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Gene Effects Controlling Heritability of Downy Mildew Resistance in Nigerian Elite Pearl Millet Lines

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Abstract: Downy mildew disease caused by the fungus *Sclerospora graminicola* Schroet, causes yield losses across the millet growing zones of Nigeria. Identification of the source of resistance and gene actions controlling resistance is useful in developing appropriate breeding strategies. Therefore there was need to study downy mildew resistance in Nigerian elite pearl millet lines. Five pearl millet parental lines; BUDUMA, SOSAT-C88, LCICDMR36-4, 20B-2 and 25B-4 were obtained from Lake Chad Research Institute, Maiduguri. From this five parents, using factorial mating scheme of North Carolina Design II, F_1s, F_2s BC_1P_1s and BC_1P_2s were generated during November, 2004 - May, 2005. The five parents, twenty-four crosses and one check (7042 S), were evaluated using Randomized Complete Block Design with three replications at the downy mildew field nursery of Lake Chad Research Institute and the Experimental Farm of the Department of Crop Production and Horticulture, Federal University of Technology, Yola during 2005 and 2006 cropping seasons. Downy mildew resistance from this study was found to be influenced by dominant gene effect, because the ratios of dominance to additive variance values were more than unity for both incidence and severity index. Narrow-sense heritability was moderately high, 66.06% for downy mildew incidence and 52.41% for downy mildew severity, indicating that there is the likelihood that improvement can be achieved by using these genotypes.

Key words: Pearl millet · Downy mildew · Gene effects · Degree of domince · Narrow-sense heritability · Broad-sense heritability

INTRODUCTION

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] known as bulrush or cattail millet, is the most important among a number of unrelated millet species grown for food worldwide [1, 2, 3]. Pearl millet grain is used for human consumption in which the whole grain is cooked and served like rice. The flour is processed into thick porridge called '*tuwo*' served with traditional vegetable soup and fried snack called *'Masa'* and non-alcoholic beverages called '*fura*' in Mali, Niger and Nigeria.

Downy mildew, as reported by Werder and Manzo [4], Zarafi *et al*. [5] and Zarafi *et al*. [6], is the most serious disease of pearl millet in Nigeria, where the epiphytotics occur annually and it is common to find systematic infection on up to 50% of the plants on farmer's fields. The choice of selection and breeding procedure to be used for genetic improvement of any crop plant largely depends on the magnitude of genetic variability and the nature of gene action governing the nature of inheritance of the desirable traits. This study is designed to determine the nature of gene action for downy mildew resistance and the degree of dominance determining resistance.

MATERIALS AND METHODS

Five pearl millet parental lines; BUDUMA, SOSAT-C88, LCICDMR36-4, 20B-2 and 25B-4 were obtained from Lake Chad Research Institute Maiduguri. From this five parents 6F_1s, 6F_2s 6BC_1P_1s and 6BC_1P_2s were generated using factorial mating design of North Carolina Design II, during November, 2004 and May, 2005 Off-season at Lake Chad Research Institute Maiduguri under irrigation. The five parents, twenty-four crosses and one check (7042S), were evaluated using Randomized Complete Block Design with three replications at the downy mildew field nursery of Lake Chad Research Institute and the Experimental Farm of Federal University of Technology, Yola during 2005 and 2006 seasons. The evaluations were done to estimate the inheritance of downy mildew resistance and the number of loci involved.

Downy Mildew Incidence: Number of diseased plants showing downy mildew symptoms expressed as a percentage of total number of plants in a plot were assessed at 30 and 60 days after sowing (DAS) by scoring for chlorosis of infected plants and at dough stage by scoring for green ears. Downy mildew incidence was

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computed using the formula developed by James [7], as the number of diseased plants expressed as:

$$\text{DMI} = \frac{\text{Number of diseased plants}}{\text{Total number of plants}} \times 100$$

Disease Severity: Disease severity was scored on a 1-5 scale as described by Williams *et al.* [8], where: 1 = no disease; 2 = symptoms on aerial tillers only; 3 = symptoms on less than 50% basal tillers; 4 = symptoms on more than 50% basal tillers; and 5 = total destruction of stand or no production of normal head. Percent disease severity index was calculated using a formula described by Williams *et al.* [8], as follows:

$$\text{DMS} = \frac{n_1(1\text{-}1) + n_2(2\text{-}1) + n_3(3\text{-}1) + n_4(4\text{-}1) + n_5(5\text{-}1)}{N\,(5\text{-}1)} \times 100$$

Where, n_1- n_5 = number of plants with different disease grades described in the 1-5 scale above; N = total number of plants assessed.

