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Analysis on the nature of gene effects involved in the expression of panicle traits in rainfed rice cultivars

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The nature and magnitude of gene effects involved in expression of panicle traits in rainfed rice cultivars were estimated among a wide range of crosses using generation mean analysis. The parental lines comprised of two low-land and six upland rain-fed rice. The lowland parents were used as pollen parents and the upland genotypes were maintained as the seed parents. Crosses were made between them to obtain the F_1 hybrids. Backcrosses were produced by crossing the F_1 hybrids to their pollen parent to obtain $BC_{1.1}$ and seed parents to produce $BC_{1.2}$. The result revealed significant differences ($P \leq 0.05$) among the genotypes for all the characters studied. Except for Max x CT7127-49 where P_2 and F_2 plants of WITA 4 x NERICA 1 that produced long panicles (29.28 and 26.13 cm) that differed significantly ($P \leq 0.05$) from other generations, F_1 plants produced the longest panicles in the other crosses followed by the F_2 plants. For most traits, F_1 generation means were higher than the mid-parent values. Significant differences observed between the F_1 and F_2 generation means in majority of the cases for percentage fertile spikelet and spikelet number per panicle is thought to be due to the diversity in these traits among the parental lines. The means of BC_1 and BC_2 tended to be located close to those of their respective recurrent parents. Digenic epistatic model was adequate to explain variation in generation means for all the panicle traits for the pooled analysis. Most of the crosses manifested non-allelic interactions for number of spikelet per panicles and fertile spikelet per panicle and is an indication that epistasis is determined to some extent by the genotypes used for the study.

Key words: Generation mean, dominance, additive, epistasis, F_1, F_2, parental line and backcross.

INTRODUCTION

In Africa, there are two rice cultivation ecosystems: The upland system on well drained soils with rain-fed crops and the lowland systems on swampy ecosystems under flooded conditions. Rain-fed upland is the major rice growing ecology in West Africa, accounting for nearly 60% of the total regional rice production area. For Nigeria upland rice accounts for 55 to 60% of the total cultivated rice land area with a productivity of 30 to 35% of total national rice production while lowland rain-fed rice production area estimates to 25% constituting some of the high yields ranging from 2 to 8 tonnes/ha, which contributes to 43 to 45% of total national rice production (Singh and Mowa, 1997). Optimizing grain yield has remained a major focus of rice production in almost all

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rice producing countries of the world. Panicle characters represent the most important part of rice plant with respect to yield improvement. Yield increase in modem rice was possible through improvement of panicle characters through long panicles, increased number of filled grains, more primary and secondary rachis (Seetharaman et al., 1973).

Genetic effect implies the capacity of a parent to produce superior progenies when crossed with another parent (Won et al., 2002). The choice of the most efficient breeding procedures predicates on the knowledge of the genetic systems controlling the characters under selection. Generation mean analysis belongs to the quantitative biometric methods based on measurements of phenotypic performances of certain quantitative traits on basic experimental breeding generations (parental, filial, backcross and segregation generations). Kearsey and Pooni (1996) reported that generation mean analysis is a useful technique in plant breeding for estimating main gene effects (additive and dominance) and their digenic (additive x additive, additive x dominance, and dominance x dominance) interactions responsible for inheritance of quantitative traits. This helps us in understanding the performance of the parents used in crosses and productivity potential of crosses for use in heterosis exploitation or in pedigree selection (Sharma and Sain, 2003). However, it is possible to ignore non-allelic (epistasis) interactions when these additive-dominance models are utilized. The presence or absence of epistasis can be detected by the analysis of generation mean using scaling test which measures epistasis accurately whether it is complementary (additive x additive) or duplicate (additive x dominance) and (dominance x dominance) at the digenic level (Farshadfar et al., 2008). The mode of inheritance and nature of genetic components of panicle characters in rice have been reported (Kim, 1987; Chang et al., 1998 Mahmood et al., 2004; Iftekharuddaula et al, 2008).

