Indian J. Genet., 72(3): 257-263 (2012)

Exploitation of heterosis through F_1 hybrid in pigeonpea (*Cajanus cajan* L.): The status and prospects

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(Received : February 2012; Revised : July 2012; Accepted: August 2012)

Abstract

India is a world leader in exploitation of heterosis in F_1 hybrids in different crops and vegetables. Pigeonpea is often cross pollinated species and with availability of male sterility it became amenable for F_1 hybrid breeding. Initial efforts in hybrid development in pigeonpea started in the 1980's with genetic male sterility (GMS) but for more than past two decades the thrust is on hybrids based on cytoplasmic-genic male sterility (CMS). Among five different available sources of cytoplasmic male sterility *viz*., A_1 to A_5, only A_2 and A_4 have been used in hybrid pigeonpea breeding. A wide range of variation in maturity, plant type etc. is now available in the CMS lines and fertility restorers (FR). Encouraging performance of the hybrids in evaluation trials has been recorded. Heterotic hybrids like AKPH 11303 and AKPH 11324 having more than 30 percent yield superiority will be useful for commercial exploitation. Various aspects of improvement of the parental lines, development of heterotic hybrids and hybrid seed production technology for better seed availability are reviewed.

Key words: Heterosis, hybrid, pigeonpea, *Cajanus cajan*

Introduction

Pigeonpea is one of the major pulse crops of dry land agriculture because of its deep tap root system and inherent drought resistance. Its ability to produce high amount of biomass per unit area makes it useful as fodder, fuel and for thatching for the rural masses. Large quantities of foliage drop add to the organic matter of the soil. The deep and well spread root system helps in soil aeration after decomposing. Hence, it is highly valued by the farmers. Pigeonpea accounts for about 14 per cent of the area under pulses and 20 per cent of the pulses production in India. The country has witnessed a large increase in pigeonpea area from 2.8 million ha in 1950 to 3.8 million ha in 1996 with an average annual growth rate of 2 per cent [1] and now it is about 4 million ha. Major area (about 78.9 per cent) lies in Maharashtra, Karnataka, Andhra Pradesh, Madhya Pradesh, Uttar Pradesh and Gujarat.

Population structure and out crossing

Flowers of pigeonpea normally open during early morning and remain open for about 36 to 48 hours [2]. Fertilization frequently occurs prior to opening of the flowers [3, 4]. Less than 1 per cent cross pollination was reported at Hawaii [5] while it was up to 25 per cent at Nagpur in Central India [6]. Howard *et al.* [7] reported 14 per cent out crossing. The degree of open pollination in pigeonpea has been reported in various studies from zero to 70 per cent [5-8]. As the pigeonpea is an often-cross pollinated crop, the landraces are populations with good amounts of genetic variation. Pigeonpea improvement in India during the 1950s was mainly based on mass selection from landraces. Mahata and Dave [4] identified a few elite early and late maturing high yielding types of pigeonpea. More than two dozen cultures were developed and released during this period in different states which include popular varieties like Type 21, Cll, UPAS 120 [9].

Later, mainly for incorporating resistance to major diseases like *Fusarium* wilt and sterility mosaic, hybridization followed by pedigree selection was resorted to. The first scientific breeding effort by Shaw *et al.* [10] described the morphological and agronomic

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Published by Indian Society of Genetics & Plant Breeding, F2, First Floor, NASC Complex, PB#11312, IARI, New Delhi 110 012
Online management by indianjournals.com

traits of 86 elite field collections in which some accessions were found to have high levels of resistance to *Fusarium* wilt disease. Such successful attempts to breed for *Fusarium* wilt resistance, resulted in the genotypes *viz.,* NPWR 15, NPWR 16, NPWR 19 and NPWR 38 [11] from a cross, NP 51 x NP 24. They served as the resistant sources for further breeding.

Development of hybrid pigeonpea

Stable genetic male sterility (GMS) [12] and cytoplasmic-genetic male sterility (CMS) [13, 14], high heterosis for grain yield [15] and abundant natural out-pollination [16-18] prompted the breeder to attempt hybrid breeding in last few decades. Saxena *et al.* [15] reported 50 to 100 per cent yield advantage of hybrids over the open pollinated varieties with a high degree of resistance to wilt and sterility mosaic diseases. Germplasm presented wide range of genetic diversity needed for heterosis breeding.

Though, attempts at F_1 hybrid breeding started in the late nineties using GMS [19-22] the hybrids could not become popular. Niranjan *et al.* [23] concluded that the cost of hybrid pigeonpea seed is within the affordable limits and the hybrid advantage is salable but the technology itself suffered from major bottlenecks, in large-scale seed production. Imperfection in hybrid seed production technology for large scale multiplication, inherent low yielding ability of early maturing seed parents, cost of rouging 50 per cent fertile plants from the GMS parent, heavy loss due to pod borers, difficulties in determining genetic purity and in quality control, were some of the major limitations. Subsequently, CGMS system could be established [13, 14].

