

Full Length Research Paper

Inheritance studies of aroma and yield attributes in rice (*Oryza sativa* L.) genotypes

Nabieu Kamara^{1*}, Maxwell Darko Asante² and Richard Akromah³

¹Crop Improvement Programme, Rokupr Agricultural Research Centre / Sierra Leone Agricultural Research Institute, Sierra Leone.

²Cereals Division, CSIR-Crops Research Institute, Kumasi, Ghana.

³Department of Crop and Soil Sciences, Collage of Agriculture and Natural Resources, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana.

Received 10 July, 2017; Accepted 11 October, 2017

Low yield is one of the main challenges of rice production in Ghana due to poor production practice, environmental stresses and plant genotype. The choice of an efficient breeding procedure depends to a large extent on knowledge of the genetic system controlling the character to be selected. This experiment was done to study the inheritance pattern of aroma attribute of rice and estimate the heritability for some yield attributes in rice (*Oryza sativa* L.). Six generations viz., P1, P2, F1, F2, BCP1 and BCP2 of a cross between IET6279 and IR70445-146-3-3 were used for the study. A randomized complete block design (RCBD) was used with three replications. All the F1 and BCP1 plants of the cross were non-aromatic indicating that the gene controlling aroma in the donor parent was recessive. The segregation ratio of aromatic to non-aromatic plants was 1:3 in F2 and 1:1 in BCP2 plants, confirming the monogenic inheritance of aroma. This shows that there would be a high probability of success in selecting for aroma using pedigree breeding in early generations of F2. High broad sense heritability estimates were observed for all the characters studied except for number of fertile spikelets per plant, suggesting that the influence of the environment was minimal for these characters. Hence, these traits would respond to selection owing to their high genetic variability and transmissibility. Thus, selection based on phenotypic value of these characters would be reliable and effective with low broad sense heritability for number of fertile spikelets per plant, indicating that influence of the environment was high for these characters. Therefore, superior genotypes selection based on phenotypic performance for this trait may not be effective. The analysis of gene effects revealed that additive, dominance and epistatic effects were involved in the inheritance of all the traits studied. However, additive effect, in general was higher in magnitude than dominance gene effect in all the characters. All the traits manifested non-allelic interactions, indicating that epistasis is determined to some extent by the genotypes used for the study. Thus, in the presence of epistasis, grain width showed significant duplicate type of gene interaction which restricted the scope of simple selection for the characters studied. Therefore delaying selections to later generations using recurrent selection will enhance success in improving yield attributes in all genotypes studied.

Key words: Aroma, inheritance, additive, gene action, heritability, monogenic, non-additive, recessive.

INTRODUCTION

Rice belongs to the genus *Oryza*, the family Gramineae, and is a widely cultivated crop (Syed and Khaliq, 2008). It is the most important staple food crop in the world consumed by more than half of the world population (Kohnaki et al., 2013).

In Ghana, rice has become a major staple in recent decades with a per capita consumption of 25 kg/annum, but most of the consumption is met by imports (MOFA, 2010). In 2009, the country imported over 350,000 tons of milled rice worth 600 million US dollars (Duffuor, 2009). MoFA (2009) revealed that, the estimated national rice consumption stands at 561,400 metric tons per year, while rice produced locally is 107,900 metric tons, leaving a gap of 453,500 metric tons which have to be imported (Directorate of Crop Services, MoFA, 2010). Low yield is one of the main challenges of rice production in Ghana due to poor production practice, environmental stresses and plant genotype.

Aromatic rice, also known as fragrant or perfumed rice, is very popular in Asia and is classified as premium quality rice in markets throughout the world, including Ghana (Diako et al., 2010). There is an increasing demand for aromatic rice being driven by improving living standards of people around the world (Chen et al., 2006). Classical examples of fragrant rice are the Basmati rice cultivars of India and Pakistan, Dulha bhog of Bangladesh, Khao Dawk Mali (Jasmine) of Thailand, Azucena and Milfor of the Philippines and Rojolele of Indonesia (Khush et al., 1979). Aromatic rice varieties are playing a vital role in global rice trading. Major feature of these aromatic rice varieties is aroma which is being appreciated by many people and represents a high value added trait (Dela and Khush, 2000). So, rice needs attention toward improvement in its cooking qualities as well as several biochemical and morphological characteristics (Golam et al., 2004). The demand for aromatic rice is increasing by the day. Unfortunately, this aromatic rice often has undesirable agronomic characters, such as low yield, susceptibility to pests and diseases, and strong shattering (Berner and Hoff, 1986). The agronomic value of a variety depends on many characteristics (Huang et al., 1991) and the most important characteristics are high yielding ability, resistance to diseases and pests, resistance to undesirable environmental factors and high quality of the products. Methods for smelling leaf tissue, grains after heating in water, and reacting with solutions of 1.7% KOH are available (Sood and Siddiq, 1978). Since rice aroma,

