Genetic analysis of variegation mutants of Pearl millet, *Pennisetum glaucum*

K. KARUNASRI and N. C. SUBRAHMANYAM

School of Life Sciences, University of Hyderabad, Hyderabad, India

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 F₁, and normal and yellow stripe in the F₂ 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 x VCM-36, IP 482 x 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 F₂s from intergenotypic crosses, the mutant phenotypes fell short of expectation, indicating differential penetrance in expression.

N. C. Subrahmanyam, School of Life Sciences, University of Hyderabad, Hyderabad-500 134, India

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. RATNASWAMY (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 SUBRAHMANYAM (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 MENCESHA (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), SUIATHA and SUBRAHMANYAM (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, their phenotype and source

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

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.

F₁ 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 × 1.8 m plots at 30 cm × 30 cm spacing. F₂ progeny were raised in plots of 1.8 m × 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 seed-bearing 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.

F₁ progeny from the crosses IP 5009 × IP 482 and the reciprocal consisted of normal and yellow
Table 2. F$_1$ progeny composition of crosses involving different variegated plants of *Pennisetum glaucum*

<table>
<thead>
<tr>
<th>Seed parent</th>
<th>Pollen parent</th>
<th>F$_2$ proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>IP 5009</td>
<td>GWS-14</td>
<td>20YS,4Y</td>
</tr>
<tr>
<td>IP 482</td>
<td>TGR 226B</td>
<td>225G</td>
</tr>
<tr>
<td>VCM-36</td>
<td>VCM-24</td>
<td>46Y</td>
</tr>
<tr>
<td>IP 13160-1</td>
<td>IP 9712</td>
<td>125Y</td>
</tr>
<tr>
<td>IP 5009</td>
<td>GWS-14</td>
<td>249G</td>
</tr>
<tr>
<td>GWS-14</td>
<td>6WS,85W</td>
<td>4WS,19Y</td>
</tr>
<tr>
<td>IP 482</td>
<td>TGR 226B</td>
<td>27YS</td>
</tr>
<tr>
<td>VCM-36</td>
<td>VCM-24</td>
<td>169G</td>
</tr>
<tr>
<td>IP 13160-1</td>
<td>IP 9712</td>
<td>2YS,24Y</td>
</tr>
</tbody>
</table>

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 x 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 (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 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. Stripping was observed on vegetative parts while peduncle, inflorescence, 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).

