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Inheritance of photo-sensitivity in pigeonpea

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Abstract

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is a short-day legume species and the late maturing genotypes are more photo-sensitive than early types. To generate information about the inheritance of photo-sensitivity, this study was conducted under natural and artificially extended (16 h) photo-periods using F_1, F_2 and BC_1F_1 generations. Under natural photo-period, F_1 hybrids showed partial dominance of earliness; while in F_2, a normal distribution that was skewed towards earliness was observed. In contrast under extended photo-period, the spread of F_2 data was wide with discontinuities recorded at day 70, 82 and 103. Chi-square tests, when applied to F_2 and BC_1F_1 data, suggested that three dominant genes (PS_3, PS_2 and PS_1) controlled the expression of photo-sensitivity. These genes were found operating in a hierarchical order with PS_2 and PS_1 genes failing to express in the presence of PS_3 gene. Similarly in the absence of PS_3 gene, PS_2 expressed but it masked the expression of PS_1. Further, PS_1 gene expressed only when both PS_3 and PS_2 were in recessive homozygous state. Hence, the proposed genetic model for photo-sensitivity in pigeonpea is $PS_3 > PS_2 > PS_1$ and photo-insensitive genotype being a triple recessive ($ps_3ps_3ps_2ps_2ps_1ps_1$).

Key words: *Cajanus cajan*, chi-square, photo-insensitivity, qualitative inheritance.

Introduction

Pigeonpea [*Cajanus cajan* (L.) Millsp.] evolved about 3500 years ago through spontaneous mutations in a photo-sensitive wild species *Cajanus cajanifolius* (van der Maesen 1980; Varshney et al. 2017). Mallikarjuna et al. (2012) postulated that with the exception of 3-4 major genes, these two species shared more or less similar genetic materials. The landraces which emerged from this base material through further spontaneous mutations and natural selections (Saxena et al. 2019) were also highly photo-sensitive and flowered only under shortening days. These landraces were under cultivation in various parts of India for centuries and over time they spread to over 100 countries through human and commodity traders (Mula and Saxena 2010).

In literature, pigeonpea is being considered as both a quantitative (Gooding 1962, Spence and Williams 1972 and Summerfield and Roberts 1985) as well as qualitative (Carberry et al. 2001; Craufurd et al. 2001) short-day species. The fact, however, remains that shortening days induce flowering in pigeonpea but its critical light hour requirement is not well researched and the results are inconsistent. For instance, Sharma et al. (1981) reported 13 h critical day length for the induction of flowering, while McPherson et al. (1985) and Silim et al. (2007) reported it to be 12 h and 11 h, respectively.

Upadhyaya et al. (2007) screened 10390 pigeonpea germplasm for their flower emergence under 16 h photo-period; and based on 50% flowering three accessions were identified as “less or total photo-period insensitive”. Wallis et al. (1981) conclusively demonstrated that in pigeonpea earliness was closely linked to photo-insensitivity. Saxena et al. (2019), while reviewing literature on the mechanisms involved in the evolution of earliness in pigeonpea, concluded that early maturity (thereby photo-insensitivity) was a product of spontaneous recessive mutations and/or transgressive segregations. They also observed that breeding of super early and early maturing cultivars

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has considerably extended the adaptation of pigeonpea. Also, the early pigeonpea types have played a significant role in the emergence of new cropping systems.

An understanding of the inheritance of photo-sensitivity can assist breeders in transferring some useful gene(s) from the photo-sensitive germplasm to elite insensitive genotypes and in developing new high yielding photo-insensitive cultivars. Unfortunately, in spite of high importance of photo-insensitive early and super early genotypes (Srivastava and Saxena 2019) and availability of diverse germplasm, only a single report (Craufurd et al. 2001) is available on the genetics of photo-sensitivity. Therefore to draw some logical conclusions on this aspect, more studies involving diverse parental materials are needed. The present study is an effort in this direction.

