



INHERITANCE PATTERN OF PIGMENTED TRAITS IN FOXTAIL MILLET (*Setaria italica* (L.) Beauv.)

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SUMMARY

This study was conducted to determine the inheritance pattern of plant, bristle pigmentation and anther color in foxtail millet. Seven parental lines with contrasting characteristics were crossed providing a total of 21 crosses. The F₁ progenies and 2 sets of 200 F₂ plants from 21 crosses were established. The development of purple pigmentation was the same in the plant as in the bristles, indicating that both traits are jointly inherited. The presence or absence of purple pigmentation appeared to be under the control of a single dominant gene, with purple (*P*) dominant over green (*p*). Orange-white anther color was determined to be under the control of 3 genes with complementary effects. Gene A in the presence of gene B and/or gene C, A_B_C_, A_B_cc, and A_bbC_, produces orange anthers. All other combinations of 3 genes produce white anthers. The pigment traits are independently inherited and should have potential use as markers in genetic studies and breeding work in foxtail millet.

Key words: Foxtail millet, pigmented traits, inheritance pattern, χ^2 test

Key findings: The inheritance pattern of pigment traits in foxtail millet indicate their potential as morphological markers in genetic studies and breeding programs.

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INTRODUCTION

The study of inheritance pattern of pigmented traits is needed for their potential use as morphological markers in genetic studies and breeding work in foxtail millet. During the development of breeding programs and the propagation of the breeding material, genetic

markers can be extremely useful for controlling crosses, determining the proportion of outcrossing, purifying populations, identifying rare genotypes, maintaining mixtures and separating populations (Chopra, 2014). Some color traits have been particularly useful as gene markers for a long time. For instance in the earlier studies, Brown-midrib (*bmr*) mutants a

kind of reddish brown pigmentation of the leaf midrib and stalk pith of some of cereals like maize, sorghum and pearl millet was successfully associated with the amount of lignin in the total biomass produced and used as models for digestibility and lignification studies (Jorgenson, 1931; Porter *et al.*, 1978; Chemey *et al.*, 1988; Cherney *et al.*, 1991; Barrière and Argillier, 1993; Jung and Deetz, 1993). The same way, Gökbayrak *et al.* (2010) linked the grapevine pigmentation in petiole or shoot tip with powdery mildew resistance and showed the success rate of selection based on presence of petiole or shoot coloration in a segregating population is up to 80% for powdery mildew resistance.

Despite the potential of pigmented traits as genetic markers, only limited genetic studies have been done on these traits in foxtail millet. The purpose of this study was to determine the inheritance and genetic variability of plant, bristle pigmentation and anther color in foxtail millet.

MATERIALS AND METHODS

Six cultivars, Srilakshmi, SiA 3085, KDR, NSR, Suryanandi and Prasad and one promising entry SiA 3220 were obtained from Regional Agricultural Research Station (ANGRAU), Nandyal and raised in net house facility in the experimental plot of Yogi Vemana University, Kadapa, Andhra Pradesh, India. In kharif 2013, these were crossed in half diallel arrangement and 21 crosses were selected arbitrarily. Staggered sowing was done to make synchronous flowering among crosses. The true hybrid plants were carefully identified based on the color traits under study and other morphological markers during rabi, 2013. During kharif 2014, 2 sets of 200 F₂ plants of 21 crosses, along with their respective parents sown separately during July and August, 2014.

Foxtail millet is highly self-pollinated crop, the cultivars were assumed to be homozygous for most loci and referred as inbred lines. All recommended agronomic and plant protection measures were taken to raise good plants. Observations were recorded on plant,

bristle pigmentation and anther color for parental lines, F₁s and F₂ population.

Chi-square test analysis and contingency tables were studied to test homogeneity of proportions between the 2 sets of F₂ populations and among different segregating crosses within each trait. The genetic model that fitted best the model was chosen. The analyses were conducted using R language version 2.5 for all statistical computations (Crawley, 2005).

