Genetic analysis of variegation mutants of Pearl millet, Pennisetum glaucum

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KARUNASRI, K. and SUBRAHMANYAM, N. C. 1994. Genetic analysis of variegation mutants of Pearl millet, Pennisetum glaucum. — Hereditas 120: 203-209. Lund, Sweden. ISSN 0018-0661. Received September 2, 1993. Accepted February 2, 1994

Intercrosses between different variegated lines of *Pennisetum glaucum* (L.) R.Br. were made to determine their allelic composition and the number of loci controlling plastid alterations. Self-pollinations of different variegated plants resulted in normal, variegated, and yellow or white progeny. Crosses among yellow stripe mutants (IP 5009, IP 9712, IP 482) resulted in normal and yellow progeny in the F_1 , and normal and yellow stripe in the F_2 generations, indicating the complementary interaction of two loci in each cross. Reciprocal crosses between the yellow stripe mutants IP 5009 and IP 13160-1 revealed similarity in their genotypes. Progeny composition from the crosses between the white stripe mutants VCM-36 and GWS-14 indicated their genotypic similarities. Crosses between yellow stripe and white stripe mutants (IP 5009 × VCM-36, IP 482 × VCM-36) indicated differences in their genotypes. Comparison of segregation patterns in the progenies of intercrosses revealed at least 4 independent loci, any one of which in recessive condition leads to mutant phenotype(s) while the development of chlorophyll is accomplished by the complementary interaction of dominant genes at these loci. Among the recessive genotypes in the F_2 s from intergenotypic crosses, the mutant phenotypes fell short of expectation, indicating differential penetrance in expression.

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Nuclear gene induced plastid mutations are known, as summarised by KIRK and TILNEY-BASSETT (1978). Following plastid mutation, normal and mutant plastids sort out from one another during successive cell divisions in a regular manner to produce variegated plants with defined striping pattern in leaves and shoots (TILNEY-BASSETT 1978). Variegations due to mutable nuclear genes and nuclear gene controlled plastid mutations show Mendelian inheritance. But variegations due to plastid mutations show non-Mendelian inheritance, thus exhibit reciprocal differences.

AYYANGAR et al. (1935) reported albinism controlled by a single recessive gene in pearl millet. VINCHON (1949) showed single gene pair control for 8 of the 10 lethal chlorophyll deficiencies. RAT-NASWAMY (1960) reported a white stripe phenotype controlled by a single recessive gene. BURTON and POWELL (1965) observed monogenic recessive inheritance in ten of the thirteen spontaneously occurring chlorophyll deficiencies, and digenic recessive inheritance in the remaining.

GILL et al. (1969) reported foliage striping of two mutants, PYS-7 and GYS-8, in the presence of 3 complementary recessive nuclear genes, while another stripe phenotype of GWS-14 was shown to be controlled by 3 different loci with duplicate, complementary, and inhibitory type of gene interactions. Subsequent studies by REDDY and SUB-RAHMANYAM (1988a) on the same white stripe mutant (GWS-14) revealed the control of striping by the delayed expression of two independently assorting recessive genes. KRISHNA RAO and Koduru (1978) reported non-Mendelian bi-parental inheritance of the variegated phenotype in a white stripe mutant. APPA RAO and MENGESHA (1984) isolated a yellow stripe mutant of IP 5009 controlled by a recessive gene. SUBRAHMANYAM et al. (1986) later demonstrated a pattern dependent plastid inheritance in the same mutant. REDDY and Subrahmanyam (1988b), Sujatha and Sub-RAHMANYAM (1991) further characterised and established the genetic basis of plastid alterations, their mode of transmission following intraplant, interspikelet, and intergenotypic crosses of stripe mutant of IP 5009.

We report here the results from intercrosses between different variegation mutants of pearl millet (*Pennisetum glaucum*) and the determination of their allelic composition based on their segregation patterns.

