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Research paper

First report of partial dominance of photo-insensitivity in pigeonpea (*Cajanus cajan* L. Millsp.)

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ABSTRACT

The time taken from sowing to flowering in pigeonpea is positively associated to its photoperiod responses; and it is expressed in terms of delay in flowering when exposed to long photoperiods. The late maturing genotypes, without exception, are photo-sensitive with critical daylength of around 11 h. The early flowering types, on the other hand, are invariably photo-insensitive. The past research on this subject has shown that the photo-insensitivity in pigeonpea was controlled by 2-3 simply inherited recessive genes. The present study was designed to understand dominance relationships among photo-sensitive and photo-insensitive alleles in six diverse crosses. It involved two photo-insensitive (Prabhat and Pant A3) and three photo-sensitive (Code 14, ICP 7065, T17) genotypes. Under long photoperiods, the three Prabhat hybrids, on average, flowered in 190.8 days, while the Pant A3 hybrids took only 82.1 days to flower. It was concluded that the two photo-insensitive genotypes carried different sets of genes for this trait. In Prabhat the photo-insensitivity was recessive in nature, while in Pant A3 it was controlled by partial dominant genes. This is the first report in pigeonpea where a photo-insensitive genotype with partial dominant genes has been identified.

Key words**:** Flowering time, Partial dominant genes, Photo-insensitivity, Photoperiod.

INTRODUCTION

The archaeologists (Kajale *et al.*, 1974), botanists (De, 1974; van der Maesen, 1980), and geneticists (Varshney *et al.*, 2017) believe that pigeonpea [*Cajanus cajan* (L.) Millsp.] evolved about 3500-4000 years ago through spontaneous mutations in a photo-sensitive wild species namely, *Cajanus cajanifolius* (Haines) Maesen. The primary mutational events were followed by the emergence of diverse photo-sensitive pigeonpea landraces on the horizon through subsequent mutations, creation of new recombinants, and selection of the adapted individuals.

The present global pigeonpea germplasm, embracing over 15,000 accessions, display a continuum of flowering from as early as 45 days to over 150 days. Saxena *et al.* (2019), while tracking the origin of earliness in pigeonpea, concluded that the early genotypes are of recent origin and they emerged following a series of recessive spontaneous mutations in the late maturing landraces and cultivars and subsequent self-fertilization of the heterozygotes and selection of the odd early flowering segregants by breeders. Saxena *et al.* (2021) opined that the time taken to flowering and photo-sensitivity were tightly linked due to their pleiotropic origin. The studies conducted by Wallis *et al.* (1981), Upadhyaya *et al.* (2007), Srivastava and Saxena (2019), and Saxena *et al.* (2021) revealed that the earliest flowering germplasm were most photo-insensitive and the late types had strong short-day requirement for flowering.

The present experiment was a part of larger hybrid breeding project; and it was conducted to assess the consistency of dominance relationships within six crosses involving photo-insensitive and photo-sensitive parents across different photoperiod regimes. Interestingly, the crosses involving the two photo-insensitive parents Prabhat and Pant A3, as a group, differed grossly for their time taken to flower under long photoperiod environments. This paper, besides analyzing the flowering patterns of the six hybrids and their parents under short- and long- photoperiods, also discusses the information on the dominance relationships among the alleles controlling photoperiod responses in pigeonpea.

MATERIALS AND METHODS

In this study two early (photo-insensitive) and three late (photo-sensitive) flowering genotypes were used. The early maturing cultivar Prabhat was bred in Kanpur (26.5 ^{0}N), while Pant A3 originated from Pant Nagar (29.0^{0}N). Among the late flowering parents, ICP 7065 is a field collection from Nagpur district (21.2 ^{0}N), Code 14 is a germplasm from Trinidad and Tobago (10.7^{0}N) - a Caribbean Island, and T-17 is a cultivar that was bred at Kanpur. Self-pollinated seeds of these genotypes were acquired from Pigeonpea Breeding Unit of ICRISAT and sown in a crossing nursery at Patancheru (17.5^{0}N). At the commencement of flowering a few branches of each plant were covered with muslin cloth bags to obtain their pure seeds. At the same time, ten crosses were also made in a 5-parent half-diallel scheme.

