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Spontaneous Chlorophyll Mutants of *Pennisetum americanum*: Genetics and Chlorophyll Quantities

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Summary. Thirteen spontaneously occurring chlorophyll deficient phenotypes have been described and their genetic basis was established. Ten of these – 'white', 'white tipped green', 'patchy white', 'white virescent', 'white striping 1', 'white striping 2', 'white striping 4', 'fine striping', 'chlorina' and 'yellow virescent' showed monogenic recessive inheritance and the remaining three – 'yellow striping', 'yellow green' and 'light green' seedling phenotypes showed digenic recessive inheritance. The genes for (i) 'white tipped green' (*wt*) and 'yellow virescent' (*yv*) and (ii) 'patchy white' (*pw*) and 'white striping 1' (*wst 1*) showed independent assortment. Further, the genes for 'white' (*w*), 'white tipped green' (*wt*) and 'yellow virescent' (*yv*) were inherited independently of the gene for hairy leaf margin (*Hm*).

In the mutants – 'white tipped green', 'patchy white', 'white striping 1', 'white striping 2', 'fine striping', 'chlorina', 'yellow virescent', 'yellow striping', 'yellow green' and 'light green' phenotypes total quantity of chlorophyll was significantly less than that in the corresponding controls, while in 'white virescent' there was no reduction in the mature stage. For nine of the mutants the quantity of chlorophyll was also estimated in F_1's (mutant × control green). In F_1's of six of the mutants – 'white tip', 'patchy white', 'chlorina', 'yellow virescent', 'fine striping' and 'yellow striping' the quantity of chlorophyll was almost equal to the wild type. In the F_1's of three of the mutants – 'white striping 1', 'white striping 2' and 'light green' an intermediate value between the mutant and wild types was observed. In 'yellow virescent' retarded synthesis of chlorophyll, particularly chlorophyll a was observed in the juvenile stage. Reduced quantity of chlorophyll was associated with defective chloroplasts. In the mutants – 'white tipped green, 'white virescent', 'fine striping', 'chlorina', 'yellow striping', 'yellow green' and 'light green' defective plastids were also observed. In 'patchy white' secondary destruction of chlorophylls and the presence of defective plastids were found to be associated with reduced chlorophyll quantity at maturity.

Paper chromatographic studies of leaf flavonoids revealed some variation between the inbreds, but there were three common spots, 7, 8 and 9, except for PDP in which the spot 8 was absent. Chlorophyll deficient mutants differed from their respective controls in the absence of one or more of the spots present in the controls and in the presence of new spots in some of the mutants.

Most of the chlorophyll mutants showed higher survival rate in the Kharif season than in Rabi season which was attributed to the higher mean day temperature and longer day light period in the Kharif season than in Rabi season.

Key words: Pearl millet – Chlorophyll deficiencies – Chlorophyll quantities – Flavonoids

Introduction

The availability of genetic markers such as chlorophyll deficient mutants is useful for basic and applied research of crop plants (Haskell 1961; Robinson and Rick 1954). In *Pennisetum americanum* (L.) Leeke (2n = 14), an important outbreeding grain and fodder crop species, there have been a number of genetic studies of chlorophyll deficiencies, both spontaneous and induced (Rangaswami Ayyangar and Hariharan 1935; Kadam et al. 1940; Krishnaswamy and Rangaswami Ayyangar 1942; Krishnaswamy 1962; Chandola et al. 1963; Burton and Powell 1965, 1966; Athwal et al. 1966; Gill et al. 1969; Tara Mohan et al. 1973; Hanna et al. 1978; Krishna Rao and Koduru 1978). In the present study the genetic basis of thirteen naturally occurring chlorophyll deficient mutants was established. Quantities of chlorophylls a and b, total chlorophyll and the chromatographic pattern of leaf flavonoid compounds were also studied.