Materials and methods

Phenotypes and sources of different accessions of Pennisetum glaucum (L.) R.Br. used in the study

Table	1,	Accessions	of	Pennisetum	glaucum	used	in	the	present
study,	th	eir phenoty	pe .	and source	_				•

Accession	Phenotype	Source			
GWS-14	Green white stripe	Dr. J. L. Minocha, Prof. of Genetics, Punjab Agric. Univ., Ludhiana, India			
IP 482	Green yellow stripe	Dr. M. Krishna Rao, Prof. of Botany, Andhra University, Waltair, A.P., India			
IP 5009 IP 9712 IP 13160-1 VCM-36 TGR 226B VCM-24	Green yellow stripe Green yellow stripe Green yellow stripe Green white stripe Green white stripe Normal green	Dr. S. Appa Rao and Dr. M. H. Mengesha, Genetic Resources unit, ICRISAT, Patancheru, A.P., 502 324, India			

are presented in Table 1. Seeds of each stripe mutant line were sown 1 cm deep in rows 30 cm apart and at a distance of 30 cm within each row in well prepared plots. Irrigation and manuring were provided as per the requirement. Reciprocal crosses were made between the parents, taking the advantage of protogyny (Burton 1980) in pearl millet. Spikes were enclosed in butter paper bags prior to the emergence of stigmas to prevent stray pollination. Pollen from male parent was collected in paper bags and dusted onto the stigmas on the spikes of female parent. To ensure cross pollination and to prevent possible selfing, the pollinations were done consecutively for 3 days by which time the stigmas withered.

 F_1 seedlings from reciprocal crosses between different accessions were raised in plastic trays in rows 3 cm apart at a distance of 1 cm from each other for a week, and scored and transplanted in 1.8 m \times 1.8 m plots at 30 cm \times 30 cm spacing. F_2 progeny were raised in plots of 1.8 m \times 1.8 m at a row to row distance of 15 cm and plant to plant distance of 1 cm. Scoring was done within two weeks after planting.

Results

Seven different variegated mutants of *Pennisetum glaucum* were used in the present study (Table 1). Four of them (IP 5009, IP 482, IP 9712, and IP 13160-1) were yellow striped and three (GWS-14, VCM-36, and TGR 226B) were white striped. The yellow stripe mutants had characteristic longitudinal yellow stripes alternating with green stripes on leaves and stems. The variegation observed on

vegetative parts extended into their inflorescence in IP 5009, IP 482, and IP 9712, whereas the inflorescence of IP 13160-1 remained normal in color. The white stripe mutants GWS-14, VCM-36, and TGR 226B showed narrow to wide longitudinal white stripes interspersed with green stripes on vegetative parts. While the variegation pattern extended from leaves and stem into the inflorescence in GWS-14, the spikes and spikelets of VCM-36 and TGR 226B were yellowish white in color. VCM-24 has a normal green phenotype. Following self pollinations, IP 5009, IP 482, IP 9712, GWS-14 and VCM-36 gave normal, yellow stripe and yellow or white progeny in varying proportions. The remaining two stripe mutants, IP 13160-1 and TGR 226B, on selfing gave only two types of progeny, normal and yellow stripe or white stripe, respectively. Yellow and white seedlings did not survive beyond two weeks. The proportions of different phenotypes among the selfed progenies depended upon the pattern and the extent of striping in the seedbearing plant. When a mutant sector was wide and uninterrupted by green regions, more yellow or white seedlings were obtained. If mutant sectors were frequently interspersed with green regions, more variegated progeny were obtained. When green sectors were wide and uninterrupted, more green progeny were obtained. The striping pattern was evident from the first leaf among the variegated seedlings. In addition, some of the green seedlings later developed stripes in all the variegated lines except in IP 9712.

Intercrosses among these eight genotypes were made to determine the allelic composition and inheritance of the variegation in different cytoplasmic backgrounds and their results are presented groupwise.

Crosses among yellow stripe mutants

When IP 5009, a non-lethal yellow stripe mutant was crossed reciprocally with another yellow stripe mutant IP 9712, varying proportions of normal and yellow seedlings were obtained, depending upon the pattern and the extent of mutant sectors in the seed-bearing plant (Table 2). In the F₂ generation variegated and normal progeny were obtained. However, the frequency of yellow stripe seedlings ranged from 6.8 to 26.6% in crosses between IP 5009 and IP 9712, and from 2.8 to 31.5% from their reciprocal.

