to that in line 1 in Table 2, this would be a noticeable but not great deviation from the expectations of the models[4,24] for random association within the triplex homologous group. The randomness could not be quantified because the configuration frequencies were not available for this homologous group alone. The effect may be indirect. If the pairing regulator lengthens the period of synaptonemal-complex correction, as *Ph* apparently does in wheat,[9] the short length of the Bs might allow correction to proceed from one end of the chromosome to the other, even without initial preferential pairing based on greater pairwise genetic similarity. The greater length of the A chromosomes in the trisomic mentioned above might be too much for total synaptonemal-complex correction in the same period and with the same nonpreferential similarity of chromosomes.

The exclusive bivalent formation among B chromosomes seems to result from a genetic regulation of pairing rather than from pairwise similarity. The Bs appear to exhibit negative chiasma interference and to decrease positive chiasma interference among the A chromosomes, thus increasing chiasma frequency among the As.

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Genetics of White Sheath and Bleached Leaf Mutants in Pearl Millet

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Two spontaneous chlorophyll-deficient mutant traits, "white sheath" and "bleached leaf," were identified from pearl millet germ plasm accessions IP 7626 (India) and IP 10729 (Sudan), respectively. Normal light green leaf sheaths of the white sheath mutant turn white one week after germination. The maximum expression occurs at flowering, although the mutant plant character persists until maturity. F₂ segregation of reciprocal crosses between normal and mutant plants indicated that the white sheath trait is controlled by a single recessive gene, *ws.* Normal leaves of the bleached leaf mutant tend to turn yellow from the tip toward the base 10 days after emergence, whereas the bottom third of the leaf blades, the midribs, and a small portion on either side of the midribs remain green. The bleached leaf expression increases until floral initiation, when the plants become green. Inheritance studies indicated that the bleached leaf mutant trait is controlled by a single recessive gene, *bl.* Linkage studies showed that there were 43 crossover units between the bleached leaf and glossy traits and 45 to 54 crossover units between the white sheath and yellow leaf traits.

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important grain crop in Asia and Africa and a forage crop elsewhere. Although the mode of inheritance of over 100 qualitative characters is known,[9,10] only two linkage groups have been established.[7,11] Two spontaneous chlorophyll-deficient mutant traits, white sheath and bleached leaf, were identified in an evaluation of the world collection of pearl millet germ plasm maintained at ICRISAT Center, Patancheru, India. These two mutant traits have not been included among the several chlorophyll-deficient mutant traits reported in pearl millet.[1,2,6,7,10] We describe the morphological features of these mutants, their mode of inheritance, and linkage relationships with some qualitatively inherited traits in pearl millet.

Materials and Methods

Two accessions—IP 7626 from India and IP 10729 from Sudan—segregated for white sheath and bleached leaf characters, respectively, during the 1981 rainy season

Table 1. Morphological differences between normal and white leaf sheath and bleached leaf mutants

| Character | White sheath (IP 7626) | | Bleached leaf (IP 10729) | |
	Normal (mean ± SE)	Mutant (mean ± SE)	Normal (mean ± SE)	Mutant (mean ± SE)
Days to 50% flowering	53.2 ± 2.6	66.4 ± 1.8	81.0 ± 2.1	90.3 ± 3.2
No. tillers	3.3 ± 1.4	9.2 ± 2.4	3.0 ± 3.4	5.3 ± 2.6
Stem thickness (mm)	9.2 ± 3.2	7.1 ± 1.9	7.4 ± 2.6	5.9 ± 2.4
No. leaves	10.2 ± 2.0	8.8 ± 1.2	11.7 ± 2.3	9.0 ± 2.8
Leaf blade length (cm)	60.4 ± 4.1	53.8 ± 2.8	69.7 ± 3.6	44.2 ± 2.2
Leaf blade width (mm)	33.3 ± 1.3	40.4 ± 2.2	34.8 ± 2.3	23.3 ± 1.8
Plant height (cm)	210.4 ± 3.5	122.3 ± 2.4	209.6 ± 4.2	112.5 ± 2.6
Spike length (cm)	25.3 ± 4.8	22.4 ± 2.7	20.4 ± 3.7	14.8 ± 2.3
Spike thickness (mm)	20.6 ± 3.2	22.5 ± 1.9	20.3 ± 2.4	18.4 ± 2.0

