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Key Plant and Grain Characteristics and Their Importance in Breeding and Adaptation of Pigeonpea Cultivars

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Abstract

Complexity of yield formation is well understood by all, and there is no specific formula for breeding high-yielding cultivars. Breeders, however for a long time, have relied on selecting various individual traits, which, they thought, will contribute to yield formation directly or indirectly, and in these ways, successes have been achieved in almost all the crops. In pigeonpea, the most important individual plant traits, known to be linked to seed yield are number of pods, primary and secondary branches, and pod-bearing bunches. All these traits are quantitative in nature and have low heritability. In this paper, an attempt has been made to identify various qualitative and quantitative traits related to seed yield, quality, and those preferred for marketing and milling. A brief description about their inheritance and association with yield has also been provided to help breeders in decision-making.

2.1 Introduction

Yield is a product of numerous direct and indirect pathways originating from various traits and their complex interactions among themselves. A number of plant and environmental studies have been conducted in different crops using sophisticated models to understand the process of yield formation. Besides this, various statistical and biometrical methods have been proposed to eliminate/minimize environmental effects to understand the role of specific trait in the determination of yield. In order to select high-yielding genotypes, breeders have attempted to establish relative contribution of individual traits in determining yield. This was done with the help of simple statistical tools such as correlations, regressions, path analyses. However, none of the approaches is foolproof and has their own pros and cons.

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Based on number of genes, the traits have been considered a qualitative (1 or 2 genes with major effect) or quantitative (more genes, each with minor effect). In general, the qualitative traits contribute relatively less to yield but are important for resistances, restoration of fertility, and certain market-preferred traits. The heritability of such traits is usually high and has a little or no environmental effect. The quantitative traits, such as plant vigor, pod and branch number, on the other hand, play relatively a greater role in yield formation, but various major or microenvironment often influences their expression. In addition, there are some 'super' traits such as photosensitivity and growth habit (determinate or non-determinate), which are controlled by fewer genes, but when expressed, they alter the phenotype of the plant by altering the expression of other traits. In such events, the estimates of gene action, based on phenotypic data, are biased and useful conclusions cannot be derived. Therefore, as suggested by Byth et al. (1981), the studies related to the estimation of various genetic parameters, and the phenotypic selection should be exercised under the environment for which the cultivar breeding is targeted.

With all these limitations, the trait-based selection is being carried out in almost every crop and it has been effective with different degrees of success. In the present paper, the potential role of different plant and grain characteristics in determining yield and stability of pigeonpea are discussed to assist breeders in selection.

2.2 Productivity Traits

Maturity: Earliness in a crop has always fascinated both researchers and farmers. The traditional pigeonpea cultivars take 6–9 months to mature. Recently, some early lines maturing in 120–130 days were bred, and they succeeded in creating new production niches. Breeders at ICRISAT continued their efforts to reduce its maturity further to help in widening its adaptation. They succeeded in breeding genotypes, which take <50 days to flower, and their maturity is achieved in 80–90 days (Vales et al. 2012). In advanced trials, such genotypes have produced about 800–1000 kg/ha yield with mean per day productivity of 10 kg/ha. Since in pigeonpea earliness is tightly linked to photo-insensitivity (Wallis et al. 1981), such cultivars can help in broadening the adaptation to warm season windows (>20 °C) at higher altitudes (up to 1600 m), wider latitudes (up to 40° N/S), and under short-fallow between two normal crops (Table 2.1).

Table 2.1 Maturity groups of pigeonpea established at 17°N

Broad group	Sub-group	Days to flower[a]	Reference variety	Remarks[a]	Prodn. system
Super early	00	<50	MN 5	Photo-insensitive	Sole crop
Extra early	0	51–60	ICPL 88039	Photo-insensitive	Sole crop
Early	I	61–70	Prabhat	Photo-insensitive	Sole crop
	II	71–80	UPAS 120	Photo-insensitive	Sole crop
	III	81–90	Pusa ageti	Photo-sensitive	Sole crop
	IV	91–100	T. 21	Photo-sensitive	Sole crop
Medium	V	101–110	Maruti	Photo-sensitive	Intercrop
	VI	111–130	Asha	Photo-sensitive	Intercrop
	VII	131–140	ICP 7035	Photo-sensitive	Intercrop
Late	VIII	141–160	Bahar	Photo-sensitive	Intercrop
	IX	>160	MAL 13	Photo-sensitive	Intercrop

