

INHERITANCE OF DOWNY MILDEW RESISTANCE IN PEARL MILLET (*Pennisetum glaucum* (R.) BR.)

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ABSTRACT

Inheritance studies of downy mildew of pearl millet was done under epiphytotic condition, in the F_1 and F_2 population of a full diallel crosses involving 10 parents. Genotypic differences were highly significant in both the generations. Combining ability analysis showed highly significant mean squares due to general combining ability (GCA) and specific combining ability (SCA) in both the generations. Significant mean square due to reciprocals were also significant. The parents 1518, 1548 and 76-32-1 were found resistant and also had negative significant GCA effects. The crosses involving these parents were also resistant. All the three analyses i.e. graphical, component and combining ability indicated that the character is controlled by both additive dominant gene effects. The resistance was found to be partially dominant over susceptibility. Graphical analysis showed that resistant parents mainly had dominant genes. Heritability estimates were high in both the generations.

INTRODUCTION

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) occupies nearly 20 million ha area throughout the world and is considered to be one of the most drought tolerant crop. The hybrid breeding programme received a great boost with the availability of the male sterile line Tifton 23-A from Georgia, U.S.A. in 1962. Since then several hybrids were released for cultivation in India and other countries. But most of the hybrids released proved unstable due to susceptibility to downy mildew and ergot diseases. Downy mildew is one of the major diseases of pearl millet causing enormous losses in yield. However, the genetics of downy mildew has not been well understood. Only a few reports are available but these are contradicting each other (Singh 1974; Singh et al. 1978 and Basavaraju et al. 1978). The present studies were conducted with a view to generate information on the inheritance of downy mildew of pearl millet.

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MATERIAL AND METHODS

A set of diallel crosses were generated involving 10 diverse elite inbred lines including two maintainers, namely 5054 B and 111-B. The other parents were 77-263-6, 77-297-2, 76-32-1, 77-268-5, 77-22-1, 77-299-4 (source : Haryana Agricultural University, Hisar) and, 1513 and 1548 (source : IARI, New Delhi). The crosses were selfed to obtain the F₂ generation.

Preparation of sick plot

The plot was infested with the fungus oospore during summer, 1975. Since then it has been supplemented with tremendous amount of oosporic inoculum every year. The sick plot was created at the Experimental Farms, Department of Plant Breeding, Haryana Agricultural University, Hisar as suggested by Thakur and Kanwar (1977). Finally the oosporic inoculum was added at the rate of 3 g/m of each row at a distance of 50 cm, keeping depth of 40-50 mm in furrows six weeks before planting. The infector rows were also planted after one month of soil inoculation with the highly susceptible cultivar NBH-3 at a distance of 1 m apart to serve as infector rows. The seeds of the test material were also mixed with the oospores before sowing to ensure effective inoculation.

Planting the test material

The experimental material of F₁ (45 F₁'s + 45 F₁'s reciprocals) and F₂ (45 F₂'s + 45 F₂'s reciprocals) diallel sets were planted along with the 10 parents, parallel to the infector rows in a compact family block design with two replications keeping row length of 4 m spaced at 50 cm apart. The parents and F₁'s had one row of each while F₂'s had four rows of each. The distance between plants was kept 10 cm, thus accomodating about 40-42 plants/row.

Observations and analysis of data

Data were recorded on 40 plants in each F₁'s and 150 plants in each F₂'s on 1 to 5 scales at different intervals. Considering, 1=No disease; 2=only nodal tillers infected; 3=less than 50% basal tillers infected; 4=more than 50% basal tillers infected and 5=all the basal tillers and main shoot infected. These scores were transformed to work out disease intensity (%) as suggested by Williams and Singh (1981). The formula used for transformation is:

$$\text{Disease intensity (\%)} = \frac{X_2 + 2X_3 + 3X_4 + 4X_5}{4N} \times 100$$

Where X₂, X₃, X₄ and X₅ = Number of plants in categories 2,3,4, and 5
N = Total number of plants

Statistical analysis of the data was done after converting the percentage disease intensity to arosin transformed values. The diallel analysis were done using the Griffing's (1956) Method 1 Model 1 and Hayman's (1954) method. For F_1 the heritability was worked out according to Crumpacker and Allard (1962) and for F_2 it was estimated by following Verhalen and Murray (1969).