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*

<table>
<thead>
<tr>
<th>Cross</th>
<th>F₁ phenotypes</th>
<th>F₂ families</th>
<th>% Germination mean (range)</th>
<th>F₂-segregation, %</th>
<th>Green</th>
<th>Stripe</th>
<th>Yellow/White*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IP 5009 (YS)</td>
<td>G</td>
<td>25</td>
<td>26(7–41)</td>
<td>86 ± 0.96</td>
<td>YS</td>
<td>14 ± 0.96</td>
<td>–</td>
</tr>
<tr>
<td>IP 9712 (YS)</td>
<td>G</td>
<td>37</td>
<td>69(27–93)</td>
<td>89 ± 2.25</td>
<td>YS</td>
<td>10.5 ± 0.7</td>
<td>–</td>
</tr>
<tr>
<td>IP 9712 (YS) × IP 5009 (YS)</td>
<td>G</td>
<td>35</td>
<td>85(27–99)</td>
<td>90 ± 0.73</td>
<td>YS</td>
<td>10 ± 0.73</td>
<td>–</td>
</tr>
<tr>
<td>IP 482 (YS)</td>
<td>G</td>
<td>6</td>
<td>88(54–100)</td>
<td>88 ± 2.40</td>
<td>YS</td>
<td>12 ± 2.40</td>
<td>–</td>
</tr>
<tr>
<td>IP 13160-1 (YS) IP 5009 (YS)</td>
<td>G</td>
<td>37</td>
<td>79(11–100)</td>
<td>76 ± 3.17</td>
<td>YS</td>
<td>24 ± 0.90</td>
<td>–</td>
</tr>
<tr>
<td>IP 13160-1 (YS) × IP 5009 (YS)</td>
<td>G</td>
<td>7</td>
<td>60(57–63)</td>
<td>92 ± 2.48</td>
<td>YS</td>
<td>8 ± 2.50</td>
<td>–</td>
</tr>
<tr>
<td>IP 5009 (YS)</td>
<td>GYS</td>
<td>1</td>
<td>44</td>
<td>94</td>
<td>YS</td>
<td>6</td>
<td>–</td>
</tr>
<tr>
<td>VCM-36 (WS) × GWS-14 (WS)</td>
<td>G</td>
<td>25</td>
<td>18(5–53)</td>
<td>88 ± 1.70</td>
<td>WS</td>
<td>11 ± 1.32</td>
<td>W</td>
</tr>
<tr>
<td>IP 482 (YS)</td>
<td>G</td>
<td>18</td>
<td>24(6–46)</td>
<td>74 ± 2.75</td>
<td>YS</td>
<td>25 ± 2.90</td>
<td>–</td>
</tr>
<tr>
<td>VCM-36 (WS)</td>
<td>G</td>
<td>6</td>
<td>4(1–10)</td>
<td>44 ± 5.90</td>
<td>WS</td>
<td>55 ± 5.90</td>
<td>–</td>
</tr>
<tr>
<td>VCM-24 (G)</td>
<td>G</td>
<td>6</td>
<td>12(3–31)</td>
<td>78 ± 3.40</td>
<td>YS</td>
<td>22 ± 3.40</td>
<td>–</td>
</tr>
<tr>
<td>IP 482 (WS)</td>
<td>G</td>
<td>10</td>
<td>13(8–23)</td>
<td>65 ± 2.64</td>
<td>YS</td>
<td>25 ± 5.98</td>
<td>Y</td>
</tr>
<tr>
<td>IP 5009 (YS)</td>
<td>G</td>
<td>9</td>
<td>36(24–58)</td>
<td>78 ± 1.69</td>
<td>YS</td>
<td>16 ± 1.26</td>
<td>W</td>
</tr>
<tr>
<td>IP 5009 (YS)</td>
<td>G</td>
<td>6</td>
<td>38(11–67)</td>
<td>77 ± 2.46</td>
<td>YS</td>
<td>16 ± 2.46</td>
<td>Y</td>
</tr>
<tr>
<td>VCM-36 (WS)</td>
<td>G</td>
<td>4</td>
<td>16(11–19)</td>
<td>64 ± 5.98</td>
<td>YS</td>
<td>15 ± 4.47</td>
<td>Y</td>
</tr>
<tr>
<td>VCM-36 (WS)</td>
<td>G</td>
<td>1</td>
<td>8</td>
<td>86</td>
<td>WS</td>
<td>7</td>
<td>W</td>
</tr>
<tr>
<td>VCM-36 (WS)</td>
<td>G</td>
<td>1</td>
<td>23</td>
<td>69</td>
<td>YS</td>
<td>29</td>
<td>W</td>
</tr>
<tr>
<td>VCM-36 (WS)</td>
<td>G</td>
<td>1</td>
<td>10</td>
<td>61</td>
<td>YS</td>
<td>13</td>
<td>Y</td>
</tr>
<tr>
<td>VCM-36 (WS)</td>
<td>G</td>
<td>1</td>
<td>2</td>
<td>–</td>
<td>YS</td>
<td>34</td>
<td>Y</td>
</tr>
<tr>
<td>VCM-36 (WS) × IP 5009 (YS)</td>
<td>G</td>
<td>15</td>
<td>24(9–47)</td>
<td>84 ± 1.69</td>
<td>YS</td>
<td>12 ± 1.39</td>
<td>–</td>
</tr>
<tr>
<td>VCM-36 (WS) × IP 5009 (YS)</td>
<td>G</td>
<td>2</td>
<td>38</td>
<td>79 ± 3.66</td>
<td>YS</td>
<td>10 ± 4.35</td>
<td>W</td>
</tr>
<tr>
<td>VCM-36 (WS) × IP 5009 (YS)</td>
<td>G</td>
<td>2</td>
<td>31</td>
<td>84 ± 4.85</td>
<td>YS</td>
<td>13 ± 4.53</td>
<td>Y</td>
</tr>
<tr>
<td>VCM-36 (WS) × IP 5009 (YS)</td>
<td>G</td>
<td>1</td>
<td>45</td>
<td>78</td>
<td>YS</td>
<td>18</td>
<td>Y</td>
</tr>
<tr>
<td>VCM-36 (WS) × IP 5009 (YS)</td>
<td>G</td>
<td>1</td>
<td>16</td>
<td>74</td>
<td>YS</td>
<td>20</td>
<td>W</td>
</tr>
<tr>
<td>VCM-36 (WS) × IP 5009 (YS)</td>
<td>G</td>
<td>1</td>
<td>37</td>
<td>96</td>
<td>–</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>IP 5009 (YS) × TGR 226B (WS)</td>
<td>GYS</td>
<td>34</td>
<td>74(41–91)</td>
<td>28 ± 3.28</td>
<td>YS</td>
<td>32 ± 4.07</td>
<td>Y</td>
</tr>
<tr>
<td>TGR 226B (WS)</td>
<td>G</td>
<td>3</td>
<td>49</td>
<td>50 ± 1.66</td>
<td>YS</td>
<td>42 ± 4.45</td>
<td>Y</td>
</tr>
<tr>
<td>IP 482 (YS) × TGR 226B (WS)</td>
<td>G</td>
<td>44</td>
<td>60(57–63)</td>
<td>85 ± 3.50</td>
<td>YS</td>
<td>15 ± 0.82</td>
<td>–</td>
</tr>
</tbody>
</table>