[a] Based on field observations on flowering at ICRISAT

Branches, pods, and pod-bearing clusters per plant: In pigeonpea, yield components such as number of branches, pods, and pod-bearing clusters are interlinked and influence the realized yield (Table 2.2). These traits are quantitative in nature and highly influenced by changes in the growing conditions and cropping systems. The heritability estimates of these traits are also low, and selection advance is limited. In spite of their low selection efficiency, pigeonpea breeders have used these traits frequently, but the results in terms of productivity gains are not very encouraging.

Seed size: There is a large variation (2–22 g/100 seeds) for seed size in pigeonpea germplasm. Seed size is an important component of yield in pigeonpea, and its relationship with yield is curvilinear in nature. D. Sharma (Pers. Comm.) studied this relationship in a large number of breeding lines and germplasm at ICRISAT, and he concluded that in the genotypes with seed size of ≤ 10 g/100 seeds, the correlation between yield and seed size was positive. This relationship, however, reversed within the large seeded (≥ 15 g/100 seeds) group of genotypes. Interestingly, there existed no relationship between these two traits in the seed size range of 11–14 g/100 seeds. Traders, millers, and consumers accept this seed size, and most breeders are now working within this range.

Pod size: In pigeonpea, the genetic variation for pod size (=seeds/pod) is large and varies from 2 to 9. In India, the large-podded genotypes are invariably consumed as a fresh vegetable, while the cultivars grown for *dal* purpose generally contain 4–6 seeds/pod. Normally, the traits such as pod size, seed size, pods/bunch, number of secondary branches are negatively associated with number of pods on a plant. The large-podded (8–9 seeds/pod) genotypes have shy pod bearing and suffer with the inherent problem of ovule abortion. In majority of the pods, 1–2 ovules fail to develop into seeds. This problem could be associated with the limited supply of food reserves to the developing ovules. In the small-podded genotypes, there is no issue of ovule abortion.

Plant biomass and harvest index: According to Y. S. Chauhan (Pers. Comm.), the high-yielding both inbred and hybrid cultivars have more or less similar partitioning and harvest indices. He further postulated that high yields recorded in hybrids were primarily due to greater biomass production and relatively with more pod-bearing sites. Bharathi and Saxena (2012) under controlled environment showed that the excessive vigor in the hybrids starts accumulating from very early seedling stage. This means that the plant vigor can be used as selection criterion, but within a given maturity, plant type, cropping system, and availability of moisture during reproductive stage.

In pigeonpea, harvest indices have little or no value for breeders, because their values are low and the estimates of genetic parameters such as genetic variation and heritability within a maturity group are not large enough to carry out any breeding exercise and expect significant genetic advances. In addition, being a perennial plant, its accurate measurement is also very difficult. Besides this, it is also proven that the plant biomass production is highly sensitive to changes in environment and cropping systems. In medium-duration cultivars, it was found to vary between 0.15 and 0.20 (Narayanan and Sheldrake 1979). Natarajan and Willey (1980) also

Table 2.2 Summary of relationships of yield with some key traits

Correlation of yield with	Reported correlations
Days to flower	+ve
Days to mature	+ve, non-sig
Plant height	+ve, −ve, non-sig
Seed size	+ve, −ve, non-sig
Seeds/pod	−ve, non-sig
Branches/plant	+ve
Pods/plant	+ve

reported large difference in the harvest indices; under pure stand of pigeonpea, it was 0.19, as compared with 0.32 in the intercrop. Matters are further complicated by pigeonpea shedding leaves throughout their growth cycle and are not normally included in the measurement.

2.3 Adaptation and Stability Traits

2.3.1 Diseases

Genetic resistances to key biotic and abiotic stresses reduce losses and provide stability to the production.

