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Genetic Control of Some Morphological and Physiological Characters in Lablab Bean (*Lablab purpureus* (L.) Sweet)

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Inheritance of growth habit, photoperiod sensitivity, pigmentation on stem and petal in lablab bean was studied. Monogenic control of growth habit was revealed from different F_2 segregating families derived from the crosses between determinate and indeterminate accessions. Although the determinate character seemed to be controlled by one locus from the crosses between wild and determinate types, inheritance of the growth habit could not be clarified because of the appearance of extreme dwarf plants and determinate plants with indeterminate lateral shoots. From the same cross photoperiod sensitivity and pigmentation on stem displayed to be governed by respective two loci. This is the first report on complementary gene control of photoperiod sensitivity in lablab bean. From the crosses between determinate and indeterminate types pigmentation on stem was controlled by three loci. Petal color was observed as governing by two loci; complementary gene action.

INTRODUCTION

Systematic improvement of lablab bean is limited (Rashid, 1993; Shivashankar *et al.*, 1993). Growth habit, pigmentation on different parts (stem, petiole, petal, sepal, pod and seed coat), pod and seed characters (number, weight, texture, size, shape and color), sensitivity to photoperiod and tolerance to diseases and insect pests are important morphological and physiological characters that could serve as effective selection criteria for improvement of this crop. The major objectives in lablab bean breeding are the development of determinate bush type, photo-insensitivity (year round and early maturity type), soft textured long pod (for vegetables), large seeds (for pulses), tolerance to insect pests (fruit borer, red mite and aphids) and wide adaptability (suitable for hot and cold weather).

The genetic control of many of the above-mentioned characters is not known. In the present paper, genetic control of growth habit, photoperiod sensitivity and pigmentation on stem and petal was described using F_2 segregating families.

MATERIALS AND METHODS

Origin and characters of the parents are presented in Table 1. The highly photoperiod sensitive accessions 60216 (wild, from Uganda) and 52510 (wild, from Zimbabwe) were

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placed in the growth chamber (25 °C, 70% RH and 12-h daylength) for flowering. Because these wild types did not flower in a plastic house of Kyushu condition or in the phytotron (25 ± 2 °C, 70 ± 5% RH and natural daylength) of Biotron Institute, Kyushu University. The photosensitive accession Tot-2456 (Thailand) was placed in 25 °C phytotron and was covered from 5:30 p.m. to 9:00 a.m. of the following day. This accession flowers outside in short day of winter season but no viable pollen was found in this condition probably due to low temperature. All other accessions were grown in the plastic house for all the year round.

Reciprocal crosses were made between determinate accession and all other eleven accessions. No fruit setting was observed in the crosses between the determinate and 52510 in both directions of. Only one way successful crosses were observed in between the determinate with 60216 and with 34777. In both cases the determinate accession was used as pollen parent.

Reciprocal crosses were also made between 60216 and 52510, between Akabana and 52510 and between Tot-2456 and 60216. Fruit setting was observed in one way crosses between 52510 and 60216, and between 52510 and Akabana, when 52510 was used as pollen parents. In all other combinations fruit setting was observed in both way crosses. In each cross, 10 to 30 flowers were used except the accession 52510 due to poor flowering.

Seeds of the determinate and Akabana (10 individuals each), 10 F₁'s from both way crosses between them and F₂ progenies (derived from each of a single F₁ plant) were sown in 12 cm diameter plastic pots containing a mixture of pumice : vermiculite : sand (1:1:1, v/v/v). They were then placed in 20 °C and 25 °C in the phytotron for the period of June to September 1999 and November 1999 to January 2000. F₂ progenies derived from

Table 1. Origin and characters of parental genotypes of lablab bean under study.

