonpea where natural cross-pollination is a common event (Table 1), the insect-aided gene flow via pollen transfer from one individual/population to another is inevitable. Recently, Reddy et al. (2015) demonstrated that the gene flow within primary gene pool of *Cajanus* was significant. Kassa et al. (2012) while analyzing genetic patterns of domestication of pigeonpea and its wild relatives reported the occurrence of a substantial gene flow from wild species to cultivated types due to natural cross-pollination; and resulted in natural genetic admixtures and alteration of allele contents in primary gene pool. Also, sometimes rare alleles not available in the primary gene pool such as trichomes and disease resistance etc., may pass from wild species to the cultivated types. The recent revelation of considerable degree of natural cross-pollination in the wild relatives of pigeonpea such as *Cajanus lineatus* (17%), *C. albicans* (10.0%), *C. scarabaeoides* (8.3%) and *C. sericeus* (2.3%) with pollen from the cultivated types, also gives a strong evidence of the possible gene flow from the primary to the secondary gene pool (Saxena and Kumar, 2010). Such events result in enhanced genetic variability which could be used by pigeonpea breeders.

7.2 Exploitation of natural hybrids

Breeding pure line cultivars: In pigeonpea the medium and long duration cultivars cover majority of the cultivated area in India and elsewhere. The open-pollinated landraces are generally grown by farmers and these provide ample opportunity to select heterotic out-crossed single plants for further pedigree breeding. In India so far 37 medium and 16 late maturing pigeonpea varieties have been released and almost half of them originated from natural hybrids identified in farmers' fields (Singh et al., 2016).

The most popular present day pigeonpea varieties such as Maruti, BDN1, LRG 30, and LRG 36 in medium group, and Gwalior-3, Bahar, and NA1 in the long duration group are the best examples where the selections from natural hybrid plants have made a great impact on Indian pulse scenario. The introduction and extensive adoption of cv. Maruti in northern Karnataka and western and southern Maharashtra have successfully eradicated Fusarium wilt, the most devastating disease of pigeonpea in the region. Similarly in Bihar and eastern Uttar Pradesh, the large scale adoption of cv. Bahar got rid of sterility mosaic virus disease. The two cultivars Gwalior 3 and LRG 30, though susceptible to diseases, still occupy large area in Madhya Pradesh and Andhra Pradesh, respectively due to their wide adaptation and high yield. Overall it is evident that the natural out-crossing in pigeonpea has been a boon to Indian farmers.

Breeding CMS systems: Saxena and Kumar (2010) documented a considerable extent of natural out-crossing in four wild species of genus *Cajanus*, and discussed its possible role in diversifying cytoplasmic base of CMS system in pigeonpea. The highest (17.1%) natural out-crossing was recorded in *Cajanus lineatus* and it was comparable to the control cultivar Asha (22.2%). *C. albicans* and *C. scarabaeoides* exhibited 10.0% and 8.3% natural out-crossing, respectively. Such "natural hybrids" with some unknown cultivated genotype, may sometimes yield traits that are not available in the germplasm collection.

Development of cytoplasmic nuclear male sterility (CGMS) system in pigeonpea is a good example where natural hybrids in wild species have been of immense value to breeders. Such natural hybrids with partial or complete male sterility have cytoplasm from wild species and nuclear genome of both wild as well as cultivated type. Some natural hybrids identified within the open-pollinated population of wild species, can be easily detected due to their abnormal growth habit (Fig. 2). These "hybrid plants" can be used to develop a CMS system by backcrossing with a good maintainer genotype. Tikka et al. (1997) from *C. scarabaeoides* and KB Saxena (unpublished) from *C. lineatus* successfully developed CGMS systems from such inter-specific natural hybrids. These were respectively, designated as A₂ and A₆ CMS systems.

7.3 Breeding composite populations

Although at present the composite population breeding does not receive favour of the breeders, but in the recent past it was one of the key breeding approaches for enhancing yield and stability in crops like maize, sorghum, and pearl millet. This methodology is based on the approach of enhancing gene frequency of favorable alleles from diverse sources and then maintaining it in a single heterogeneous population through random mating using natural cross-pollination. These populations, besides serving as a gene pool for deriving useful variability, can also be released as heterogeneous population for cultivation, especially for stressed rainfed environments. However, it is a cumbersome breeding approach as it requires large scale hybridization and selection of genotypes with favourable genetic constitution.