From the available selfed and crossed seeds, three lots were prepared for sowing. To provide significant daylength variation for the experiment, three diverse sowing dates were identified. These were the normal July 7 (13 h, followed by short days), November 3 (11 h, followed by short days), and the delayed February 20 (12 h, followed by long days) sowings. For each planting, a basal doze of di-ammonium phosphate was applied @ 100 kg/ha; and ridges were constructed at 75 cm spacings. In each experiment, a pre-sowing irrigation was given to assure uniform germination. Two replications of 4m long two-row plots were sown in a randomized complete block design. Seeds were dibbled at inter-hill spacing of 25 cm. In the experiment plots, the seedling establishment was adversely affected by the infestation of collar rot (*Sclerotium rolfsii*) disease. After 3-4 weeks, the hybrid progenies were examined for their true hybridity. This was done by using the phenotypic markers (growth habit, stem colour, and leaf size) of the pollen parents. For accuracy of data, any suspected self-pollinated plant within the hybrid rows was uprooted.

On each plant the time taken from sowing to first flower opening was recorded. Due to variable population (21-33 plants/plot) in the trials caused by the disease, the scheduled data analysis was not performed, and instead, for each planting date the entry-wise data over the two replications were pooled and their standard errors were estimated. In view of small (22.5 x 9 m) and uniform experimental area and good crop management it was thought that, in spite of limited plant population, the study of pooled data over the replications would provide some logical information about the inheritance of genes responsible for photo-sensitivity. Further, the information generated from this study may also be of value in designing elaborate future studies on this subject.

RESULTS AND DISCUSSION

Daylength sensitivity for flowering time in pigeonpea- a brief overview

Garner and Allard (1920) were the first to study the effect of daylength on flowering time of plants. They hypothesized that the photoperiod requirement of different plant species may vary, quantitatively or qualitatively, from day-neutral to short or long days. In case of pigeonpea, the available information on critical daylength for inducing flowers is limited and unclear. Sharma *et al.* (1981), for example, reported 13 h critical daylength, while McPherson *et al.* (1985) and Silim *et al.* (2007) reported it to be 12 h and 11 h, respectively. This inconsistency could be attributed to the differences in genotypes or methodologies used in their experiments.

So far there is no direct experimental evidence in pigeonpea to show the existence of a basic vegetative phase. In this context, Byth *et al.* (1981) opined that since the pigeonpea seedlings show variable responses under different photoperiods with respect to growth rate and flowering time, there may not be any notable basic vegetative phase in this crop. In some crops besides photoperiod, the temperature is also known to play role in the emergence of flowers. Unfortunately, on this aspect also, little information is available from the controlled-environment studies to reliably pronounce the effects of temperature on flowering (Turnbull, 1986; Lawn and Troedson, 1990; Troedson *et al.*, 1990).

Carberry *et al.* (2001) defined the qualitative photoperiod sensitive response as "one in which flowering does not occur when photoperiod exceeds a critical value" and accordingly they classified pigeonpea as a qualitative short-day species. This statement is in divergences with the conclusions of Summerfield and Roberts (1985) and Saxena *et al.* (2021) who classified pigeonpea into a quantitative short-day plant. Carberry *et al.* (2001) also opined that pigeonpea germplasm, irrespective of maturity class, respond as qualitative short-day species. This theory, however, was refuted by Wallis *et al.* (1981), Turnbull (1986), Upadhyaya *et al.* (2007), Srivastava and Saxena (2019), and Saxena *et al*. (2021) who demonstrated that in comparison to late types, the earlier flowering pigeonpea genotypes were relatively photo-insensitive.

Akinola and Whiteman (1974), Sharma *et al*. (1981), Singh and Saxena (1981) and Saxena and Sharma (1990) reported that the time taken from sowing to flowering was highest in the sowings made prior to the longest day; and it reduces progressively as the sowings are delayed into the shortening days. Recently, Saxena *et al*. (2021) reported that the flowering time and photo-sensitivity in pigeonpea shared a strong positive relationship. They attributed this linkage to their pleiotropic origin; and hence, ruled out the existence of any late maturing photo-insensitive pigeonpea germplasm.