Accession	Origin	Growth habit ^a	Pigmentation ^b on		Response to photoperiod ^c
			petal	stem	
Determinate	India	D (bush)	W	G	IS
Akabana	Japan	I (SV)	P	P	IS
60216	Uganda	I (LSV)	RP	P	HS
52510	Zimbabwe	I (LSV)	RP	P	HS
Tot-2456	Thailand	I (LSV)	LP	LPG	S
34777	India	I (SV)	W	G	LS
52504A	Angola	I (SV)	LP	M	LS
52532	India	I (SV)	W	G	LS
52506B	Angola	I (SV)	LP	M	LS
76998	Zambia	I (MSV)	W	G	LS
34783	India	I (MSV)	W	G	LS
36903	USSR	I (MSV)	P	M	LS

^a D; Determinate, I; Indeterminate, SV; Small vine, MSV; Medium spreading vine, LSV; Large spreading vine.

^b W; White, P; Purple, RP; Reddish purple, LP; Light purple, G; Green, LPG=Light green and purple, M; Mixed (green and purple).

^c IS; Insensitive, HS; Highly sensitive, S; Sensitive, LS; Less sensitive

a single F₁ plant (60216 × determinate) were grown in the plastic house from the period of September 2000 to January 2001. All other F₁s were grown in a greenhouse and the plastic house.

Data were analyzed by the standard procedures. The χ^2 test was applied to confirm the segregation ratios in F₂ progenies.

RESULTS AND DISCUSSION

Growth habit

Growth habit of 86 F₁s, derived from the crosses between the determinate and eleven other different indeterminate accessions is presented in Table 2. All the F₁s irrespective of the direction of crosses, genotypes (cultivated or wild) or growing environment (plastic house, green house or phytotron and summer or winter season) were indeterminate in growth habit except one F₁ derived from the cross between 34777 (female) and the determinate (male). No successful reciprocal crosses obtained from this combination. Both parents were from Indian origin and no remarkable morphological, biochemical (isozymes) or molecular (RAPD) markers were identified except growth habit and seed shape (Sultana *et al.*, 2000, 2001). The parent 34777 was indeterminate and its seed shape was oval, and the pollen parent was determinate in growth habit and produced round shaped seeds. From these results it is suggested that there are two indeterminate genes; one is dominant and the other is recessive to determinate gene.

In most cases, indeterminate growth habit was found dominant over determinate and controlled by a single gene pair with simple Mendelian inheritance. Some examples are reported in lablab bean (Harland, 1920), soybean (Bernard, 1971, 1972; Halvankar and Patil, 1994), pigeon pea (Gupta and Kapoor, 1991), chickpea (Rheenen *et al.*, 1994), winged bean (Uemoto and Okubo, 1993), lima bean (Allard and Allard, 1953) and tomato (Yeager, 1927; Currence, 1933). In contrast, Hutchins (1940) found that determinate

Table 2. Growth habit of parents and F₁s observed in some selected crosses.

Cross	Growth habit ^z	No. of F ₁ s checked	Observed growth habit	
			Determinate	Indeterminate
Determinate × Akabana	D × I	25	0	25
Akabana × Determinate	I × D	25	0	25
Determinate × Tot-2456	D × I	10	0	10
Tot-2456 × Determinate	I × D	10	0	10
60216 × Determinate	I × D	10	0	10
34777 × Determinate	I × D	1	1	0
Determinate × 39078	D × I	1	0	1
52504A × Determinate	I × D	1	0	1
52532 × Determinate	I × D	1	0	1
Determinate × 52560B	D × I	1	0	1
Determinate × 76998	D × I	1	0	1
Total		86	1	85

^z D; Determinate, I; Indeterminate.

growth habit in cucumber is dominant over indeterminate and controlled by a single gene pair. Denna (1971) suggested that in cucumber most indeterminate cultivars possess a number of modifier genes and penetrance of the determinate character varied depending on the source of both the determinate and indeterminate parents.