Fusarium wilt and sterility mosaic are major pigeonpea diseases causing severe yield losses each year. For wilt resistance, both recessive and dominant genes have been reported (Saxena et al. 2012); while for sterility mosaic, the genetics of resistance is unclear. Singh et al. (1983) reported that resistance to sterility mosaic virus was controlled by two dominant and two recessive alleles. Sharma et al. (1984) reported that the resistance to this virus was controlled by four alleles at two major loci. Of these, one each of dominant and recessive alleles together gives immune reaction. In both wilt and sterility mosaic, some prominent biotypes/races have also been observed. For fusarium wilt, the situation with respect to races and their resistance sources is inconclusive. For sterility mosaic disease, three prominent races, specific to area, have been identified. These are designated as Patancheru, Bangalore, and Dholi (Bihar) races, and their resistance sources are well defined.

In addition to wilt and sterility mosaic, Phytophthora stem blight is another potential disease. For this disease also, the existence of races has been established, but their biology and genetics of resistance are unclear. The race situation for Phytophthora blight is still unclear. Alternaria blight, though a minor disease, can cause severe damage in the post-rainy season sowings. A single recessive gene (Sharma et al. 1987) controls the resistance to Alternaria blight.

2.3.2 Insects

Helicoverpa armigera is the most common pod-boring insect of pigeonpea. The annual losses caused by this insect to pigeonpea are estimated to be around US $317 m. The genetic solutions to manage this constraint have not been successful and so far farmers resort to excessive use of chemicals to protect their crops. As an alternate breeding approach, the use of an endotoxin of *Bacillus thuringiensis* (*Bt*) is being tried in pigeonpea at ICRISAT. In pigeonpea, Sharma et al. (2006) reported the development of transgenic for pod borer resistance through direct organogenesis of axillary bud following 72 h co-cultivation with *A. tumefacience*. According to Sharma et al. (2008) although the transgenic pigeonpea plants with *Bt* are available at ICRISAT, the expression of the target genes in the selections for efficiently controlling pod borers under field conditions has been very low, and work is in progress to develop plants with better events.

2.3.3 Waterlogging

Temporary waterlogging in soils with high water-holding capacity poses a serious threat to pigeonpea productivity (Reddy and Virmani 1981). In India alone, about 1.1 m ha of land is waterlogged annually, causing losses of about 25–30% in the productivity (Choudhary et al. 2011). Under waterlogged situations, the useful aerobic bacteria become inactive while their anaerobic counterparts (both facultative/obligate bacteria) become active, and this results in the shortage of oxygen in the soil (Jackson 1990). This adversely affects general plant health. For screening waterlogging tolerance, a reliable technology was developed by Chauhan et al. (2008), and recently, a number of tolerant genotypes have been identified (Sultana et al. 2013). The resistance to waterlogging is controlled by a single dominant gene (Perera et al. 2001).

2.3.4 Drought

Drought is a universal abiotic constraint, and it may affect the crop at early, intermittent, or terminal growth stages with variable intensity (Lopez et al. 1996). In pigeonpea, very little work has been done to understand this constraint, and so far, no genotype with noticeable genetic resistance has been identified.

2.4 Grain Quality Traits

Pigeonpea produces quality grains with 20–22% protein. To produce more protein and meet the requirements, there is a need to breed cultivars with high (20–22%) protein and seed yield as good as traditional cultivars. At ICRISAT, breeding for high protein was taken up using wild species as donor parents. The newly bred lines had protein between 28 and 30% with yield as good as cultivar BDN 1 (Saxena and Sawargaonkar 2015). An estimate of protein yield from this genotype showed (Table 2.3) that the cultivation of such high-protein cultivars, in one hectare additional 100,000 gram protein could be harvested for the farming families.

2.5 Market-preferred Traits

Pigeonpea seeds are non-endospermic with a tightly glued seed coat. To prepare *dal* of good quality with minimum losses, the commercial millers and traders have preferences for various seed traits. These include seed size, shape, and color, besides overall *dal* recovery. Generally, seed size of 10–14 g/100 seeds is preferred for quality *dal* production. Millers easily accept round seeds with white or brown color, but seed lots with mixed colors/size fetch fewer rates in the market. Most millers consider *da*l recovery of about 70% in commercial milling economical. In eastern and southern Africa, the preferred varieties are those with large (>15 g/100 seeds) and white/cream grain color.