Analysis of variance across environment was based on the genetic model;

Yijkl = *u* + *m*i + *f*j + (*mxf*)ij + Ek + *m*ilk + *f*jkl + *mf*ijkl + eijkl,

Where:

Yijkl	=	The *k*[th] observation on *ixj*[th] progeny in the *l*[th] location
u	=	The general mean
*m*i	=	The effect of the *i*[th] male
*f*j	=	The effect of the *j*[th] female
*(mxf)*ij	=	The interaction effect between the *i*[th] male and *j*[th] female
Ek	=	The effect of the K[th] location
*m*ilk	=	The interaction effect of the i[th] genotype and j[th] year
*f*jkl	=	The interaction effect between i[th] genotype in the k[th] location
*mf*ijkl	=	The effect of the k[th] location on i[th] genotype on the j[th] year
eijkl	=	Random error

Estimation of gene effects was based on components of generation mean, a non-weighted analysis approach developed by Hayman [9] as used by St.Amandi and Wehner [10]. Parents, F_1, F_2, backcross means and variances of each cross were used to determine additive, dominance and epistatic gene effects. Gene effects were defined using the following notations; *m* = mean value, *d* = additive gene effects, *d*= dominant gene effects, *aa* = additive x additive gene effects, *ad* = additive x dominance, *dd* = dominance x dominance gene effects. Where:

$m = F_2$
$a = B_1\text{-}B_2$
$d = F_1 - 4F_2 - 0.5P_1 - 0.5P_2 + 2B_1 + 2B_2$
$aa = 2B_1 + 2B_2 - 4F_2$
$ad = B_1 - 0.5P_1 - B_2 - 0.5P_2$
$dd = P_1 + P_2 + 2F_1 + 4F_2 - 4B_1 - 4B_2$

The genetic component calculation were based on an estimate of the net effects of all loci at which the parents differ in the measured traits assuming epistatic effect is not significant.

Genetic parameters of appropriate model were tested within the limit of their standard errors where significant of the genetic effects is tested in a similar manner as done in the scaling tests. Parameters determined to be different from zero ($p \leq 0.05$) were considered to contribute significantly to the model.

Degree of dominance was calculated as the ratio of dominance variance to additive variance = $\sqrt{D}/^{A}$

Estimates of broad sense and narrow sense heritability were calculated for downy mildew incidence (DMI) and downy mildew severity (DMS) in pearl millet by using the variance of the parents, F_1, F_2 backcross generations to estimate phenotypic (V_P), environmental (V_E), total genetic (V_G), additive genetic (V_A), and dominance genetic variances (V_D). Where:

$V_P = V_{F2}$
$V_E = 0.25\,(V_{P1}) + 0.25\,(V_{P2}) + 0.25\,(V_{F1})$
$V_G = V_{F2} - V_E$, $V_A = 2\,(V_{F2}) - V_{BC1P1} - V_{BC1P2}$
$V_D = V_{BC1P1} + V_{BC1P2} - V_{F2} - V_E$

(i). Broad sense heritability

$$h_b^2 = (V_A + V_D)/V_{F2}, = \frac{d^2F_2 - d^2e}{d^2F_2} = \frac{d^2g}{d^2F_2}$$

Where; V_A + V_D represent the genetic variance of F_2 according to Allard [11] and Erin (3)

(ii) Narrow sense heritability = $h^2_n = V_A/V_{F2} = 2\delta^2F_2 - (\delta^2B_1 + \delta^2B_2) / \delta^2F_2$ described Warner [12] as used by Karen *et al.* [13].