Development of CGMS system

Ariyanayagam *et al.* [24] reported development of maternally inherited male sterility through chemical and physical mutagensis Kaul [25] showed that wide hybridization involving interspecific and intergeneric crosses could be a good source for CMS system. So far, seven CMS systems have been reported with varying degree of success [26]. Reddy and Paris [27] crossed *Cajanus scarabaeoides,* a wild species with fertile F_1 plants of *Cajanus cajan* x *C. scarabaeoides.* The resulting BC_1F_1 plants were fertile but in BC_1F_2 generation some male-steriles segregated but the male-sterility was linked with female-sterility. Ariyanayagam [28] crossed *Cajanus sericeus* with a short-duration advanced breeding line of pigeonpea. The F_1 progeny was partially male-sterile and the backcrosses (BC_1F_1-BC_3F_1) with limited population size (2-19 plants) were found segregating for male-sterility. The maternally inherited male-sterility in the BC_1F_1 (15 plants) ranged between 8-99 per cent. The CMS derived from it (ICPA 88034 and ICPA 13092) were temperature sensitive [29]. In the last decade of twentieth century, six national centres viz., Indian Institute of Pulses Research, Kanpur; Indian Agricultural Research Institute, New Delhi; Sardar Patel Agricultural University, Sardar Krushinagar; Panjabrao Deshmukh Krishi Vidyapeeth, Akola; Tamilnadu Agricultural University, Coimbatore and Punjab Agricultural University, Ludhiana joined the efforts to develop CMS through inter-specific crosses. Some male sterile plants were found in crosses involving *C. sericeus* and C. *mollis* with cultivated C. *cajan* at Bhabha Atomic Research Centre, Trombay and Banaras Hindu University, Varanasi respectively. Wanjari [30] used the wild species *C. sericeus, C.volubilis, C. cajanifolius, C. lineatus, C. lanceolatus* as the probable sources of alien cytoplasm. Male sterility isolated from the derivatives of *C.volubilis* x *C.cajan* var. ICPL-83024 [31] was found to have cytoplasmic inheritance. However, the effort to identify the fertility restorer was not successful. Another CMS with the cytoplasm from *C. lanceolatus* was recorded [32]. It has been diversified into six agronomic backgrounds *viz.,* AKT9827, AKWR-376, AKMR-875, AKMR-840, MDDRL-11, AKT-8811 [33]. First stable cytoplasmic male-sterile line *viz.,* CMSGT 288A was established with cytoplasm from *C. scarabaeoides* and nuclear genome of ICPL 288 [13]. It was stable across environments [29]. This source was used for development of diversified CMS lines at various centers. Another reports appeared on CMS derived with the cytoplasm from *Cajanus scarabaeoides* [14] and also from *C. cajanifolius* [34]. Saxena *et al.* [35] enlisted five sources of cytoplasmic male-sterility as A_1 from *Cajanus sericeus* [28], A_2 from *Cajanus scarabaeoides* [13, 14], A_3 from *Cajanus volubilis* [31], A_4 from *Cajanus cajanifolius* [34] and A_5 from *Cajaus cajan* [36].

Fertility restorers for CMS lines based on different cytoplasm

Search for the fertility restorers from the population derived from the cross *Cajanus scarabaeoides* x *Cajanus cajan* and some cultivated germplasm led to the establishment of 18 fertility restorers in different maturity groups *viz*., GTR 1 to 18 against CMS based on *C. scarabaeoides* at Sardar Krushinagar [29]. Saxena and Kumar [14] reported eight fertility restorers for the CMS based on *C. scarabaoides.* IIPR Kanpur and AICRP centers at Akola, Sardar Krushinagar and Faizabad made extensive efforts using hybrid combinations with; more than 2400 germplasm lines and identified 223 fertility restorers with variation in the degree of fertility restoration [37]. Environment played an important role in fertility restoration [38]. Efforts were made to look for fertility restorers in F_2 populations derived from fertile hybrids and the fertility restoration mechanism with the Kenyan germplasm line ICP-10875 was discovered against the CMS based on *C. scarabaeoides* [39, 40]. AK-200355 has been found to be a better source of restorer [40]. However, this line was associated with undesirable agronomic traits such as late flowering/ maturity, determinate flowering, highly affected due to terminal drought resulting in shy pod setting. It was indicated that selection *per se* for fertility in the derivatives can be a good criterion for obtaining better fertility restorer lines. Lad and Wanjari [41] studied F_3 and BC_1F_2 progenies derived from the fertile plants in F_2 and BC_1 respectively and reported that better anther dehiscence has been largely associated with higher pollen fertility in the derivatives. Such derivatives when used for hybridization with CMSGT 288 produced highly fertile hybrids with better autogamous seed setting. About 60 stable fertility restorer lines have been established from the derivatives of the hybrids involving ICP-10875.