In this investigation six generations (parental, F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$) was undertaken to study gene action on panicle traits in two lowland and six upland rice genotypes using their generation means.

MATERIALS AND METHODS

The experimental materials consisted of six generations [P_1, P_2, F_1, F_2, $BC_{1.1}$ (P_1 x F_1)] and $BC_{1.2}$ (P_2 x F_1). The parental lines consisted of two lowland and six upland rice genotypes chosen for their differing panicle characters: WITA 4, Max, WAB 96-1-1, IR57689-73, EMPASC 105, Fofifa 16, CT7127- 49 and NERICA 1. Crosses between these genotypes with different rain-fed ecologies were performed to obtain hybrids. The lowland genotypes were used as pollen parents while the upland ones were used as the seed parents and crosses were made between them to obtain the F_1 hybrids. Backcrosses were produced by crossing the F_1 plants back to both their seed and pollen parents. All entries were grown in randomised complete block design with three replications at the Teaching and Research Farm of the Federal University of Technology, Owerri, Nigeria during the season of 2009. Each generation was planted in 1 m × 1 m plot with a spacing of 20 cm × 20 cm within and between plots. Panicle lengths and primary branches of panicle were measured in centimetre from five randomly selected plants and the mean data were used for statistical analysis. Similarly, number of spikelet per panicle and number of seeds per primary branch of panicle were determined. All measurements were taken according to SES of rice (1988).

The statistical analysis and genetic effects were performed using the GLM procedure of the SAS program (SAS institute, 1999) according to the randomized complete block design considering experiments and genotypes as fixed effects. Analyses of variances and F-tests following Steel and Torrie (1980) and Obi (2002) were carried out on six populations (P_1, P_2, F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$) within each cross to determine the significance of genotypic differences for the traits studied. The least significant difference (LSD) was used to separate the treatment means.

The estimate of gene effects of the panicle traits was determined using the mean data from the parental lines (P_1 and P_2), F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$ populations as described by Gamble (1962) and modified by Yang et al. (1997**)** as follows:

$M = F_2$;
$a = BC_{1.1} - BC_{1.2}$;
$d = - ½ P_1 - ½ P_2 + F_1 - 4 F_2 + 2BC_{1.1} + 2BC_{1.2}$;
$aa = - 4F_2 + 2BC_{1.1} + 2 BC_{1.2}$
$ad = - P_1 + P_2 + 2BC_{1.1} – 2BC_{1.2}$
$dd = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_{1.1} - 4BC_{1.2}$

Where: a = additive effect; d = dominance effect; aa = additive × additive type of epistasis; ad = additive × dominance type of epistasis; dd = dominance × dominance type of epistasis; $BC_{1.1}$ =Back Cross one (1), and BC1.2 = Back Cross two (2).

RESULTS

Generation mean analysis of the lowland x upland rice genotypes

The result of the mean performance of the crosses between eight genotypes of rice studied is presented in Table 1. Significant differences (P ≤ 0.05) were observed among the genotypes for all the characters studied. For panicle length, significant differences (P ≤ 0.05) were observed for all crosses. Except for Max x CT7127-49 where P_2 produced the longest panicle (29.28 cm) followed by F_1 plants (29.18 cm) and WITA 4 x NERICA 1 where F_2 produced the longest panicles (26.13 cm), F_1 plants produced the longest panicles in all the other crosses followed by the F_2 plants. The F_1 and F_2 plants produced more secondary branches per panicle in WITA 4 x IR57689-73, WITA 4 x WAB 96-1-1 and WITA 4 x NERICA1. The F_2 plants produced more fertile spikelets in WITA 4 x IR57689-73 (93.77%), WITA 4 x CT7127- 49 (94.53%), WITA 4 x Fofifa 16 (90.57%), WITA 4 x NERICA 1 (95.15%), Max x CT 7127- 49(95.52%) Max x EMPASC 105 (92.23 %) and Max x WAB 96-1-1 (93.22%) than the other generations. Similarly, P_2 plants were more fertile in WITA 4 x EMPASC 105 (93.4%), Max x Fofifa 16 (96.43%) and Max x NERICA 1 (93.17%) crosses. Significant differences (P≤ 0.05) were recorded for number of spikelets per panicle in all the crosses. The

Table 1. Generation means and least significant differences (LSD) for panicle traits in eight rain-fed rice crosses.

