

Inheritance of stripe in pearl millet

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ABSTRACT: A nonlethal chlorophyll-deficient mutant named stripe was detected in a pearl millet (*Pennisetum americanum* (L.) Leeke) accession IP-5009 collected from Nigeria. The stripe plants showed longitudinal yellow stripes alternating with green stripes on leaf blades, leaf sheaths, stems, peduncles, inflorescences, and spikelets. The stripe plants segregated yellow, stripe, and green depending on the number and size of the yellow stripes on the leaf blade. Segregation data from crosses of green and stripe plants did not fit a finite Mendelian ratio. The spikes of the stripe plants have yellow and green spikelets and when yellow spikelets were crossed with green spikelets, segregation data indicated that the yellow spikelet color was monogenic recessive to the green color. Since the yellow and green sectors that are genetically different from each other lie adjacent to each other, the stripe plants are considered to be chimeras.

WHILE EVALUATING the world collection of pearl millet (*Pennisetum americanum* (L.) Leeke) at ICRISAT, an unusual chlorophyll-deficient phenotype was observed and isolated during the postrainy season of 1977-78. This "mutant" was named stripe according to the suggested nomenclature of Burton and Powell². As the "mutant" was morphologically different from those previously described^{3,6,8} its mode of inheritance was studied.

Materials and Methods

The stripe "mutant" was isolated from the selfed progeny of IP-5009, an introduction from Nigeria. In a progeny of 193 plants, two stripe plants were found that were subsequently maintained by selfing. The morphological characteristics of the "mutant" along with normal green plants were studied during the rainy season of 1982, utilizing the standard pearl millet descriptors⁷.

The stripe plants were visually classified into 10 groups corresponding to the number and size of yellow stripes on the leaf blades (Figure 1C) and spikelets (Figure 1B). Reciprocal crosses were made between the normal and the stripe plants taking advantage of protogyny as de-

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scribed by Burton¹. The progenies from each of the selfs and crosses were classified as yellow, stripe, or green within 10 days after their germination in sand beds or in the field.

Results and Discussion

The stripe "mutant" was conspicuous from emergence. The first formed leaf showed longitudinal yellow stripes of different sizes alternating with green. All the subsequent leaves including the flag leaf of that particular tiller produced yellow stripes (Figure 1A). The number and relative size of the yellow stripes were almost the same in all the leaves. However, in a few tillers the size of the yellow stripe gradually increased in the subsequent leaves leading to the development of a yellow flag leaf with a thin green streak. In a few plants the number and size of the yellow stripes decreased in the subsequent tillers. The pattern of yellow-green stripes varied from plant to plant, tiller to tiller within a plant, and even from leaf to leaf on the same tiller (Figure 1A). Although it is easy to distinguish the "mutant" from normal green at any stage, the maximum expression of the "mutant" character was at boot leaf stage at which time the yellow stripes were strikingly different. The yellow stripes extended to the leaf sheath, internode, peduncle, and inflorescence. Spikelets developing on the green rachis were green, in the yellowish area, yellow (Figure 1C). The borderline spikelets were a mixture of yellow and green.

Table I. Morphological differences between normal and stripe "mutant" (planted on June 23, 1982 with three replications, plot size 3 m²)

| Character | Normal mean ± SE | Stripe mean ± SE |
|-----------------------|---------------------|---------------------|
| Days to 50% flowering | 59 ± 0.67 | 61 ± 1.20 |
| Plant hgt (cm) | 212 ± 10.14 | 197 ± 23.51 |
| Spike lgh (cm) | 32 ± 0.27 | 31 ± 1.65 |
| Spike thickness (mm) | 21 ± 0.76 | 21 ± 1.07 |
| Stem thickness (mm) | 10 ± 1.60 | 7 ± 1.28 |
| Leaf blade lgh (cm) | 71 ± 4.33 | 63 ± 3.06 |
| Leaf blade width (mm) | 41 ± 1.33 | 34 ± 0.58 |
| Total tillers (no.) | 5 ± 1.33 | 4 ± 0.20 |

The "mutant" was slow growing in the initial stages, and if not isolated from the green plants it was suppressed in growth and 13 percent of the plants did not flower. However, when isolated from green plants or space planted, the "mutant" flowered and only 1.7 percent of the plants died before the three-leaf stage. The "mutant" plants were highly variable for all the characters studied depending on the relative proportion of green and yellow area. Plant height, leaf blade length, width and stem thickness were reduced in the "mutant" compared to normal green (Table I).