a polygenic quantitative trait with complex inheritance pattern, is highly influenced by environment, it is difficult to identify genes that determine this trait (Pachauri et al., 2010). Genetic studies on the inheritance of aroma in rice revealed that a recessive nuclear gene controls aroma in rice. Dong et al. (2000) reported that aroma is controlled by a single recessive gene in Jasmine 85 and p1467917 and by two genes in Amber and Dragon Eyeball. Digenic segregation for aroma was also reported by Lin (1991). Sood and Siddiq, (1978) reported that aroma is monogenic recessive to non-aromatic that is, a digenic segregation of 15:1 (Geetha, 1994), 13:3 (Tsuzuki and Shimakawa, 1990) and trigenic ratio of 37 non-aroma: 27 aroma. Further, the recent inheritance studies on aroma indicated 3:1 (non-scented: scented) segregation ratio indicating monogenic, recessive gene control (Lorieux et al., 1996). There is no consensus yet on the nature of inheritance in aromatic characters as described earlier. The lack of agreement among many investigators appears to be related to the differences in the aromatic varieties used and also the differences in the methods used in evaluating aroma.

Rice grain length and width are the two important quantitative traits also closely related to the exterior quality of the rice (Shi et al., 2000). Genetic analyses of length and width of rice kernels have been reported by some of the researchers and most of the studies have shown that rice grain shape is quantitatively inherited (Zhang et al., 2005). It has been shown that rice grain shape is controlled by triploid endosperm genes, cytoplasmic genes, and maternal genes (Shi et al., 2005) and their genotype into environment interaction effects. The length, width and seed thickness is one of the quantitative measures of grain shape. The objective of the present study was to understand the nature of inheritance of aroma, grain length, grain width, number of spikelets per plant and number of fertile spikelets per plant.

MATERIALS AND METHODS

A field experiment was carried out in Fumesua, Kumasi in a forest region of Ghana with soil classification of gleyic Lixisol soil having clay loam texture with moderate soil fertility (N06° 45' 05.3" latitude and W001° 32' 19.3" longitude). The experimental material consisted of two lowland varieties (Table 1). Seeds of the two rice varieties were obtained from the Cereals Division, CSIR-Crops Research Institute, Kumasi - Ghana. Crosses were made between

*Corresponding author E-mail: kamara.nabieu@yahoo.com.

Table 1. Salient features of the parents used for the development of F1, F2, BCP1 and BCP2 populations.

Accession	Pedigree	Plant height	Duration	Grain type	Yield (t ha ⁻¹)	Salient features
IET6279	Indian	Tall	Late	Short, bold	8.5	Non- aromatic
IR70445-146-3-3	IRRI	Medium	Medium early	Long, slender	6.0	Aromatic

the two parents to obtain F1 individuals. The F1 were grown and backcrossed to both parent. The two parents, F1, F2, BCP1 and BCP2 generations were grown in the field at the same time.

Pot culture of F1 plants

The F1 seeds were pre-germinated in a white tissue paper and Petri dish for three days, nursed for 21 days with one seedling transplanted per bucket. The buckets were filled with sterilized top soil to avoid soil contamination. Sowing of the varieties were staggered over a three-week's period in order to synchronize flowering in the varieties. The hybrid plants were provided with 10 g of N P K (15:15:15) at tillering and 10 g of urea at panicle initiation. Standard agronomic operations like irrigation, application of insecticides and hand weeding were employed whenever necessary. Some F1 plants were selfed to produce F2. Some panicles from the same F1 plants were backcrossed to either parent to generate the backcross populations. New crosses between parents were also made to generate fresh F1 seeds.

Field experiment

All seedlings were transplanted to an irrigated lowland field in a randomized complete block design in three replications at CSIR-CRI Fumesua during the minor season of 2015. Each replicate had 60 plants of parents, 25 F1s, 300 F2, 60 BCP1 and BCP2 plants. Spacing of 40 and 20 cm between-row and within-row was followed, respectively at a density of a single plant per hill and data were taken on individual plants for all the populations. The recommended fertilizer rate of 90-60-60- Kg/ha- N-P2O5-K2O was applied: 60-60-60 kg/ha applied two weeks after transplanting top-dressed with 30 kg/ha N at panicle initiation. Weeds were controlled by spraying with a post emergence selective weedicide, Pronil-plus and Propanil. This was followed by hand picking. Field was irrigated whenever necessary using rain water from a fabricated lake through canals with flood method.