RESULTS

Data recorded on plant and bristle pigmentation in foxtail millet between the parental lines, F₁s and F₂ populations for all 21 crosses revealed that both parts of the plants are equally pigmented. The purple pigmentation started at seedling stages after emergence on the first leaf sheaths and progressed consecutively upward on the nodes, midribs, leaf blades, internodes, bristles and peduncle. Bristle color was observed after 5 days of flowering where the intensity of pigmentation was the same as that on the basal parts of the plant (Table 1). The F₂ populations of the 3 crosses among the 3 green parents, KDR, Suryanandi and Prasad were all green plants while the F₂ populations of the 6 crosses among the 4 purple parents NSR, SiA 3220, SiA 3085 and Srilakshmi were all purple plants. These results were confirmed by the data obtained from the corresponding F₂ populations, planted on August, 2014 (Table 2). There was no genotypic variation for pigmentation either among the parents with purple plants or among the parents with green plants. The only difference may exist between purple and green parents. In contrast to the F₂ populations of the crosses between green x green and purple x purple, each F₂ population of the 5 crosses between purple x green and the 7 crosses between green x purple, planted on July 2014 segregated for purple and green plants in a ratio of 3 purple to one green (Table 2). Although the observed frequencies of green plants are generally slightly higher than the expected numbers, the chi-square values and their corresponding P values on each and over all the eleven crosses show a good fit to a 3:1 ratio.

Table 1. Plant/bristle pigmentation among F₁ progenies among 7 foxtail millet lines during kharif 2013.

Parental Lines	KDR	NSR	Suryanandi	SiA 3220	SiA 3085	Srilakshmi	Prasad
KDR	Green	Purple	Green	Purple	Purple	Purple	Green
NSR		Purple	Purple	Purple	Purple	Purple	Purple
Suryanandi			Green	Purple	Purple	Purple	Green
SiA 3220				Purple	Purple	Purple	Purple
SiA 3085					Purple	Purple	Purple
Srilakshmi						Purple	Purple
Prasad							Green

Table 2. Segregation of plant pigmentation among the F₂ progenies for crosses among 7 foxtail millet lines and their chi-square tests during kharif 2014.

Cross	Plant pigmentation on set 1					Plant pigmentation on set 2				
	Purple	Green	Ratio	χ^2	P	Purple	Green	Ratio	χ^2	P
Purple x Purple										
SiA 3220 x NSR	202	0	1:0			198	0	1:0		
SiA 3085 x NSR	202	0	1:0			199	0	1:0		
NSR x Srilakshmi	199	0	1:0			200	0	1:0		
SiA 3085 x SiA 3220	201	0	1:0			202	0	1:0		
SiA 3220 x Srilakshmi	203	0	1:0			198	0	1:0		
SiA 3085 x Srilakshmi	204	0	1:0			202	0	1:0		
Green x Purple										
KDR x NSR	144	56	3:1	0.96	0.33	149	52	3:1	0.08	0.78
KDR x SiA 3085	152	47	3:1	0.20	0.65	145	55	3:1	0.66	0.41
KDR x Srilakshmi	151	50	3:1	0.00	0.97	146	57	3:1	1.03	0.31
Suryanandi x SiA 3085	144	56	3:1	0.96	0.33	147	53	3:1	0.24	0.62
Suryanandi x Srilakshmi	154	46	3:1	0.43	0.51	154	47	3:1	0.28	0.60
Prasad x SiA 3085	147	56	3:1	0.72	0.40	144	56	3:1	0.96	0.33
Prasad x Srilakshmi	149	51	3:1	0.03	0.87	146	54	3:1	0.43	0.51
Purple x Green										
SiA 3220 x KDR	152	50	3:1	0.01	0.94	152	48	3:1	0.11	0.74
NSR x Suryanandi	141	59	3:1	2.16	0.14	145	57	3:1	1.12	0.29
NSR x Prasad	148	56	3:1	0.65	0.42	146	54	3:1	0.43	0.51
SiA 3220 x Suryanandi	149	51	3:1	0.03	0.87	154	48	3:1	0.17	0.69
SiA 3220 x Prasad	147	53	3:1	0.24	0.62	148	52	3:1	0.11	0.74
Green x Green										
Suryanandi x KDR	0	201	0:1			0	198	0:1		
KDR x Prasad	0	200	0:1			0	200	0:1		
Suryanandi x Prasad	0	200	0:1			0	200	0:1		
				6.39	0.90				5.59	0.94

The deviations are probably due to bias caused in thinning F₁ populations to 5 plants per row. The segregation ratios of 3 purple to one green for each of the eleven crosses are strongly supported by the data recorded on each F₂ population from the corresponding crosses planted on August, 2014 (Table 2). Both data fit a 3:1 ratio. The total chi square values over all the segregating F₂ populations $\chi^2 = 6.39$ and $\chi^2 =$

5.59 on the first and second data sets respectively and their corresponding *P* values, *P* = 0.90 and *P* = 0.94 are evidence for the 3 purple to one green ratio.