The stripe "mutant" did not breed true even after 13 generations of selfing. In all generations it produced three types of progenies: stripe, normal green, and yellow; the latter died within a week after emergence. Relative frequencies of the different types varied enormously (Table II) from plant to plant depending on the size and number of yellow stripes (Figure 1C). In those plants in which the boot leaf was yellow except for the midrib (group I) only yellow seedlings were obtained. Plants in which the yellow area predominated over green (group II) produced mostly yellow seedlings with a low frequency of stripe plants. Wherever the alternating yellow-green stripes were more pronounced (group III), the frequency of stripe seedlings was at a maximum with a low frequency of yellow and green plants. As the area of yellow stripes was more or less equal to the green area (group IV) all of the three types were obtained. With an increase in the green leaf area (group V), there was an increase in the frequency of green plants. The progeny consisted of mostly green plants with only a thin yellow streak (group VI). Green plants recovered from the stripe plants (group VII) produced predominantly green and a low frequency of stripe plants. The segregation patterns of the different groups of stripe plants clearly indicate that the size of the yellow and green stripes along with the number of interspersions determined the type and frequency of the progeny. The extent of uninterrupted green or yellow stripes on the leaves was related to the frequencies of green or yellow seedlings: as the proportion of uninterrupted yellow area increased the frequency of yellow seedlings increased. The number of interspersions on the leaf was related to the frequency of stripe progeny, in that the frequency of stripe seedlings increased with an increase in the number of interspersions.

Table II. Segregation of different groups of stripe plants (see text)

| Stripe group | No. families | Total seedlings | Percent of | | |
|--------------|--------------|-----------------|------------|--------|-------|
| | | | stripe | yellow | green |
| I | 6 | 1558 | 0.00 | 100.00 | 0.00 |
| II | 5 | 583 | 8.06 | 91.94 | 0.00 |
| III | 4 | 2162 | 92.92 | 5.13 | 1.94 |
| IV | 16 | 3492 | 16.15 | 77.58 | 6.27 |
| V | 8 | 1276 | 7.60 | 75.39 | 17.00 |
| VI | 5 | 2062 | 8.48 | 6.62 | 85.88 |
| VII | 10 | 1151 | 10.05 | 15.09 | 74.76 |
| VIII | 10 | 143 | 80.06 | 12.06 | 7.88 |
| IX | 10 | 2046 | 6.02 | 2.06 | 91.92 |
| X | 10 | 453 | 0.00 | 100.00 | 0.00 |

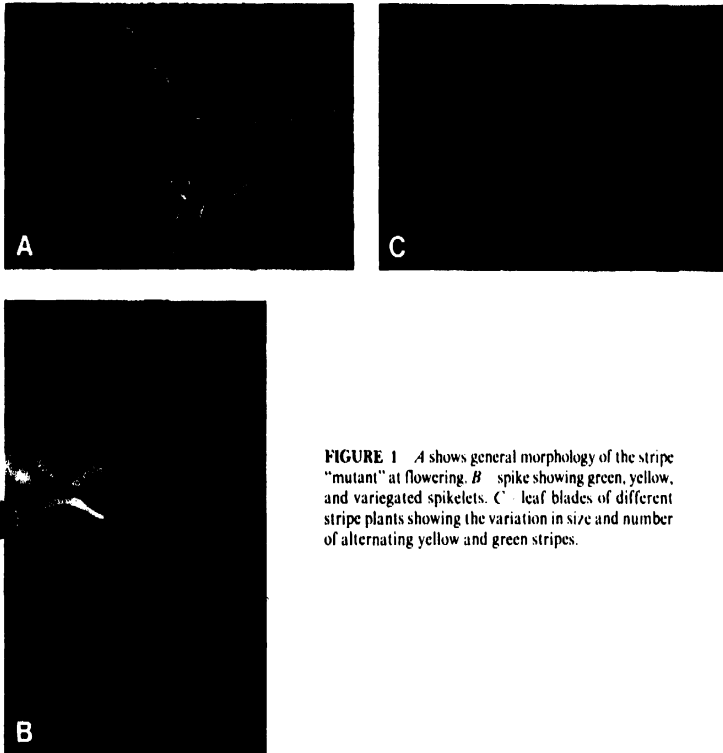


FIGURE 1 A shows general morphology of the stripe "mutant" at flowering. B spike showing green, yellow, and variegated spikelets. C leaf blades of different stripe plants showing the variation in size and number of alternating yellow and green stripes.

The spikelet color (Figure 1B) greatly influenced the type and frequency of progeny. Variegated spikelets found on the borderline areas (group VIII) produced three types of progeny, although stripe plants were predominant. Green spikelets found on the green rachis (group IX) produced predominantly green progeny. The yellow spikelets found on the yellow rachis (group X) exclusively produced yellow progeny. These observations suggest that the ovules borne on yellow sectors contain plastids that are different from those ovules borne on green sectors, while the ovules borne on the var-

iegated spikelets contain both types of plastids. This pattern is similar to the behavior of variegated phenotypes observed in other plants⁵.