Data collection

After 60 days of seeding, determination of presence or absence of aroma was made according to the method described by Sood and Siddiq (1978) and Dong et al. (2001b). Two grams of green leaves were harvested from individual plants cut into small pieces and kept in the test tubes. About 10 ml of 1.7% potassium hydroxide (KOH) solution was added to each test tube. The test tubes were covered immediately after the addition of alkali and left under room temperature for about ten minutes. The test tubes were opened one by one and the content in each was immediately evaluated by smelling. The samples were classified according to the degree of aroma, at a rating scale from zero to three; with zero indicating no aroma, one indicating faint aroma, two indicating aroma and three indicating strong aroma. The evaluation of aroma for individual plants was conducted in three replications by 5 panelists. To

prevent overwhelming panel member's senses, no more than 20 samples were evaluated at a time. For each set of data the aromatic and non-aromatic parents were included as controls; where a panel member failed to evaluate the controls, the data was rejected. Samples were divided into three groups based on the average of rating scale values: (i) aromatic (1.5 - 3.0); (ii) questionable (1.2 - 1.4) and (iii) non-aromatic (less than 1.2). Any questionable sample was re-evaluated until it was classified as either aromatic or non-aromatic. Grain length and grain width were measured in millimeter (mm) after harvesting. Number of spikelets per plant was determined by counting total number of spikelets after harvesting. Number of fertile spikelets per plant was also determined by pressing the spikelets with the fingers and noting those that do not have grains after harvesting.

Data analysis

Analysis of variances was done for six population (the two parents, F1, F2, BCP1 and BCP2) within each cross with respect to all the studied traits, and generation means analysis using linear mixed models (REML) was done to estimate genetic effects of the four quantitative traits according to the methodology proposed by Mather and Jinks (1971). Statistical and genetic analyses were performed using Genstat software (15.1). The means and variances obtained were used to estimate genetic parameters such as broad sense and narrow sense heritability.

Gene action controlling four quantitative traits in IET6279 × IR70445-146-3-3 cross

The generation mean analysis model is stated as:

$$Y = m + \alpha a + \beta d + \alpha 2aa + 2\alpha\beta ad + \beta 2dd$$

Where α and β are the coefficients for a and d , respectively, Y = the observed mean, m = mean = mean of the F2, a = pooled additive effects, d = pooled dominance effects, aa = additive × additive gene interaction effects, ad = additive × dominance gene interaction effects, dd = dominance × dominance gene interaction effects. The mode of inheritance of the four yield attribute was estimated by generation mean analysis. Their means and variances were used to perform generation mean analysis.

Heritability in the broad sense

Broad sense heritability (H^2_b) was estimated using the formula of Allard (1960).

$$H^2_b = (VF2 - VE) / VF2$$

Where; H^2_b = Broad sense heritability;
 VE = Error variance = $(VP1 + VP2 + VF1) / 3$;
 $VF2$ = Variance of F2 family;

VP1 = Variance of parent 1;
 VP2 = Variance of parent 2;
 VF1 = Variance of F1 family.

Narrow sense heritability

Narrow sense heritability (h^2_n) was calculated according to the method of Halloran et al. (1979) as follows:

$$h^2_n = [2VF2 - VBCP1 - VBCP2] / VF2$$

Where: VF2, VBCP1, and VBCP2 are the variances of the F2, IET6279 × F1 and IR70445-146-3-3 × F1, respectively.

Aroma

Chi-square values of the aroma data obtained from segregating population of the crosses were computed following the procedure described by Gomez and Gomez (1984).

RESULTS

The result of analysis of variance revealed significant differences ($P < 0.01$) among generations for all the characters investigated indicating the presence of sufficient genetic variability and depicting the possibility of selection for desirable yield attributes in rice. The F1 and the backcross to IET6279 (BCP1) from these cross were non-aromatic. The F2 and the backcross to IR70445-146-3-3 (BCP2) from these cross were aromatic (Table 2). The F2 generation was segregated into 203 aromatic and 589 non-aromatic plants fitting into 1:3 ratio ($\chi^2 = 0.14$). The backcross to IR70445-146-3-3 (BCP2) cross was segregated into a ratio of 79 aromatic to 92 non-aromatic plants fitting into a 1:1 ratio ($\chi^2 = 0.84$). This indicates that aroma in IR70445-146-3-3 is under the control of a single recessive gene (Table 3). The highest mean performance for number of spikelets per plant was recorded for IET6279 (3785) followed by BCP1 (2662); while IR70445-146-3-3 (2194) recorded the lowest mean. The means of F1, F2, BCP1 and BCP2 are all within parental limits. The range of variation in BCP1 was higher than BCP2, F2, F1 and parents. BCP1 recorded the highest CV (4.16%) followed by BCP1 (2.95%); while F1 recorded the lowest (1.28%).