 F_1 progeny from the crosses IP $5009 \times IP$ 482 and the reciprocal consisted of normal and yellow

Seed parent	Pollen parent									
	IP 5009 (YS)	GWS-14 (WS)	IP 482 (YS)	TGR 226B (WS)	VCM-36 (WS)	VCM-24 (G)	IP 13160-1 (YS)	IP 9712 (YS)		
IP 5009 (YS)	44G 20YS,4Y		79G 68Y	14G 101YS,47Y	225G 46Y		225G 4YS,19Y	39G 125Y		
GWS-14 (WS)		249G 6WS,85W								
IP 482 (YS)			15G 28YS,55Y	72G 186Y	129G 74Y		248G 89Y			
TGR 226B (WS)				24G 40WS						
VCM-36 (WS)	225G 4W	152G 3WS,220W			18G 48WS,4W	165G 53W				
VCM-24 (G)						132G				
IP 13160-1 (YS)	349G 27YS						52G 8Y			
IP 9712	169G							18G 2VS 24V		

Table 2. F₁ progeny composition of crosses involving different variegated plants of Pennisetum glaucum

Phenotypes: YS-Yellow stripe; WS-White stripe; G-Green; Y-Yellow; W-White

Yellow/White seedlings did not survive beyond two weeks

seedlings in varying proportions (Table 2). The F_2 progeny derived from selfing of different green F_1 progenies consisted of normal and yellow stripe in different proportions. The frequency of stripe progeny ranged from 2.8 to 31.5% and from 7.4 to 23% in the crosses IP 5009 × IP 482 and the reciprocal, respectively.

Progeny obtained on crossing IP 5009 with pollen from IP 13160-1 consisted of normal, yellow stripe, and yellow seedlings (Table 2). The reciprocal cross gave normal and yellow stripe progeny in varying proportions in the F_1 generation. However, the frequencies of variegated progeny were low from crosses involving IP 13160-1 as the seed parent (Table 2). The normal F_1 plants were randomly selected and selfed. Normal and yellow stripe seedlings were obtained in the F_2 generation. The frequency of variegated progeny in the F_2 generation, when IP 5009 was crossed with IP 13160-1, ranged from 1.6 to 31.6%, whereas the reciprocal cross gave about 8% variegated progeny.

Crosses between white stripe mutants

The pattern and extent of striping in VCM-36 varied from plant to plant, tiller to tiller and even leaf to leaf on the same tiller. Striping was observed on vegetative parts while peduncle, inflores-

cence, and spikelets were yellowish white in colour. Cross between VCM-36 and a normal inbred line VCM-24 resulted in various proportions of normal and white seedlings in the F_1 generation, depending upon the pattern and extent of white striping on the seed-bearing plant (Table 2). The normal seedlings did not show any striping even up to flag leaf stage. Some F_1 plants were selected randomly and selfed. Normal F_1 families segregated into white stripe and normal seedlings in the F_2 generation (Tables 2, 3).

Normal, stripe and white seedlings were obtained in the F_1 generation when VCM-36 was crossed with GWS-14, similar to that of selfed progeny of both parents (Table 2). Of the 25 randomly selected and selfed normal F_1 families, four gave normal, white stripe, and white progeny while the other F_1 families segregated into normal and white stripe progeny in the F_2 generation. The frequency of stripe plants in F_2 generation ranged from 4 to 28.9%.

Crosses between yellow stripe and white stripe mutants

When yellow stripe mutant IP 482 was crossed with pollen from the white stripe mutant VCM-36, F_1 progeny consisted of normal and yellow progeny (Table 2). Normal F_1 plants on selfing,

Table 3. F₂ segregation ratios of F₁ families on crossing different stripe plants of Pennisetum glaucum