Materials and Methods

Preparation of experimental area

Pigeonpea plants are known to produce certain volatile chemicals and nectar during flowering (Saxena et al. 2016); and these invite a variety of flying insects. The foraging and nectar harvesting by such insects often result in cross-pollination and fertilization. The natural cross-pollination occurs in almost all the pigeonpea growing countries but their extents vary considerably (Saxena et al. 2016). The out-crossing does not allow a genotype to retain its genetic identity under open-field conditions and makes it unfit for any quality genetic study. Under these circumstances, it was decided that all the experimental materials, irrespective of its filial generation and population size, will be grown under controlled pollination. Therefore, to keep the potential insect pollinators away from the crop, nylon nets were fixed over the entire experimental area using aluminium frames, well before the commencement of flowering.

The experiments were conducted at the University of Queensland research station located at Redland Bay, about 30 km away from Brisbane city. For sowing, two blocks were prepared, one each for natural and extended photoperiod, and to avoid interference from artificial lights, these were separated by about 150 m. To provide extended (16 h) light in the illuminated block, one 60 Watt incandescent bulb was hanged over a 6' x 6' grid. These bulbs were placed about 2' above the plant canopy level. To maintain this scenario throughout the experiment, height of the bulbs was raised every week. To control the duration of light an automatic timer was used.

Selection of experimental materials

A photo-period insensitive pigeonpea line QPL 1 was selected from the breeding materials grown at the University farm. This genotype was introduced earlier from ICRISAT. It flowered in 51+3 days at Patancheru (17^{o} N), 57+1 days at Hissar (29^{o} N) and in 54+2 days at Redland Bay (27^{o} S). The photo-sensitive parental genotypes MS 3A and MS 4A are genetic male sterile lines developed at ICRISAT under hybrid pigeonpea breeding project. These are known photo-sensitive genotypes and did not flower under the extended photo-period until 125 days when the experiment was terminated. At this time in this material not even the floral bud formation was observed. Seeds of these genotypes were also imported from ICRISAT.

Sowing, hybridization and generation advancement

To kick-off the genetic study, seeds of QPL 1, MS 3A sib, MS 4A sib were sown at the onset of rainy season on ridges, 75 cm apart under natural day length. A basal dose of di-ammonium phosphate was applied @ 100 kg/ha with irrigations given as and when found necessary. Seeds of MS 3A and MS 4A were maintained by crossing the male sterile with their fertile sibs. To develop hybrid generation, the male sterile segregants were crossed with QPL 1. To facilitate hybridization between the two genotypes with diverse flowering time, the plants of QPL 1 were maintained in their reproductive stage by cutting back (ratooning) the top of canopy and periodic removal of flowers and young pods (Saxena et al. 1976) until the late flowering parents commenced flowering. Seeds of QPL 1, the two hybrids and sib-mated male steriles were harvested. In the subsequent season, both the F_1 hybrids were sown to produce F_2 and backcross seeds. For some reasons, the backcross seed could be produced only in cross MS 3A x QPL 1. In the final experimentation, seeds of the parents, F_1s, F_2s and backcrosses were sown the same day in both the blocks and a healthy crop was maintained.

Data recording and analyses

Each plant in the two blocks was tagged for the number of days it took from sowing to the opening of its first flower. This exercise was carried out on alternate days and continued up to 125 days from the date of sowing. The flowering data of F_2 and BC_1F_1 populations, generated from the extended photo-period plot were

subjected to the standard chi-square test.

Results and Discussion

Pigeonpea germplasm is known to harbour a vast (45 to >160 days) genetic variation for time taken from sowing to flowering. Saxena and Sharma (1990), while reviewing the genetics of flowering time in pigeonpea concluded that it is conditioned by a few genes with additive effects and partial dominance of earliness. Overall, the literature on this subject in pigeonpea is inconsistent and not properly understood. Such ambiguity in literature could be due to the (i) use of different or impure parental materials, (ii) variation in photo-thermal regimes in different studies, (iii) genotype x photo-period x temperature interactions and (iv) methodology used in recording data.