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Materials and Methods

Chlorophyll deficient mutants were obtained by inbreeding the stocks Vg 212, IP 457, IP 482, IP 1475, IP 2361, PDP and Tift 23 DB. Chlorophylls from fresh leaf samples extracted in 80% acetone were studied using a Spectronic 20 spectrophotometer and the quantity of the pigments was calculated using the formulae of Arnon (1949). The variation in the chromatographic pattern of the leaf flavonoid compounds was studied using the method of Fröst et al. (1970). The chromatograms were developed in ammonia vapour and longwave UV light (Torres and Levin 1964; Giannasi and Rogers 1970). The position and colour of the spot in each chromatogram was noted. Free hand unstained sections of the fresh plumules or leaves were mounted in tapwater to observe the morphology of the plastids in the mutants and the controls.

Observations

The Mutants

The thirteen mutant phenotypes, their proposed gene symbols and the source are given in Table 1.

'White' is a seedling lethal mutant; a few colourless tiny plastids were present in the hypodermal cells of the plumules while the sub-hypodermal cells were devoid of plastids. The recessive mutant genes found in the two inbred lines were allelic. 'White tipped green' was light yellow at the plumule stage; greening started from the base of the second leaf (4-6 day old seedlings) but the tip of the lamina remained white or yellow in the second to fourth leaves. Subsequent leaves showed uniform green colour. Adult plants were weak and had yellow interveinal longitudinal streaks on the leaves. Ears were short and lax with light yellow glumes. Plumules of the mutant had light yellow plastids in the hypodermal and sub-hypodermal cells. In 20-day old seedlings, which appeared light green, plastids were less distinguishable from those of normal green plants. 'Patchy white' showed scattered white patches from the plumule stage onwards. At maturity the entire leaf developed interveinal streaks which showed yellow green plastids. White tiny plastids were present in the white areas and numerous green plastids were present in the green areas. The plumules of the 'white virescent' showed initiation of greening between four to six days. The first leaf was initially yellow but soon turned green, starting from the tip. The young seedlings were light green and weak. The plumules contained leucoplasts. 'White striping 1' was expressed as white or light yellow longitudinal stripes on the margins of the leaf blade in the seedlings but in the mature leaves stripes were produced on the sheath as well. Though mutants can be spotted at the plumule stage, clear manifestation of the mutant phenotype occurs at maturity. Four week old seedlings appeared normal green as chlorophyll developed in the white regions also. However, between 40-50 days, stripes reappeared on the new leaves. Spikelets appeared yellow and the seeds had a brownish yellow pericarp; fertility was normal. A few yellow, tiny plastids were present in the striped regions and normally developed green plastids were present in the green areas. In the inbred IP 457 a family homozygous for a spontaneously occurring chromosomal interchange was located. The homozygosity for the interchange produced a semi-dwarf darkgreen phenotype and 'white striping 2' was obtained as a segregant in one of the selfed families. Stripes were white to light yellow and were expressed from the plumule stage. The extent of striping increased during maturity of the plant but even at the flowering stage about 50% of the leaf area was green. Plants flowered 15-20 days later than the controls. Meiosis and fertility were normal. The hypodermal and sub-hypodermal cells of the striped regions had light yellow and colourless plastids of variable sizes. 'White striping 4' was expressed late in development, about 15 to 20 days before flowering. Stripes first appeared as short dull white interveinal areas in the middle part of the lamina. At flowering time stripes extended on either side. The striped regions had light yellow to pale green plastids. 'Fine striping' mutants were greenish yellow at the plumule stage but at the 2-3 leaf stage narrow white longitudinal stripes appeared. In the adult plants stripes appeared very narrow so that the leaf was predominantly green. Seedlings as well as the mature plants were weak but fertility was normal. A few light yellow plastids were present in the hypodermal cells of the striped regions. 'Chlorina' was characterised by chlorophyll deficient leaves at all stages of growth from the 4-6 leaf stage. Younger seedlings looked as green as control seedlings.