Segregation and goodness of fit tests of eight F_2 families derived from both way crosses between determinate and Akabana (each family derived from a single different F_1 plant), grown in the controlled environment (20 and 25 °C, phytotron) are presented in Table 3. All families segregated into a 3:1 ratio of indeterminate to determinate irrespective of growing temperature or season. The result suggests that determinate and indeterminate growth habit of lablab bean is controlled by a single gene pair and indeterminate growth habit is dominant over determinate.

Segregation and goodness of fit tests of growth habit, photoperiod sensitivity, pigmentation on stem and petal of F_2 families derived from a cross between 60216 (female) and determinate (male) and both way crosses between Akabana and determinate are presented in Table 4. F_2 plants from the cross between 60216 and determinate were grown in the plastic house in the period of September 2000 to January 2001 (non-inductive season for changing determinate plants to indeterminate, Kim *et al.*, 1992). Among 125 F_2 plants, 80 were indeterminate (viny), 25 were dwarf and determinate (flower at the tip of main stem), five were normal dwarf (dwarf but no flower), 10 were determinate (flower at the tip of main stem) with viny lateral branches and five were extreme dwarf (abnormal dwarf). The number of true indeterminate and determinate plants, 80 and 25, respectively, fits well to 3:1 ratio of indeterminate to determinate. Again it proved from this result that determinate and indeterminate growth habits of lablab bean are monogenic and indeterminate growth habit is dominant over determinate.

Inheritance of the growth habit could not be clarified in this study because of the appearance of extreme dwarf plants and determinate plants with indeterminate lateral shoots. The presence of extreme dwarf was also found in *Phaseolus vulgaris*. Nakayama (1957) reported abnormal dwarfness in garden bean (*Phaseolus vulgaris*) due to duplicate recessive gene dw_1dw_2 . Lamprecht (1934) pointed out that in garden bean some indeterminates are relatively short. He suggested *Fin* and *fin* from finites for the

Table 3. Segregation and goodness-of-fit tests of growth habit of F_2 derived from the crosses between Akabana (indeterminate) and determinate grown in the phytotron in summer and winter seasons.

Family	Cross	Growth condition in the phytotron	No. of plants			χ^2 (3:1)	P
			Indeterminate	Determinate	Total		
1	Determinate \times Akabana	Summer, 20 °C	31	9	40	0.03333	0.85513
2	Akabana \times Determinate	Summer, 20 °C	27	13	40	0.83333	0.36131
3	Determinate \times Akabana	Summer, 25 °C	39	11	50	0.10667	0.74397
4	Akabana \times Determinate	Summer, 25 °C	35	15	50	0.42667	0.51363
5	Determinate \times Akabana	Winter, 20 °C	39	11	50	0.10667	0.74397
6	Akabana \times Determinate	Winter, 20 °C	34	16	50	0.96	0.32719
7	Determinate \times Akabana	Winter, 25 °C	44	11	55	0.49091	0.48352
8	Akabana \times Determinate	Winter, 25 °C	41	14	55	0.00606	0.93795

Table 4. Characters of parents, F₁ and F₂ segregation for growth habit, photosensitivity and pigmentation on stem and petal.

Characters	Cross	F ₁	F ₂	Ratio	χ ²	P	Ratio	χ ²	P		
Growth habit ²	P ₁ I×P ₂ D	I	Dom. I vs. D ²	I	80	3:1	0.02857	0.86577	54:10	4.73235	0.0296
			Rec.	D	25						
			Viny vs. Dwarf	Viny Dwarf	80	3:1	7.49067	0.0062	39:25	0.3226	0.54178
Photosensitivity ³	P ₁ HS×P ₂ IS	SE	Inter.	IS	66	3:1	31.6827	0.0000	9:7	0.47251	0.49184
				HS to SE	59						
Pigmentation on stem ⁴	P ₃ Purl.×P ₂ Gr.	PB	Inter.	Purl. to PB	168	3:1	12.3504	0.00044	54:10	0.34283	0.5582
				Gr.	27						
	P ₂ Gr.×P ₃ Purl.	PB	Inter.	Purl. to PB	172	3:1	17.4376	0.0000	54:10	1.88904	0.16931
				Gr.	23						
Pigmentation on petal ⁵	P ₁ Purl.×P ₂ Gr.	PB	Inter.	Purl. to PB	62	3:1	41.6667	0.0000	9:7	1.98413	0.15896
				Gr.	63						
	P ₂ W×P ₃ Purl.	LP	Inter.	Purl. to LP	54	3:1	10.0148	0.00155	9:7	0.37319	0.54127
				W	36						

