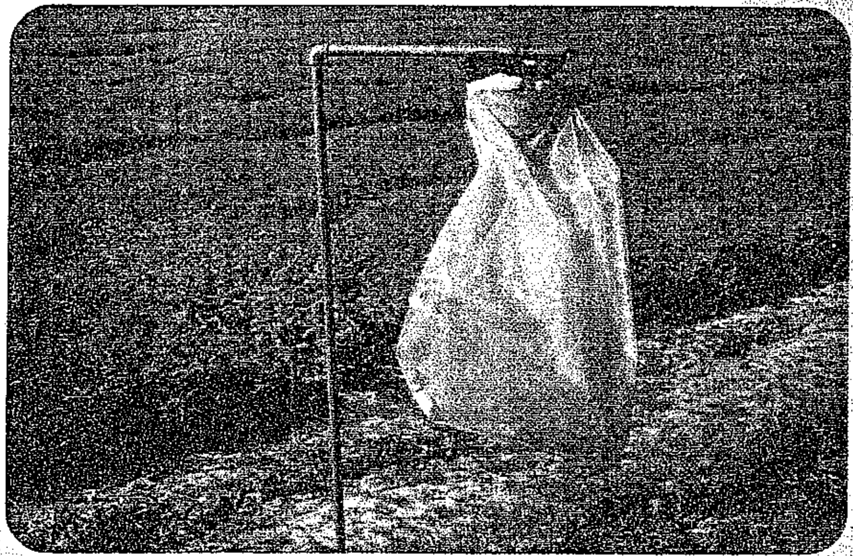
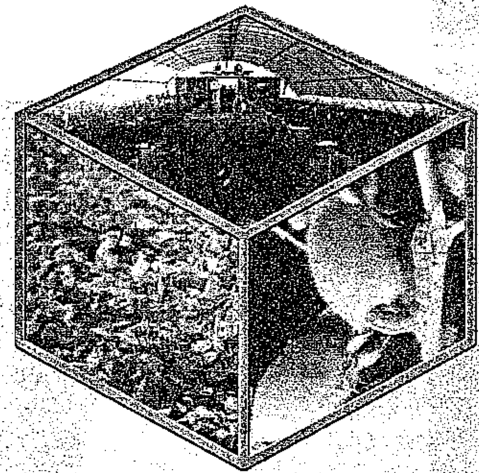


Advances in Management of Biotic and Abiotic Stresses in Pulse Crops



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Breaking Yield Barrier in Pigeonpea through Hybrid Breeding

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ABSTRACT

In pigeonpea (*Cajanus cajan (L.) Millsp.)*, an important pulse crop of Indian subcontinent, East Africa and the Caribbean, traditionally pure line cultivars and land races are cultivated. In the last few decades a steady progress in pigeonpea production has been recorded but the productivity has remained low. The knowledge about male-sterility, however, paved the way for breaking yield barrier in this crop through hybrid breeding. Six hybrids with about 25-35% superiority over inbred varieties have been released for commercial cultivation in India. The potential of pigeonpea hybrids to perform well in diverse and stress environments is likely to help in enhancing its productivity in a variety of production systems. A considerable progress has been made to overcome the large-scale hybrid seed production problems associated with genetic male-sterility by developing cytoplasmic male-sterility in pigeonpea. This paper highlights the advances made in hybrid pigeonpea research.

Pigeonpea (*Cajanus cajan* (L.) Millsp) is one of the major pulse crops of the tropics and subtropics. Endowed with several unique characteristics, it finds an important place in small holder farming systems. Research on the genetic improvement of pigeonpea started in the early part of this century with the selection of disease resistant genotypes from landraces and later some cultivars were also developed from hybridization programmes. These varieties either had shorter maturity, shorter plant types or increased resistance to one or more diseases which resulted in increased production at the national level but over decades the productivity of the crop has remained unchanged around 750 kg/ha. This highlights the point that breeding for increasing yield potential of the crop has not met with success. For developing such pure line cultivars traditionally additive genetic variation has been exploited through pedigree selection and the substantial level of non-additive genetic variation present in crop (18) has not been exploited profitably for genetic improvement of yield as has been demonstrated in many cereals and vegetables.

