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Research Note

Inheritance pattern of photoperiod responsive flowering, growth habit and flower colour in Indian bean [*Lablab purpureus* (L.) Sweet.]

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Abstract
Photoperiod responsive flowering and growth habit have played key role in evolution and domestication of Indian bean. Most of the land races of this crop exhibit photoperiod sensitive flowering and indeterminate growth habit. To deduce inheritance pattern of photoperiod responsive flowering, growth habit and flower colour, four crosses were made between genotypes having extreme phenotypes keeping determinate and photoperiod insensitive variety GNIB-21 as common female parent. Pure hybrids were selected on the basis of male dominant traits to raise true F_2 generations. Segregation patterns of 3 : 1 in all F_2 generations and χ^2 estimates indicated that photoperiod insensitive flowering, determinate growth habit and white flower colour are monogenic recessive in nature, while photoperiod sensitivity, indeterminate growth habit and purple flowers are dominant in nature. Linkage analysis in the cross GNIB-21 x GP-189 revealed that loci governing photoperiod responsive flowering and growth habit are placed at the distance of 22.99 cM $\pm$ 0.022. The analysis also revealed coupling phase of linkage between photoperiod insensitive flowering and determinate growth habit. The information obtained from present study will be helpful for molecular dissection of photoperiod responsive flowering and growth habit in Indian bean utilizing new genomics tools.

Key words
Photoperiod insensitivity, growth habit, flower colour, linkage mapping, evolution

Indian bean [*Lablab purpureus* (L.) Sweet], with 2n = 22 chromosomes belongs to Fabaceae family, is a very important short day pulse crop of tropical countries especially the tribal areas. The green pods along with green seeds of Indian bean are used as vegetable while dried seeds are used as split pulse. It is also used as a forage and cover crop. Being a legume, it fixes atmospheric nitrogen, hence famous as intercrop to enrich soil fertility. Though wide variability is present in India and Africa for this crop, it is not extensively studied. Growth habit and photoperiod responsive flowering has played very important role in domestication history of this crop. Most of the land races and cultivars of Indian bean are photoperiod sensitive and indeterminate which flower only during short day length of winter season in India making its cultivation difficult across the year. Photoperiod sensitive flowering also poses difficulties in germplasm conversion when breeder is interested to transfer valuable traits from sensitive types to insensitive ones. However, few determinate and photoperiod insensitive types are available which flowers within 40 to 50 days across the year. Due to synchronous flowering and maturity, determinate growth habit and photoperiod insensitive flowering enables solitary cultivation as well as inter cropping especially in plantation crops throughout the year. Determinate types exhibit compact and pole type growth habit with low production, however, modulating crop geometry equalizes their production with indeterminate types as more number of compact plants can be accommodated in unit area. In many genotypes of Indian bean, pigmentation is observed on various plant parts like stem, leaf, flower, pod and seed. Generally pigmented pods are not preferred by the consumers, however, if purple flowers are coupled with green pods, the flower colour could be a very important traits for varietal identification.

Knowledge on inheritance of determinate growth habit and photoperiod responsive flowering is necessary for yield and quality improvement in Indian bean. Prasanthi (2005) observed simple dominance of photoperiod sensitive flowering in two crosses of Indian bean. Keerthi *et al.* (2014) found monogenic control of photoperiodic response to flowering time; photoperiod sensitivity being dominant to insensitivity. Keerthi *et al.* (2016) revealed biallelic monogenic control of flower colour in F_2 and F_3 generations. While, in their study, growth habit was controlled by two genes with complementary epistasis. The dominant alleles, at two different unlinked pairs of genes were necessary for plants to exhibit indeterminate growth habit. The genes controlling growth habit and photoperiod responsive flowering were linked. Knowledge on inheritance pattern of these traits paves the way to decide molecular breeding strategies in this crop. Hence, the study was

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conducted to assess the genetics of photoperiod responsive flowering, growth habit and flower colour among four different crosses obtained from five contrasting parents in Indian bean.

With a view to study the genetics of various qualitative traits, crosses were made keeping released variety GNIB-21 as female possessing determinate growth habit, white flowers and photoperiod insensitive flowering with contrasting male parents GP-1, GP-167 GP-189 and GP-Kh-120 which are indeterminate, purple flowered and photoperiod sensitive short day plants except GP-Kh-12 that possessed white flowers. Emasculation and crossing was carried out during *Kharif-Rabi*, 2014-15 at College Farm, N. M. College of Agriculture, Navsari Agriculture University, Navsari, Gujarat. Subsequently, F_1s and F_2s were evaluated during the years 2015-16 and 2016-17, respectively. True F_1s were identified on the basis of dominant nature of traits possessed by male parents and selfed to obtain respective F_2s. The parents, F_1s and F_2s of these four crosses were sown keeping inter and intra row spacing as 90 cm and 45 cm, respectively.