² P₁; 60216, wild (Uganda), P₂; Determinate, cultivated (India), I; Indeterminate, D; Determinate, Dom.; Dominant, Rec.; Recessive. ³ Twenty of 125 were uncoded because of complexed expression of growth habit. ⁴ HS; Highly sensitive (flower only in controlled condition), IS=Insensitive (flower all the year round except in extreme long day and high temperature), SE; Sensitive (flower only in short day), Inter.; Intermediate. ⁵ P₃; Akabana, cultivated (Japan), Purl.; Purple, Gr.; Green, PB; Purple blotch on green stem. ⁶ W; White, Purl.; Purple, LP; Light purple.

gene pair involved in determinate and indeterminate. Later, Rudolf (1958) designated *in*⁺ indeterminate and *in* determinate. Like garden bean, relatively short indeterminate accessions present in lablab bean (Sultana *et al.*, 2001). The Indian accession 34777 was this kind of indeterminate. And the expression of determinate growth habit in F₁ between 34777 and the determinate might be explained in this way that there might be some interaction among modifier or inhibitory genes. Or the chromosome carrying determinate growth habit controlling genes might be preferentially transmitted in F₁ (preferential transmission was identified in lablab bean by Kundori *et al.* (2000)).

Ladizinsky (1997) conducted a series of intra- and inter-specific crosses in search of dwarfing gene in the genus *Lens*. He concluded that dwarf phenotype is controlled by two complementary genes, Df₁ and Df₂ and these two genes are suppressed by the dominant allele of dwarf inhibitory gene *Dfi*. In fact, it revealed from the present experiment that the factors controlling growth habit, plant height and flowering or photoperiod sensitivity in lablab bean are related in a complex form.

Photoperiod sensitivity

Degree of photoperiod sensitivity expressed in F₁ from the crosses between parents having different degrees of photoperiod sensitivity is presented in Table 5. Among ten cross combinations, F₁s from seven combinations were intermediate in respect to photoperiod sensitivity. F₁s between HS (highly sensitive) and IS (insensitive) and between S (sensitive) and IS (insensitive) were all intermediate indicating that there is no complete dominance in this character. Due to the similar characters in other three

Table 5. Response to photoperiod in parents and F₁s observed in some selected crosses.

Cross	Degree of photoperiod sensitivity ^a	
	in parents	in F ₁ plants
60216 × Determinate	HS × IS	S to LS
Akabana × 52510	IS × HS	S to LS
60216 × 52510	HS × HS	HS
60216 × Tot-2456	HS × S	S to HS
Tot-2456 × 60216	S × HS	S to HS
Akabana × Determinate	IS × IS	IS to LS
Determinate × Akabana	IS × IS	IS to LS
Tot-2456 × Determinate	S × IS	LS
Determinate × Tot-2456	IS × S	LS
Determinate × 34773	IS × LS	LS

^a IS; Insensitive to photoperiod (flower all the year round), LS; Less sensitive (flower twice a year), S; Sensitive (flower only in very short day condition, HS=Highly sensitive (no flower at all in Kyushu).

combinations, character expression in F₁s in these combinations was not clear. Shanmugasundaram (1980) and Coyne (1966) reported that photoperiod sensitivity in soybean is controlled by polygenes. In contrast, Rao (1987) reported that photoperiod sensitivity in lablab bean is controlled by a single pair of gene.