Considering ever increasing demand of pigeonpea in the country, it is essential to make concerted efforts to enhance its productivity and breeding for hybrids is a potential avenue to achieve this breakthrough. To accomplish this an effective pollen transfer mechanism is essential which is provided by insect-aided natural cross-pollination. The utilization of

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natural cross-pollination in commercial hybrid breeding program was ruled out mainly due to the non-availability of male-sterility in pigeonpea (14,24). Both at ICRISAT as well as at ICAR considerable research efforts have been devoted to develop stable male-sterility systems and hybrid seed production technology. This paper besides summarizing the present status discusses prospects of heterosis breeding technology in pigeonpea.

GENE ACTION AND HETEROSIS

Since there is little inbreeding depression in pigeonpea, beyond F_2 generation dominance does not appear to be an important genetic component in determining yield in this crop. Predominance of additive gene action for yield and yield components has been observed (15). Importance of both additive and non-additive gene actions for yield has been reported (12). The predominance of non-additive gene action has also been observed (15). In pigeonpea predominance of additive gene action is known for seed size, days to flower and plant height (4,7,21,22,23).

Although critical information on the occurrance and magnitude of the non-additive variance (dominance and epistasis) responsible for the manifestation of heterosis is lacking in pigeonpea, considerable hybrid vigor over the mid-parent and better parent values have been observed by several workers for grain yield and other economic characters. Hybrid vigour up to 24.5% over the better parent for grain yield has been reported (25). Subsequently, a number of reports have appeared on the existence of hybrid vigour for yield and yield components (18). In multilocational trials 20 to 49% heterosis over the recommended control cultivar in medium and short duration pigeonpea hybrids has been observed (17).

Most of the information on hybrid vigour are from experiments conducted in a single environment, and such estimates suffer from bias due to genotype x environment interaction. This bias is considerably accentuated if a particular phenological group is better adapted to a particular test environment. Hence, a single location study may give an impression of pseudo-heterosis.

Component analyses of hybrids have shown high yield in the heterotic crosses to be closely associated with heterosis for yield components such as number of pods, number of primary branches and plant height, that all contribute to increased total biomass (2,27,17). To realize significant hybrid vigour for yield, selection of parental lines belonging to diverse maturity groups has been suggested.

NATURAL CROSS POLLINATAION

Self-fertilization is not the rule in pigeonpea and a considerable degree of natural cross-pollination occurs (Table 1). This created serious problem in maintaining the genetic purity in germplasm and released cultivars. There are 24 insect species that affect cross-fertilization (10) and the degree of natural cross-pollination at any particular location depends on the presence and activity of these pollinating vectors (19). The hybrid seed production feasibility studies conducted at ICRISAT revealed that the present level of natural cross-pollination is sufficient for an effective hybrid seed production program. In the sterile plants, however, significant flower drop is observed initially but in a few weeks normal pod set due to outcrossing is observed. This happens because these plants continue to produce flowers until enough pods were set by insect pollination to cease further flowering.

Table 1. Natural outcrossing (%) in pigeonpea recorded at various locations in India

Place	Mean	Range
Pusa	-	1.6-12.0
Nagar	25.0	3.0-48.0
Niphad	16.0	11.6-20.8
West Bengal	30.0	—
Ranchi	-	3.8-26.7
Coimbatore	13.7	—
Varanasi	—	10.3-41.4
Badnapur	—	0.0-8.0
Coimbatore	—	10-70.0
Hyderabad	27.9	0.9-42.1

MALE-STERILITY SYSTEMS

Genetic male sterility: An easily identifiable genetic male-sterile source (ms) characterized by translucent anthers was identified at ICRISAT (11). Subsequently, another genetic male-sterile source (ms_2) with brown arrowhead shaped anthers was discovered at the University of Queensland, Australia (20). These male sterile sources are controlled by non-allelic single recessive genes. Microsporogenesis studies revealed that in ms_1, the tetrad fails to separate from the pollen mother cell and gradually degenerates through vacuolation while the tapetum persists (11). In ms_2, on the other hand, male sterility is caused by the degeneration of tetrads at an early prophase stage (5). These male sterile genes have so far not been found linked to any marker trait to assist pre-flowering identification of male-sterile plants.