Crosses/generation	Panicle length (cm)	Primary branch /panicle	Fertile spikelet (%)	No of spikelet/panicle	Seed/primary branch of panicle
WITA 4 × IR 57689-73					
P1	24.40	9.00	87.82	85.33	9.67
P2	22.03	9.33	92.81	84.38	9.16
F1	25.57	10.33	78.57	74.50	8.67
F2	24.53	9.83	93.77	91.83	11.17
BC1	24.35	9.33	80.73	79.67	9.83
BC2	24.22	8.67	61.37	66.33	9.67
LSD(0.05)	1.262	1.146	6.42	15.282	1.461
WITA 4 × CT 7127 – 49					
P1	26.22	11.17	80.98	98.50	11.17
P2	26.20	11.50	91.02	139.40	13.19
F1	29.22	10.67	83.6	86.17	8.12
F2	27.05	9.17	94.53	115.67	13.83
BC1	24.15	11.17	77.02	90.17	9.50
BC2	25.75	8.33	58.77	65.33	10.33
LSD(0.05)	2.513	2.113	8.894	24.964	2.759
WITA 4 x EMPASC 105					
P1	21.90	10.50	88.27	94.50	10.67
P2	22.47	10.83	93.40	114.8	12.17
F1	23.90	9.83	78.32	81.17	8.67
F2	22.32	10.00	87.93	115.17	12.00
BC1	22.23	10.67	70.27	77.83	9.00
BC2	21.72	8.67	58.32	64.17	10.33
LSD(0.05)	2.075	1.853	12.754	23.843	1.231
WITA 4 x Fofifa 16					
P1	22.98	10.33	84.77	96.17	10.17
P2	22.98	9.33	89.57	91.00	10.90
F1	25.25	10.17	75.27	71.67	7.33
F2	24.42	10.67	90.57	99.00	10.83
BC1	22.57	10.50	78.42	81.33	10.17
BC2	22.54	7.50	71.20	76.67	9.17
LSD(0.05)	2.027	2.659	8.40	13.758	2.340
WITA 4 x WAB96-1-1					
P1	25.02	9.83	81.52	94.83	9.97
P2	24.29	10.17	90.88	95.50	10.83
F1	27.05	10.50	65.63	71.83	9.17
F2	25.15	9.93	91.82	108.67	9.04
BC1	24.28	10.34	78.50	81.00	9.50
BC2	23.22	8.83	73.83	79.67	9.47
LSD(0.05)	1.995	1.435	7.454	17.055	1.856
WITA 4 x NERICA 1					
P1	23.27	9.83	81.15	113.29	11.16
P2	22.56	10.15	94.50	96.83	10.82
F1	24.50	10.5	86.42	84.34	8.92
F2	26.13	10.66	95.15	102.36	10.71
BC1	22.82	10.16	79.23	99.53	9.53
BC2	21.75	8.91	78.98	81.64	9.17
LSD(0.05)	1.378	1.435	8.423	20.641	1.856

Table 1. Contd.