Cross	F ₁ phenotypes	F ₁	% Germination	F ₂ -segregat	ion, %	
		families	mean (range)	Green	Stripe	Yellow/ White*
IP 5009 (YS)	G	25	26(7-41)	86 ± 0.96	YS 14 ± 0.96	_
IP 9712 (YS) IP 9712 (YS)			(,,			
(P 5009 (YS)	G	37	69(27-93)	89 ± 2.25	YS 10.5 ± 0.7	_
IP 5009 (YS) × IP 482 (YS)	G	35	85(27-99)	90 ± 0.73	YS 10 ± 0.73	-
IP 482 (YS × IP 13160-1 (YS)	G	6	88(54-100)	88 ± 2.40	YS 12 ± 2.40	-
IP 5009 (YS) × IP 13160-1 (YS)	G	37	79(11-100)	76 ± 3.17	YS 24 ± 0.90	**************************************
IP 13160-1 (YS)	G	7	60(57-63)	92 ± 2.48	YS 8 ± 2.50	_
IP 5009 (YS)	YS	I	44	94	YS 6	-
VCM-36 (WS) × GWS-14 (WS)	G	25	18(5-53)	88 ± 1.70	WS 11 ± 1.32	W 1 ± 1.00
IP 482 (YS) × VCM-36 (WS)	G	18	24(6-46)	74 ± 2.75	$\begin{array}{ccc} {\rm YS} & 25 \pm 2.90 \\ {\rm WS} & 0.7 \pm 0.74 \\ {\rm YWS} & 0.3 \pm 0.04 \end{array}$	-
VCM-36 (WS) × VCM-24 (G)	G	6	4(1-10)	44 ± 5.90	WS 55 ± 5.90	-
IP 5009 (YS)	G	6	12(3-31)	78 ± 3.40	YS 22 ± 3.40	=
× VCM-36 (WS)		3	13(8-23)	65 ± 2.64	YS 25 ± 5.98	Y 10 ± 4.49
, ,		10	26(16-39)	78 ± 1.92	YS 16 ± 2.06 WS 6 ± 1.32	_
		9	36(24-58)	78 ± 1.69	YS 16 ± 1.26 WS 4 ± 0.71	W 2 ± 0.3
		6	38(11-67)	77 ± 2.46	YS 16 ± 2.46 WS 4 ± 0.51	Y 3 ± 0.65
		4	16(11-19)	64 ± 5.98	YS 15 ± 4.47 WS 7 ± 2.04	Y 4 ± 0.65 W 10 ± 5.2
		1	8	86	WS 7	W 7
		1	23	69	YS 29	W 2
		1	10	61	YS 13	Y 13, W 13
		1	2	-	YS 34	Y 33, W 3
VCM-36 × IP 5009 (YS)	G	10	11(2-24)	82 ± 3.25	YS 18 ± 3.21	
1 3003 (15)		15	24(9-47)	84 ± 1.69	YS 12 ± 1.39 WS 4 ± 0.62	
		2	38	79 ± 3.66	YS 16 ± 4.35 WS 3 ± 0.45	W 2 ± 0.23
		2	31	84 ± 4.85	YS 13 ± 4.53	
		1	45	78	YS 18	Y 3, W 1
		1	16	74	YS 20 WS 3	Y 3
		1	37	96	_	Y 1, W 3
IP 5009 (YS)	YS	34	74(41-91)	28 ± 3.28	YS 32 ± 4.07	
TGR 226B (WS)	G	3	49	50 ± 1.66	YS 42 ± 4.45	Y 8 ± 5.4
IP 482 (YS) ** TGR 226B (WS)	G	44	60(57-63)	85 ± 3.50	YS 15 ± 0.82	

^{*} Yellow/White seedlings did not survive beyond two weeks

segregated into normal, yellow stripe, white stripe, and yellow white stripe seedlings, the proportions of which varied from one F₁ family to the other.

Similar results were obtained when yellow stripe mutant IP 5009 was crossed with pollen from white stripe mutant VCM-36. Normal and yellow seedlings were obtained in the F_1 generation. However, the reciprocal cross gave normal and white progeny in the F_1 generation (Table 2). The frequency of normal to yellow or white progeny varied depending upon the extent of striping in the seedbearing plant. The normal F_1 plants from the reciprocal crosses gave different proportions of normal, yellow stripe, white stripe, yellow, and white seedlings in their F_2 generation.

The yellow stripe mutants IP 5009 and IP 482 when crossed with pollen from TGR 226B (a white stripe mutant), yielded different F_1 progenies. The progeny of the cross IP $5009 \times TGR$ 226B consisted of a low frequency of normal, yellow stripe, and yellow seedlings (Table 2). Yellow stripe and normal F_1 plants on selfing gave different proportions of normal, yellow stripe and yellow progeny in the F_2 generation. IP 482 was used as a seedbearing parent and TGR 226B as pollen parent, the F_1 progeny consisted of normal and yellow seedlings (Table 2). Green F_1 families on selfing, segregated into normal and yellow stripe progeny. Yellow stripe seedlings ranged from 2.3 to 31.5%.