In the case of number of fertile spikelets per plant, the maximum and minimum means were recorded for IET6279 (3181) and IR70445-146-3-3 (2057), respectively. The means of F1, F2, BCP1 and BCP2 were all within parental limits. The range of variation in BCP1 was higher than F1, F2, BCP2 and parents. BCP1 recorded the highest CV (3.47%) followed by IR70445-146-3-3 (1.96%); while IET6279 recorded the lowest (0.53%). For grain length, the highest mean was recorded for IR70445-146-3-3 (10.92) followed by BCP2 (9.73); while IET6279 (8.19) recorded the lowest mean.

The means of F1, F2, BCP1 and BCP2 were all within parental limits. The largest range of variation was recorded in BCP1 followed by F2; while IET6279 recorded the smallest range. BCP1 recorded the highest CV (8.34%) followed by BCP1 (7.80%) while IET6279 recorded the lowest (2.89%).

In the case of grain width, IET6279 recorded the highest mean (2.73) followed by F2 (2.71); while IR70445-146-3-3 (2.49) recorded the lowest. The means of F1, F2, BCP1 and BCP2 were all within parental limits. The range of variation in BCP1 was higher than BCP2, F2, F1 and parents. BCP1 had the highest CV (3.17%) followed by BCP2 (1.95%); while F2 recorded the lowest (0.25%) (Table 4).

Heritability was estimated for four agro - morphological characters (Table 5). Broad sense heritability estimates were high for number of spikelets per plant, grain length and grain width but low for number of fertile spikelets per plant. Grain width recorded highest broad sense heritability (86%) with a narrow sense heritability (08%) followed by grain length which recorded 79% and narrow sense of (14%) heritabilities. This was followed by number of spikelets per plant which recorded 65% and narrow sense of (38%) heritabilities, respectively; while heritability estimates of number of fertile spikelets per plant were observed to possess low broad sense heritability. These further indicated that the trait was highly influenced by the environments (Table 5).

The analysis of gene effects in six-parameter model revealed that additive, dominance and epistatic effects were involved in the inheritance of all traits. The additive (a) and dominance (d) genetic effects had a significant contribution in all the characters studied. Additive gene effects were found to be relatively more important, as indicated by the fact that in all cases the additive (a) values were higher than the dominance (d) values. Regarding the non-allelic interactions, the additive × dominance gene effect (ad) was significant for all the characters studied except for grain width, additive × additive gene effect (aa) was significant for grain width and grain width and dominance × dominance (dd) genetic effects was only significant for grain width. The additive × additive and dominance × dominance (dd) interaction were larger in magnitude than their corresponding additive × additive (aa) effects. The dominance (d) and dominance × dominance (dd) effects were in the opposite direction, suggesting that duplicate type of epistasis exists for grain width (Table 6).

DISCUSSION

The inheritance study of quantitative characters in various crosses will help breeders to choose appropriate breeding methods. IR70445-146-3-3 was used as donor in an attempt to incorporate aroma into IET6279. F1 of

Table 2. Number of plants expressing aromatic and non-aromatic grain type according to KOH test in two rice genotypes.

Parents	No. of plants tested	No. of plants	
		Aromatic plants	Non-aromatic plants
IET6279	25	0	25
IR70445-146-3-3	60	60	0
F1	45	0	45
F2	792	203	589
BCP2	171	79	92
BCP1	60	0	60

Table 3. Inheritance pattern of aroma in F2 and BCP2 populations in two rice genotypes.

Cross	No. of plants tested	No. of plants				Ratio	Chi-square	P value
		Non-aromatic plants		Aromatic plants				
		Observed	Expected	Observed	Expected			
F2	792	203	198	589	594	1:3	0.14	3.84
BCP2	171	79	85.5	92	85.5	1:1	0.84	3.84

IET6279/IR70445-146-3-3 was non-aromatic.