Cytoplasmic male sterility: Considerable efforts have been made to develop cytoplasm male-sterility (CMS) through mutagenesis and wide hybridization. High levels of maternal inheritance for male sterility within the derived lines have been recovered. In the selected progenies of the sodium azide (0.025%) treated QMS 1, 87% male sterile plants were recorded at ICRISAT. A preliminary electrophoretic assay of esterase indicated that sterile lines developed through mutation were different from the ms_1 male-sterile parent. Segregation pattern and the electrophoretic assay together suggested that the mutagenic treatment has an effect on the maternal inheritance of sterility.

In order to develop CMS through wide hybridization, attempts have been made to place pigeonpea genome in alien cytoplasm. The investigations has indicated differences in the occurrence of male-sterility between species, and among accessions within species. For instance, the use of *Cajanus sericeus*, *C. scarabaeoides* and *C. acutifolius* as the female parent gave rise to a higher frequency of sterile progenies than *C. albicans*. Similarly, there were differences among accessions within these three promising species. The advanced lines available at ICRISAT have shown high level of male-sterility. Such 'A' lines are maintained by crossing with appropriate 'B' lines (Table 2).

SEED PRODUCTION TECHNOLOGY

Male sterile lines: For uniform expression of heterosis in hybrids, genetic purity of male sterile stocks is essential. Since genetic male sterility is controlled by a single recessive gene, it must be maintained as a heterozygote by harvesting seeds from male sterile plants pollinated by fertile heterozygote. To multiply male sterile lines, seeds harvested from male sterile plants are grown in isolation and at flowering a young bud from each plant is manually opened and anthers examined for the presence or absence of pollen grains.

Table 2. Segregation for male-sterility in advanced CMS lines at ICRISAT during 1998-99 rainy season

	No of plants		
Progeny	Total	Sterile	% steriles
2691	134	125	93
2692	35	28	80
2693	178	178	100
2694	12	12	100
2695	124	124	100
2696	65	65	100
2698	37	37	100
Total	585	569	97

At maturity, seeds from male sterile plants alone are harvested. Immature pods are removed from fertile segregants, if necessary, to extend the period of pollen availability. A problem often encountered in the maintenance of male sterile stocks is incorrect identification of fertile and sterile plants. This is largely due to the bushy nature of the plants and the consequent intermingling of branches of neighbouring plants. This problem is overcome by widely spacing of plants and maintaining rows of male-sterile and pollinator plants in a proportion of 6:1, respectively. For maintaining seeds of cytoplasmic male-sterile lines after every six rows of 'A' line one row of 'B' line should be planted in isolation. This ratio may be changed to suit local environment and pollinator activity.

Pollinator lines: Genetic purity of pollinators is also essential for uniform expression of hybrid vigour. To prevent genetic contamination due to natural outcrossing the pollinator must be grown in isolation and off-types, if any, should be rogued before the commencement of flowering. Small quantities of pollinator seeds can be produced under insect-proof cages.