Observations on photoperiod responsive flowering, flower colour and growth habit were recorded from individual plants. GNIB-21 flowers within 40 to 45 days across the year being photoperiod insensitive. While, photoperiod sensitive male parents flowered during short day conditions of winter season. Segregating individuals flowering within 40-45 days were considered as photoperiod insensitive and plants flowering later than that were considered as photoperiod sensitive. GNIB-21 has determinate growth habit where main shoot discontinues vegetative growth and terminates into raceme. Due to their indeterminate nature, main shoot of male parents continued vegetative growth without bearing flowers at the tip. Growth habit of segregating individuals was classified as determinate and indeterminate accordingly. GNIB-21 manifested white flowers while male parents GP-1, GP-167 and GP-189 exhibited purple flower. The segregation patterns and linkage were statistically confirmed using χ^2 test. For linkage analysis, recombination fraction was calculated by maximum likelihood method (Immer, 1930) and converted into map distance using Kosambi map function (Kosambi, 1944). The standard error for recombination frequency was calculated according to Adams and Joly (1980).

Plant growth habit and photoperiod responsive flowering have played very important role in domestication of pulse crops and Indian bean is not an exception to this. Looking to the increasing demand of determinate and photoperiod insensitive cultivars of Indian bean among the farmers, an effort was made to trace inheritance of plant growth habit, photoperiod responsive flowering and flower colour by utilizing four crosses *viz*., GNIB-21 x GP-1, GNIB-21 x GP-167, GNIB-21 x GP-189 and GNIB-21 x GPkh-120. Morphological status of five parents and four hybrids are mentioned in Table 1. Deliberately, the variety GNIB-21 was kept as female parent to identify true F_1s showing dominant characters of male parents. Total 30 plants were sown for each F_1 along with respective parents for comparison. These true F_1s exhibited purple flower, photoperiod sensitive flowering and indeterminate growth habit except GNIB-21 x GPkh-120 which had white flowers. Seeds were harvested from these true F_1s to raise F_2 generations in all four crosses. Observations recorded for three qualitative traits in four segregating generations are mentioned in Table 2.

Out of total 244 plants observed in F_2 generation of the cross GNIB-21 x GP-1, 176 and 68 exhibited indeterminate and determinate growth habit, respectively, suggesting monogenic recessive nature of determinate growth habit. Similar results were obtained for two F_2 generations obtained from the crosses GNIB-21 x GP-189 and GNIB-21 x GP-kh-120. Non-significant χ^2 values at 5 % level of significance also confirmed monogenic dominant nature of indeterminate growth habit in these three crosses. Total 185 plants were observed for flower colour in the cross GNIB-21 x GP-1. Of these, 130 plants manifested purple flower while 55 plants had white flower. χ^2 test pointed out monogenic recessive nature of white flower in three crosses *viz*., GNIB-21 x GP-1, GNIB-21 x GP-189 and GNIB-21 x GP-kh-120. Flowering response to photoperiod was observed only in one cross GNIB-21 x GP-189. The observed data and χ^2 test confirmed perfect agreement with 3 : 1 segregation ratio of photoperiod sensitive and photoperiod insensitive flowering suggesting dominant nature of flowering under short day conditions. Out of total 720 plants observed for the cross GNIB-21 x GP-Kh-120, 543 plants were found to be indeterminate and 177 were observed to be determinate type. χ^2 test indicated monogenic recessive nature of determinate growth habit for this cross also.

Linkage between determinate growth habit and photoperiod insensitive flowering was apparent upon keen observation of F_2 generations. However, to confirm it statistically, each and every plant of the cross GNIB-21 x GP-189 were observed for their growth habit and photoperiod responsive flowering (Table 3). Out of total 386 plants observed, 253 and 50 plants were found to be IDT/PS and DT/PIS, respectively, indicating their parental nature and coupling phase of linkage between the loci governing photoperiod responsive flowering and growth habit. Out of total 83 recombinants, 32 and 51 recombinants were found to be IDT/PIS and DT/PS. Highly significant χ^2 value (62.52) indicated statistical deviation of F_2 segregation data from expected independent assortment as well as presence of linkage between photoperiod responsive flowering and growth habit. Recombination fraction was calculated as 0.22 by maximum likelihood method. Applying Kosambi's mapping function, linkage distance was calculated as 22.99 cM $\pm$ 0.021.