RESULTS AND DISCUSSION

The mean squares due to genotypes were highly significant for downy mildew reaction in both the generations (Table 1). The mean disease intensity of different genotypes is depicted in Table 2. A perusal of the Table 2 showed that parents 76-32-1 and 1513 were highly resistant 77-263-6, 77-268-5, and 77-22-1 were susceptible. On the other hand parents 5054-B, 1548 and 111-B were moderately resistant whereas the parents 77-297-2, 77-299-4 were moderately susceptible. Among the crosses 5054-B x 76-32-1; 1513x76-32-1; 1513x1548; 76-32-1x1548; 5054B x 111-B; 5054B x 1513 and 5054Bx 1548 were free from downy mildew infection in F_1 , thus were highly resistant. Most of these crosses had disease intensity below 5% in F_2 and F_2 reciprocals. These crosses involved mostly resistant x resistant or resistant x moderately resistant parents. These crosses could be further utilised for the selection of resistant and desirable plants in the advance generations.

Table 1. Analysis of variance for downy mildew intensity in F_1 and F_2 population of pearl millet

Source	Degree of freedom	Mean sum of squares	
		F_1	F_2
Replication	1	227.99	3.58
Treatment	99	407.01**	414.41
Error	99	11.14	2.75

** Significant at $P=0.01$

Combining ability analysis

Analysis of variance for combining ability indicated the mean squares associated with general combining ability (GCA), Specific combining ability (SCA) and reciprocals were highly significant in both the generations (Table 3). Thus indicating the importance of both additive and non-additive gene effects in the inheritance of downy mildew in the present study. Similar results have been obtained by Singh et al. (1978). The significance of reciprocal differences revealed the importance of cytoplasmic genes in the inheritance of downy mildew resistance. These genes may be situated most likely on mitochondrial DNA. Therefore, while breeding for the resistance of this disease one should take care of cytogenes along with nuclear genes.

The estimates of GCA and SCA effects are presented in Table 4. Highly significant and negative GCA effects were recorded for the parentt 5054B, 111-B, 76-32-1,

Table 2. Mean downy mildew disease intensity (%) in parents, F₁ and F₂ generations (above diagonal) and their reciprocal (below diagonal) of pearl millet

Parents	Population	5054B	111-B	77-263-6	77-297-2	76-32-1	77-268-5	77-22-1	77-299-4	1513	1548
5054B	F ₁	—	0.0	4.0	3.7	0.0	21.2	16.5	4.0	0.0	0.0
	F ₂	—	2.9	31.6	21.9	4.1	29.1	27.4	22.8	4.0	6.3
111B	F ₁	8.7	—	12.8	11.9	2.0	23.1	19.9	15.9	1.7	2.8
	F ₂	6.5	—	34.3	22.3	5.5	23.6	29.0	6.0	3.5	4.7
77-263.6	F ₁	16.5	12.7	—	33.4	5.3	57.5	60.4	32.4	2.4	4.0
	F ₂	38.0	35.3	—	55.0	29.0	66.1	50.0	52.5	25.0	22.5
77-297-2	F ₁	8.7	16.2	29.3	—	3.5	34.1	33.4	25.4	1.8	4.4
	F ₂	27.0	31.0	55.6	—	18.7	63.1	61.2	56.3	23.2	21.3
76-32-1	F ₁	0.0	3.0	3.1	3.2	—	16.2	5.6	10.4	0.0	0.0
	F ₂	5.5	6.6	15.6	2.4	—	32.6	17.5	22.5	0.0	0.0
77-268-5	F ₁	23.4	26.2	60.6	39.5	15.0	—	61.8	40.9	4.6	10.8
	F ₂	33.4	26.7	64.5	65.8	37.6	—	71.8	65.6	23.1	25.3
77-22-1	F ₁	21.2	25.0	47.7	40.6	12.6	58.1	—	41.9	9.7	9.9
	F ₂	31.3	26.6	64.8	63.0	22.8	65.4	—	61.5	21.7	24.6
77-299-4	F ₁	14.1	20.1	33.2	26.5	5.3	44.9	44.6	—	4.3	6.2
	F ₂	23.1	32.0	61.2	58.3	25.2	54.3	59.0	—	17.1	18.3
1513	F ₁	0.0	0.7	2.5	2.5	0.0	7.2	6.0	2.2	—	0.0
	F ₂	6.6	5.0	18.4	10.0	0.0	16.5	16.0	11.2	—	0.0
1548	F ₁	0.0	0.3	11.3	10.9	0.0	13.4	7.1	5.9	0.0	—
	F ₂	6.0	7.2	19.2	19.3	2.5	16.4	19.4	15.1	1.0	—
Parent mean	F ₁	2.5	5.0	56.5	19.4	0.0	50.6	55.2	34.0	0.0	3.1
	F ₂	2.5	5.0	56.5	19.4	0.0	50.6	55.2	34.2	0.0	3.1