Table 1. Seasonal variation in the survival rate of chlorophyll deficient mutants of *P. americanum*

Chlorophyll deficient phenotypes	Gene symbol	Inbred line	Per cent survial	
			Kharif season	Rabi season
White striping 4	*wst 4*	PDP	94.00	93.00
Chlorina	*c*	IP 482	92.33	90.00
Yellow striping	yst_1, yst_2	IP 457	91.33	89.33
White striping 1	*wst 1*	IP 2361	89.00	85.00
Patchy white	*pw*	Vg 212	75.33	66.00
White striping 2	*wst 2*	IP 457	73.33	60.67
Fine striping	*fst*	PDP	56.00	–
White tipped green	*wt*	PDP	55.00	17.67
White virescent	*wv*	Vg 212	34.00	–
Yellow green seedlings	yg_1, yg_2	Vg 272	13.50	3.50
Light green seedlings	lg_1, lg_2	IP 482		
		Tift 23 DB	12.67	3.50
Yellow virescent	*yv*	IP 1475	4.75	0.33
White	*w*	IP 1475		
		PDP	0.00	0.00

Table 2. Comparison of chlorophyll quantities of mutants with their respective controls and with F_1's (mutant X control): mg/gm fresh weight

Genotype	Total chlorophyll	a/b ratio
	Plumule stage	
White tipped green	0.82 (91.20) ± 0.012	0.985
Control	0.927 ± 0.006	1.6981
	Mature stage	
White tipped green	1.918 (58.80) ± 0.013	1.542
F_1 plants	4.608 ± 0.014	1.607
Control	4.650 ± 0.062	1.531
Patchy white	1.164 (74.28) ± 0.003	1.318
F_1 plants	4.401 ± 0.02	1.522
Control	4.526 ± 0.063	1.501
White virescent	4.770 (0.82) ± 0.006	1.593
Control	4.810 ± 0.028	1.551
White striping 1	3.580 (27.82) ± 0.028	1.166
F_1 plants	4.002 ± 0.210	1.510
Control	4.960 ± 0.045	1.552
White striping 2	2.552 (67.75) ± 0.024	1.402
F_1 plants	4.172 ± 0.062	1.498
Control	7.912 ± 0.076	1.535
Fine striping	2.904 (39.55) ± 0.028	1.587
F_1 plants	4.534 ± 0.008	1.527
Control	4.804 ± 0.069	1.613
Chlorina	2.164 (67.57) ± 0.030	1.518
F_1 plants	6.586 ± 0.080	1.440
Control	6.672 ± 0.062	1.421
	Plumule stage (3 day old seedlings)	
Yellow virescent	0.062 (91.60) ± 0.009	0.512
Control	0.739 ± 0.009	1.280
	2nd leaf stage (7 days old seedlings)	
Yellow virescent	0.163 (91.68) ± 0.011	0.691
Control	1.960 ± 0.011	1.317
	Mature stage (70 days old plants)	
Yellow virescent	1.886 (61.26) ± 0.037	1.334
F_1 plants	4.474 ± 0.025	1.545
Control	4.868 ± 0.025	1.541
Yellow striping	5.948 (10.85) ± 0.040	1.508
F_1 plants	6.640 ± 0.040	1.452
Control	6.672 ± 0.062	1.421
Yellow green seedlings	4.412 (11.20) ± 0.020	1.533
Control	4.968 ± 0.028	1.516
Light green seedlings	3.054 (54.23) ± 0.053	1.449
F_1 plants	5.237 ± 0.046	1.523
Control	6.672 ± 0.062	1.421

Figures in brackets indicate per cent reduction in the mutant

The mutant plants did not bear tillers and flowered 14-20 days later than the controls. 'Chlorina' is distinguishable from 'yellow virescent' by its greenish yellow leaves and vigorous stature. The mutant had numerous yellow green plastids. The 'yellow virescent' mutants appeared yellow at the plumule stage. Seedlings turned to light green by 10-14 days during the Kharif season; but in the Rabi season less than 1.0% of the seedlings had turned to light green even by 20 days. Mature mutant plants were weak with narrow leaves and narrow short ears but poduced more tillers than the control plants. Meiosis was normal but the seed set was less compared to the control plants. Pale yellow to light green plastids were present in the mature leaves. All the seedlings of the inbred line IP 457 exhibited interveinal longitudinal 'yellow stripes' from 20-53 days after sowing. The yellow regions had large light green plastids while the green areas had green plastids. 'Yellow green' seedlings segregated in the F_2 families of two crosses (i) Vg 272 x IP 1475 and (ii) PDP x IP 1475

which were originally made to study the genetics of hairy lamina and hairy leaf margin, respectively. The mutants were yellow green at the plumule stage with signs of chlorophyll development in a basipetal manner. In the plumules plastids were pale green in the hypodermal cells and light yellow in the sub-hypodermal cells. The 'light green' phenotype was expressed from the first leaf stage and resulted in weak and short plants bearing narrow leaves. Flowering time was delayed by 10-15 days relative to the control plants. Ear heads were thin and shorter but seed setting was normal. There was no visible difference in the plastid phenotype of the mutant. Foliar spraying of 0.001% gibberellic acid at weekly intervals starting from the 2-4 leaf stage enhanced the growth rate of the seedlings.