Discussion

A general feature of the seven stripe mutant lines is the production of normal, variegated, and yellow or white progeny on self pollination (Table 2). Relative frequencies of different phenotypic classes in each of the lines are dependent upon the nature and extent of variegation. This generality is consistent with the earlier findings in IP 5009 and GWS-14 (SUBRAHMANYAM et al. 1986; REDDY and SUBRAHMANYAM 1988a,b). Production of normal, variegated, and yellow or white progeny in the F_1 generation of the crosses IP 5009 × IP 13160-1, IP $5009 \times TGR$ 226B, and GWS-14 \times VCM-36 (Table 3) reflect the similarities in the genotypic composition of the parents in each of the respective crosses. Variegation in IP 5009 is governed by the genotype (vi/vi) (REDDY and SUBRAHMANYAM 1988b) which will be referred as vi_1/vi_1 from now on. Thus, it is inferred that IP 13160-1 and TGR 226B have the same (vi_1/vi_1) genotype at this locus. Since white striping in GWS-14 is controlled by two loci (REDDY and SUBRAHMANYAM 1988a), VCM-36 is likely to have the same genotype as GWS-14. Production of normal and yellow seedlings in the F_1 generation and the appearance of stripe progeny in the F_2 generation in the reciprocal crosses between IP 5009 and IP 9712 indicate that two complementary loci are involved in these two mutants, which may be designated as vi_1/vi_1 in IP 5009 and vi_2/vi_2 in IP 9712. The genetic behaviour of IP 482 in crosses with IP 5009 also indicates that variegation in IP 482 is controlled by a different locus from that of IP 5009 but complementary to each other. Whether IP 482 has the same genotype as IP 9712 or not remains to be examined.

Production of normal and yellow progeny in the F_1 generation of the cross IP 5009 × VCM-36, and normal and white F₁ progeny in their reciprocal cross, is indicative of the differences in the genotypic composition of these two lines. The genotype of VCM-36 is tentatively designated as vi_3/vi_3vi_4 vi₄ since VCM-36 behaved similar to GWS-14 in crosses with IP 5009 in the present study and from the results reported earlier (REDDY and SUBRAH-MANYAM 1988a). From the F_1 composition of the cross IP 482 × TGR 226B, it is evident that these two lines differ in their genotypes in the development of variegation. While TGR 226B showed similarity in behaviour as that of IP 5009 in the present study, IP 482 was found to be different from IP 5009 (REDDY and SUBRAHMANYAM 1988b). Based on the results of the cross IP 482 × VCM-36 it can be inferred that IP 482 has a distinct genotype from VCM-36. Thus the production of two kinds (normal and yellow or white) of progeny in the F₁ generation of different intercrosses between variegated lines, indicates that the recessive nuclear gene(s) controlling striping in each parent are non-allelic and are similar to the differences between the stripe mutants *Iojap* (RHOADES 1943, 1946) and chloroplast mutator (STROUP 1970) of maize. The dominant alleles from both the parents complement in their F₁ hybrids (heterozygous at each locus) and give rise to normal F₁ plants. The stripe mutant IP 5009 (700430) of P. glaucum is shown to be homozygous for a recessive gene vi (variation inducer in the plastids, REDDY and SUBRAHMANYAM 1988b). In homozygous (vi_1/vi_1) condition, some plastids within a cell fail to develop chlorophyll and become yellow, producing cells with a mixture of green and yellow plastids. From such heteroplastidic cells, the normal and altered plastids sort out

into pure homoplastidic cells and cell lineages. This is in accordance with the earlier findings of RHOADES (1943) in *Iojap* mutant of maize and of HAGEMANN and SCHOLZ (1962) in the albostrain of barley. Yellow stripe seedlings in varying proportions in the F_2 generation of the above mentioned crosses did not fit the modified Mendelian ratio of 9:7 (p < 0.01). This suggests a differential penetrance among homozygous recessive plants similar to that of chloroplast mutator gene of maize (STROUP 1970).

Absence of yellow seedlings in the F_2 generation is not surprising because there is no mutant sector in the F_1 normal progeny and thereby no homoplastidic mutant egg cells. Stripe progeny in the F_2 generation represents the proportion of homozygous recessive plants in which alteration of plastids occurred. This is a general phenomenon with all the variegated lines and is consistent with the earlier findings in IP 5009 (REDDY and SUBRAHMANYAM 1988b).