Anther color on emergence of all the parents, except SiA 3085, was orange with a tinge of varying degree of brown. After dehiscence and consequent drying, the orange anthers turned brown. The plants of SiA 3085

had unique white anthers, which even when dry remained white (Table 3). The F₂ progenies of all 21 crosses, 15 between orange x orange, 3 between orange x white, and 3 between white x orange, resembled the parental orange anther color. These results indicate that orange anther color is dominant over white. The first data set on the segregation for orange and white anther color of the 21 crosses among the 7 parents show that there was no segregation for white anthers in all the

crosses between orange x orange (Table 4). These results are in perfect agreement with the data recorded on the second set of the corresponding F₂ populations planted on August, 2014 (Table 5), thus verifying the lack of segregation in the crosses between parents with orange phenotype x orange phenotype. The absence of segregation may suggest genotypic uniformity among the 6 parents with orange anther color.

Table 3. Anther color among the F₁s for crosses among 7 foxtail millet lines during rabi 2013.

Parental Lines	KDR	NSR	Suryanandi	SiA 3220	SiA 3085	Srilakshmi	Prasad
KDR	Orange	Orange	Orange	Orange	Orange	Orange	Orange
NSR		Orange	Orange	Orange	Orange	Orange	Orange
Suryanandi			Orange	Orange	Orange	Orange	Orange
SiA 3220				Orange	Orange	Orange	Orange
SiA 3085					White	Orange	Orange
Srilakshmi						Orange	Orange
Prasad							Orange

Table 4. First data set of the segregation for anther color among the F₂ populations for crosses among 7 foxtail millet lines and their chi-square tests during kharif 2014.

Cross	Anther colour		One gene model			Three gene model		
	Orange	White	Ratio	χ^2	P	Ratio	χ^2	P
Orange x Orange								
KDR x NSR	200	0	1:0			1:0		
Suryanandi x KDR	198	0	1:0			1:0		
SiA 3220 x KDR	202	0	1:0			1:0		
KDR x Srilakshmi	201	0	1:0			1:0		
Prasad x KDR	200	0	1:0			1:0		
NSR x Suryanandi	194	0	1:0			1:0		
SiA 3220 x NSR	202	0	1:0			1:0		
NSR x Srilakshmi	197	0	1:0			1:0		
NSR x Prasad	204	0	1:0			1:0		
SiA 3220 x Suryanandi	199	0	1:0			1:0		
Suryanandi x Srilakshmi	199	0	1:0			1:0		
Suryanandi x Prasad	200	0	1:0			1:0		
SiA 3220 x Srilakshmi	203	0	1:0			1:0		
SiA 3220 x Prasad	198	0	1:0			1:0		
Prasad x Srilakshmi	200	0	1:0			1:0		
Orange x White								
KDR x SiA 3085	149	48	3:1	0.04	0.84	45:19	2.67	0.10
Suryanandi x SiA 3085	136	63	3:1	4.71	0.03	45:19	0.36	0.54
Prasad x SiA 3085	111	92	3:1	44.70	0.00	9:7	0.20	0.65
White x Orange								
SiA 3085 x NSR	142	60	3:1	2.38	0.12	45:19	0.00	1.00
SiA 3085 x SiA 3220	145	56	3:1	0.88	0.35	45:19	0.32	0.57
SiA 3085 x Srilakshmi	142	61	3:1	2.76	0.10	45:19	0.01	0.91
				55.47 ^a	0.00 ^b		3.58 ^a	0.73 ^b

^aTotal chi square values over all segregating crosses and ^btheir corresponding P values with df = 6, $\chi^2 = 24.34$; $P < 0.00$, chi square test for homogeneity of proportions across segregating crosses

Table 5. Second data set of the segregation for anther color among the F₂ populations for crosses among 7 foxtail millet lines and their chi square tests during kharif 2014.