Flowering under natural photo-period

Under natural photo-period (13.8 h max.) the late maturing parents MS 3A and MS 4A, respectfully took 118+1.7 and 120+2.4 days to flower; while QPL 1 flowered in 44+1.9 days. The hybrid plants flowered in 81+2.1 days in cross 1(MS 3A x QPL 1) and 84+2.8 days in cross 2 (MS 4A x QPL 1). In F_2 generation of cross 1, a total of 202 plants were raised and the days to first flower ranged from 46-116 days, while in cross 2 (87 plants), this range was from 49 to 119 days. F_2 distribution in both the crosses followed more or less normal distribution but with a slight skew towards earliness. In cross 1, the backcross to early parent flowered in 60-67 days, while with that of late parent it took 95-101 days.

Segregation for flowering under extended photo-period

Garner and Allard (1920) were the first to recognize the influence of day-length on flowering of plants. They hypothesized that the photo-period requirement of different species may vary, quantitatively or qualitatively, from day-neutral to short or long days; and it is determined by the amount of light absorbed by phytochormes present in the plant system.

In the present experiment the photo-period insensitive line QPL 1 took about a week more to flower when compared to natural photo-period regime and flowered in 53 +1.6 days. In contrast, the photo-period sensitive parents MS 3A and MS 4A did not flower in this environment until 125 days when the experiment was terminated. The hybrid generation in both the crosses also took about a fortnight more to flower when compared to the natural photo-period. In F_2 generation, the earliest segregants in cross 1 and cross 2, respectively took 49 and 52 days to flower. Under this environment in cross 1 and 2, respectively 215 and 197 F_2 plants failed to flower when the experiment was terminated. In cross 1, the backcross to photo-period insensitive parent flowered in 74+3.1 days; while with that of the sensitive parent it took 117+4.6 days to flowwer.

In each F_2 population, the spread of individual plant flowering data were thoroughly examined and four clear discontinuities at day 103, 82 and 70 (Fig. 1) were observed; and these considered the

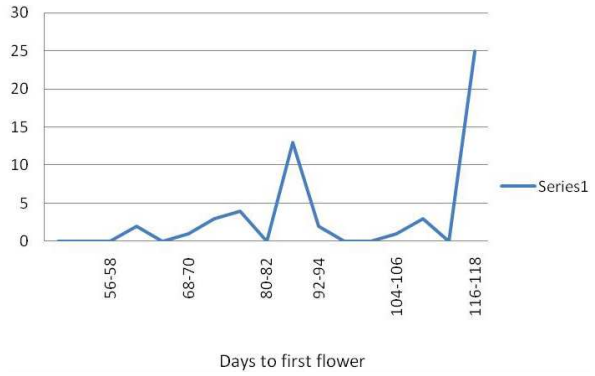

Fig. 1. F_2 frequency distribution for days to first flower under 16 h light

phenotypic photo-period response classes. The frequency of plants recorded within each of the four phenotypic groups and the standard chi-square tests were applied for genetic interpretations. The data (Table 1) fitted well to the expected ratio of 48 (late): 12 (medium): 3 (early): 1(extra early). The backcross population involving the insensitive parent also segregated in the same four phenotypic classes. The recorded counts (Table 1) fitted well (Prob. = 0.170) to the expected ratio of 4 (late): 2 (medium): 1 (early): 1 (extra early). These segregation patterns suggested that the photo-sensitivity in pigeonpea was conditioned by three dominant genes with epistatic effects. These genes, designated as PS_3, PS_2 and PS_1, were expressed only under extended photo-period regime. Also, they followed a unique hierarchical order where the genes PS_2 and PS_1 failing to express in the presence of PS_3 gene. Similarly, in the absence of PS_3 and presence of PS_2 gene, only PS_2 expressed and the expression of PS_1 gene was masked. Further, PS_1 gene was expressed only in the situations when PS_3 and PS_2 genes were in recessive homozygous