A recessive gene, therefore, controls aroma in IR70445-146-3-3. The F2 for IET 6279/IR70445-146-3-3 was segregated into 203 aromatic: 589 non-aromatic plants, indicating a 1: 3 ratio ($\chi^2 = 0.14$). A backcross (test cross), BCP2 (IET6279/IR70445-146-3-3//IR70445-146-3-3) segregated into 79 aromatic: 92 non-aromatic plants were obtained, indicating a 1:1 ratio ($\chi^2 = 0.84$). BCP1 (IET6279/IR70445-146-3-3//IET6279) plants were all non-aromatic. The segregation ratios (F2 and BCP2) indicated that a single recessive gene controls aroma in IR70445-146-3-3. These show that there would be a high probability of success in selecting for aroma using pedigree breeding in early generations of F2 (Table 2). Single gene control of aroma has been widely reported (Pinson, 1994; Dong et al., 2000, 2001a, b). However, multiple gene control of aroma has also been reported (Geetha, 1994; Pinson, 1994; Dong et al., 2000, 2001b). This report has also validated Pinson (1994)'s report that J85 was under the control of a single recessive gene. It must be noted that some researchers have used the same method on different cultivars and have reported both monogenic and digenic inheritance depending on the cultivar used (Pinson, 1994; Dong et al., 2000, 2001b). Tsuzuki and Shimokwa (1990) reported that the lack of agreement among researchers as to whether a single recessive gene, or two or three recessive or dominant genes control aroma in rice, appears to be related to the differences in the aromatic varieties used and also the differences in the methods used in evaluating aroma. It is suggested that some aromatic

cultivars contain a single gene whilst others contain two or more aroma genes; and that the difference in opinion on the inheritance of aroma is mainly due to cultivar differences.

The magnitude of heritability is classified as low (below 30%), medium (30 to 60%) and high (above 60%) (Babu et al., 2012). High broad sense heritability was recorded for number of spikelets per plant, grain length and grain width. High heritability values indicate that the characters under study are less influenced by environment in their expression, which suggests that these traits would respond to selection owing to their high genetic variability and transmissibility. Thus, selection based on phenotypic values would be effective for these traits. These findings are in agreement with those of Pallabi et al. (2013) for number of spikelets per plant in rice, Kiani (2013) and Tuhina et al. (2015) for both grain length and grain width. However, these results were contrary to the finding of Rafii et al. (2014) who reported low broad sense heritability for grain length and grain width in rice, respectively. In contrast, number of fertile spikelets per plant had low heritability which indicates greater role of environment on the expression of the traits. Thus, direct selection for these traits will be ineffective. Therefore, methods of selection based on families and progeny testing are more effective and efficient. On the contrary, Pallabi et al. (2013) reported high broad sense heritability for number of fertile spikelets per plant in rice, possibly because the author might have used different genotypes and environmental conditions under which their study was conducted.

Table 4. Mean performance, standard deviation, ranges and coefficient of variation (CV) yield attributes of six generations in two rice genotypes.

Traits	Generation	Mean	StDev	Range	C.V
Number of spikelets per plant	IET6279	3785	59.70	3723-3843	1.58
	IR70445-146-3-3	2194	29.10	2173-2227	1.33
	F1	2219	28.40	2190-2247	1.28
	F2	2652	70.70	2570-2693	2.67
	BCP1	2662	110.60	2593-2789	4.16
	BCP2	2596	76.500	2534-2682	2.95
Number of fertile spikelets per plant	IET6279	3182	16.90	3165-3199	0.53
	IR70445-146-3-3	2057	40.30	2017-2098	1.96
	F1	2182	35.90	2146-2218	1.65
	F2	2333	22.60	2320-2356	0.97
	BCP1	2299	79.70	2238-2389	3.47
	BCP2	2140	14.70	2130-2157	0.69
Grain length (mm)	IET6279	8.19	0.24	7.68-8.63	2.89
	IR70445-146-3-3	10.92	0.36	10.19-11.65	3.31
	F1	9.31	0.33	8.67-9.99	3.54
	F2	9.62	0.68	7.53-11.83	7.11
	BCP1	9.22	0.77	7.72-11.81	8.34
	BCP2	9.73	0.76	7.48-11.9	7.8
Grain width (mm)	IET6279	2.73	0.01	2.72-2.74	0.37
	IR70445-146-3-3	2.49	0.02	2.47-2.52	0.87
	F1	2.55	0.09	2.52-2.59	1.53
	F2	2.71	0.21	2.72-2.74	0.25
	BCP1	2.67	0.18	2.61-2.77	3.17
	BCP2	2.55	0.14	2.48- 2.57	1.95

Table 5. Heritability estimates for yield attributes calculated from estimated variance component in of rice genotypes.