Ariyanayagam *et al.* [28] identified fertility restorers for the CMS derived from *C. sericeus.* Later, ICPL 129, ICPL 89 and HPL24 were identified as good fertility restorers [29]. Search for fertility restorers for CMS based on *C.volubilis* cytoplasm using more than 250 germplasm lines was not successful [30, 39]. Saxena *et al.* [34] reported that among the crosses of CMS lines based on *C. cajanifolius* with more than 500 genotypes as pollinators, about 12 per cent behaved as maintainer and 9.2 per cent restored fertility well and rest had mixed unclear effect. The fertility restorers in different genetic backgrounds could be used to develop base populations and heterotic gene pools for improvement of restorer lines for better combining ability.

Some of the restorers produced hybrids, which did not set seeds when placed inside the net-cages because of the likelihood failure of effective self pollination. Auto-gammy would be highly desirable in the hybrid to make it practically more stable in productivity in the event of lack of sufficient population of insect vectors for pollination. The fertility restorer source from a Kenyan germplasm line *viz*., TCP-10875 [39] enables autogamous pod setting in hybrids. Their derivatives are very much desirable in this respect.

Inheritance of fertility traits and selection for fertility restoration

Lad and Wanjari [42] presented interesting segregation in the selfed progeny of fertile F_2 plants of CMS-GT288 x ICP10875 in F_2, F_3 and BC_1F_2 generations. On the basis of segregation pattern in different plant-to-row progenies for each of these traits, the possibility of involvement of complex epistasis of more than three genes for each of the three fertility traits *viz.,* anther color (translucent white vs. yellow), dehiscent vs. non-dehiscent anther and quality of dehiscence (good vs. poor) was recorded. There is a possibility of effective selection of highly fertile plants in the segregating generations for use as better fertility restorer [41, 43]. The selection for pollen fertility can be improved if dehiscence of the anthers is used as a secondary criterion [40].

Saxena [34] presented an observation that the majority of hybrids based on *C. cajanifolius* CMS had no perfect fertility restoration due to intra-accession variation in the cultivated genotypes used as male parent. It was attributed to differential inter-genomic and cytoplasmic-genomic interactions which may involve complex epistasis. Dalvi *et al.* [44] studied genetics of fertility restoration in five crosses in CMS based on *C. cajanifolius.* In three crosses a single dominant gene restored the fertility, while in other crosses two dominant genes with duplicate gene action or two dominant genes with complimentary action governed the fertility restoration. Saxena [45] reported that fertility restoration in CMS system based on *C. cajanifolius* was not perfect and a large variation ranging from 50 to 95 per cent of pollen fertility was observed. This variation could be due to differential intergenomic or cytoplasmic genomic interactions. Abdalla and Hermsen [46] opined that polymorphism arising due to different genes can also yield inconsistent expression of both male sterility and fertility restoration.

Hybrid seed production technology

GMS based hybrids are not used now but the experiences in hybrid seed production with GMS would be useful in commercial seed production of CGMS based hybrids. The hybrid seed yields based on early duration GMS lines were low firstly because of inherent lower productivity of determinate male sterile line like ms Prabhat or ms GT 288 within a limited flowering span and secondly for the fact that fertile segregates of genetic male sterile lines have better seedling vigor and which suppresses sterile plants and have delayed flowering when sterile and fertile plants grow close to each other [47]. In GMS parents the recovery of male sterile plants was lower, when more than one seed germinated in a single hill, than when a single seed grew in a hill. If one of the two seedlings in a hill happens to be a fertile plant, it will suppress the growth and vigor of male sterile seedling. Moreover, while uprooting the fertile plant in rouging the root system of sterile plant is disturbed. Thus, there was double disadvantage for the male sterile plants. Intra-row spacing of 10 to 15 cm with sowing single seed per hill was found to be desirable [47]. Based on these observations, the seed production technology package for hybrid seed production has been developed [48].

Saxena *et al.* [35] maintained that for seed production in pigeonpea an isolation distance of 500 m may suffice. However, later it was found that the isolation distance of 500 meters cannot be universal and need to be reviewed. Row proportion of female: male at 4:1 was reported to give a good seed yield. It can be 8:1 (female: male) at the location with high activity of pollination vectors. Use of honey bee hives can promote the hybrid seed yield from the seed plots [49].