Table 1. Frequency distribution in F_2 and BC_1F_1 generations in four response groups under extended photo-period and probability of segregation for photo-sensitive (*PS*) genes

Gen (F_2/BC)/ FI group (d)	*PS* gene present	Expected ratio	Ratio (number of plants)		Probability	
			Cross 1	Cross 2	Cross 1	Cross 2
< 70	None	1	4	3	-	-
71-82	1(PS_1)	3:1	16:4	16:3	0.676	0.279
83-103	2 (PS_2, PS_1)	12:3:1	52:16: 4	56:16:3	0.371	0.323
104- >125	3 (PS_3, PS_2, PS_1)	48:12:3:1	215: 52:16: 4	197:56:16:3	0.223	0.211
	Total	64	287	272	-	-
BC_1F_1	PS_3, PS_2, PS_1	4:2:1:1	64:25:16:11	-	0.170	-
	Total	8	116			

Cross 1: MS 3A x QPL 1; Cross 2: MS 4A x QPL 1

state. Thus, the hierarchy was summarised as $PS_3 > PS_2 > PS_1$. In this genetic model the photo-insensitive genotype will be a triple homozygous recessive ($ps_3ps_3ps_2ps_2\ ps_1ps_1$). In some crops, the photo-sensitivity may also involve one or more genes with minor effects, as observed by Tsao (1977) in *Phaseolus vulgaris*. In the present study, however, no evidence of such gene(s) was detected.

Like most crops in pigeonpea also, the ambient temperatures are known to influence the time taken to flower (Turnbull et al. 1981; Wallace et al. 1993, Silim et al. 2007). The prevailing minimum (16.8 - 19.4°C), maximum (26.7 - 29.1°C), and mean (23.4 - 25.7°C) temperatures recorded during the experimentation remained more or less uniform (www.longpadedock.qld.gov.au/silo/point-data/). Byth and Wallis (1981) and Turnbull et al. (1981) opined that the ranges recorded in the ambient temperatures at the research farm were not large enough to confound the present results. The flowering data also revealed that both the crosses behaved more or less in the same way under both the test environments; and this could be due to the close genetic relationship between the two photo-period sensitive parents used in this study (Reddy et al. 1977).

In case of pigeonpea earliness has been reported to be partially dominant over lateness and its degree may vary in different genotypes and the environments (Saxena and Sharma 1990). Craufurd et al. (2001) reported the presence of two flowering genes in pigeonpea which expressed only under 15 h photo-period environments. Besides pigeonpea in some other crops also, the presence of major genes, expressing exclusively under extended photo-period, has also been reported. These include, common bean (*Phaseolus vulgaris*) which, under long days, had two dominant genes and three response groups (Kornegay et al. 1993). Similarly in an F_2 population of *Phaseolus vulgaris*, Coyne (1966) observed quantitative uni-model segregation for flowering in environment I and a qualitative bi-modal (9:7) segregation in environment II (Coyne 1967). He attributed this difference to the presence of two major genes which expressed only in the second (conducive) photo-period environment, and not in the first.

A perusal of inheritance patterns in some other pulse crops revealed that photo-period sensitivity is rather simply inherited. For instance, in *Vigna unguiculata* (Ishiyaku and Singh 2001), *Vigna radiata* (Sen and Ghosh 1961) and *Vigna mungo* (Sinha 1988) the photo-period sensitivity was controlled by monogenic recessive gene. On the other hand, a single dominant gene was responsible for photo-period sensitivity in *Cicer arietinum* (Or et al. 1999) and *Lablab purpureus* (Prasanthi 2005). Tsao (1977), however, reported that photo-period insensitivity in *Phaseolus vulgaris* was under the control of four dominant genes.