Max x IR 57689-73					
P1	21.65	9.83	89.63	83.50	10.83
P2	22.12	10.00	87.33	112.60	12.38
F1	23.72	10.83	63.35	76.50	9.32
F2	22.78	10.00	91.23	97.17	10.84
BC1	23.03	9.17	83.83	89.83	10.47
BC2	24.4	7.67	71.67	94.16	12.96
LSD(0.05)	1.32	2.074	7.679	10.009	1.761
Max x CT 7127-49					
P1	25.83	12.14	83.91	119.53	11.33
P2	29.28	12.17	94.85	122.83	13.32
F1	29.18	12.67	87.00	96.17	12.64
F2	25.72	11.50	95.52	123.17	12.67
BC1	24.22	11.00	79.63	101.67	10.83
BC2	25.12	10.00	54.92	77.67	11.00
LSD(0.05)	1.79	1.62	8.411	26.758	2.648
Max x EMPASC 105					
P1	21.48	11.00	81.08	96.83	12.83
P2	22.48	12.15	91.80	110.17	12.19
F1	23.93	10.33	81.93	86.92	10.02
F2	21.83	11.50	92.2	116.67	11.17
BC1	21.57	11.17	73.02	8217	10.17
BC2	22.37	9.333	61.05	78.00	11.50
LSD(0.05)	2.002	1.686	9.481	33.119	2.894
Max x Fofifa 16					
P1	22.60	10.83	85.58	95.33	11.33
P2	22.46	10.57	95.43	92.67	10.33
F1	25.37	9.67	84.30	81.67	8.67
F2	23.05	9.62	90.15	93.17	11.50
BC1	22.02	9.17	81.72	81.72	9.83
BC2	22.10	8.83	68.48	61.33	10.33
LSD(0.05)	2.574	1.424	7.478	19.05	2.383
Max x WAB 96-1-1					
P1	24.48	10.83	86.83	92.17	11.33
P2	24.03	11.17	91.33	97.33	10.67
F1	27.32	10.67	83.78	94.50	9.83
F2	26.15	10.83	93.22	113.22	11.17
BC1	24.20	9.67	84.20	86.00	10.00
BC2	22.23	8.67	66.72	63.50	9.93
LSD(0.05)	2.40	1.24	7.175	25.171	2.451
Max x NERICA 1					
P1	22.72	12.83	81.87	110.18	11.83
P2	22.58	11.83	93.17	96.37	15.51
F1	23.77	12.33	86.33	69.81	9.50
F2	23.33	11.17	90.37	130.13	14.17
BC1	21.65	10.83	74.61	94.17	11.67
BC2	22.15	9.67	70.38	81.56	11.83
LSD(0.05)	1.859	1.869	6.47	20.189	2.194

Table 2. Estimates of genetic effects on panicle traits of the rice genotypes studied in 2009.

Characters	M	A	D	AA	AD	DD	Type of epistasis
Panicle length (cm)	24.49	0.58*	-0.512	-2.76	0.673	7.644**	-
Primary branch/panicle	10.46	0.94*	-2.92*	-2.76*	2.16**	6.72*	Duplicate
Spikelet /panicle	106.13	7.72*	-102.17**	-91.4**	18.58**	140.063**	Duplicate
Fertile spikelet (%)	95.59	9.66**	-89.15**	-83.083**	23.062**	129.334**	Duplicate
Seed/primary branch/panicle	11.95	-0.05	-6.575*	-5.622*	0.313	8.952*	Duplicate

P_2 and F_2 plants produced more spikelets which differed from others in WITA 4 x CT7127- 49, WITA 4 x EMPASC 105, Max x CT7127- 49, Max x EMPASC 105, Max x WAB 96-1-1 while P_1 and F_2 in WITA 4 x IR57689-73, WITA 4 x Fofifa 16, WITA 4 x NERICA 1, Max x Fofifa 16 and Max x NERICA 1 produced more spikelet than others. P_2 and F_2 produced more seeds per secondary branch of panicle in WITA 4 x CT7127- 49, WITA 4 x EMPASC 105, WITA 4 x Fofifa 16, WITA 4 x WAB 96-1-1, Max x CT7127- 49 and Max x NERICA 1. On the other hand, P_1 and F_2 produced more seeds than plants from other generations in Max x Fofifa16 and Max x WAB 96-1-1.