Characters	Heritability	
	Broad sense (%)	Narrow sense (%)
Number of spikelets per plant	65	38
Number of fertile spikelets per plant	27	10
Grain length (mm)	79	14
Grain width (mm)	86	08

The analysis of gene effects in six-parameter model revealed that additive, dominance and epistatic effects were involved in the inheritance of all traits studied. The additive (a) and dominance (d) genetic effects had a significant contribution in almost all the characters studied. Additive gene effects were found to be relatively more important, as indicated by the fact that in all cases the additive (a) values were higher than the dominance

(d) values. These findings are in agreement with Hasib et al. (2002) and Mahalingam and Nadarajan (2010). Snape (1987) pointed out that dominance could be small due to its ambi directional nature. However, previous studies have revealed that epistasis as a basic mechanism cannot be ignored. Thus, formulating breeding policies on the basis of only main gene effects that is, additive and dominance could be misleading (Sand and Lal, 2014).

Table 6. REML estimates of variance components for genetic effects of yield attributes obtained through generation mean analysis in two rice genotypes.

Variables	Characters			
	Number of spikelets per plant	Number of fertile spikelets per plant	Grain length (mm)	Grain width (mm)
m	2656**	2289**	9.569**	2.679**
a	796.7**	546.5**	-1.363**	0.1043**
d	-953.4**	-1592*	-1.192*	-0.9191**
aa	-119.6	-245.4	-0.5698**	-0.4617**
ad	-1499**	-836.2**	1.705*	0.04939
dd	66.14	911.1	0.3792	0.3826**
Type of epistasis	-	-	-	Duplicate

*and **: significant at 5 and 1% probability levels, respectively. (a) additive; (d) dominance; (aa) additive × additive; (ad) additive × dominance; (dd) dominance × dominance gene effects.

The performance of all of the characters studied manifesting non-allelic interactions is an indication that epistasis is determined to some extent by the genotypes used for the study. The additive effects and gene interaction dominance × dominance (dd) or other type digenic complementary gene interaction can be exploited effectively by selection for the improvement of characters. It might be possible to follow 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 or 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. Presence of non-additive gene for number of spikelets per plant, number of fertile spikelets per plant, grain length and grain width indicate that conventional selection procedure may not be effective enough for improvement of yield. Therefore postponement of selection in later generations or inter-mating among the selected segregants followed by one or two generations of selfing could be suggested to break the undesirable linkage and allow the accumulation of favorable alleles for the improvement of these traits. The results agreed with the findings of Patel et al. (2014) and Jarwar et al. (2014) who reported the influence of both additive and non-additive gene action in control of grain length and grain width in rice while Munhot et al. (2000) and Annadurai and Nadarajan (2001) reported non additive genetic variance for grain yield attribute in rice. Verma et al. (1994) indicated that epistasis plays a vital role in grain components yield except grain number in panicle in rice, Abebe et al. (2017) reported the predominance of non-additive gene action in controlling spikelet traits in rice, and Pallabi et al. (2013) reported

the role of additive gene action governed for number of spikelets per plant in rice. Duplicate type of epistasis as evidenced from opposite sign of (d) and (dd) was noticed from the expression of grain width. This type of epistasis tends to cancel or weaken the effect of each other in hybrid combination and hinders the progress made under selection and therefore, selection would have to be deferred till late generations of segregation where dominance effects are dissipated.

Conclusion

Result from this study favored a single recessive gene control of aroma as opposed to multiple gene control. However, a careful review of literature compared to this work suggests that, there are differences in the number of genes controlling aroma in different varieties. An F₂ ratio of 1:3 (aromatic: non-aromatic) plants and a backcross (IET6279/ IR70445-146-3-3 // IR70445-146-3-3) ratio of 1:1 indicate that a single recessive gene controls aroma in IR70445-146-3-3. Broad sense heritability estimates were high for number of spikelets per plant, grain length and grain width, while low broad sense heritability estimate was observed for number of fertile spikelets per plant. The analysis of gene effects revealed that additive, dominance and epistatic effects were involved in the inheritance of all the traits. However, additive effect, in general was of higher magnitude than dominance gene effect in all the characters studied. All the traits manifested non-allelic interactions, indicating that epistasis is determined to some extent by the genotypes used for the study. Thus, in the presence of epistasis, grain width showed that significant duplicate type of gene interaction restricted the scope of simple selection for the characters studied. Therefore delaying selections to later generations using recurrent selection

will enhance success in improving yield attributes in all the genotypes studied.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGMENTS

The authors appreciate the kindness of the West African Agricultural Productivity Program (WAAPP–1C SL) for the sponsorship of the research work. They are also grateful to the staff of CSIR-Crops Research Institute Kumasi, Ghana for providing the rice germplasm used for the research.