Photo-insensitivity in relation to adaptation

In an effort to enhance pigeonpea production at international level it has been emphasized that new

photo-period insensitive early maturing cultivars, which can be grown successfully in non-traditional areas at varying altitudes and latitudes, should be developed (Sharma et al. 1981). In this context, the breeding of new super early pigeonpea genotypes which take <90 days to mature (Srivastava and Saxena 2019) can further enrich the scope of crop diversification.

Since in pigeonpea, photo-period insensitivity and earliness are closely linked to each other (Wallis et al. 1981; Turnbull et al. 1981, Wallace et al. 1993), the selection for earliness can help in breeding near photo-period insensitive lines. In order to develop such cultivars breeding methodologies like bi-parental mating, selection of transgressive segregants and spontaneous mutants have been used successfully in the past (Saxena et al. 2019). For success in this endeavour; it is necessary that the selection environment should have a photo-period regime that is long enough to allow the expression of triple recessives ($ps_3ps_3ps_2ps_2ps_1ps_1$). At this point, an example of breeding photo-period insensitive pigeonpea genotype MN 5 using two diverse natural photo-period sites would be appropriate. In the early 90s some short duration (110-120 d) advanced inbred lines, developed at 17^0 N (Patancheru) under natural photo-period, were sent to Minnesota (45^0 N) for testing their adaptation under 16 h natural photo-period. At this location although these lines were early, but exhibited significant intra-line variability for days taken to flower (Davis et al. 1995). The selections for the earliest flowering segregants at this location produced a new super early photo-insensitive inbred line MN 5. This selection, when brought back and grown at Patancheru, flowered in around 45 days and its maturity was achieved in 85-90 days. From this breeding/ testing experience it is hypothesized that although the originally introduced ICRISAT-bred line appeared pure for earliness under short days and perhaps carried the photo-period sensitive gene PS_1 in both homozygous and heterozygous forms which did not express under short days of Patancheru. When this material was exposed to long day environment of Minnesota, the heterozygous (PS_1ps_1) genotypes segregated and generated variation for flowering, which allowed the selection of triple recessive genotypes; and this turned out to be a super early and photo-period insensitive. These observations suggested that the genotypes bred under long days can be grown successfully at lower latitudes as well, but not the *vice versa*. Since the high latitude locations may not be accessible easily to breeders, some alternatives need to be worked out. One possible approach is to screen the breeding materials under artificially extended photo-period and advance the early and super early selections through speed breeding (Saxena et al. 2017).

The importance of early maturing photo-period insensitive pigeonpea is now well established for widening its adaptation. The present study showed that there are three dominant genes in pigeonpea which govern the expression of photo-period sensitivity. Further, the positive pleiotropic relationship between photo-period sensitivity and time taken to flower suggested that in this crop long duration photo-period insensitive cultivars cannot be bred. The photo-period insensitive early and super early cultivars, however, can be bred by screening the segregating populations under extended (16 h) photo-period and selecting the desired early flowering segregants. For this breeding activity some recently developed molecular technologies such as SSR (simple sequence repeat) and SNP (single nucleotide polymorphism) can also be used (Bohra et al. 2020). These will provide a viable breeding platform to implement marker-assisted selection (MAS); markers-assisted back-crossing (MABC) and early generation selection (EGS) to help in identifying the plants with triple recessive ($ps_3ps_3ps_2ps_2ps_1ps_1$) genetic constitution. The development of parallel genome sequencing and whole genome re-sequencing in recent times can also facilitate the genomics-based breeding of photo-period insensitive genotypes more accurately and at a faster pace.

Authors' contribution

Conceptualization of research (KBS, DEB); Designing of the experiments (KBS, DEB, ESW); Contribution of experimental materials (ICRISAT, UQ*); Execution of field/lab experiments and data collection (KBS, ESW); Analysis of data and interpretation (KBS, YSC, DEB, ESW); Preparation of manuscript (KBS, YSC).

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Declaration

The authors declare no conflict of interest.

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