Estimates of gene effects of panicle traits on lowland x upland rice genotypes

There were variations in gene effects on the panicle traits in the chosen parents and in the crosses. The results of generation mean analysis provide estimates of the main and first order interaction gene effects (Table 2). The additive and dominance gene effects were involved in the expression of the characters studied. In spite of the fact that most values of dominant effect (d) were negative, the mean of the F_2 (m) and additive effect (a), recorded values that were significantly different from zero (Table 3) indicating that the generation means were not only controlled by the additive and dominance effects of the genes and thus suggests that a non allelic interaction (epistasis) was influencing the expression of the characters. The result of the pooled estimate of genetic effect showed predominant positive additive (a) components which had lower values for most negative dominance (d) components and higher values for all traits except for number of seeds per primary branch of panicle. Among the crosses, additive gene effect influenced the inheritance of primary branch per panicle only in WITA 4 x CT 7127-49, WITA 4 x EMPASC 105, WITA 4 x Fofifa 16 and Max x EMPASC 105 as well as percentage fertile spikelet in all the hybrids except WITA 4 x CT 7127-49, WITA 4 x EMPASC 105, WITA 4 x Fofifa 16. On the other hand, dominance gene affected the inheritance of seeds/primary branch of panicle in WITA 4 x WAB 96-1-1 and fertile spikelet/ panicle and seeds/primary branch of panicle in WITA 4 x NERICA 1. Dominance gene effects recorded very high and significant values for spikelet/ panicle, fertile spikelet/ panicle and number of seeds/ primary branch of panicle indicating that alleles responsible for the less yield-related characters were dominant over the alleles controlling the high ones. The three types of gene interaction namely: Additive, dominance and epistasis were observed to be significant though negative in dominance effect in the pooled result (Table 2) in primary. Duplicate epistasis was involved in all the parameters measured in the cross of Max x WAB 96-1-1
branch/panicle, fertile spikelet/panicle and spikelet/panicle. Similar results were recorded for fertile spikelet/panicle in WITA 4 x IR 57689-73, WITA 4 x CT7127-49**,** Max x IR 57689-73, Max x CT 7127- 49, Max x Fofifa 16 and Max x WAB 96-1-1. Among the digenic epistasis, dominance x dominance had higher and more significant values than additive x additive effect which were mostly negative.

Gene interaction did not influence the inheritance of panicle length and primary branch per panicle in WITA 4 x IR 57689-73, WITA 4 x EMPASC 105, WITA 4 x WAB 96-1-1, WITA 4 x NERICA 1 as well as seed per primary branch of panicle in Max x EMPASC 105, Max x Fofifa 16 and Max x NERICA 1.

DISCUSSION

Considerable amount of variability was observed in the characters evaluated for generation mean analysis. High mean value was the main selection criterion for a long time. Gilbert (1958) suggested that the parents with good mean performance would result in better genotypes since it is the actual realized value in the experiment. The result showed that the means of BC_1 that is P_1F_1 and BC_2 that is P_2 F_1 tended to be located close to those of their respective recurrent parents. For most traits, F_1 generation means were higher than the mid-parent values. Significant differences were observed between the F_1 and F_2 generation means in majority of the cases for percentage fertile spikelets and spikelet number per panicle which is thought to be due to the diversity in these traits among the parental lines. Panicle length contributes to grain yield in rice (Zafar et al., 2004). Maximum panicle length was observed for CT 7127-49 (29.41 cm) among the parents while among the

Table 3. Estimates of the genetic effects of the panicle traits of the lowland x upland rice genotypes studied in 2009.