Allelism and Interrelationships

'White tipped green' and 'yellow virescent' were crossed reciprocally to study their allelic and linkage relationships. Breeding behaviour in F_1 (225 plants, all green) and F_2 (562 green: 428 chlorophyll deficient giving a 9:7 ration, $\chi^2 = 1.078$; $p = 0.3 - 0.2$) showed independent assortiment of the two non-allelic genes. Genes for 'patchy white' and 'white striping 1' are also non-allelic (210 green F_1 seedlings) with independent segregation in the F_2 (Table 4).

Distribution of long hairs along the margin and submarginal areas of the basal part of the lamina was observed in several inbred lines. Presence of the marginal hairs, expressed from the second leaf stage, was inherited as a monogenic dominant trait (Krishna Rao and Koduru 1979). Interrelationship between hairy leaf margin (*Hm*) and three of the chlorophyll deficient mutants – 'white tipped green' (*wt*), 'white' (*w*) and 'yellow virescent' (*yv*) was investigated. *Hm* showed independent assortment from the three genes *wt*, *w* and *yv* (Table 4).

Discussion

Genetics

The genetics of the eight mutants – 'white tipped green', 'patchy white', 'white striping 1', 'white striping 2', 'white striping 4', 'fine striping', 'chlorina' and 'yellow green'

Table 3. Comparison of leaf flavonoids of inbred and chlorophyll deficient genotypes at maturity

Inbred / Mutant	Total No. of spots	1	2	3	4	5	6	7	8	9	10	11	12	13	14[a]
		Y	B	Yg	Lg	Y	Yg	Dy	Gy	B	Gy	Y	Y	Dy	Y[b]
		0.08	0.33	0.59	0.59	0.65	0.69	0.68	0.75	0.85	0.55	0.90	0.91	0.96	0.81[c]
		0.08	0.07	0.09	0.11	0.42	0.09	0.52	0.11	0.14	0.09	0.58	0.13	0.13	0.92[d]
Vg 212	5	–	–	–	–	–	+	+	+	+	+	–	–	–	–
Patchy white (green areas)	3	–	–	–	–	–	–	+	+	+	–	–	–	–	–
Patchy white (white areas)	2	–	–	–	–	–	–	+	+	–	–	–	–	–	–
PDP	5	–	–	–	–	+	–	+	–	+	–	–	+	+	–
White tipped green	3	–	–	–	–	–	–	–	+	+	–	–	+	–	–
White striping 4	3	–	–	–	–	–	–	+	–	+	–	–	+	–	–
IP 457	6	+	–	–	–	–	+	+	+	+	–	–	–	–	+
White striping 2	5	–	–	–	+	+	+	+	+	–	–	–	–	–	–
IP 482	6	–	+	+	–	+	–	+	+	+	–	–	–	–	–
Chlorina	3	–	–	–	–	–	–	+	+	(+)	–	–	–	–	–
Light green	3	–	–	–	–	+	–	–	+	+	–	–	–	–	–
IP 1475	5	–	+	+	–	–	–	+	+	+	–	–	–	–	–
Yellow virescent	3	–	–	–	–	–	–	+	+	+	–	–	–	–	–
IP 2361	5	–	–	–	–	–	+	+	+	+	–	+	–	–	–
White striping 1	4	–	–	–	–	–	+	+	+	–	–	+	–	–	–

[a] number of the spot
[b] colour of the spot: B = blue; Dy = deep yellow; Gy = greenish yellow; Lg = light green; Y = yellow and Yg = yellow green
[c] R_f = value in the solvent 1
[d] R_f = value in the solvent 2. + = present; – absent; (+) = weak spot

Table 4. Allelic and interrelationships between chlorophyll deficient and hairy genes