REFERENCES

- Abebe T, Alamerew S, Tulu L (2017). genetic variability, heritability and genetic advance for yield and its related traits in rainfed lowland rice (*Oryza sativa* L.) Genotypes at Fogera and Pawe, Ethiopia. *Adv. Crop Sci. Technol.* 5(2):1-8.
- Allard RW (1960). Principles of plant breeding. John Wiley, New York pp. 83-108.
- Annadurai A, Nadarajan N (2001). Combining ability for yield component and physiological traits in hybrid Rice. *Madras Agric. J.* 88:300-303.
- Babu RV, Shreya K, Singh DK, Usharani G, Shankar AS (2012). Correlation and path coefficient analysis studies in popular rice hybrids of India. *Int. J. Sci. Res. Pub.* 2(6):1-5.
- Berner DK, Hoff BJ (1986). Inheritance of scent in American long grain rice. *Crop Sci.* 26(5):876-878.
- Chen S, Wu J, Yang Y, Shi W, Xu M (2006). The *ggr* gene responsible for rice fragrance was restricted within 69kb. *Plant Sci.* 171:505-514.
- Dela CN, Khush GS (2000). Rice grain quality evaluation procedures. In: *Aromatic rices*. Singh RK, Singh US, Khush GS (Eds). Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, India. pp. 16-28.
- Diako C, Sakyi-Dawson E, Bediako-Amoa B, Saalia FK, Manful JT (2010). Consumer perceptions, knowledge and preferences for aromatic rice types in Ghana. *Nature Sci.* 8(12):12-19.
- Dong JY, Tsuzuki E, Terao H (2000). Inheritance of aroma in four rice cultivars (*Oryza sativa* L.). *IRRI. Int. Rice Res. Notes* 25:2.
- Dong Y, Tsuzuki E, Terao H (2001a). Trisomic genetic analysis of aroma in three Japanese native rice varieties (*Oryza sativa*, L). *Euphytica* 117:191-196.
- Dong Y, Tsuzuki E, Terao H (2001b). Genetic analysis of aroma in three rice cultivars (*Oryza sativa*, L). *J. Genet. Breed.* 55:39-44.
- Duffuor K (2009). Budget Statement and Economic Policy of the Government of Ghana for the (2010) Fiscal Year. *Ecology* 22(1):43-45.
- Geetha S (1994). Inheritance of aroma in two rice crosses. *Int. Rice Res. Notes* 19(2):5.
- Golan F, Mohamad O, Hadjim K, Craig AM (2004). Inheritance of kernel elongation in rice. *Int. J. Agric. Biol.* 5:813-815.
- Gomez AK, Gomez AA (1984). *Statistical Procedures for Agricultural Research*. John Wiley, New York. pp. 458-465.
- Halloran GM, Knight R, McWhirter KS, Sparrow DHB (1979). *Plant Breeding* (Ed. R. Knight). Poly-Graphics Pty. Ltd. pp. 61-62.
- Hasib KM, Ganguli PK, Kole PC (2002). Genetic analysis of some quantitative characters in aromatic rice involving induced mutants. *Trop. Agric. Res. Ext.* 5(1-2):1-6.
- Huang J, David CC, Duff B (1991). Rice in Asia: Is it becoming an inferior good? *Comment. Am. J. Agric. Econ.* 73:515-521.
- Jarwar AD, Dela Cruz QD, Junejo GS, Jarwar M (2014). Gene action of some agronomic, yield and quality characters in aromatic rice (*Oryza sativa* L.) varieties and their F1 hybrids under lowland and upland environments. *Pak. J. Agric. Eng. Vet. Sci.* 30(1):1-7.
- Khush GS, Paule CM, DeLa Cruz MN (1979). Rice quality evaluation and improvement at IRRI. In *Proceedings of the workshop on chemical aspects of rice grain quality*, International Rice Research Institute. Los Banos, Laguna, Philippines pp. 21-31.
- Khattak GSS, Haq MA, Ashraf M, Mcneilly T (2001). Genetic basis of variation of yield and yield components in mungbean (*Vigna radiata* L). *Hereditas* 134:211-217.
- Kiani G (2013). Heritability and diversity analysis of quantitative traits in rice. *Agric. Conspect. Sci.* 78(2):113-117.
- Kohnaki ME, Kiani G, Nematzadeh G (2013). Relationship between morphological traits in rice restorer lines at F3 generation using multivariate analysis. *Int. J. Adv. Biol. Biomed. Res.* 1(6):572-577.
- Lin S (1991). Rice Aroma: Methods of Evaluation and Genetics. In: *Rice Genetics II*, (Eds.) International Rice Research Institute, Manila, Philippines.