RESULTS AND DISCUSSION

Results from the generation mean estimates for downy mildew incidence (DMI) are presented in Table 1.

Table 1: Estimates of gene effects, significant levels±standard errors for Downy mildew incidence (DMI) in pearl millet determined from the generation mean for combined locations (Maiduguri andYola) and years (2005 and 2006 seasons)

Crosses	m	a	d	aa	ad	dd
20B-2 X BUDUMA	15.15±4.77**	4.90±5.13	17.73±23.15	17.84±22.79	-1.6±6.15	-1.86±21.16
25B-4 X BUDUMA	27.08±5.36**	-11.47±5.8	-62.70±33.3	-42.26±33.05	-12.35±6.70	88.15±39.58**
20B-2 X SOSAT-C88	21.43±5.02**	0.07±1.76	-55.38±20.50**	-52.86±20.39**	12.20±3.99**	69.93±21.70**
25B-4 X SOSAT-C88	16.26±5.44**	-4.29±2.12	-35.99±22.40	-24.34±22.30	13.55±3.13**	38.14±24.21
20B-2 X DMR36-4	16.19±27.28**	-7.8±1.58*	-6.49±29.78	-3.08±29.59	2.40±3.42	-1.9±31.60
25B-4 X DMR36-4	20.62±3.00**	-5.53±3.02	-40.92±14.89**	-34.66±14.04**	10.30±4.19**	72.43±19.61**

Note: *, ** significant at 5% and 1% levels of probabilities respectively.

Table 2: Estimates of gene effects, significant levels±standard errors for Downy mildew severity (DMS) in pearl millet determined from the generation mean for combined locations (Maiduguri andYola) and years (2005 and 2006 seasons)

Crosses	m	a	d	aa	ad	dd
20B-2 X BUDUMA	11.19±3.66**	4.44±2.35	-14.06±16.85	-6.22±16.24	-2.53±5.72	40.92±22.20**
25B-4 X BUDUMA	32.34±9.50**	-2.81±2.14	-106.53±38.51**	-99.74±38.38**	-5.05±4.15	121.04±39.99**
20B-2 X SOSAT-C88	9.91±5.06	-6.64±1.50**	-29.94±20.63	-23.48±20.47	-0.43±2.65	23.41±21.65
25B-4 X SOSAT-C88	8.98±3.07	-4.51±1.36**	-34.68±12.61**	-23.89±12.37	6.42±2.69**	38.19±14.10**
20B-2 X DMR36-4	9.37±8.25	-1.69±0.95	-14.17±33.19	-9.72±33.12	3.60±2.63	5.67±33.83
25B-4 X DMR36-4	21.48±4.36**	0.90±1.14	70.52±18.17**	73.81±18.03**	10.91±3.15**	68.28±7.27**