Cross	Anther colour		One gene model			Three gene model		
	Orange	White	Ratio	χ^2	P	Ratio	χ^2	P
Orange x Orange								
KDR x NSR	201	0	1:0			1:0		
Suryanandi x KDR	198	0	1:0			1:0		
SiA 3220 x KDR	199	0	1:0			1:0		
KDR x Srilakshmi	201	0	1:0			1:0		
Prasad x KDR	198	0	1:0			1:0		
NSR x Suryanandi	197	0	1:0			1:0		
SiA 3220 x NSR	198	0	1:0			1:0		
NSR x Srilakshmi	200	0	1:0			1:0		
NSR x Prasad	198	0	1:0			1:0		
SiA 3220 x Suryanandi	202	0	1:0			1:0		
Suryanandi x Srilakshmi	198	0	1:0			1:0		
Suryanandi x Prasad	194	0	1:0			1:0		
SiA 3220 x Srilakshmi	197	0	1:0			1:0		
SiA 3220 x Prasad	200	0	1:0			1:0		
Prasad x Srilakshmi	196	0	1:0			1:0		
Orange x White								
KDR x SiA 3085	149	50	3:1	0.00	0.96	45:19	1.98	0.16
Suryanandi x SiA 3085	129	71	3:1	11.76	0.00	45:19	3.24	0.07
Prasad x SiA 3085	103	97	3:1	58.91	0.00	9:7	1.83	0.18
White x Orange								
SiA 3085 x NSR	139	58	3:1	2.07	0.15	45:19	0.01	0.94
SiA 3085 x SiA 3220	150	52	3:1	0.06	0.81	45:19	1.51	0.22
SiA 3085 x Srilakshmi	142	60	3:1	2.38	0.12	45:19	0.00	1.00
				75.19 ^a	0.00 ^b		8.57 ^a	0.20 ^b

^aTotal chi square values over all segregating crosses and ^btheir corresponding p values with df=6
 $\chi^2 = 34.75$; $p=0.00$, chi square test for homogeneity of proportions across segregating crosses

Segregation of F₂ progenies from the 3 crosses between orange x white and the 3 crosses between white x orange resulted in varying ratios of orange to white anther color (Table 4 and 5). Of the 200 F₂ plants grown from each of these crosses, the plants with orange anthers varied from 111 to 149 on the first data set and from 103 to 149 in the second data set. The observed differences in segregating ratios were statistically significant as shown by the large chi-square values, $\chi^2 = 24.34$ and $\chi^2 = 34.75$, in the first and second data set respectively. The differences in segregating ratios among the 6 crosses suggest that there is genotypic variation among the parents with orange anthers. Because the crosses involved the same parent with white anthers, any variation in segregation ratios is expected to occur only if parents with orange anthers had different genotypes. The genotypic variation among the parents with orange anthers suggests that orange-white anther color is controlled by

more than one gene. The chi-square tests for a single gene with dominant effects, 3:1 ratio, on the first data set are represented in Table 4. The chi square values and their corresponding P values show that the data of the crosses KDR x SiA 3085 and SiA 3085 x SiA 3220 fit the 3 oranges to one white ratio, but the other crosses fit it poorly or not at all, especially the data from the crosses Suryanandi x SiA 3085 and Prasad x SiA 3085. Furthermore, the total of chi square values over all the segregating crosses $\chi^2 = 55.47$ indicated that the 3:1 ratio does not fit the data. These results are in close agreement with those obtained on the second set of F₂ populations planted on August, 2014 (Table 5). The total chi-square value $\chi^2 = 75.19$ is even larger than for the first data set. These results clearly indicate that a single gene model is not appropriate to explain the general inheritance of orange and white anther color in foxtail millet.