Parents	Cross	Total population	F_2 phenotypes				X^2 (9:3:3:1/9:3:4)	p – value
			A- B-	*A- bb*	*aa B-*	*aa bb*		
Vg 212 X IP 2361	Patchy white X White striping 1 (*aa BB* X *AA bb*)	1206	697	216	235	58	5.317	0.2-0.1
PDP X Vg 212	White tipped green, hairless leaf margin X Green, hairy leaf margin (*aa bb* X *AA BB*)	2512	1410	482	475	145	1.214	0.9-0.7
PDP	Hairy leaf margin, green selfed (*Aa Bb*)	1204	680	210	314		1.671	0.5-0.3
IP 1475 X Vg 212	Green, hairy leaf margin X Yellow virescent, hairless leaf margin (*AA BB* X *aa bb*)	3092	1755	563	774		0.628	0.9-0.7

seedlings was studied and the first seven were inherited as monogenic recessives. The gene symbols *wt*, *pw*, *wst 1*, *wst 2*, *wst 4*, *fst* and *c* are proposed for these mutants. The last phenotype was inherited as a digenic recessive and the gene symbols yg_1, yg_2 are proposed. Results of the remaining five mutants were consistant with the earlier reports.

Chlorophyll Estimations

In spite of vast information available on the genetic control of chlorophyll deficient mutants in different plant species, information on the quantities of chlorophyll pigments in the mutants in relation to their controls is limited (Maclachlan and Zalik 1963; Starnes and Hadley 1965; Pettigrew et al. 1969; Tai and Todd 1972; Flemming and Palmer 1975). Chlorophyll quantities in eleven of the thirteen mutants described above were estimated (Table 2). In ten of the mutants the quantity of chlorophyll was significantly reduced compared to the corresponding normals. On the basis of the quantities of chlorophylls a and b, the eleven mutants were divided into four groups (i) those in which the a/b ratio in the mutant was less than that in the control ('patchy white', 'white striping 1', 'white striping 2', 'fine striping' and 'yellow virescent'); (ii) those in which the a/b ratio in the mutant was higher than that in the control ('chlorina' and 'yellow striping') (iii) those in which the a/b ratio remained unaltered ('white tipped green', 'yellow green' and 'light green') and (iv) those in which the mutants showed little difference in the quantities of chlorophylls from the control at maturity ('white virescent').

For nine of the mutants, the quantities of chlorophylls were also estimated in the F_1 hybrids of the mutant × control. In the F_1's of six of these mutants the quantity of chlorophyll was almost equal to the wild type; thus, in these the wild type is completely dominant over the mutant ('white tipped green', 'patchy white', 'chlorina', 'yellow virescent', 'fine striping' and 'yellow striping'). In the F_1's of the other three of the mutants – 'white striping 1', 'white striping 2' and 'light green', an intermediate value between the mutant and wild type was observed. A heterotic effect for chlorophyll quantity was not observed in any case. Thus, in all but one case the amount of chlorophylls a, b and total chlorophyll at maturity was lowest in the homozygous mutants and highest in homozygous greens. Earlier Maclachlan and Zalik (1963) in barley, Starnes and Hadley (1965) in soybeans, Pettigrew et al. (1969) in wheat and Tai and Todd (1972) in groundnut reported reduced quantities of chlorophylls in the mutants compared to their controls at maturity and attributed the reduction to several factors, including inability of the mutant to synthesize normal quantity (Tai and Todd 1972), defective plastid organisation (Maclachlan and Zalik 1963) and secondary destruction of chlorophyll (von Wettstein 1961).

In the present study the reduced chlorophyll quantity

of the mutants can be attributed to some of these factors. The quantities of chlorophylls at different developmental stages of 'yellow virescent' (Table 2) suggest retarded pigment synthesis in the juvenile stage. It is interesting to note that at this stage chlorophyll a was more affected than b. The quantities of chlorophylls a and b increased by the second leaf stage and this trend continued further. Moreover, ill defined smaller plastids were associated with lesser pigment content (plumule stage) while normally developed plastids were associated with increased chlorophyll content. Though the plastids in mature plants looked normal, normal chlorophyll quantity was not restored. The exact reasons for this pigment deficiency are not known but one possibility is defective plastid organization which can not be detected with the light microscope. In the mutant 'white tipped green' the gradual change in the light microscopic plastid phenotype from abnormal in the plumule to the apparently normal in the adult was also accompanied by an increase in chlorophyll quantities; however, normal quantity was not restored. Therefore, as in the 'yellow virescent', in this mutant the reduced chlorophyll content can possibly also be attributed to defective plastid organization.