Photoperiod responses of parents and their hybrids

Parental lines: A medium maturing (165-185 days) photo-sensitive pigeonpea cultivar, when sown in July at Patancheru (17^{o}N), starts flowering in October when the day light starts reducing beyond 11.8 h. Any significant change in this planting schedule alters the time taken from sowing to flowering. Such changes are minimal in photo-insensitive genotypes and quite significant in the photo-sensitive types.

In the present experiment the two photo-insensitive genotypes Prabhat and Pant A3, respectively took 64.3±4.1 and 73.4±3.3 days to flower in July sowing. In the November (short day) and February (long day) sowings also, they took around the same (60-70 days) time to flower (Table 1). These observations suggested that both these genotypes were insensitive to vastly different photoperiods. The three photo-sensitive genotypes took 125-148 days to flower in July sowing. In the November sowing, however, their flowering time reduced considerably, and it increased significantly when the crop was sown in the month of February. For instance, genotype T 17 flowered in 147.9±11.7 days in July sowing; but in the November and February sowings it took respectively, 118.1±12.4 and 250.3±8.2 days to flower. These data demonstrated that this genotype was highly sensitive to the changes in photoperiods.

Intra-maturity hybrids: The lone insensitive x insensitive hybrid followed the flowering pattern of its parents, Prabhat and Pant A3; and demonstrated its photo-insensitive reaction under the three testing environments (Table 1)**.** The three sensitive x sensitive crosses behaved identically with respect to their flowering time in the three planting dates. In the July sowing, these hybrids flowered earlier than their parents, suggesting partial dominance of earliness. In the November planting, the hybrids and their parents took less time to flower than that of July sowing. On the contrary, the February-sown hybrid plants remained vegetative for a long eight months before flowering in the month of October when the photoperiods started declining. In conclusion, it can be said that the two insensitive parental lines had alleles for photo-insensitivity, and they responded identically when exposed to the three different photoperiods. Similarly, the three sensitive parents had similar genetic constitution with respect to photo-sensitivity. In both photo-insensitive and photo-sensitive genotypes, additive genetic variance played significant role in the expression of flowering under variable photoperiods.

Photo-insensitive x photo-sensitive hybrids: Six hybrids were produced by crossing two photo-insensitive with three photo-sensitive parental lines. The flowering data recorded on these hybrids and their parents in three planting dates (Table 1) revealed that all the six crosses behaved more or less alike, both in the July and November sowings. In the normal (July) sowing these hybrids exhibited partial dominance of earliness. In the November sowing, the flowering time of all the genotypes telescoped and the hybrids flowered around their mid-parent values, suggesting the expression of additive gene effects.

In the February (long days) sowing, the Prabhat and Pant A3 hybrids, as separate groups, yielded contrasting results. The three hybrids involving Prabhat responded to long days and their flowers appeared 192 to 199 days after sowing, suggesting dominance of photo-sensitivity in these crosses.

In contrast, the three hybrids involving cv. Pant A3 responded differently when exposed to the long photoperiod regime (Fig 1). In this sowing, the insensitive parent (Pant A3) flowered in 55.7±5.6 days while the sensitive parents took 245 to 250 days to flower. Under long days the hybrids Pant A3 x Code 14, Pant A3 x ICP 7065, and Pant A3 x T 17, respectively flowered in 82.8±4.1, 80.0±5.4, and 83.6±3.7days with a mean of 82.13 days. These hybrid values were found leaning towards the insensitive parent (55.7±5.6 days), but at a distance from the sensitive parents (245 to 250 days). These observations (Fig 1) revealed that under long-day conditions, the Pant A3 hybrids exhibited partial dominance of photo-insensitivity.