The database of seed production research needs to be critically developed for each hybrid to be promoted. Synchronization of flowering and extended flowering in male is necessary to coincide with the flowering in female line. It needs to be ensured and managed with irrigation and nutrient management. Some more research will be needed on the use of growth regulators (retardants as well as promoters) to improve seed yield from the seed production plots. Promotion of the seed production of a single hybrid on very large area at one place may help coping with the problem of isolation distance.

GMS or CGMS based hybrid seed production can be assisted by the use sterility linked seedling markers. Similarly, the seedling linked markers can be better used in identification of the parents and hybrids in grow out test. Patil *et al.* [50] established seven seedling markers. They include epicotyls pigmentation (purple *vs* green), stem pigmentation (present *vs* absent), first primordial leaves (broad *vs* narrow, long *vs* short, normal *vs* tiny), unifoliate first leaf immediately after the first primordial pair of leaves and two unifoliate leaves in sequence after the first primordial pair of leaves. They are likely to be useful in identification of the hybrids, particularly when they are monogenically inherited. Wanjari *et al.* [51] reported that the epicotyl pigmentation is governed by single dominant gene however, it was not linked with the male sterility gene *ms_1* responsible for GMS [12].

Heterotic performance of CMS based hybrids

Saxena *et al.* [15] reported encouraging performances of the hybrids based on A_4 cytoplasm over seven locations with as high as 119 per cent and 52 percent standard heterosis over the check variety in early and mid-late groups, respectively. In the Indian national program the pigeonpea hybrids are being developed with CMS based on A_2 cytoplasm. During 2011-12 few promising hybrids expressed more than 20 per cent standard heterosis at Akola. In Medium maturity group AKPHM-11303 was promising in Co-ordinated Advanced Hybrid Trial as well as in Multilocation Hybrid Trial with about 39 and 25% yield superiority respectively, over the best check variety. It was also superior to standard check by about 41 per cent in an experiment under Emeritus Scientists project (Table 1). The hybrids from early maturity group *viz*., AKPHE-04012 and AKPHE 02402 expressed 14 to 29 per cent superiority over the check (Table 2). In another experiment conducted under Emeritus Scientist's project also AKPH 04012 expressed 37% heterosis over standard check [52].

Recently, Rane [53] observed that CMS lines grown inside the insect proof cages did not set pods in the absence of hand pollination, from first few flushes. However, in a later part of their life cycle beyond late December there were a few plants to set more than ten pods. The observations on the progenies raised from such seed pointed to the possibility of apomictic development of pods without sexual reproduction although only a few of the progenies bred true to the mother traits.

Table 1. Promising medium duration hybrids at Akola during *kharif* 2011-12

Trial®	Best check (kg/ha)	Promising hybrids	Yield (kg/ha)	Heterosis over best varietal check
AHT Medium	Maruti (1562)	AKPHM-11303	2171	38.98
MHT Medium	BSMR-736 (3155)	AKPHM-11324	4221*	33.74
		AKPHM-10277	4159*	31.79
		AKPHM-11303	3936*	24.72
Emeritus Scientist Project	PKV TARA (2451)	AKPHM-11303	3451	40.79
		AKPHM-11324	3222	31.47
		AKPHM-13359	3191	30.21

®AHT=Advanced Hybrid Trial, MHT= Multilocation Hybrid Trial, * Significantly superior to the check at p=0.05

Table 2. Promising early duration hybrids at Akola during *kharif* 2011-12

Trial®	Best check (kg/ha)	Promising hybrids	Yield (kg/ha)	Heterosis over best varietal check
AHT Early	GTH-1 (1206)	AKPHE-04012	1447	19.85
MHT Early	AKT-8811 (1632)	AKPHE-04012	2103	28.84
		AKPHE-02402	2014	23.40
		AKPHE-05178	1860	13.95
		AKPHE-02002	1826	11.92
Emeritus Scientist Project	AKT-8811 (1551)	AKPHE- 10402	2612	48.46
		AKPHE-04012	2415	37.28
		AKPHE-05178	2284	29.82

@AHT=Advanced Hybrid Trial, MHT= Multilocation Hybrid Trial

To conclude, the CMS based hybrid pigeonpea research has a short history, but it has been successful in producing a large number of CMS lines and their fertility restorers with promising high yielding hybrid combinations. The bottleneck lies in commercial seed production, mainly because of the dependence on pollination vectors. The effort to identify heterotic hybrid combinations, to diversify nuclear base of parental lines, to train human resource and expand seed production and marketing systems may continue. Breeding new stable parental lines with better combining ability and heterotic cross combinations with grower friendly seed production technology need careful planning in future. Apomixis will be useful in species like pigeonpea where commercial hybrid seed production is facing difficulty.

Acknowledgements

The financial support extended by Indian Council of Agricultural Research and physical co-operation rendered by Dr. Panjabrao Deshmukh Agricultural University, for the Emeritus Scientist Project during 2010-2012 are gratefully acknowledged.

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