Note: *, ** significant at 5% and 1% levels of probabilities respectively

There were significant differences among the individual crosses and their generations. The result indicated highly significant additive x dominant (ad) gene effect in crosses such as 20B-2 x SOSAT-C88 (12.20±3.99**), 25B-4 x SOSAT-C88 (13.55±3.13**) and 25B-4 x DMR36-4 (10.30±4.19**). Genes controlling the resistance of downy mildew incidence was expressed as over-dominance (dd) as indicated in all the crosses involving 25B-4 x BUDUMA (88.15±39.58**), 20B-2 x SOSAT-C88 (69.93±21.70**) and 25B-4 x DMRD6-4 (72.43±19.61**). Net effect of genes controlling downy mildew incidence was expressed as over-dominance (dd) in all the crosses except for 20B-2 crosses involving either BUDUMA or DMR36-4 male parents. This study further confirms the findings of Appadurai *et al.* [14], Singh [15] and Gill *et al*. [16, 17], who demonstrated that resistance for downy mildew resistance in pearl millet, is controlled by one or two dominant genes. Estimates of gene effects from the generation mean for downy mildew severity index (DMS) are presented in Table 2. Result indicated significant dominant gene effect for downy mildew severity in the crosses involving 25B-4 X DMR36-4 (70.52±18.17**) with epistatic effect (aa= 73.81±18.03**) while additive x dominant gene effect is responsible in generation involving SOSAT-C88 donor parent such as 20B-2 X SOSAT-C88 (6.42±2.69**) and DMR36-4 such as 25B-4 X DMR36-4 (10.30±4.19**). Genes controlling the resistance of downy mildew severity was generally expressed as over-dominance (dd) as indicated in the crosses involving 20B-2 X BUDUMA (40.92±22.20**), 25B-4 X BUDUMA (121.04±39.99**), 25B-4 X SOSAT-C88 (38.19±14.10**) and 25B-4 X DMR36-4 (68.28±7.27**). Estimates of gene effects for downy mildew severity index (DMS) showed that additive x dominance gene effect was highly significant for crosses involving SOSAT-C88 as male or donor parent, which demonstrated that there were genes in the nucleus controlling downy mildew resistance. Dominant gene effects (d), for downy mildew severity index was highly significant for all crosses involving 25B-4 as female or recipient parent as evidenced in its crosses with either BUDUMA, SOSAT-C88 or DMR36-4. In the case where one gene with complete dominance was responsible for downy mildew resistance in pearl millet, mode of inheritance is simple and its utilization is straightforward.

The net effect of genes conferring resistance to downy mildew incidence and severity in the crosses is observed to be dominant, considering the fact that the ratios of dominance to additive variance (degree of dominance) values ranged from 0.91-2.99 with a mean value of 1.95 for incidence and from 1.78-8.88 with overall mean value of 5.33 for severity index (Table 3).

Estimates for broad-sense heritability for resistance to downy mildew incidence ranged from 37.78-88.64% with overall mean value of 63.21%. Narrow-sense heritability ranged from 43.48-87.69% with mean value of 66.06%. Crosses involving SOSAT-C88 as a donor parent had both the highest broad and narrow-sense heritability for

Table 3: Estimates for heritability (%) controlling resistance to downy mildew incidence and severity in pearl millet for combined locations (Maiduguri and Yola) and years (2005 and 2006 seasons).

	Heritability (%)					
	DMI			DMS		
Crosses	Degree of dominance	Broad sense	Narrow sense	Degree of dominance	Broad sense	Narrow sense
20B-2XBUDUMA	1.90	39.25	84.65	1.78	-13.99	8.20
25B-4XBUDUMA	2.33	76.34	43.48	6.16	88.50	92.26
20B-2XSOSAT-C88	2.81	82.34	87.69	2.12	81.96	93.00
25B-4XSOSAT-C88	2.99	88.64	80.01	2.77	47.24	78.46
20B-2XDMR36-4	0.91	85.09	86.98	2.90	93.06	96.62
25B-4XDMR36-4	2.72	37.78	52.22	8.83	74.20	72.10
Range	0.91-2.99	37.78-88.64	43.48-87.69	1.78-8.88	-13.99-93.06	8.2-96.62
Mean	1.95	63.21	66.06	5.33	81.07	52.41

incidence (Table 3). Broad-sense heritability estimates for resistance to downy mildew severity ranged from -13.99-93.06% with a mean of 81.07% and narrow-sense heritability estimates were between 8.2-96.62% with overall mean of 52.41% (Table 3). This shows that genes conferring resistance to downy mildew is highly heritable and would respond to selection techniques which could be facilitated by the modern biotechnological tools, such as marker assisted breeding techniques. According to Erin [18], high heritability estimates can increase the prevalence of a particular trait under selection. In this study the high heritability estimates for downy mildew incidence and severity indicates that transfer of resistance to recipients parents by donor parents was highly possible. The simplest use of narrow-sense heritability value for breeders is to decide how effective selection might be, particularly for phenotypic selection. In this study the high narrow-sense heritability (which is a predictive value) for downy mildew incidence and severity indicates that there was the likelihood that improvement or change could be achieved by using specific breeding stock, such as hybrids involving SOSAT-C88. Methods such as selection indices and best linear unbiased prediction have been developed to combine information from relatives to achieve this goal.

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