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 F1 generation. However, the reciprocal cross gave normal and white progeny in the F1 generation (Table 2). The frequency of normal to yellow or white progeny varied depending upon the extent of striping in the seed-bearing plant. The normal F1 plants from the reciprocal crosses gave different proportions of normal, yellow stripe, white stripe, yellow, and white seedlings in their F2 generation.

The yellow stripe mutants IP 5009 and IP 482 when crossed with pollen from TGR 226B (a white stripe mutant), yielded different F1 progenies. The progeny of the cross IP 5009 × TGR 226B consisted of a low frequency of normal, yellow stripe, and yellow seedlings (Table 2). Yellow stripe and normal F1 plants on selfing gave different proportions of normal, yellow stripe and yellow progeny in the F2 generation. IP 482 was used as a seed-bearing parent and TGR 226B as pollen parent, the F1 progeny consisted of normal and yellow seedlings (Table 2). Green F1 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 (Subrahmanyan et al. 1986; Reddy and Subrahmanyan 1988a,b). Production of normal, variegated, and yellow or white progeny in the F1 generation of the crosses IP 5009 × IP 13160-1, IP 5009 × TGR 226B, and GWS-14 × 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 Subrahmanyan 1988b) which will be referred as vii/vi from now on. Thus, it is inferred that IP 13160-1 and TGR 226B have the same (vi/vi) genotype at this locus. Since white striping in GWS-14 is controlled by two loci (Reddy and Subrahmanyan 1988a), VCM-36 is likely to have the same genotype as GWS-14. Production of normal and yellow seedlings in the F1 generation and the appearance of stripe progeny in the F2 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 vi1/vi1 in IP 5009 and vi2/vi2 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 F1 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 vi3/vi3vi4/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 Subrahmanyan 1988a). From the F1 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 Subrahmanyan 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 lojap (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 Subrahmanyan 1988b). In homozygous (vi/vi) 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 heteroplasmatic 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 Jojap mutant of maize and of Hagemann and Scholz (1962) in the albostain of barley. Yellow stripe seedlings in varying proportions in the F₂ 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 F₂ generation is not surprising because there is no mutant sector in the F₁ normal progeny and thereby no homoplastidic mutant egg cells. Stripe progeny in the F₂ 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 x 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 vi₃/vi₄vi₄/vi₄.

When IP 5009 was crossed with TGR 226B (white-stripe mutant) F₁ and F₂ 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 F₁ and F₂ generations from the cross IP 482 x TGR 226B is also indicative of the similarity in their genotypes in at least one locus vi₂/vi₂. Thus, TGR 226B is the likely vi₁/vi₁vi₂/vi₂ 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

<table>
<thead>
<tr>
<th>Accessions</th>
<th>Genotype</th>
<th>Earlier designation</th>
</tr>
</thead>
<tbody>
<tr>
<td>IP 5009</td>
<td>vi₁vi₁vi₂vi₂vi₃vi₃vi₄vi₄</td>
<td>st st (Appa Rao and Mengesha 1984)</td>
</tr>
<tr>
<td>IP 13160-1</td>
<td>vi₁vi₁vi₂vi₂vi₃vi₃vi₄vi₄</td>
<td>vi vi (Reddy and Subrahmanyam 1988)</td>
</tr>
<tr>
<td>IP 9712</td>
<td>vi₁vi₁vi₂vi₂vi₃vi₃vi₄vi₄</td>
<td></td>
</tr>
<tr>
<td>IP 482</td>
<td>vi₁vi₁vi₂vi₂vi₃vi₃vi₄vi₄</td>
<td></td>
</tr>
<tr>
<td>TGR 226B</td>
<td>vi₁vi₁vi₂vi₂vi₃vi₃vi₄vi₄</td>
<td>gws₁ gws₁ gws₂ gws₂ (Gill et al. 1969)</td>
</tr>
<tr>
<td>GWS-14</td>
<td>vi₁vi₁vi₂vi₂vi₁vi₁vi₄vi₄</td>
<td></td>
</tr>
<tr>
<td>VCM-36</td>
<td>vi₁vi₁vi₂vi₂vi₁vi₁vi₄vi₄</td>
<td></td>
</tr>
</tbody>
</table>

* 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 heteroplastic 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.

References