Table 3. Analysis of variance for general (GCA) and specific combining ability (SCA) for downy mildew disease in F₁ and F₂ population of pearl millet

Source	d.f.	Mean sum of squares	
		F ₁	F ₂
GCA	9	2009.06**	2063.23**
SCA	45	32.24*	30.44*
Reciprocals	45	13.64*	12.76*
Error	99	5.57	1.37

* Significant at P = 0.05

** Significant at P = 0.01

1513 and 1548, accordingly these were good general combiners for downy mildew resistance. On the contrary, parents 77-263-6, 77-297-2, 77-268-5, 77-22-1 and 77-299-4 were poor general combiners for downy mildew resistance. Most of the SCA effects (Table 4) were non-significant in F₁, however, the crosses 77-263-6 x 76-32-1, 77-263-6 x 1513, 76-32-1 x 77-22-1; 77-268-5 x 1513; and 77-22-1 x 1548 exhibited negative SCA effects. This implied the importance of non-additive genetic variance in these crosses for the inheritance of downy mildew.

Graphical and component analysis

In Wr-Vr graph (Fig. 1 a, b) the regression lines had its intercept the origin indicating partial dominance in both the generations. The resistant parents 1513, 1548, 76-32-1 and 5054B were nearer the origin and thus appeared to have maximum dominant genes, whereas the susceptible parents 77-263-6, 77-22-1, 77-268-5, 77-299-4 and 77-297-2 had the maximum recessive genes. The graphical analysis revealed that downy mildew resistance is governed by dominant genes which was also corroborated from the correlation between Wr x Vr and parental mean which was positive and significant (0.62).

The component analysis (Table 5) showed the significance of additive (D) and dominance (H₁ and H₂) components. Net dominance (h²) effect was significant. The degree of dominance (H₁/D)^{1/2} indicated partial dominance. The ratio (h²/H₂) showed that four effective factors or gene group showing dominance were involved in controlling downy mildew resistances in this material. The proportion of genes with positive and negative effects (H₂/4H₁) among the parents was found to be asymmetrical. The ratio (4H₁)^{1/2} + F/(4DH₁)^{1/2}-F, also showed the unequal distribution of gene among the parents. The high heritability estimates (55%) confirm the role of additive genetic variance in the inheritance of downy mildew in pearl millet.

The crosses involving resistant x resistant parents viz; 1548 x 1513, 1548 x 76-32-1, 1513 x 76-32-1 produced resistant F₁, s, F₂ and their reciprocals. The crosses involving resistant x susceptible parents showed higher disease intensity than those

Table 4. Estimated of GCA (diagonal), SCA (upper) to (diagonal) and reciprocal effects (lower to diagonal) of combining ability in F₁ and F₂ populations of pearl millet for downy mildew reaction