Characters	M	A	D	AA	AD	DD	Type of Epistasis
WITA 4 x IR 57689-73							
Panicle length (cm)	24.53	0.13	1.35	-1.00	-2.10	1.433	-
Primary branch/panicle	9.83	0.67	-2.17	-3.33	1.67	6.33	-
Spikelet /panicle	91.83	13.33	-86.17**	-75.33*	26.67	103.00*	Duplicate
Fertile spikelet (%)	93.77	19.37**	-101.11**	-90.87**	38.73**	141.43**	Duplicate
Seed/primary branch/panicle	11.17	-1.83	-8.67	-3.63	-9.67	19.33**	-
WITA 4 x CT7127-49							
Panicle length (cm)	27.05	-1.60	5.39	-8.40	-3.22	19.45**	-
Primary branch/panicle	9.17	2.83*	1.67	2.33	6.00**	-2.67	-
Spikelet /panicle	115.67	24.83	-184.00**	-151.67**	49.67*	290.00**	Duplicate
Fertile spikelet	94.53	18.25**	-113.96**	-106.57**	36.53**	184.24**	Duplicate
Seed/primary branch/panicle	13.83	-0.83	-18.83**	-15.67**	-1.67	22.33**	Duplicate
WITA 4 x EMPASC 105							
Panicle length (cm)	22.32	0.517	0.533	-1.367	1.03	5.27	-
Primary branch/panicle	10.00	2.00*	-2.17	-1.33	4.33*	- 3.67	-
Spikelet /panicle	115.17	13.67	-200.00**	-176.67**	27.33	264.00**	Duplicate
Fertile spikelet (%)	87.93	11.95	-104.08**	-94.57**	23.03	169.72**	Duplicate
Seed/ primary branch/panicle	12.00	-1.33	-15.08**	-13.33**	-3.17	20.83**	Duplicate
WITA x Fofifa 16							
Panicle length (cm)	24.42	0.00	-5.13	-7.41	0.00	13.60*	-
Primary branch/panicle	10.67	3.00*	-6.33	-6.667	5.01	10.67*	-
Spikelet /panicle	99.00	4.67	-98.91*	-80.02	14.50	100.50	-
Fertile spikelet (%)	90.57	7.22	-72.43**	-63.03**	14.23	83.67**	Duplicate
Seed/ primary branch/panicle	10.83	1.00	-5.25	-4.67	0.50	8.50	-
WITA 4 x WAB 96-1-1							
Panicle length (cm)	25.15	1.07	-3.52	-5.63	2.03	14.63*	-
Primary branch/panicle	9.93	1.15	0.03	-1.66	1.12	7.26	-
Spikelet/panicle	108.01	1.33	-136.67**	-113.33**	3.33	126.03*	Duplicate
Fertile spikelet (%)	91.82	4.67	-86.17**	-62.61**	8.71	67.60*	Duplicate
Seed/ primary branch/panicle	9.04	0.92	21.61**	3.12	0.82	-1.24	-
WITA 4 x NERICA1							
Panicle length (cm)	26.13	1.08	13.78**	-15.37**	1.47	21.03**	Duplicate
Primary branch/panicle	10.16	-0.56	0.38	-0.08	1.16	7.16	-
Spikelet /panicle	133.67	17.89	45.47	-47.1	19.32	63.56	-
Fertile spikelet (%)	95.15	0.25	-68.8*	-64.17*	0.5	3.18	-
Seed/ primary branch/panicle	9 .76	-0.69	20.11**	0.46	102.67**	7.94	Duplicate
Max x IR 57689-73							
Panicle length (cm)	22.78	-1.367	5.8	3.73	-2.733	-7.867	-
Primary branch/panicle	10	1.5	-5.417	-6.333	3.167	14.167*	-
Spikelet /panicle	97.17	4.333	-4.5	-38	8.667	7.333	-
Fertile spikelet (%)	91.23	12.163*	-79.052**	-53.921**	22.026*	46.58	-
Seed/secondary branch/panicle	10.83	-2.463	1.215	3.5	-3.432	-8.514*	-
MAXx CT7127-49							
Panicle length (cm)	25.72	-0.91	-0.85	-4.22	-1.84	15.57*	-
Primary branch/panicle	11.53	1.03	-3.42	-4.12	2.17	11.53*	-
Spikelet/panicle	123.17	24.02	-159.00*	-134.00*	51.333	209.99**	Duplicate
Fertile spikelet (%)	95.52	24.72**	-116.97**	-112.97**	49.43**	26.98**	Duplicate
Seed/ primary branch/panicle	12.67	-0.17	-7.67	-7.04	-0.33	15.33*	-

Table 3. Contd.