2.6 Naked-Eye Polymorphic Markers

Some distinctive morphological traits could be used to ensure genetic purity of breeding lines and cultivars. Such marker traits (Table 2.4) are controlled by recessive genes and popularly called as ‘naked-eye polymorphic markers.’ Some of such markers identified in pigeonpea germplasm are described herewith.

Obcordate leaf shape: One such important morphological trait is ‘obcordate leaf.’ This marker is controlled by a single recessive gene (Saxena et al. 2011), and it can be incorporated easily into popular cultivars and hybrid parents. This leaf marker expresses within a month from sowing. The out-crossed hybrid seedlings will have dominant normal (lanceolate) leaves. Such plants can be identified easily with naked eyes for rouging before flowering.

Sesame leaf shape: The plants have long narrow leaves with greenish-yellow color and can be identified easily with naked eyes. Since the sesame leaf trait is controlled by single recessive gene, it can be incorporated easily into the genotypes of interest and can be used as

Table 2.3 Seed and protein yields harvested from high-protein lines

Genotype	Maturity (days)	100-seed wt (g)	Yield (kg/ha)	Protein (%)	Protein yield (g/ha)
HPL 40–5	169	9.6	2100	26.9	452,000 (21.2)
HPL 40–17	169	8.5	2070	26.5	440,000 (18.0)
BDN 1 (C)	168	9.6	2020	23.2	373,000
SEm±	0.9	0.18	160	0.46	–
CV (%)	0.9	3.4	17.3	3.0	–

Source: Saxena and Sawargaonkar (2015); () % advantage over control

Table 2.4 List of potential naked-eye polymorphic traits in pigeonpea

S. no	Plant part	Recessive phenotype	Dominant phenotype
1	Stem	Green	Purple
2		Determinate	Non-determinate
3		Corky	Smooth
4		Single culm	Branching
5		Decumbent	Strait
6	Leaf	Obcordate	Lanceolate
7		Narrow	Lanceolate
8		Sesame	Normal
9	Flower	Cleistogamous	Normal
10		Yellow color	Red color
11	Pod	Green color	Purple color
12	Stature	Dwarf	Tall

marker for maintaining genetic purity in pigeonpea.

Genetic dwarfs: In a well-managed crop, the pigeonpea plants often grow to a height of 2–3 m, and it becomes difficult to manage insects with chemical sprays. The only viable alternative is to tackle this issue by reducing plant height at genetic level. Earlier efforts in this direction succeeded in identifying various dwarfing sources, but the breeders could not succeed in transferring this trait to high-yielding genotypes.

Determinate growth habit: The non-determinate plants have a vegetative terminal bud, which allows the plant to grow in height and spread under adequate moisture conditions. In such plants, the flowers and pods are borne in bunches on the axillary inflorescences arising from nodes. The alternative form of this plant type is designated as 'determinate.' The determinate pigeonpea plants are short in stature and are characterized by reproductive terminal buds. Such plants when they reach flowering stop growing in height. The cultivars with determinate growth habit are not popular because of their greater susceptibility to pod borers. In most cases, the determinate growth habit is controlled by a single recessive gene and can be distinguished easily with naked eyes (Kapoor and Gupta 1991).

Green stem: Genotypes with uniform green stem color were used as 'naked-eye polymorphic marker' in studying the extent of natural out-crossing in pigeonpea (Bhatia et al. 1981). A single recessive gene controls this trait, and its alternate form has dark purple-colored stem.

2.7 Evolution-related Traits

Biologists often ask a question about the evolution of pigeonpea from its wild form to the domesticated types, and some believe that pigeonpea plant is still evolving in nature. The presence of certain plant traits indicates that, in spite of 3000 years of cultivation, the crop is not fully domesticated. The traits such as absence of annual growth cycle, creation of food reserves in stem and other parts, photosensitivity, extensive flower drop, presence of strophiole, and pod shattering in certain germplasm support this view. According to De (1974) and Maesen (1980), the cultivated form of pigeonpea originated from *Cajanus cajanifolius*, a wild relative of pigeonpea, through a single gene mutation. Perhaps a careful comparison of the two species at morphological and genomics levels can through some light on this issue.

