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Original scientific article

GENE ACTION AND HETEROSIS FOR AGRO-NUTRITIONAL QUALITY TRAITS OF MAIZE HYBRIDS IN HUMID AGRO-ECOLOGIES OF NIGERIA

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Maize is a staple food of sub-Saharan African (SSA) populace but deficient in protein. Quality protein maize (QPM) has been developed to contain essential amino acids including lysine and tryptophan to alleviate malnutrition in SSA. This study was conducted to assess general and specific combining ability (GCA and SCA) effects, gene actions and heterosis among QPM hybrids for lysine and tryptophan at three locations in humid agro-ecologies of Nigeria. Grains from sib-mated full-sibs were analysed for lysine and tryptophan among ten inbreds, 45 hybrids generated by half-diallel and two checks. Results showed lysine and tryptophan contents ranged from 2.71% - 0.73% (Kishi) to 3.41% - 0.96% (Ibadan). Gene actions for expression of lysine and tryptophan varied with location; thus, additive gene action was preponderance in inheritance of lysine and tryptophan in Ibadan and Ile-Ife, whereas non-additive gene action was involved in inheritance of these traits in Kishi. Inbreds TZEEQI-8, TZEEQI3, TZEEQI-10, TZEEQI-12, TZEEQI-2 were best combiners for lysine and tryptophan. Hybrids TZEEQI-8×TZEEQI-16, TZEEQI-2×TZEEQI-12, TZEEQI 10×TZEEQI-7,TZEEQI-10×TZEEQI-12 and TZEEQI-8×TZEEQI-12 were adjudged as the top five hybrids for exhibiting positive and significant standard heterosis over commercial

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check with a range of 12.8%-16.7% for lysine and 15.4%-20.0% for tryptophan across locations. The relationship between grain yield with lysine and tryptophan was negative and significant across locations. Hence, breeding for high yielding QPM genotypes with high lysine and tryptophan contents at the same time, requires careful monitoring of lysine and tryptophan contents in the laboratory.

Keywords: Quality protein maize, lysine, tryptophan, grain yield, combining ability, heterosis

INTRODUCTION

Maize (*Zea mays* L.) is an important staple food crop widely grown in sub-Saharan Africa (SSA). Globally, it is the third most important cereal after wheat and rice and the first in SSA, where over 80% of the population depend on it as a source of livelihood (ASARECA, 2014; PARDEY *et al.*, 2016). It is one of the major sources of food for human, livestock and industrial raw materials (brewery, confectionery) (OLAKOJO, 2001). I*n about 94 developing countries, more than 4.5 billion people rely* on it for *at least 30%* of their entire daily calories *(*CIMMYT and IITA, 2011; SHIFERAW *et al.*, 2011), *while* about twelve countries in SSA, rely on it for at least 20% of their entire daily calorie intake and up to 60% for their total daily protein intake (KRIVANEK and VIVEK, 2006). Its utilization was predicted to increase by 50% globally and 93% in SSA between 1995 and 2020 (CIMMYT, 2001). In Nigeria, maize is the most available staple crop and it plays a vital role in food security, employment and income generation for both small-holder families and large-scale businesses. Nigeria is the 10th largest producer of maize in the world and adjudged as the major producer of maize in Africa, followed by South Africa (usaid 2010; faostat, 2012), demonstrating the importance of maize to Nigeria and Africa.

There is an increase in world population from 1.7 billion in 1900 to about 7.2 billion in 2013, with an expectation of increasing to 9.6 billion in 2050 and with over 2 billion people currently faced with protein deficiency, especially among children due to poverty (ISAAA, 2014). For instance, daily protein intake in Nigeria is as low as 5 g/day compared to 46-56 g/day for a normal person and 96 g/day for nursing mothers and pregnant women as recommended by FOOD AND NUTRITION BOARD ACADEMY OF SCIENCE (1980). This has led to incidence of the disease known as *Kwashiorkor*. The disease is associated with stunted growth, skin lesions, oedema, underweight and susceptibility to hosts of infection.