Table 2. Inheritance of white leaf sheath and bleached leaf mutant characters in pearl millet

| Cross/phenotype | Generation | No. progenies | No. F_2 plants | | χ^2 (3:1) | P | Heterogeneity | |
			Normal	Mutant			χ^2	P
White sheath								
Normal × mutant	F_2	4	3,817	1,244	0.48	.5–.3	1.20	.8–.7
Mutant × normal	F_2	9	8,217	2,726	0.05	.9–.8	0.84	>.99
White sheath	F_3	10	0	1,574	—	—	—	—
Green sheath	F_3	14	2,498	812	0.39	.7–.5	4.38	.99–.98
Green sheath	F_3	6	1,445	0	—	—	—	—
Bleached leaf								
Normal × mutant	F_2	3	1,872	590	1.41	.3–.2	0.34	.9–.8
Mutant × normal	F_2	2	1,558	482	2.05	.2–.1	0.04	.9–.8
Bleached leaf	F_3	10	0	903	—	—	—	—
Green leaf	F_3	20	2,959	956	0.71	.5–.3	8.92	.98–.95
Green leaf	F_3	12	1,584	0	—	—	—	—

Table 3. Linkage relationships of genes governing some seedling markers in pearl millet

| Cross[a] | R/C[b] | No. progenies | No. F_2 plants | χ^2 (9:3:3:1) | P | Heterogeneity | | Recombination value ± SE |
						χ^2	P	
PPWsWs × ppwsws	C	4	3,316	1.66	.7–.5	10.23	.5–.3	
ppwsws × PPWsWs	C	5	8,269	0.56	.95–.9	6.16	.95–.9	
gl_lgl_lWsWs × Gl_lGl_lwsws	R	6	9,439	2.30	.7–.5	10.79	.8–.7	
WsWsyy × wswsYY	R	4	3,316	16.58[c]	<.001	7.89	.7–.5	54.20 ± 1.24[c]
wswsYY × WsWsyy	R	3	2,409	12.08[c]	.01–.001	10.24	.2–.1	45.03 ± 1.61[c]
$wswsD_3D_3$ × $WsWsd_3d_3$	R	4	3,316	5.59	.2–.1	3.59	.95–.9	
blblpp × BlBlPP	C	3	2,462	1.58	.7–.5	4.51	.7–.5	
$blblGl_lGl_l$ × $BlBlgl_lgl_l$	R	3	3,503	24.71[c]	<.001	6.78	.5–.3	43.55 ± 1.36[c]
blblYY × BlBlyy	R	3	2,040	3.04	.5–.3	5.75	.5–.3	

[a] P = purple; pp = green; Ws = green sheath; wsws = white sheath; Gl = nonglossy; glgl = glossy; Y = green; yy = yellow; D = tall; dd = dwarf; Bl = green; blbl = bleached leaf.
[b] R = repulsion; C = coupling.
[c] Significant at the 5% level.

at the ICRISAT Center. Morphological characters were recorded on 20 random plants from four replicates for the mutants and their respective normal plants, using the descriptors for pearl millet.[8] Reciprocal crosses were made during the post-rainy season of 1986 between the normal and the mutant plants to study the mode of inheritance. Several F_2 and F_3 progenies were grown for each cross. Heterogeneity tests indicated good agreement among the progenies. Therefore, data were pooled to

determine the segregation ratios, and goodness of fit was tested with a chi-square test.[12]

Linkages with white sheath and bleached leaf traits were determined by crossing true-breeding genetic stocks: IP 1995 for yellow leaf (yy), IP 8277 for glossy (gl_lgl_l), IP 10401 for dwarf (d_3d_3), and IP 8166 for purple foliage (PP), each of which is controlled by a single gene.[3-5] The recombination values were calculated by the product ratio method of Stevens.[13]

Results and Discussion

White Sheath Mutant

Mutant plants were distinguishable from normal plants one week after germination. All leaf sheaths of mutant plants including tillers were white, whereas in normal plants leaf sheaths are green (Figure 1). In mature leaves, there is a tendency for the white color to extend toward the base of the leaf blades as longitudinal white stripes alternating with green. Maximum expression of the mutant character occurs at flowering, although it persists up to maturity. The intensity of the white sheath character varies from plant to plant but is consistent between the leaf sheaths of a single tiller and among different tillers of the same plant. The stem also remains white, and the spikelets are pale yellow. Stem thickness, number of leaves, spike length, and spike thickness did not differ significantly between normal and mutant plants (Table 1). However, they differed considerably in regard to days to 50% flowering, plant height, tiller number, and leaf blade length and width (Table 1).

In a population of 40 plants from IP 7626, two plants showed the white sheath character whereas the remainder were normal green. In subsequent generations, all white sheath plants bred true, some of the green plants segregated for green and white sheath, and other green plants bred true. The F_1 plants from crosses between green and white sheath plants had green sheaths, indicating that white sheath is a recessive trait (Table 2). In the F_2 generation, white sheath and green plants segregated in a 1:3 ratio (Table 2). In the F_3 generation, all white sheath plants bred true, confirming the recessive nature of white sheath. In a population of 20 selfed F_2 green plants, 14 segregated in a 3:1 ratio as did the F_2 plants, and 6 bred true, giving a good fit (P = .8–.7) to a 2:1 ratio, as was expected for a trait controlled by a single recessive gene. Thus, the white sheath mutant was found to be monogenic recessive. We propose ws as the gene symbol for the white sheath trait.