- Lorieux M, Petrov M, Haung N, Guiderdoni E, Ghesquiere A (1996). Aroma in rice: Genetic analysis of a quantitative trait. *Theor. Appl. Genet.* 93:1145-1151.
- Mahalingam L, Nadarajan N (2010). Genetic analysis of grain yield and milling quality characters of two line rice hybrids. *Elect. J. Plant Breed.* 1(4):977-982.
- Mather K, Jinks L (1971). *Biometrical genetics*. Ithaca, NY: Cornell University Press.
- Ministry of Food and Agriculture (MOFA) (2010). *Agriculture in Ghana-Facts and Figures*. Statistics, Research and Information Directorate (SRID), Ministry of Food and Agriculture, Accra, Ghana P 58.
- Ministry of Food and Agriculture (MOFA) (2009). *National Rice Development Strategy*. Draft. Ministry of Food and Agriculture, Accra, Ghana P. 26.
- Moreno-Gonzalez J, Cubero JI (1993). Selection Methods. In: *Plant Breeding: Principles and Prospects*, Hayward, M.D., I. Romagosa and N.O. Bosemark (Eds.). Chapman and Hall, London, UK. pp. 281-313.
- Munhot MK, Sarawgi AK, Rastogi NK (2000). Gene action and combining ability for yield, grain quality and other related characters in rice. *Oryza* 37(1):1-6.
- Pachauri V, Singh MK, Singh AK, Singh S, Shakeel NA, Singh VP, Singh NK (2010). Origin and Genetic Diversity of Aromatic Rice Varieties, Molecular Breeding and Chemical and Genetic Basis of Rice Aroma. *J. Plant Biochem. Biotechnol.* 19(2):127-143.
- Pallabi D, Partha ND, Borua PK (2013). Morphological Traits as Selection Indices in Rice: A Statistical View. *Univ. J. Agric. Res.* 1(3):85-96
- Patel JR, Saiyad MR, Prajapati KN, Patel RA, Bhavani RT (2014). Genetic variability and character association studies in rainfed upland rice (*Oryza sativa* L.). *Elect. J. Plant Breed.* 5(3):531-537.
- Pinson SRM (1994). Inheritance of Aroma in Six Rice Cultivars. *Crop Sci.* 34:1151-1157.
- Rafii MY, Zakiah MZ, Asfaliza R, Iffah Haifaa MD, Latif MA, Malek MA (2014). Grain Quality Performance and Heritability Estimation in Selected F1 Rice Genotypes. *Sains Malaysiana* 43(1):1-7.
- Sand AS, Lal JP (2014). Estimation of Generation Mean- Five Parameter Model for the Evaluation of Drought Tolerant Lines in Rice (*Oryza sativa* L.). *Int. J. Sci. Footprints* 2(4):1-17.
- Shi C, Wu J, Wu P (2005). Genetic analysis of developmental behavior for amylose content in filling process of rice. *J. Sci. Food. Agric.* 85:791-796
- Shi C, Zhu J, Wu J, Fan L (2000). Genetic and genotype x environment interaction effects from embryo, endosperm, cytoplasm and maternal plant for rice grain shape traits of Indica rice. *Field Crops Res.* 68:191-198.
- Snape JW (1987). Conventional methods of genetic analysis in wheat. In: *Lupton F G H (ed) Wheat breeding, its scientific basis*. Chapman and Hall, London, New York pp. 109-128.
- Sood BC, Siddiq EA (1978). A rapid technique for scent determination in rice. *Indian J. Genet. Plant Breed.* 38:268-271.

- Syed E, Khaliq I (2008). Quantitative inheritance of some physiological traits for spring wheat under two different population densities. Pak. J. Bot. 40(2):581-587.
- Tsuzuki E, Shimokawa E (1990). Inheritance of aroma in rice. Euphytica 46:157-159.
- Tuhina KM, Mohamed MH, Mohd RY, Wong MY, Faezah MS, Jannatul F (2015). Genetic variation, heritability, and diversity analysis of upland rice (*Oryza sativa* L.) genotypes based on quantitative traits. BioMed Res. Int. 1:1-7.
- Verma PK, Katoch PC, Kaushik RP (1994). Genetics of harvest index and grain characters eliminating and allowing the inadequacy of testers using selfing generation of triple test cross in rice. Ann. Biol. 10:216-222.
- Zhang M, Guo B, Peng Z (2005). Genetic effects on grain characteristics of indica black rice and their uses on indirect selections for some mineral element contents in grains. Genet. Resour. Crop Evol. 52:1121-1128.