Monogenic recessive nature of white flower, determinate growth habit and photoperiod insensitive flowering observed in present study is in accordance with previously reported results by Hanumantha Rao C. (1987), Prasanthi (2005), Keerthi *et al*. (2014) and Keerthi *et al*. (2016). However, Keerthi *et al*. (2016) observed complementary epistasis for growth habit where two dominant genes were necessary for a plant to be indeterminate type. They also reported the linkage distance of 25.48 cM between photoperiod responsive flowering and growth habit. Knowledge on inheritance of growth habit and photoperiod responsive flowering paves the way towards molecular dissection of photoperiod responsive flowering and determinate growth habit in Indian bean. Determinate growth habit and photoperiod insensitivity have played very important role in evolution and domestication of Indian bean, however, the actual genes responsible for these traits have not been identified. Even reports on inheritance pattern of these traits in Indian bean are very scanty. In common bean, the recessive *fin* (determinacy) and the dominant *Ppd* (photoperiod sensitivity) loci are located on the B1 linkage group (Kwak *et al*., 2008). Ten loci *viz*., *E1-E9* and *J* controlling flowering time and maturity have been characterized at phenotypic and genetic levels in soybean. Of these, *E3* locus causes similar flowering delays under long days with different light qualities, indicating this gene is less sensitive to light quality (Cober *et al*. 1996b). The recessive *e3* allele is associated with the control of long day insensitivity under fluorescent light with a high R:FR ratio (Buzzell 1971). Yamanaka *et al* (2005), Watanabe *et al*. (2009) and Watanabe *et al*. (2011) characterized and fine mapped *Dt1* linked *FT3* locus corresponding to *E3* locus in soybean located on chromosome number 19 utilizing RHL (Residual Heterozygous Line). The linkage between growth habit and photoperiod responsive flowering in common bean, soybean and Indian bean suggest that photoperiod insensitivity in Indian bean may be governed by mutation or deletion of *E3* homologue.

Kong *et al*. (2010) detected two *FT* homologues *GmFT2a* and *GmFT5a* involved in the control of photoperiodic flowering in soybean. They concluded that loss-of-function alleles of the two *PHYA* genes (*e3e4*) and *FT* homologues coordinately control flowering and enable the adaptation of soybean to a wide range of photoperiodic environments. suggested the possibility of involvement of complicated *CO-FT* regulons in the photoperiod regulation of flowering time in soybean. pointed out that *GmCOL1a/b* may serve as suppressors of photoperiodic flowering in soybean under long day conditions by suppressing the florigens *GmFt2a/GmFT5a* in cordination with *E1*, *E2*, *E3* and *E4*. This indicates that such *CO-FT* regulons might also exist in Indian bean. Gene discovery using public sequence databases of model plants is useful especially for specialty crops that do not have this type of information yet (Mahalakshmi and Ortiz, 2001). The information available on characterized genes for photoperiod responsive flowering and determinate growth habit from soybean and other legumes may be utilized in Indian bean for isolation, characterization and mapping of genes involved in regulation of flowering and growth habit. Utilization of next generation sequencing based genomics tools and mapping population like recombinant inbred lines, near isogenic lines and residual heterozygous line (RHL) may further accelerate this process of molecular dissection of flowering in Indian bean.

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Table 1. Morphological status of parents and four hybrids for three qualitative traits in Indian bean

Particulars	Trait		
	Plant growth habit	Photoperiod responsive flowering	Flower colour
Parents			
GNIB-21	Determinate	Photoperiod insensitive	White
GP-1	Indeterminate	Photoperiod sensitive	Purple
GP-167	Indeterminate	Photoperiod sensitive	Purple
GP-189	Indeterminate	Photoperiod sensitive	Purple
Gpkh-120	Indeterminate	Photoperiod sensitive	White
Crosses			
GNIB-21 x GP-1	Indeterminate	Photoperiod sensitive	Purple
GNIB-21 x GP-167	Indeterminate	Photoperiod sensitive	Purple
GNIB-21 x GP-189	Indeterminate	Photoperiod sensitive	Purple
GNIB-21 x GP-Kh-120	Indeterminate	Photoperiod sensitive	White

Table 2. Chi-square test for segregation of three quality traits in Indian bean

Cross	Trait	Phenotypic classes	Observed frequencies in F_2	Expected frequencies in F_2	Expected ratio	χ^2 estimate[@]
GNIB-21 x GP-1	Growth habit	IDT	176	183.00	3: 1	1.07
		DT	68	61.00		
	Flower colour	Purple	130	138.75	3 : 1	2.20
		White	55	46.25		
GNIB-21 x GP-167	Flower colour	Purple	81	81.00	3 : 1	0.00
		White	27	27.00		
GNIB-21 x GP-189	Growth habit	IDT	285	289.50	3 : 1	0.28
		DT	101	96.50		
	Flower colour	Purple	306	289.50	3 : 1	3.76
		White	80	96.50		
	Photoperiod responsive flowering	PS	304	289.50	3 : 1	2.90
		PIS	82	96.50		
GNIB-21 x GP-Kh-120	Growth habit	IDT	543	540.00	3 : 1	0.07
		DT	177	180.00		

[@] : χ^2 table value at 1 degree of freedom and 0.05 probability level is 3.84

Table 3. Linkage mapping between photoperiod responsive flowering and growth habit

Growth habit	**IDT**	**IDT**	**DT**	**DT**	**χ^2 estimate (3 df)[@]**	**Recombination fraction**	**Linkage distance (cM)**
Photoperiod responsive flowering	**PS**	**PIS**	**PS**	**PIS**			
Observed number of plants in F_2	253	32	51	50	62.52**	0.22	22.99 ± 0.021
Expected frequencies for independent assortment	217.13	72.38	72.38	24.13			

[@] : χ^2 table value at 3 degree of freedom and 0.05 probability level is 7.81