Max x EMPASC 105							
Panicle length (cm)	21.83	-0.8	2.483	0.533	-0.6	3.433	-
Primary branch/panicle	11.51	1.83*	-5.67*	-5.04	3.67*	6.67	-
Spikelet /panicle	116.67	4.17	-160.17**	-146.33*	21.667	212.33*	Duplicate
Fertile spikelet (%)	92.23	11.97*	-103.31**	-100.81**	20.65	177.42**	Duplicate
Seed/ primary branch/panicle	11.17	-1.33	-1.17	-1.33	-2.67	9.67	-
Max x Fofifa 16							
Panicle length (cm)	23.05	-0.08	-1.21	-3.97	-0.17	11.67*	-
Primary branch/panicle	9.62	0.33	-3.75	-2.67	0.5	7.5	-
Spikelet /panicle	93.17	15.02	-99.67*	-97.33**	47.33	193.33**	Duplicate
Fertile spikelet (%)	90.15	13.23**	-61.91**	-60.20**	27.93**	100.42**	Duplicate
Seed/ primary branch/panicle	11.50	-0.54	-3.83	-5.67	-2.01	12.33	-
Max x WAB 96-1-1							
Panicle length (cm)	26.15	1.97	-8.68	-11.73*	3.48	22.02**	Duplicate
Primary branch/panicle	10.83	1.05	-7.00*	-6.67*	2.33	13.33**	Duplicate
Spikelet /panicle	113.52	22.5	-160.25**	-155**	60.17*	244.53**	Duplicate
Fertile spikelet (%)	93.22	17.48**	-77.58**	-71.03**	34.97**	117.43**	Duplicate
Seed/ primary branch/panicle	12.17	0.667	-8.5*	-10.00*	1.33	19.67**	Duplicate
Max x NERICA 1							
Panicle length (cm)	23.33	-0.5	-4.62	-5.73	-1.13	10.97*	-
Primary branch/panicle	11.17	1.167	-3.67	-3.67	1.33	12.04*	-
Spikelet /panicle	130.33	12.67	-121.84*	-89.98	8.34	81.61	-
Fertile spikelet (%)	90.37	4.22	-77.03**	-71.55**	8.43	137.93**	Duplicate
Seed/ primary branch/panicle	14.17	1.83	-8.33	-5.67	4.33	10.06	-

m= mean of F_2; a = additive gene effect; d = dominance gene effect; aa = additive × additive gene effect; ad = additive × dominance gene effect; dd = dominance x.

progenies the F_1 of CT 7127-47 x Fofifa 16 (29.32 cm) had the longest panicle. The highest number of secondary branch per panicle (14) were observed for CT 7127-49 and NERICA 1 among the parental lines and in F_1 (14.13), BC_1 (13.96) and F_1 of CT7127-49 x EMPASC 105 (12.67). The number of spikelet per panicle which is assessed after heading, greatly influences grain yield in rice and measures yield related characters. The highest number of spikelet per panicle were observed in CT 7127-49(139.4) and EMPASC 105 (124.21) amongst parental lines while among the progenies F_1 and F_2 hybrids of CT 7127-49 x EMPASC 105 had 153.86 and 128.36 respectively. Likewise, F_2 hybrids of Max x CT 7127-49 had 123.17. Percentage fertile spikelet which is determined by feeling the ripened spikelet to ensure there is grain in it; recorded highest values for Fofifa 16 (96.43%) and NERICA 1(96%) among the parents while the F_2 of WAB 96-1-1 x NERICA1(97.9%) and Fofifa 16 x NERICA1(97.45%) had the highest among the progenies.