The segregation of the stripe plants even after 13 generations of selfing, and the occurrence of lethal yellow seedlings in the progeny can be explained by assuming that stripe plants have normal and "mutant" plastids. The spikelets borne on yellow sectors contain "mutant" plastids, the spikelets borne on green sectors contain normal plastids. In the spikelets borne on borderline cells there are a mixture of normal and "mutant" plastids. In *Pelargonium*, Tilney-Basset⁹ reported that the variegated embryos contained plastids from both parents usually in disproportionate amounts. The phenotypes of the

descendant were determined by the type of plastids the ovules contained. The fact that the yellow spikelets on selfing produced exclusively yellow seedlings confirmed this assumption. Segregation of the selfed stripe plant was probably due to sorting-out of normal and "mutant" plastids during successive rounds of cell division as suggested by Hagemann⁵. The production of yellow-green stripes depends on the ratio of green to "mutant" plastids. This assumption was further supported by the fact that the proportion of yellow, stripe, and green seedlings was dependent on the size of yellow-green stripes and the number of interspersions.

When the normal and stripe plants were crossed, reciprocal differences were observed in the F₁ generation (Table III). Crosses involving stripe as female and normal as male produced normal green and yellow as well as a low frequency of stripe plants. When the stripe plant was used as male parent the progeny consisted of green plants only. Reciprocal differences were confirmed after crossing stripe with a dominant marker, purple pigmentation on stem and leaves. When a male sterile line (5141A) was crossed with the stripe "mutant" as male parent, the progeny consisted of green plants only. The breeding behavior of the mutant and reciprocal differences in the F₁ clearly suggest a maternal effect on the expression of the stripe "mutant." Since crosses were made taking advantage of protogyny, without emasculating, at least some of the maternal types found in the F₁ might be due to selfing. This was overcome by making use of a dominant marker gene, purple pigmentation and also a male-sterile line.

The striped F₁ plants produced normal green, stripe and yellow plants like the parent stripe "mutant" whereas the normal green F₁ plants produced stripe and green plants in varying proportions (Table IV). The F₂ segregation did not fit into any definite Mendelian ratio. When the stripe plant was crossed with the purple stock, all the expected four phenotypes were observed, but in a non-Mendelian ratio. However, in the subsequent generations stripe plants with purple pigmentation were observed indicating the influence of a nuclear gene. It was possible to transfer the stripe trait into dwarf and purple background even when the stripe was used as male parent. This indicates that the stripe trait

Table III. F₁ behavior in various crosses of normal and stripe

| Parents* | No. spikes | Frequency of seedlings in F ₁ | | | |
|-----------------|------------|--|--------|-------|--------|
| | | stripe | yellow | green | purple |
| Stripe X green | 15 | 156 | 5729 | 7613 | 0 |
| Green X stripe | 15 | 0 | 0 | 8526 | 0 |
| Stripe X purple | 5 | 39 | 643 | 265 | 146 |
| Purple X stripe | 5 | 0 | 0 | 0 | 198 |
| 5141A X stripe | 5 | 0 | 0 | 396 | 0 |
| YSL X GSL | 5 | 0 | 13 | 48 | 0 |
| GSL X YSL | 5 | 0 | 0 | 165 | 0 |

* YSL = yellow colored spikelets; GSL = green colored spikelets

Table IV. F₂ segregation

| Cross* | F ₁ phenotype | No. families | Purple normal | Purple stripe | Green normal | Green stripe | Yellow | χ ² |
|-----------------|--------------------------|--------------|---------------|---------------|--------------|--------------|--------|----------------|
| | | | | | | | | (3:1) |
| Stripe X green | stripe | 20 | — | — | 1843 | 153 | 284 | — |
| Stripe X green | green | 20 | — | — | 2046 | 198 | 53 | — |
| Green X stripe | green | 38 | — | — | 5683 | 436 | 86 | — |
| 5141A X stripe | green | 10 | — | — | 547 | 48 | 5 | — |
| Stripe X purple | purple | 10 | — | — | 896 | 53 | 78 | — |
| Stripe X purple | green | 10 | — | — | 634 | 25 | 8 | — |
| Stripe X purple | purple | 8 | 493 | 89 | 328 | 50 | 3 | — |
| Purple X stripe | purple | 7 | 894 | 145 | 517 | 86 | 10 | — |
| YSL X GSL | green | 5 | — | — | 398 | 105 | — | 4.56 |
| GSL X YSL | green | 5 | — | — | 532 | 146 | — | 4.34 |

* YSL = yellow colored spikelets; GSL = green colored spikelets

also was transmitted through the male parent.