Parents	Population	5054B	111-B	77-263-6	77-297.2	76-32-1	77-268-5	77-22-1	77-299-4	1513	1548
5054B	F ₁	-7.2*	-0.8	-4.5	-2.2	-0.2	1.1	0.4	-2.2	3.0	2.2
	F ₂	-6.9*	-2.6	2.9	-0.1	-0.1	-2.4	-0.1	-0.1	3.8	2.5
111-B	F ₁	-7.6*	-2.8*	-2.6	0.8	3.2	-1.6	-1.3	1.6	1.2	-1.3
	F ₂	2.5*	-7.4*	0.1	1.6	2.1	-3.5	-0.4	-3.9	2.4	2.7
77-263-6	F ₁	6.0*	3.5*	8.9*	1.5	-6.5*	7.1*	6.0*	6.0*	-7.0*	4.3
	F ₂	1.9*	-2.2*	10.8*	0.4	-2.4	1.9	-1.2	2.5	-0.1	-1.9
77-297-2	F ₁	3.0*	2.1*	-1.2	3.2*	-1.8	-0.2	1.9	1.1	-2.0	1.5
	F ₂	1.5	2.8*	0.1	7.5*	0.4	4.6	4.7	6.6*	-0.8	0.6
76-32-1	F ₁	0.0	0.4	-1.5	-0.2	-11.0*	0.2	-7.1*	0.9	5.7	2.0
	F ₂	0.9	0.6	-4.6*	1.8*	-9.7*	4.7*	-2.1	3.3	2.1	-0.1
77-268-5	F ₁	0.7	1.0	0.9	1.4	0.4	13.8*	4.6	2.7	-7.0*	-4.4
	F ₂	1.3*	1.0*	-0.4	0.8	1.3	11.8*	3.1	3.2	2.4	-3.6
77-22-1	F ₁	1.9	1.8	-3.6*	2.1	6.1*	1.1	11.9*	4.5	-2.9	-6.2*
	F ₂	1.2	-0.7	4.3*	0.5	0.6	-3.7*	10.4*	4.7*	-1.6	-1.3
77-299-4	F ₁	5.3*	1.5	0.3	0.5	-2.8	-0.5	2.2	5.7*	-2.7	-2.3
	F ₂	0.1	10.1*	2.3*	1.4*	0.8	-3.3*	0.7	6.4*	-1.3	-1.1
1513	F ₁	-1.1	-3.7*	0.1	0.5	0.0	1.3	-1.9	-1.6	13.1*	4.1
	F ₂	1.0	1.0	-2.2*	-5.1*	0.5	-2.3*	-2.1*	-2.4*	-12.4*	0.4
1548	F ₁	-1.8	-2.5	4.1*	3.6*	0.0	1.1	-1.3	-0.21	0.0	-9.4*
	F ₂	-0.2*	1.4	-1.6	-0.8	-0.2	-3.5*	-1.8*	-0.2	0.3	-10.4*