In pigeonpea, the idea of cultivating a mixture of genotypes varying in flowering for enhanced pod set and yield was mooted by Howard et al. (1919). In Uganda, Khan (1973) recommended

the breeding of composite populations using natural out-crossing to enhance productivity of pigeonpea. Green et al. (1981) recommended the use of a recessive trait (obcordate leaf) to identify natural hybrids in recurrent selection scheme; while Byth et al. (1981) proposed the use of genetic male sterility and natural out-crossing to breed high yielding composite populations. Onim (1981) reported 2% yield gains per cycle of selection. This is certainly a potential breeding approach to accumulate alleles contributing to yield and stability and need careful consideration.

7.4 Enabling large-scale hybrid seed production

Economically viable mass cross-pollination is the key for success of any commercial hybrid programme. In pigeonpea the hybrid technology is new (Saxena, 2015) and information on its large-scale seed production is still being generated. In the last few years the breeders were able to identify some seed production hot spots in the country. These include Rewa, Indore, Seoni, Katni, Jabalpur, and Tikamgarh (Table 3). Zeng-Hong et al. (2011) reported that even with 70% less insect visits on the male sterile plants, the amount of cross-pollinated seed yield (384 g/plant) produced on them was similar to that of more frequently visited fertile plants (357 g/plant). Almost similar results were also reported by Saxena et al. (2005). These observations indicated that for good pod set on the male sterile plants, very high insect activity may not be essential to produce reasonably good quantities of hybrid seed in the isolation plots. The hybrid yield ranging between 1333 - 3040 kg/ha was recorded. A perusal of the seed production information compiled by Singhal (2013) revealed that the level of natural out-crossing in pigeonpea is sufficient to produce hybrid seed for commercialization and it is comparable to other crops.

VIII. SUMMARY

According to Price (1975) the co-evolution of flowering plants and their pollinators started about 225 million years ago and that the lack of pollinators in sufficient number leads to poor adaptation and yield. Besides reproduction, it has also been recognized that the natural cross-pollination and mutations had been important forces in the evolution of plant species by producing the fittest individuals. It has been estimated that more than 85% of the crop species relied on partial or complete cross-pollination for their reproduction and these species needed some external pollinating agents such as animals, wind or water (Pratap 2001). The frequency of out-crossing in the wind-pollinated species is generally higher than those out-crossed by insects; and the legumes belong to the latter group.

Among legume crops also, a large variation in natural cross-pollination exists with a number of environmental and biological factors being responsible for it. The pigeonpea flowers are visited by both pollinivore and nectarivore insects, but the cross-pollination is predominantly a function of the latter group. It has also been observed that the pollinators visit fertile plants more frequently than those with no pollen. More research, however, is needed to understand the behaviour of insects in relation to their preferences, collection of pollen and nectar, and their effectiveness in cross-pollinating the fertile/sterile flowers. The competitive advantage of foreign pollen over self-pollen with respect to their germination and pollen tube growth helps in cross-fertilization. In addition the members of genus *Cajanus* are

characterized by extra-floral nectaries on leaf surface and stipules and appear as scattered small disc like gland (Bharati and Maheswari, 1976) but their significance in relation to cross-pollination has not been fully understood. It seems that pigeonpea breeders have very well exploited the natural out-crossing to (i) develop high yielding inbred cultivars by selecting heterotic natural hybrid plants within landraces, (ii) develop cytoplasmic nuclear male sterility which provided platform to develop a viable hybrid technology and, (iii) develop economically viable hybrid seed production technology that helped in successful commercialization of hybrids with on-farm yield advantage of 25-30% in the productivity. For fruitful hybrid seed production identification of eco-friendly chemical molecules with least harm to the pollinator insects will help in adoption of hybrids on a large-scale with greater efficiency and profitability.