Perenniality: Botanically, all the pigeonpea genotypes are perennial. This perennial nature, however, is not very strong across the germplasm, and genetic variation has been observed. In general, the pigeonpea plants survive for

3–5 years. No information is available on the physiology or genetics of this trait.

Photosensitivity: In pigeonpea, long hours of darkness induce flowering, therefore it is classified as a`short-day plant.' Day and night temperatures also interact with prevailing photoperiod to influence the emergence of flowers. The information on the threshold levels for inducing flowering is inconclusive. Wallis et al. (1981) studied the response of extended (16 h) photoperiod on flowering in a range of genotypes and concluded that in pigeonpea, earliness and photo-insensitivity were inversely correlated. Saxena (1981) studied the inheritance of photoperiod reaction in pigeonpea and concluded that three major dominant genes (Ps_1, Ps_2, and Ps_3) were responsible for lateness, and these genes exhibited pleiotropic effects under extended daylength to determine the photoperiod sensitivity. He further concluded that it is not possible to breed late maturing photo-insensitive cultivars in pigeonpea.

2.7.1 Temperature

Inherently, pigeonpea is a warm season pulse and it grows well in the temperature range of 25-35 °C. In both low as well high temperature regimes its growth, flowering and pod set are adversely affected. Under low (<10 °C) temperatures the photosynthesis in the plants is adversely affected due to moisture stress and internal injury causing of cell sap; while the high (>40 °C) temperatures often lead to pollen abortion/sterility and flower drop. In pigeonpea, this has not been an area of serious research and very little and unconfirmed information is available with respect to critical/threshold temperature levels and genetic variation for the tolerance for this abiotic factor.

2.7.2 Need a Section on Temperature Influence

Cleistogamy: Natural out-crossing has been recognized as a major constraint in maintaining genetic purity in pigeonpea. Saxena et al. (1992) selected segregants from an interspecific cross with modified flowers that does not permit natural out-crossing. Since this floral variant is easy to identify and it is controlled by single recessive gene, it offers opportunities to breed cultivars with least or no out-crossing.

Male sterility: In pigeonpea genetic (GMS), cytoplasmic nuclear (CMS), and temperature-sensitive (TGMS) male sterility systems have been discovered. A total of 11 GMS sources were reported from different researchers (see review by Saxena et al. 2010; Saxena 2014). At present, these are not being used in any plant breeding activity, but their maintenance would be a positive step toward conserving biodiversity. Two CMS systems (A_2 and A_4) in pigeonpea have been stabilized, but only A_4 with *C. cajanifolius* cytoplasm is being used in commercial hybrid breeding. The other six CMS sources need to be stabilized for cytoplasmic diversification of pigeonpea hybrids.

Some rare traits: Sometimes, certain rare traits also appear in the crop. This generally happens due to spontaneous recessive mutation and subsequent segregation. Invariably, such traits are lost because of their inability to compete or survive. Most of these traits have no economic value, but can be considered important from academic point of view. Some of such mutants identified at ICRISAT were corky stem (Saxena et al. 1988a, 1988b), open carpel (Saxena et al. 1988a, 1988b), and prostrate or decumbent growth (Saxena et al. 1989) habit. These mutants must be maintained in genetically pure form.

2.8 Traits of Interest in the Wild Species

The cultivated species of crops have originated from their wild ancestors, and it has taken centuries to evolve through natural phenomenon of mutation and selection. Such processes gradually led to species differentiation within a given genera. During this process, some important alleles (mostly recessive and those with minor

Table 2.5 List of important traits available in secondary and tertiary gene pools

Traits lacking in primary gene pool	Potential donor species in secondary gene pool
High protein	*C. scarabaeoides*
	C. albicans
	C. sericeous
Pod borer resistance	*C. scarabaeoides*
Salinity tolerance	*C. sericeous*
CMS inducing cytoplasm	*C. scarabaeoides*
	C. albicans
	C. sericeous
Temperature-sensitive male sterility	*C. sericeous*

effects) were also lost, and the cultivated species lacked these vital traits. Over a period of time, the gene frequencies in highly self-pollinated and those with strong crossability barriers were more or less stabilized, while those with out-crossing continued to maintain such variability.