Bleached Leaf Mutant

Mutant plants were indistinguishable from normal plants until 10 days after emergence. The first two leaves were normal green in color, whereas subsequently emerging leaves became yellow from the tip of the leaf toward the base and on either side of the midrib. In fully expanded leaves, the bottom third of the leaf blade was green, whereas the top third was bleached

yellow. The middle portion of the leaf blade, except the midrib and on either side of the midrib, was bleached yellow (Figure 2). The extent of greenness on either side of the midrib decreased from the base toward the tip. The relative proportion of green area and the intensity of the green color were greater in older leaves than in younger leaves. All tillers of the same plant showed similar expression. The intensity of the mutant plant expression was maximal at the time of internode elongation, after which the leaves tended to become normal green. However, mutant plants were distinguishable even after flowering. There were no significant differences between normal and mutant plants in days to flowering, number of tillers, stem and spike thickness, and number of leaves. There were significant differences in leaf blade length and width, plant height, and spike length (Table 1).

In a population of 82 plants from IP 10729, five plants showed the bleached leaf character. In the subsequent generations, these bleached leaf plants bred true, whereas some of the green plants segregated for green and bleached leaf plants. The F_1 plants from normal green and bleached leaf crosses were normal green, indicating that the bleached leaf character is recessive (Table 2). The F_2 segregation fit a monogenic ratio of 3 green : 1 bleached leaf plant (Table 2). In the F_3 generation, all bleached leaf plants bred true, whereas 20 of the 32 green plants segregated in a manner similar to that of the F_2 generation. The remaining 12 green plants bred true for green color, confirming that bleached leaf is a monogenic recessive trait. We propose *bl* as the gene symbol for this trait.

Linkage Relationships

Genes controlling white sheath and bleached leaf were studied for linkage relationships with genes controlling glossy, yellow foliage, dwarf (monogenic recessive traits),[2-4] and purple (monogenic dominant)[5] (Table 3). Segregation for white leaf sheath and yellow leaf showed a significant deviation from a ratio of 9:3:3:1, indicating the presence of linkage with a recombination value of 45.03 to 54.2 between these two traits (Table 3). However, the F_2 segregation of white leaf sheath with each of the traits—purple, glossy, and dwarf—corresponded well to the 9:3:3:1 ratio, indicating independent assortment (Table 3).

Linkage data from crosses between bleached leaf and the glossy trait showed

Figure 1. Culms of pearl millet showing white leaf sheaths (left) and green leaf sheaths (right).

a significant deviation from the 9:3:3:1 ratio expected on the basis of independent assortment, suggesting the presence of linkage, with a recombination value of 43.55 between these two traits (Table 3). Linkage data from crosses between bleached leaf, purple, and yellow corresponded well with the 9:3:3:1 ratio, indicating their independent assortment (Table 3).

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Linkage Relationships of Genes Affecting Bitterness and Flesh Color in Watermelon

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The genetic basis of two traits of watermelon fruit was investigated in a backcross generation resulting from hybridization between an interspecific F₁ hybrid of *Citrullus lanatus* and *C. colocynthis* with the cultivated parent *C. lanatus*. Bitterness of the fruit, a trait that characterizes wild *C. colocynthis*, was found to be governed by a single dominant gene (*Bi*) linked to the isozyme marker *Pgm-1* at a distance of 11.3 cM. The appearance of red color in the fruit is determined by a single recessive gene (*red*) that is linked to the isozyme marker *Gdh-2* at a distance of 12.8 cM. These two marker loci and the two newly identified genes are on linkage group 3. Using another backcross population between *C. lanatus* and *C. colocynthis* and an F₂ population between *C. colocynthis* and *C. ecirrhosus*, we identified three new linkage groups: linkage group 5 with *6Pgd-1* and *Aps-2*, linkage group 6 with *Dia-1* and *For-1*, and linkage group 7 with *Est-1* and *Adh-1*. Three marker loci—*Prx-2*, *Prx-3*, and *Got-4*—were added to linkage groups 1 and 4.

The two wild species in the genus *Citrullus*—*C. ecirrhosus* and *C. colocynthis*—are crossable with the cultivated watermelon (*C. lanatus*) and may constitute a potential source of desirable traits.[5] The fruit of the wild species is characterized by white flesh and an extremely bitter taste as a result of the presence of the toxic compound cucurbitacin.[3]

We previously had constructed a linkage map of *Citrullus*, using 19 isozyme and seed protein markers.[4] In this study, we utilized an interspecific cross to map the gene for

Figure 2. Bleached leaf mutant showing yellowish green leaf blades.

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