Segregation of F₂ progenies derived from a cross between 60216 (HS) and the determinate (IS) accessions, grown in short day conditions, is presented in Table 4. Among 125 F₂ plants 66 flowered and 59 did not. The number of plants with flowering to non-flowering fits well in 9:7 ratio indicating the involvement of two pair of complementary genes for this character.

A close relationship between growth habit and photoperiod sensitivity was found in the genus *Phaseolus* (Rudorf, 1958). In *Phaseolus* indeterminate growth, *fin*⁺, retards flowering as compared with *fin*. The F₂ crosses between the indeterminate (*fin*⁺) short day (*neu*⁺, photo sensitive) *Phaseolus aborigineus* and the determinate (*fin*) day neutral (*nue*, photo insensitive) *P. vulgaris* gives 3:1 ratio when grown with a short photoperiod, but with long day segregates 9 indeterminate short day (*fin*⁺*neu*⁺): 3 indeterminate day neutral (*fin*⁺*neu*): 4 determinate day neutral (*fin neu*⁺ and *neu*). The third generation established that *fin* is epistatic to *neu*⁺. In the present study similar relationship was observed but the ratio was different. Among 125 F₂ plants, 32 plants were indeterminate with flower, 48 were indeterminate but no flower, 25 were dwarf and flowered at the tip of main stem (determinate), five were dwarf but no flower (normal dwarf), 10 were determinate (flower at the tip of main stem) with viny lateral branch and five were extreme dwarf with no flower. It seems from the result that determinate growth habit and photoperiod sensitivity has close relationship in lablab bean and controlled by more than two loci and the degree of sensitivity is modified by some genes, but for clear recommendation it requires further studies.

According to Coyne (1966) photoperiodism in soybean is a complex trait and might

be controlled by many genes. Some varieties may respond at only one or two loci while other varieties may differ at many loci. Under short day it appears that qualitative genes are not expressed and the variation expressed in segregating generation is mainly due to the action of polygenes and environment.

Pigmentation on stem

Stem color of F_1 s from the crosses between green stem and green stem plants was green, that between purple stem and purple stem plants was purple and that between green stem and purple stem plants was all purple blotch (purple blotch on green stem). Stem color segregation was counted from F_2 plants of the crosses between Akabana (purple stem) and determinate (green stem), grown in the phytotron. Among 195 F_2 plants (Akabana \times determinate), 168 were purple (both light and deep) and 27 were green. In the reciprocal cross, 178 plants had purple and 23 had green stem colors. The number of purple to green plants fitted well in 54:10 ratio of purple to green plants (Table 4), suggesting that pigmentation on stem is controlled by three loci. Rao (1987) inferred that pigmentation on stem was controlled by three dominant genes and the presence of any two of three genes caused the purple pigmentation in agreement with the present findings.

In another F_2 family derived from the cross between 60216 and determinate, 62 plants showed purple stem color, whereas 63 plants were green. This number does not fit in 3:1 or 54:10 ratio but fits in 9:7 ratio, suggesting that this character is governed by two loci. Monogenic dominant gene action for stem color of lablab bean was reported by Raut and Patil (1985), while Nakahade *et al.* (1979) recorded digenic interaction. On the other hand Meenakshi and Sunderesan (1964) reported four genes controlling stem pigment in lablab bean.

Pigmentation on petal

All F_1 s between white petal color and white petal color plants produced white petal color plants, those between purple petal color and purple petal color plants showed purple and those between purple petal color and white petal color plants were all light purple. Segregation of 90 F_2 plants was recorded from a cross between Akabana (purple petal) and determinate (white petal). Purple to light purple petal was observed in 54 plants and white petal was observed in 36 plants. The ratio of purple to white was 9:7 suggesting that petal color of lablab bean is controlled by two pairs of complementary genes, whereas Raut and Patil (1985) reported monogenic control of purple flower color. However, the result obtained in the present study was in full agreement with Harland (1920).

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