Hybrids: Identification of heterotic crosses generally requires testing a large number of combinations. Seeds for these experimental hybrids is best produced by hand-pollinating male sterile plants. A trained person can pollinate about 400 floral buds in a day and 30-40% pod set can be expected which yields enough seed to include the hybrid in a small replicated yield trial. To produce large quantities of hybrid seed, seeds from male-sterile plants in the maintenance block are planted in isolation with the required pollen parent. At ICRISAT full pod set has been obtained if one pollinator row is planted after every six male-sterile rows. In using the genetic male sterility, hybrid seed production requires fertile segregants within female rows to be rouged. The first floral bud that appears on each plant has to be examined and male-sterile plants tagged while fertile segregates must be rogued before opening of flowers to prevent transfer of their pollen to sterile plants. In pollinator rows flowering terminates when the potential pod load is realized. In the absence of sufficient pod load due to lack of insect vectors or non-synchrony of flowering in parents, sterile plants continue to flower till the potential number of pods are set. To ensure an adequate hybrid yield, flowering in the pollinators can be extended by periodically removing young developing pods and frequently irrigating the plants. In the hybrid seed production with cytoplasmic male sterility, a combination of six rows of 'A' line and one row of 'R' line is ideal. The ratio of male: female rows may have to be changed if the recommended 6 female: 1 male ratio is found to be not optimal due to an insufficient number of pollinating insect vectors and/or variable plant growth.

Isolation Specifications: Isolation specifications of pigeonpea differ considerably on account of the varying degrees of natural cross-pollination. For quality variety seed production, two varieties must be separated by at least 100 m, whilst a distance of 200 m between varieties is essential if the seed is to be used by breeders. (6) The studies at ICRISAT suggested that although uniform isolation standards are difficult to specify, the FAO specifications are suitable, both, for the production of hybrid pigeonpea seeds and the maintenance of male-sterile and pollinator lines.

Estimated cost of hybrid seed production: Seed cost plays an important role in the wide scale adoption of hybrid pigeonpea and management practices are clearly a critical factor in determing production costs. Studies jointly conducted by ICRISAT and Tamil Nadu Agricultural University ((TNAU) to determine the cost of producing seed of pigeonpea hybrid ICPH 8 was Rs 6.25 per kg during 1988 and rouging contributed 45.12% to the production cost (9). Similar studies conducted at Punjab Agricultural University (PAU) Ludhiana showed a large variation in the production costs of male sterile and the estimated production cost of hybrid PPH 4 was Rs 13.8 per kg (26). These studies

revealed that with good management the genetic male sterility could be exploited for production of hybrid seed at a cost acceptable to both farmers and seed growers.

The production costs can be reduced by adopting a multiple harvest system. In tropical environments with warm winters, pigeonpea produces several flushes of pods within a year and the perennial nature of this crop can be exploited to produce quality hybrid seed at low cost. Multiple harvests help to substantially reduce the cost of hybrid seed production as there is no need to rogue after the first crop and same seed production nursery can be used in subsequent years (17). Plants in such a seed production system should be ratooned at a manageable height as they tend to grow tall making insect control and harvesting difficult.

PROSPECTS FOR PIGEONPEA HYBRIDS

Commercial hybrids and their yield potential: Among the hybrids developed at ICRISAT ICPH 8, a cross between ms Prabhat (DT) and ICPL 161, was found to be most promising. It was released for cultivation in the central zone of India in 1991. Evaluation from 100 trials showed ICPH 8 to be superior to controls, UPAS 120 and Manak by 30.5 and 34.2%, respectively. The performance of ICPH 8 in diverse environments from 1981 to 1989 is summarized in Table 3. Extensive testing of ICPH 8 in the northwest plains, central and southern zones clearly established its superiority over the controls. Testing of ICPH 8 mini kit trials of 12 locations in the central zone during 1989 exhibited superiority of 25.6 and 60.7% over ICPL 87 and ICPL 151, respectively. PPH 4, a short-duration hybrid pigeonpea, suitable for a pigeonpea-wheat rotation was released by PAU. This hybrid was developed by crossing Ms Prabhat (DT) with ICPL 81 (AL 688). On-farm trials conducted in 1994 (28) showed that PPH 4 outyielded the control AL 201 by 20%. An indeterminate short-duration hybrid CoH1 (IPH 732), developed by crossing ms T 21 and ICPL 87109, was released by TNAU in 1994. In 17 on-farm trials conducted in 1994, CoH1 recorded a 32% higher yield over the control VBN 1 (8).