In the F_3 , stripe F_2 plants segregated like the stripe parent. Of the 20 normal green F_2 plants, five bred true for green, while 15 segregated into stripe and green seedlings. Crosses made between F_1 s using stripe plants as female parent and normal green plants as male parents produced green, stripe, and yellow seedlings while the reverse cross produced only green plants.

When the yellow spikelets of a stripe plant were crossed with the green spikelets, of a stripe plant, the F_1 consisted of yellow and green seedlings, while in the reverse cross, only green seedlings were recovered. As yellow seedlings are lethal, it is not possible to know their spikelet color. However, it was assumed that they should have produced yellow spikelets. The green F_1 plants from both the crosses had green spikelets suggesting that the yellow spikelet color was recessive to the green spikelet color. The green F_1 plants recovered from both the crosses segregated in the F_2 into normal green and stripe in an approximate 3:1 ratio (Table IV) indicating that the stripe is a monogenic recessive trait. However, there is a considerable deficit of the stripe plants. This deficit may be due to the fact that the yellow seedlings, some of which would have developed as stripe plants, died at an early stage. As the seedlings carrying exclusively "mutant"

plastids are lethal, the "mutant" plastids can exist only in association with the normal plastids, i.e., as stripe plants only.

The yellow sector containing "mutant" plastids are genetically different from the green sector containing normal plastids. Hence the stripe plants were considered to be chimeras as defined by Gramer⁴. The gene symbol *sp* is proposed for this trait. As the yellow sectors extend from the epidermis in towards the center of the leaf, stem, inflorescence, and spikelets, stripe plants are considered to be sectorial chimeras. If crosses were made ignoring the spikelet color, irregular segregation would be expected. In fact, such an irregular segregation was observed when the stripe and green plants were crossed (Table IV). Such an irregular segregation also was observed by Gill et al.³ who reported that it was determined by three complementary and inhibitory types of gene interaction. White striping-3, a similar trait, reported by Rao and Koduru⁸ exhibited non-Mendelian, biparental inheritance with a suggestion of dominating maternal influence. However, as white striping-3 died at the 3-5 leaf stage, it is different from the present stripe "mutant." As the stripe mutant is distinguishable at all stages of growth (emergence to maturity) and produces enough seed, it is of considerable interest in basic research.

References

1. BURTON, G. W. Pearl millet. In *Hybridization of Crop Plants*. Am. Soc. Agron., Madison, Wisconsin. p. 457-469. 1980.
2. ——— and J. B. POWELL. Six chlorophyll-deficient seedlings in pearl millet, *Pennisetum typhoides*, and a suggested system for their nomenclature. *Crop Sci.* 5:1-3. 1965.
3. GILL, B. S., S. S. VIRMANI, and P. S. PHULL. Inheritance of foliage striping in pearl millet. *Indian J. Genet.* 29:473-477. 1969.
4. GRAMER, P. J. Chimaeras. *Biblio. Genetica* 16: 193-381. 1954.
5. HAGEMANN, R. Genetics and molecular biology of plastids of higher plants. *Stadler Symp.* 11: 91-115. 1979.
6. HANNA, W. W., G. W. BURTON, and J. B. POWELL. Genetics of mutagen induced nonlethal chlorophyll mutants in pearl millet. *J. Hered.* 69:273-274. 1978.
7. ICRISAT/IBPGR. Descriptors for pearl millet. ICRISAT, Patancheru, A. P., India/IBPGR, Rome, Italy. 1981.
8. RAO, M. K. and P. R. K. KODURU. Biparental plastid inheritance in *Pennisetum americanum*. *J. Hered.* 69:327-330. 1978.
9. THUNEY-BASSETT, R. A. E. A search for the rare type II (G>V<W) plastids segregation pattern among cultivars of *Pelargonium* × *Hortorum* Bailey. *Ann. Bot.* 38:1089-1092. 1974.

To the memory of Gregor Mendel: 1822–1884

In 1965, Czechoslovakia issued memorial stamps to celebrate the 100th anniversary of Mendel's law. This year, 1984, West Germany has issued special Mendel stamps to commemorate the 100th year of his death. Dr. Peter Meinecke of Hamburg, on learning from C. C. Li's biography (E. B. Spiess: *Am. J. Med. Genetics* 16: 603-630. 1983) that he had lost the 100 Mendel memorial stamps he bought in Brno, Czechoslovakia, promptly sent Dr. Li 50 newly issued Mendel stamps as replacement. We thank Drs. Meinecke and Li for sharing the memorial stamps with the readers of the *Journal*.—Ed.