Table 1. Days to first flower in the parents (P_1 , P_2) and their hybrids (F_1) in three planting dates at Patancheru

Sowing time	Generation			Generation		
	P_1	P_2	F_1	P_1	P_2	F_1
	(E x E) Cross 1: Pant A3 x Prabhat			**(L x L) Cross 2: Code 14 x ICP 7065**		
July 7	64.3±4.1	73.4±3.3	63.3±4.4(68,4)	125.0± 3.7	131.8± 5.9	122.7±4.0(128.4)
Nov 30	69.1±3.0	70.1±3.0	66.1±2.9(69,6)	92.8±4.4	92.1±9.4	88.0±6.4(92.5)
Feb 20	55.7±5.6	63.4±4.5	53.3±3.7(59.6)	245.1±10.7	246.4±11.4	242.2±8.5(245.8)
	(L x L) Cross 3: Code 14 x T 17			**(L x L) Cross 4: ICP 7065 x T 17**		
July 7	125.0± 3.7	147.9±11.7	128.9±4.2(136.5)	131.8± 5.9	147.9±11.7	135.3±6.0(139.9)
Nov 30	92.8±4.4	118.1±12.4	112.5±7.6(105.5)	92.1±9.4	118.1±12.4	114.8±10.3(105.1)
Feb 20	245.1±10.7	250.3±8.2	245.1±8.2(247.7)	246.4±11.4	250.3±8.2	243.4±12.9(248.4)
	(E x L) Cross 5: Prabhat x Code 14			**(E x L) Cross 6: Pant A3 x Code 14 (E x L)**		
July 7	73.4±3.3	125.0± 3.7	95.0± 4.7(99.2)	64.3±4.1	125.0±3.7	86.7± 4.3(94.7)
Nov 30	70.1±3.0	92.8±4.4	79.6±4.5 (81.5)	69.1±3.0	92.8±4.4	78.9± 4.1(81.0)
Feb 20	63.4±4.5	245.1±10.7	198.8±7.4(154.3)	55.7±5.6	245.1±10.7	82.8±4.1(150.4)
	(E x L) Cross 7: Prabhat x ICP 7065 (E x L)			**(E x L) Cross 8: Pant A3 x ICP 7065 (E x L)**		
July 7	73.4±3.3	131.8± 5.9	89.0± 4.1(102.6)	64.3±4.1	131.8± 5.9	87.3± 3.7(98,5)
Nov 30	70.1±3.0	92.1±9.4	78.0±5.1(81,1)	69.1±3.0	92.1±9.4	76.6±4.9(80.6)
Feb 20	63.4±4.5	246.4±11.4	191.7±9.0(154.9)	55.7±5.6	246.4±11.4	80.0±5.4(151.1)
	(E x L) Cross 9: Prabhat x T 17 (E x L)			**(E x L) Cross 10: Pant A3 x T 17 (E x L)**		
July 7	73.4±3.3	147.9±11.7	96.7± 6.3(110.7)	64.3±4.1	147.9±11.7	90.7± 5.0(106.1)
Nov 30	70.1±3.0	118.1±12.4	89.2±5.1(94.1)	69.1±3.0	118.1±12.4	89.2±5.7(93.6)
Feb 20	63.4±4.5	250.3±8.2	194.9±8.1(156.9)	55.7±5.6	250.3±8.2	83.6±3.7(153.0)

( ) mid-parent value of the cross

Under long photoperiod conditions, Saxena *et al.* (2021) recorded significant increases in the flowering time of both, the photo-sensitive parent (MS 3A) and its hybrid (MS 3A x QPL 1) with insensitive genotype QPL 1. This hybrid, like Prabhat hybrids, showed dominance of photo-sensitivity. But in the Pant A3 hybrids, partial dominance of photo-insensitivity with epistatic effects was evident. In these crosses the photo-sensitive genes (present in the late maturing parents) failed to express to their complete dominance in the presence of photo-insensitive genes contributed by Pant A3; and instead, partial dominance of photo-insensitivity was expressed. The authors believe that this is the first report in pigeonpea where partial dominance of photo-insensitivity was recorded and this would be a valuable asset in breeding in breeding pigeonpea.