Although percentage fertile spikelet contributes positively to grain yield in rice (Anyanwu, 2009), yet, highest percentage filled grain is not the only factor responsible for grain yield. In the present study, Fofifa 16 and NERICA 1 which recorded highest percentage filled grains did not have corresponding values for spikelet number per panicle and other yield related traits recorded lower yields. Generation mean analysis is commonly utilised in evaluation of effect of the genes which are involved in quantitative traits in rice breeding programmes. The analysis of gene effects revealed that additive, dominance and epistatic effects were involved in the inheritance of most traits. The result of the pooled analysis of genetic effects of the traits agrees with the work of Kim (1987) who obtained non allelic gene interactions for all the panicle traits he studied. On the other hand, Chang et al. (1998) reported epistasis for number of primary branches per panicle and number of spikelet per panicle. However, they explained the inheritance of primary branch length using the additive-dominance genetic model. The performance of most of the crosses manifesting non-allelic interactions for number of spikelet per panicles and fertile spikelet per panicle is an indication that epistasis is determined to some extent by the genotypes used for the study.

Recurrent selection has been suggested for non-allelic inheritance traits in rice (Subraman and Rangasamy, 1989; Vijayakumar et al., 1996), wheat (Sharma et al., 1995) and mungbean (Khattak et al., 2001). The present study suggests the use of recurrent selection for panicle traits in most of the genotypes used especially in WITA 4 x CT 7127-49, WITA 4 x EMPASC 105, Max x CT 7127-49 and Max x WAB 96-1-1. Except for WITA 4 x IR 57689-73 and Max x EMPASC 105 where panicle length was not affected by gene interaction, epistasis influenced its expression in the other crosses. It could therefore be improved through recurrent selection in the other cross combinations. It might be possible to follow the recommendation of Khattak et al. (2001) to use a bi-parental approach *inter se* crossing and/or recurrent selection for developing high yielding rice lines in advanced generations if we want to exploit all types of gene effects.

Mather and Jinks (1982) reported that when opposite signs of additive x additive (aa) and dominance x dominance (dd) are involved in a cross, that it indicates prevalence of duplicate epistasis and complementary epistasis when both signs are the same. Duplicate epistasis was observed in most of the crosses for spikelet/panicle and fertile spikelet (%) as well as seeds/primary branch of panicle except for Max 4 x IR 57689-73. Similarly, positive dominance x dominance gene action was recorded for WITA 4 x Fofifa 16, WITA 4 x NERICA 1 and Max x NERICA 1 while duplicate epistasis was observed only for percentage fertile spikelet. This effect would tend to obscure the manifestation of any genetic progress made since in the early generations. Falconer and Mackay (1996) had earlier suggested that in self- pollinated plants, epistasis is more important than dominance which lasts for a short time with progressive selfing but non allelic interaction can generate segregates some of which may represent real genetic advance over their parents. It might be possible to follower the suggestion of Moreno-Gonzalez and Cubero(1993) that where epistasis is more important, recurrent selection and reciprocal recurrent selection can be efficient techniques for selecting desirable cultivars.

Conclusion

The analysis of gene effects revealed that additive, dominance and epistatic effects were involved in the inheritance of most traits. Most of the crosses manifested non-allelic interactions for number of spikelet per panicles and fertile spikelet per panicle indicating that epistasis is determined to some extent by the genotypes used for the study. The presence of significant duplicate epistasis restricted the scope of simple selection for the characters studied. Therefore delaying selections to later generations will enhance success in improving panicle characters in the genotypes studied. Recurrent selection could be used in improving panicle traits in WITA 4 x CT 7127-49, WITA 4 x EMPASC 105, Max x CT 7127-49 and Max x WAB 96-1-1.

Conflict of Interest

The authors have not declared any conflict of interests.

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