The segregation ratios among the 6 crosses were found to agree with a 3 gene model with complementary effects. Under this model, gene A in the presence of gene B and/or C produces orange anthers; otherwise the anthers are white. So there would be 3 types of genotypes, A_B_C_, A_B_cc, and A_bbC_ responsible for orange anthers, and 5 genotypes, aaB_C_, A_bbcc, aaB_cc, aabbC_ and aabbcc responsible for white anthers. The crosses KDR x SiA 3085, Suryanandi x SiA 3085, SiA 3085 x NSR, SiA 3085 x SiA 3220 and SiA 3085 x Srilakshmi segregated approximately for 45 orange to 19 white anthers, while the cross Prasad x SiA 3085 segregated 9 orange to 7 white anthers (Table 4). However, the crosses between Prasad and other parents with orange anthers produced plants with orange anthers only. The total chi square value ($\chi^2 = 3.58$) and its p value ($P = 0.73$) support the 45:19 and 9:7 (orange/white) ratios as the best fit to the data. These ratios were confirmed by the results found in the second data set (Table 5). Although, the deviations from the expected numbers were slightly higher than those in the first set, the data are still in good agreement with the 45:19 and 9:7 (orange/white) ratios.

DISCUSSION

In foxtail millet, the crosses involving all types of variation detected genotypic variation and led to understanding the inheritance of plant/bristle pigmentation and anther color. The observations on plant and bristle pigmentation suggest that purple pigmentation in foxtail millet can be explained jointly by gene(s) of pleiotropic effects. There is no single study on the joint performance of purple plant and bristle pigmentation reported in foxtail millet with which to compare. However, Appa Rao *et al.* (1988) and Varalakshmi *et al.* (2012) reported that purple pigmentation of leaf sheaths, leaf blades, internodes, bristles and glumes in pearl millet (*Pennisetum glaucum* L.) is inherited together. Because the development of purple pigmentation on the plant was the same as that in the bristles cumulatively denoted as plant pigmentation. Crosses between purple and green plants or between green and purple plants produced purple F₁ plants which indicate that

purple pigmentation is dominant over green.

The 3:1 ratio denotes the action of a single gene, with dominant effects. A dominant homozygote and heterozygote genotypes are responsible for purple pigmentation, while a recessive homozygote produces green plants. Therefore, in light of the present data, it may be postulated that purple/green plant pigmentation is controlled by a single dominant gene, with purple dominant over green. This agrees with the results reported by MacVicar and Parnell (1941). However, it is not in accord with the 4 gene and 2 gene models suggested by Ayyangar *et al.* (1935) and Li *et al.* (1945) respectively.

It must be recognized that pigmentation intensity within the purple type and within the different plant parts did vary. The variation may be associated with genetic effects (Ayyangar *et al.*, 1935), it was observed that not only the pigmentation intensity, but also the development of the pigment on the different parts of the plant is, to some extent, affected by changes in environmental conditions (Li *et al.*, 1945).

Regarding anther color, the segregation ratios among the 6 crosses were found to agree with a 3 gene model with complementary effects. Gene A in the presence of gene B and/or C produces orange anthers; otherwise, the anthers are white. So, there would be 3 types of genotypes, A_B_C_, A_B_cc and A_bbC_, responsible for orange anthers, and 5 genotypes, aaB_C_, A_bbcc, aaB_cc, aabbC_ and aabbcc responsible for white anthers. The parental lines, KDR, NSR, Suryanandi, SiA 3220 and Srilakshmi have 3 pairs of dominant genes, AABBCC, while the parent line, SiA 3085, has 3 pairs of recessive genes, aabbcc. The genotype of Prasad can be either AABBcc or AAbbCC. Ayyangar and Narayanan (1932) proposed a single gene, with orange dominant over white, which agrees with the segregation ratios found in some of the crosses. However, as was discussed, the one gene model was not appropriate to explain the other observed ratios. Because their conclusions were drawn based on one natural segregating population and one orange x white cross, it can be assumed that their study did not include enough genetic material to identify the other 2 genes. Contrary to the one gene model, Li *et al.* (1945) postulated a gametophyte gene linked with orange anther

color. They invoked this gene because they observed some sterility in the F₂ progeny. However, the F₃ progeny failed to confirm their hypothesis. They attributed it to small population size.

It can be concluded that presence or absence of purple plant/bristle pigmentation and the orange or white anther color although it is under the control of pathway linked oligogenes should have potential use in further understanding regulating genes through genome wide association studies in foxtail millet.

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