Experimental hybrids: A large number of broad-based experimental hybrids are usually tested to identify heterotic cross combinations. During the past few years, a number of promising hybrids have been evaluated at different agro-ecological zones in India. Some of the short- and medium-duration hybrids which produced significantly high yield over the controls in different trials are listed in Table 4. A few hybrid such as IPH 550 (5.08 t/ha) and IPH 732 (5.58 t/ha) demonstrated a great yield potential. Such genetic combinations can form a solid scientific platform to accomplish a possible breakthrough in yield

Table 3 Zonal weighted mean seed yield of hybrid ICPH 8 and controls UPAS 120 and Manak in different zones in India, 1981-89

Zone	Years	Number of trials	Yield ($t\ ha^{-1}$) ICPH 8	UPAS120	Manak	% increase over ICPH 8 UPAS 120	Manak
Northwest plains	6	36	2.85	2.10	2.34	35.0	31.0
Central	4	30	1.56	1.16	0.93	32.9	52.5
Southern	4	30	1.42	1.22	1.26	23.6	27.3
Northwestern hills	1	2	1.56	1.50	1.19	4.3	31.0
North eastern hills	1	1	1.68	1.15	—	45.6	-
Western	1	1	2 .06	1.41	1.59	45.6	29.5
Mean			1.99	1.53	1.35	30.5	34.2

potential of pigeonpea. Studies on these hybrids may help in understanding the physiology of yield in pigeonpea, which can be utilized in breeding high yielding pure line cultivars.

Hybrids for higher stress tolerance

As pigeonpea is generally grown under rainfed conditions, it is subjected to intermittent drought stresses. Drought resistance, therefore, is an important requirement in the crop for realizing higher yields. ICPL 87 and UPAS 120 are two popular short duration cultivars released in recent years. The hybrid ICPH 8 was found to perform well both under excessive and deficit moisture regime against these cultivars. Hybrids have also been shown to have a more vigorous root system and this may account for their superior performance (16).

Pigeonpea diseases cause considerable economic losses. The annual crop loss due to wilt disease alone has been estimated at US$ 41 million (13). Under severe disease situations, wilt resistant hybrids have shown greater yield advantage over resistant varieties. In an experiment conducted for two years, it was observed that the advantage of hybrids over varieties increased more than three-folds under disease stress conditions (Table 5).

In India, pulses are a major source of vegetarian cuisine especially among middle and lower income masses. To meet the increasing national needs of the pulses a proportional increase in their production is essential. Pigeonpea production in India has recorded a significant increase over the last few decades but it has mainly come through increase in its area and not through increasing its productivity. The attempts made by breeders in the past to develop high yielding cultivars did not produce desired results and a breakthrough in the yield potential of the crop is long awaited to cater the nutritional needs for 21st century. Heterosis, a commonly known genetic mechanism for phenomenal yield increases, has been successfully exploited in cereals and vegetables and in pigeonpea also a similar unconventional breeding approach is needed to achieve breakthrough in yield. Fortunately, pigeonpea flowers allow this opportunity due to a built-in mechanism of natural out-crossing. Therefore, in this crop both additive as well as nonadditive genetic variances can be utilized in breeding programs to enhance yield levels. Considering the prospects and potential of heterosis breeding, both ICRISAT and ICAR explored this breeding avenue and the first hybrid ICPH 8 was released in 1991. The experimental hybrids, besides demonstrating yield potential as high as 5 t/ha have also exhibited high stability and tolerance to stress factors such as drought and diseases.