Based on the crossability barrier, Harlan and de Wit (1971) classified the germplasm into three broad groups and called them gene pools. The primary gene pools consisted of cultivated types and were easy to cross with other sister lines. The secondary and tertiary gene pools were involved all the wild relatives of species. In the former group, the crossable wild species were included, while the non-crossable species constituted the tertiary gene pool. Similar to primary gene pool, in the secondary and tertiary gene pools also, a considerable intra-species genetic variability for different traits exists (Saxena et al. 1990, 1996). This means that for the genetic improvement of cultivated types using its wild relatives, a careful scanning of traits within wild species and their documentation is essential (Table 2.5). From the species representing the secondary gene pool, so far traits such as high protein have successfully been transferred (Saxena and Sawargaonkar 2015). In addition *C. scarabaeoides*, *C. sericeus*, *C. reticulatus*, and *C. cajanifolius* were used to breed cytoplasmic nuclear male sterility systems (Saxena et al. 2010). Due to strong crossability barriers, the transfer of useful traits from the tertiary gene pool is not easy. The only successful example is *C. platycarpus*. Mallikarjuna and Moss (1995) crossed this species with cultivated type using embryo rescue technology. They succeeded in transferring *Phytophthora* blight resistance and earliness to the cultivated types.

2.9 Inheritance of Key Traits

For planning a sustainable genetic enhancement programme, information on gene action of the key traits is essential. In pigeonpea, limited information is available in different maturity groups. The information available from literature (Saxena and Sharma 1990) has been summarized (Table 2.6) for the benefit of the readers. For any detailed information, the original research papers need to be consulted. A perusal of the table shows that both additive as well as non-additive gene actions govern the key traits. For yield enhancement in pigeonpea, both pure line and hybrid breeding programs are in use.

2.10 Genomic Approaches for Trait-Based Breeding

Breeding program in pigeonpea is expected to be enriching through collaborative approaches incorporating genomics interventions. Benefits of combining genomics tools with breeding have been identified in a number of crop species (Varshney et al. 2006). However, in the case of

Table 2.6 Summary information on gene action of some key traits

Trait	Additive	Non-additive	Add. + Non-add.
Days to flower	*		*
Plant height	*	*	*
Plant width	*		*
Days to mature	*	*	*
Pods/plant		*	*
Seeds/pod	*		*
Seed size	*	*	*
Seed yield	*	*	*
Protein %		*	*

Table 2.7 List of traits tentatively identified for genomics research

Trait	Target gene	Donor source	Priority
Wilt resistance	Dominant gene	ICPL 87119	1
SM resistance	Genes from 3 races	ICP 7035	1
Alterneria blight	Recessive gene	ICPL 366	4
Phytophthora blight	Dominant gene	Wild relatives	4
Waterlogging	Dominant gene	ICP 5028/MAL 15	2
High protein	Recessive gene	Wild relatives	3
Fertility restoration	Dominant gene	ICPL 87119	1
Cytoplasmic male sterility	–	ICPA 2039	1
Cleistogamous flower	Recessive gene	ICPL 99050	2
Obcordate leaves	Recessive gene	ICP 5277	2

pigeonpea with few exceptions such as markers for purity testing in hybrids and few preliminary studies on marker trait associations, larger gains from genomics have not realized. Successfully applying genomics in harnessing the genetic gains requires diverse genetic resources, trait phenotyping, genomics tools, bioinformatics, and proof of gene function in crop, i.e., proof of concept. In order to implement genomics in pigeonpea improvement two major milestones have been achieved (1) understanding the desired phenotypic traits in the field (Table 2.7) and (2) developed ample genomics resources including draft genome sequence (Pazhamala et al. 2015). Now, the further challenge is to effectively combine different genomics approaches, integrating information to maximize for pigeonpea improvement. Once marker trait associations established will provide easy/accurate means of selection and transferring desired traits in required genetic backgrounds.

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