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AUTHORS

First Author – KB Saxena, Former Principal Scientist, ICRISAT, Patancheru, India, Present address: 17- NMC Housing, Al Ain, Abu Dhabi, U.A.E. kbsaxena1949@gmail.com
Second Author – AN Tikle, Sr Pulse Breeder, RAK Agricultural College, Sehore, MP, India. antiklep@gmail.com
Third Author – RV Kumar, Senior Manager, ICRISAT Patancheru, India, rvku3ar@gmail.com
Fourth Author – AK Choudhary, Principal Scientist, ICAR Research Complex, Darbhanga, India, akicar1968@gmail.com
Fifth Author – Bir Bahadur, Department of Botany, Kakatiya University, Warangal, India. birbahadur5april@gmail.com

Table 1: Variation for natural out-crossing in pigeonpea reported in different countries

Country/ Location	Author (year)	% Out-crossing	
		Range	Mean
India			
Pusa	Howard et al. (1919)	2 – 12	NR
	Shaw (1932)	2 - 3	NR
Nagpur	Mahta and Dave 1931	3 – 48	NR
	Deshmukh and Rekhi (1963)	NR	25.0
Niphad	Kadam et al. (1945)	12 -21	16.0
Bengal	Sen and Sur (1964)	NR	30.0
Ranchi	Prasad et al. (1972)	4 – 27	NR
Coimbatore	Veeraswamy et al. (1973)	NR	13.7
Varanasi	Bhatia et al. (1981)	10 – 41	NR
Badnapur	Bhatia et al. (1981)	0 – 8	NR
Hyderabad	Sharma and Green (1977)	NR	27.9
	Bhatia et al. (1981)	0 – 42	NR
	Bhatia et al. (1981)	3 – 15	NR
	Saxena et al (1987)	4 – 26	NR
	Githiri et al (1993)	10 – 24	13.1
New Delhi	Reddi et al. (2001)	0 – 21	9.0
Kenya			
Katumani	Onim (1981)	NR	17.7
Kibos	Onim (1981)	NR	12.6
Makueni	Onim (1981)	NR	21.0
Mtwapa	Onim (1981)	NR	22.0
Kabete	Onim (1981)	23 – 46	NR
Other countries			
Australia	Byth et al. (1982)	2– 40	NR
Cameroon	Pando et al. (2011)	15-39	NR
China	Yang et al. (2003)	0 – 60	24.6
Hawaii	Krass (1932)	NR	<1.0
Hawaii	Wilsie and Takahashi (1934)	6 – 30	18.5
Myanmar	Kyu Kin Lay (Pers. Comm.)	20-40	NR
Nepal	Saxena (Pers. Comm.)	20-25	NR
Puerto Rico	Abrams (1967)	5 – 6	NR
Sri Lanka	Saxena et al. (1994)	1 – 20	NR
Trinidad	Ariyanayagam (1976)	2 – 40	NR
Uganda	Khan (1973)	8 – 22	NR

NR= Not Reported

Table 2. An account of popular pigeonpea cultivars developed by selection from natural hybrids identified in farmers' fields in three maturity groups in India.

Maturity	Total releases	Germ. selection	% of Total	Popular cvs	Year of release
Early	33	6	18.2	UPAS 120	1976
				AL 15	1981
				Co 2	1974

Medium	37	17	46.0	C 11	1975
				BDN1	1978
				LRG 30	1982
				Maruti	1985
				HY 3C	1985
Late	16	9	56.3	Type 7	1960
				Type 17	1978
				Gwalior 3	1980
				Bahar	1980
				NA 1	1997
Total	86	32	37.2	-	-

Table 3: Nectarivore/pollinivore-aided seed production of hybrids and CMS lines in Madhya Pradesh, India

Location	Genetic material	Area (ha)	Yield (kg/ha)
Rewa	ICPH 2740	1.0	1740
Indore	ICPH 2671	0.15	2267
Seoni	ICPH 2740	1.0	2500
Katni	ICPH 2740	3.0	1450
Jabalpur	ICPH 2740	1.5	1333
Tikamgarh	ICPH 2740	5.0	3040



Fig. 1. The mutant flower (left) with all 10 free stamen has <2% out-crossing as compared to normal (9+1) flower which registers >30% out-crossing. (Source: ICRISAT photo lab)



**Fig. 2. Comparative plant morphology of three wild relatives of pigeonpea (left) and their natural hybrids (right).
Source: ICRISAT Photo lab.**