In the mutants 'yellow striping', 'chlorina', 'light green' and 'yellow green', phenotypically different plastids were present at maturity. This was associated with lesser pigment content in the mutant compared to their controls. The decreased chlorophyll quantity in the mutants – 'white striping 1', 'white striping 2' and 'fine striping' can be attributed to the presence of chlorophyl – less sectors containing a few ill-defined leucoplast-like bodies. The mutant 'patchy white' showed a different pattern. The patches developed some green colour during later stages of vegetative growth. However, at about flowering time there was no distinct patchy appearance; instead the leaves developed longitudinal interveinal yellow streaks containing deformed plastids, thus indicating a secondary destruction of chlorophyll. Secondary destruction of the plastids was noticed in the variegated mutants of *Humulus japonicus* (von Wettstein 1961) and in the 'aureus' mutant of groundnut (Tai and Todd 1972).

Leaf Flavonoids

Chlorophyll deficient mutants of barley differed from their control plants in the chromatographic pattern of leaf flavonoids (Fröst et al. 1970; Holm and Fröst 1972). In *P. americanum*, Singh and Gill (1978) reported that the synthesis of leaf flavonoids was controlled by 42 genes and that different flavonoids showed different genetic ratios. The present analysis revealed the absence of some spots in the mutants which were present in their controls and also that the inbred lines differed from each other (Table 3). Of the six inbreds investigated, five resembled each other in having three common spots – 7, 8 and 9 (Vg 212, IP 457, IP 482, IP 1475 and IP 2361) while the sixth one, PDP, was lacking spot 8. Based on the presence or absence of these common spots the eight chlorophyll mutants investigated fall into two groups: (i) those having the three common spots ('patchy white', 'chlorina', and 'yellow virescent') and (ii) those lacking in one or more of these spots ('white tipped green', 'white striping 1', '-2', '-4' and 'light green'). Incidentally, it is interesting to note that the pairs of mutants – 'patchy white' and 'white striping 1' and 'white tipped green' and 'yellow virescent' which were found to be non-allelic – do not belong to the same flavonoid group.

Seasonal Variation in the Survival Frequency of the Mutants

In general, homozygous chlorophyll deficient mutants showed seasonal effects on the germination period, growth rate and survival value. During the Kharif season (May-June sowings) with mean day temperatures between 28°C-32°C, the radicles emerged within 16-20 hours after sowing in petri dishes, while in the Rabi season (December-January sowings), with cooler days (with mean day temperatures between 21°C-24°C), the radicles emerged within 36-40 hours. Thus temperature has profound influence on the germination time.

The data in Table 1 indicate that the survival frequency of the chlorophyll deficient mutants was low in the Rabi season and in particular the mutants 'yellow virescent', 'yellow green' and 'light green' were almost lethal. This lethality appears to be due to a slow rate of chlorophyll synthesis in the mutants in the Rabi season as evidenced by the prolonged time taken for greening in such mutants as 'white tipped green' and the inability to develop any green colour in 'yellow virescent'. This slow rate of chlorophyll synthesis coupled with reduced day length had a cumulative negative effect on the photosynthetic efficiency of the mutants. Burton and Powell (1965) also noticed that lower temperature coupled with shorter light period did not favour pigment synthesis in the pale yellow, pale yellow 2 and yellow virescent mutants in this species. Pettigrew et al. (1969) found that the rate of synthesis of chlorophylls a and b in the yellow mutant of hexaploid wheat was influenced by day length. Virescent mutants of maize showed retardation in greening at low temperatures which do not influence the greening of control plants (Rumball and Grogan 1972; Hopkins et al. 1975; Hopkins and Walden 1977). Thus it appears that in general the ability of chlorophyll deficient mutants to synthesize the necessary quantity of chlorophyll for their survival is dependent on temperature and day length.

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