F₁ SE GCA = 1.05 F₂ SE GCA = 2.49
 SE S (I) = 3.17 SE S (II) = 2.37
 SE R (I) = 1.66 SE R (II) = 0.82

*Significant at P = 0.05

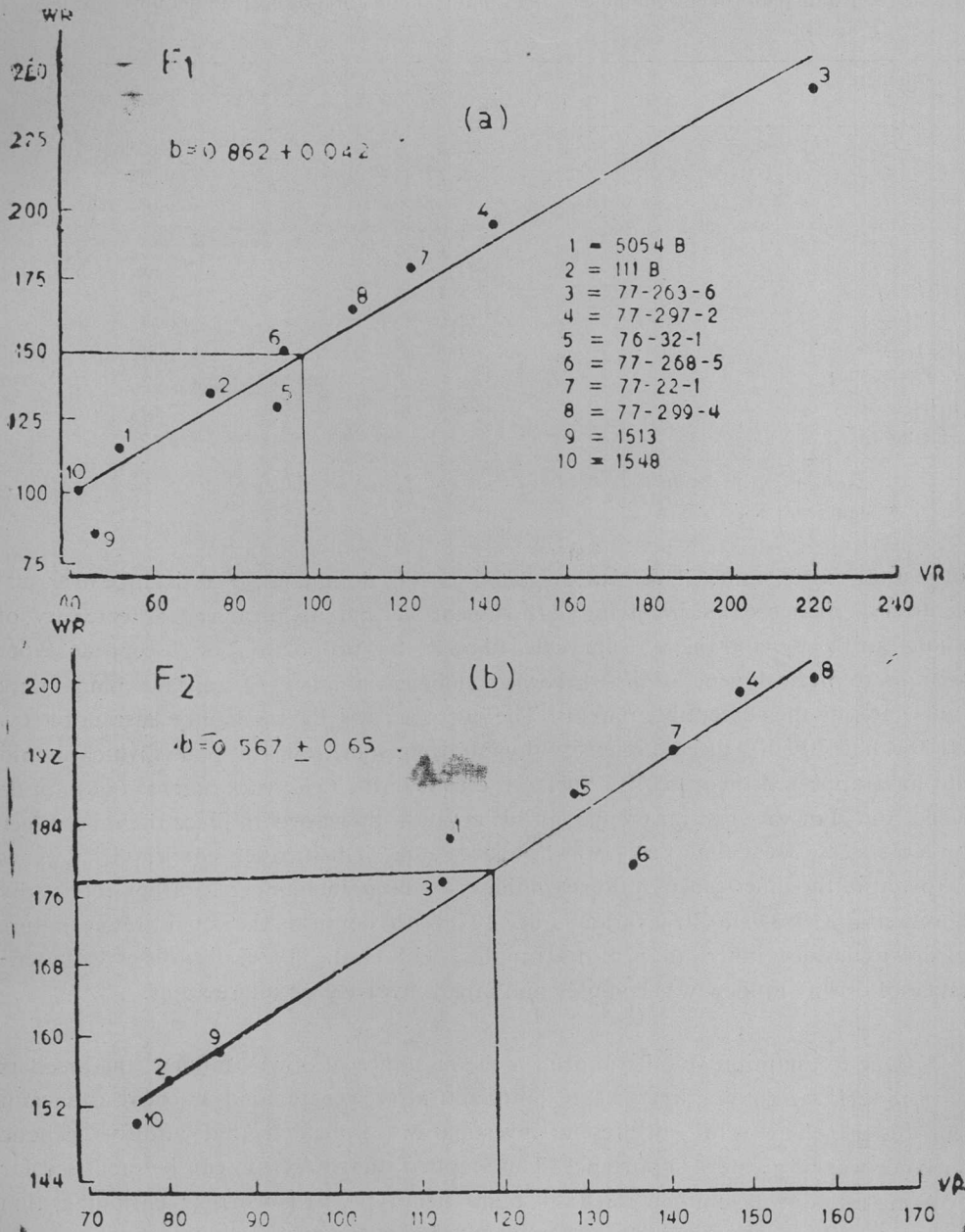


Fig 1 REGRESSION OF WR ON MR FOR DOWNY MILDEW INTENSITY IN PEARL MILLET

Table 5. Estimate of genetic component of F₁ and F₂ population of pearl millet downy mildew reaction

Component	Generation	
	F ₁	F ₂
D	322.1** ± 8.91	325.63** ± 10.4
H ₁	68.57** ± 19.14	380.31** ± 22.1
H ₂	51.18** ± 10.27	224.0** ± 18.8
F	-59.98** ± 20.75	-95.0** ± 23.9
h ²	28.93** ± 10.89	567.68** ± 12.6
(H ₁ /D) ^{1/2}	0.47	0.54
H ₂ /4H ₁	0.04	0.15
(4 DH ₁) ^{1/2} + F	0.67	0.57
(4 DH ₁) ^{1/2} - F		
h ₂ /H ²	0.57	2.62
Heritability	55.1	68.2

*Significant at P = 0.05

**Significant at P = 0.01

of resistant x resistant. This also suggested partial dominance of resistance over susceptibility. The crosses involving both susceptible parents produced all category of plants in F₁, F₂ and their reciprocals, though the proportion of susceptible types were more in both generations. Likewise sufficient number of resistant plants were found among the susceptible parents. The infector rows having highly susceptible cv. NHB-3 had 70-80% disease intensity thus showing some resistant plants which should not have appeared theoretically. Such an escape in the field experiment could not be ruled out. For the resistant x susceptible crosses, the efforts to place the inheritance on a classical Mendelian basis was not successful. This further confirms that genes involved in the inheritance of downy mildew are large in numbers. Earlier reports by Singh et al. (1978) and Basavaraju et al. (1978) also confirms the quantitative nature of downy mildew inheritance in pearl millet. Gill et al. (1978) also observed inheritance of downy mildew was complex and might involve gene interactions.

Due to quantitative inheritance for the resistance of downy mildew, the breeders have to seek the guiding lines based on quantitative genetic analysis of resistance of this disease. The result of present investigation indicated that additive genetic variance was of greater importance. This implied that selection can be practised for evolving the downy mildew resistant bajra genotype. It is worth mentioning that reciprocal effects were found to be significant. Therefore proper choice of cytoplasmic source should be combined with the appropriate male parent. Since dominance genetic variance was also significant, the selection of resistant genotypes arising from a cross should be deferred till sufficient homozygosity reached in the later generation. The crosses 77-263-6 x 76-32-1; 76-32-1 x 77-22-1 and 77-263-6 x 1513 should be exploited for evolving the resistant genotype.

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