Absence of stripe progenies following intercrosses between variegated lines with different genotypes further substantiates the earlier reports (REDDY and SUBRAHMANYAM 1988a,b) that the altered plastids in the presence of normal plastids in the heteroplastidic egg cells develop normally on acquiring a dominant allele from the pollen parent. Thus the interaction between the normal plastid and the nuclear gene leads to the normal development of otherwise altered plastids. The absence of striping in the F₁ and reappearance in the F₂ generation (Tables 2, 3) in the cross VCM- $36 \times VCM-24$, indicates that the stripe phenotype is under the control of a recessive nuclear genotype. Although the low frequency of germination led to small sample size, results from crosses with GWS-14, a white stripe mutant controlled by two independently assorting recessive genes (GILL et al.

1969; REDDY and SUBRAHMANYAM 1988a), indicate that VCM-36 carries the same genotype $vi_3/vi_3vi_4/vi_4$.

When IP 5009 was crossed with TGR 226B (white-stripe mutant) F_1 and F_2 progeny consisted of normal, yellow stripe, and yellow progeny. Appearance of yellow stripe and absence of white stripe progeny in both these generations could be due to the similarity of the genotype (vi/vi) at one locus. Normal, yellow stripe, and yellow progeny in the F_1 and F_2 generations from the cross IP $482 \times TGR$ 226B is also indicative of the similarity in their genotypes in at least one locus vi_2/vi_2 . Thus, TGR 226B is the likely $vi_1/vi_1vi_2/vi_2$ genotype.

The results from different possible intercrosses between different stripe mutants of pearl millet revealed at least four (possibly five) loci which control plastid alteration (Table 4). In the F₂ generation derived from intercrosses between different genotypes, the proportion of stripe progeny fell short of the expected recessive genotypes from complementary ratios (9:7, 27:37 or their regroupings). This reflects incomplete penetrance among the homozygous recessive genotypes. Crosses between different variegated mutants which differ in their genotypes (Table 4) result in prevention of the development of chlorophyll in a proportion of plastids in the zygotic cell. Invariably such altered plastids revert back to normal on acquiring corresponding dominant allele(s) through pollen from a normal genotype in the presence of normal plastids as in heteroplastidic egg cells. This substantiates earlier findings of REDDY and SUBRAHMANYAM (1988a,b). From the wide range of intercrosses between yellow stripe and white stripe lines there was no evidence for bi-parental transmission of mutant plastids as suggested by Krishna Rao and KODURU (1978). Occurrence of yellow-white stripe progeny in the F₂ generation from the

Table 4. Genotypic composition of different variegation mutants of Pennisetum glaucum

Accessions	Genotype	Earlier designation
IP 5009	$vi_1vi_1Vi_2Vi_2Vi_3Vi_3Vi_4Vi_4$	st st (Appa Rao and Mengesha 1984) vi vi (Reddy and Subrahmanyam 1988)
IP 13160-1	$vi_1vi_1Vi_2Vi_2Vi_3Vi_3Vi_4Vi_4$	
IP 9712	$Vi_1Vi_1vi_2vi_2Vi_3Vi_3Vi_4Vi_4$	
IP 482	$Vi_1 Vi_1 vi_2 vi_2 Vi_3 Vi_3 Vi_4 Vi_4^*$	
TGR 226B	$vi_1vi_1vi_2vi_2Vi_3Vi_3Vi_4Vi_4$	
GWS-14	$Vi_1Vi_1Vi_2Vi_2vi_3vi_3vi_4vi_4$	gws ₁ gws ₁ gws ₂ gws ₂ (Gill et al. 1969)
VCM-36	$Vi_1Vi_1Vi_2Vi_2vi_3vi_3vi_4vi_4^*$	

^{*} Subject to further confirmation

crosses between yellow stripe and white stripe mutants indicates that loci controlling yellow stripe are likely to be involved at a different step from that of the loci controlling white stripe in blocking the chlorophyll developmental pathway. Yet, each one of them interacts with the normal plastid in the reversal of altered plastids to normal in the heteroplastidic egg cells on acquiring dominant allele(s) through pollen. Thus the present findings provide a unique base for the study of nuclear-plastidic interactions.

Acknowledgements. - Fellowship to K. Karunasri from University Grants Commission (India) is gratefully acknowledged.

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