Pigeonpea is known for its slow growth in its early stages, which restricts biomass accumulation especially in short-duration photoperiod insensitive genotypes. Despite their small seeds and photoperiod insensitivity the hybrids produce higher seedling vigor than their parents. The early growth vigor of hybrids becomes pronounced with time and makes them suitable for high productivity as they establish quickly and utilize light and water resources more efficiently. Short duration hybrids have also shown good plasticity at plant densities ranging from 16 to 66 plants/m^2 without adversely affecting its seed yield (16). Higher crop growth rate of the hybrids ultimately results in as high as 20 t/ha biomass production (1). A significant proportion (18-20%) of this harvestable biomass is 'lost' due to leaf fall but could be considered to add to the organic matter reserve of the soil. Also large quantity of harvestable stems provide useful fuel wood. In pigeonpea variation in yield is primarily accounted for differences in growth rates. High yield in pigeonpea hybrids due to higher crop growth while retaining their partioning ability at least at the same level as that of traditional varieties have been demonstrated (1).

Inspite of high yield potential of the hybrids they could not find high adoption

Table 4. Yield potential of some of the experimental pigeonpea hybrids developed at ICRISAT.

Hybrid No.	Days to 50% Flowering	Days to Maturity	Plant Height (cm)	Yield ($t\ ha^{-1}$) Hybrid	Yield ($t\ ha^{-1}$) Control	SE	CV (%)
Short-duration :							
IPH 550	66	110	133	5.08	1.75	±0.585	30
IPH 575	68	113	143	4.81	2.13	±0.533	26
IPH 526	73	116	213	5.28	3.19	±0.520	22
IPH 583	89	130	289	4.26	2.2	±0.369	18
IPH 656	83	127	190	4.82	2.79	±0.834	36
IPH 732	86	129	193	5.58	2.15	±0.679	26
IPH 700	81	124	163	4.49	2.15	±0.679	26
IPH 719	75	117	198	4.93	2.15	±0.679	26
IPH 503	69	113	188	4.82	2.43	±0.715	32
IPH 495	71	115	185	5.00	2.43	±0.715	32
IPH 752	71	120	89	4.53	2.44	±0.251	15
IPH 786	72	119	94	4.64	2.99	±0.158	8
IPH 784	71	118	80	4.10	2.99	±0.158	8
IPH 1227	71	120	138	3.80	2.57	±0.440	23
IPH 1380	76	112	—	3.12	0.91	±0.329	25
Medium-duration							
IPH 487	140	199	245	4.35	2.61	± 0.291	11
IPH 479	132	196	247	4.18	2.61	± 0.291	11
IPH 482	135	193	258	4.01	2.61	± 0.291	11
IPH 483	136	196	257	3.90	2.61	± 0.291	11

Source : K.B. Saxena, ICRISAT

due to the genetic nature of the male-sterility which poses practical difficulties in large scale seed production. To simplify seed production technology, the resources have now been shifted towards developing cytoplasmic male-sterility in pigeonpea. Todate a significant progress has been made in developing cytoplasmic male-sterile lines and concerted efforts need to be continued in identifying heterotic cross combinations in diverse genetic backgrounds and to develop efficient seed production technology to achieve the ultimate goal of increasing productivity of pigeonpea.

Table 5. Yield (t ha⁻¹) of some disease resistant hybrids and varieties in disease-free and sick fields at Patancheru, rainy season 1993 and 1994.

Hybrid	Disease-free field			Sick field		
	1993	1994	Mean	1993	1994	Mean
Hybrids						
IPH 1326	2.6	2.5	2.53	2.1	1.2	1.64
IPH 1395	2.2	2.3	2.26	2.0	1.5	1.72
IPH 1327	2.4	1.8	2.13	1.9	1.5	1.6
Mean	2.40	2.2	2.31	2.0	1.4	1.68
Varieties						
ICPL 87119	2.6	1.9	2.25	1.07	0.7	0.88
ICPL 87051	1.5	1.6	1.60	1.32	0.9	1.11
Mean	2.05	1.75	1.93	1.20	0.8	1.00
Advantage of hybrid (%)	17.1	25.7	19.7	66.7	75.0	68.0

Source : K.B. Saxena, ICRISAT

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