Earlier, Craufurd *et al.* (2001) reported two dominant photo-sensitive genes in pigeonpea which expressed under 15 h photoperiod environment. In a recent publication, Saxena *et al.* (2021) reported that there were three dominant genes which controlled photo-sensitivity in pigeonpea. These genes followed a unique hierarchical (PS_3 > PS_2 >PS_1) pattern in their expression and the photo-insensitive genotype was a triple homozygous recessive. In *Phaseolus vulgaris* four dominant genes were found to control the photo-insensitivity

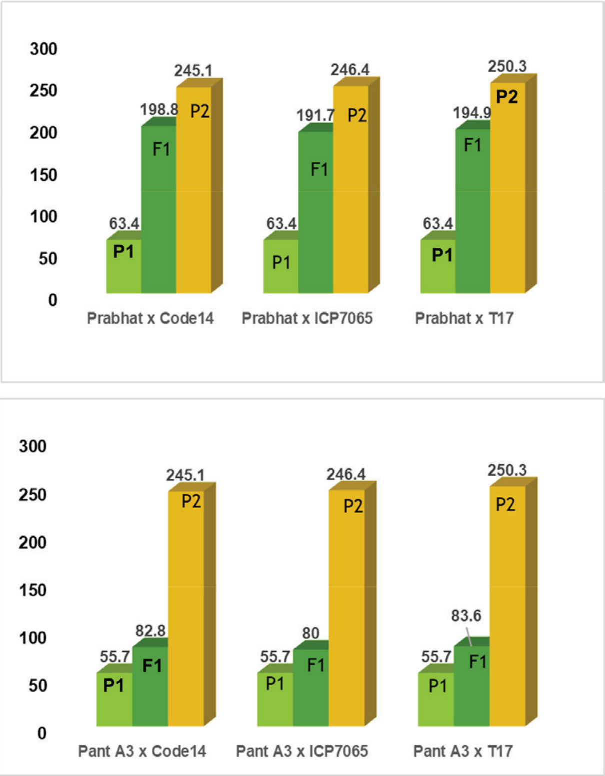

Fig 1. Flowering patterns of photo-sensitive (Code 14, ICP 7065, T 17) and photo-insensitive (Prabhat and Pant A3) genotypes and their hybrids under long photoperiods. Note the flowering time of F_1 hybrids in the two graphs.

trait (Tsao, 1977), while monogenic dominant gene controlled the photo-insensitivity in the three *Vigna* species – *V. unguiculata* (Ishiyaku and Singh, 2001), *V. radiata* (Sen and Ghosh, 1961), and *V. mungo* (Sinha, 1988). In contrast, a single dominant gene was found responsible for photo-sensitivity in *Cicer arietinum* (Or *et al*., 1999) and *Lablab purpureus* (Prasanthi, 2005). While Kornegay *et al*. (1993) and Coyne (1967) reported two dominant genes which controlled the expression of photo-sensitivity in *Phaseolus vulgaris*.

CONCLUSION

The results showed that the two photo-insensitive genotypes Prabhat and Pant A3 carried different sets of photo-insensitive gene(s). In Prabhat the photo-insensitivity genes were recessive, while in Pant A3 the presence of partial dominance of photo-insensitivity was evident. This paper presents the first report of the partially dominant genes for photo-insensitivity with epistatic effects. These genes are activated under long photoperiod environment and partly inhibit the expression of the photo-sensitivity genes. The traditional late maturing pigeonpeas are cultivated within an adaptation zone of 0-35° latitudes; and this restriction is posed due to inherent characteristic of the crop to flower under short days. Although, some photo-insensitive cultivars are available, but they produce little biomass and are have poor competitive abilities, and hence, do not fit in the traditional inter-cropping systems. Therefore, to overcome this limitation, there is need for breeding of longer duration photo-insensitive cultivars which could flower at the locations characterized by long hours of day light. The authors also believe that the partial dominant photo-insensitive genes, present in Pant A3 can be identified using modern genomics tools and used in breeding programmes to develop new pigeonpea cultivars which will find adaptation beyond 35° latitudes where long photoperiods prevail.

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