The normal endosperm maize has poor nutritional value for monogastric animals including humans, because of reduced content of essential amino acids such as lysine and tryptophan, making it impossible to alleviate protein deficiency without supplementing with other rich protein sources, which are needed for growth and development of humans and animals (BHARTI *et al.*, 2017). Thus, quality protein maize (QPM) has been developed to contains twice the levels of tryptophan and lysine found in most normal endosperm maize and could contribute about 70-73% of human protein needs, compared to 46% obtainable from normal maize endosperm (OLAKOJO *et al.*, 2007; VIVEK *et al.*, 2008; ANNOR and BADU-APRAKU, 2016).

Genetic information on the estimates of combining ability to assess nature of gene actions involved in inheritance of traits is vital to a crop improvement programme (PANHWAR *et al.*, 2008). Hence, several studies on combining ability using different mating designs for QPM inbreds under different environments to ascertain the nature of gene actions and adaptation of QPM germplasm to target environments in SSA, had been conducted (WEGARY *et al.*, 2013;

BADU-APRAKU *et al.*, 2015; ANNOR and BADU-APRAKU, 2016). However, conflicting reports have been reported among authors on the nature of gene action responsible for inheritance of maize grain lysine and tryptophan contents as reported by OSORNO and CARENA (2008); NGABOYISONGA *et al.* (2008); WEGARY *et al.* (2011) in QPM germplasm at different locations in SSA. For instance, WEGARY *et al.* (2011) reported that additive gene effects were responsible for variation of tryptophan concentration in QPM grain at different environments, whereas NGABOYISONGA *et al.* (2008); OSORNO and CARENA (2008) reported that non-additive gene control inheritance of tryptophan in QPM. Thus, knowledge on the genetic control of grain lysine and tryptophan are inadequate. Studies on gene actions involved in inheritance of these traits would assist in the exploitation of heterosis for maize quality traits improvement. Therefore, this study was conducted to assess general and specific combining ability (GCA and SCA), gene actions and heterosis among quality protein hybrids for lysine and trptophan at three locations in humid agro-ecologies of Nigeria.

MATERIALS AND METHODS

Description of experimental sites

The experiment was conducted at three locations in humid agro-ecologies of Nigeria: Ibadan located in Forest-Savanna transition (latitude 7.38‘N, longitude 3.84‘E, 160 m above sea level). Cropping history of the experimental location in Ibadan showed that the site had been subjected to continuous cultivation of maize for more than fifteen years without fallowing, which resulted to depletion soil N nutrient and always receive low amount of rainfall as a result of severe rain cessation peculiar with the location (ANJORIN, 2013, AKINYOSOYE *et al.*, 2018). This location was chosen to simulate small farmers’ production fields in SSA, because most of the farm lands available for cultivation of maize by resource-limited rural farmers in Nigeria are depleted of N due to monocropping and non-availability of fertilizer (AKINYOSOYE *et al.*, 2018). Ile-Ife located in the Rain Forest ecology (latitude 7.55’N, longitude 4.56’E, 280 m above sea level), and Kishi located in the Southern Guinea Savanna ecology (latitude 8.98'N, longitude 3.94'E, 380m asl). The dominant soils types at the experimental sites were classified as Ferric Luxisols in Kishi and only as Ferric Lixisols in Ibadan and Ile-Ife (SONNEVELD, 2005). Experimental locations during the evaluation in 2017 and 2018, received rain of 152.50 mm and 147.50 mm in Ibadan; 164.50 mm and 154.50 mm in Ile-Ife; 169.50 mm and 166.50 mm in Kishi, respectively.

Genetic materials

Ten quality protein inbred lines (Table 1) were obtained from Maize Improvement Programme of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. A total of six plants were sib-mated in each plot at each location during the on-station evaluation of the forty-five (45) hybrids generated by half-diallel mating scheme, ten (10) parents and the two checks in the previous study (unpublished). At harvest, the sib-mated plants in each plot at three locations were harvested separately for chemical analysis in the laboratory. The kernels from the mid portion of the six ears for all sib-mated plots were used for the chemical analysis to ensure uniformity as kernels are more uniform at the middle of each cob.

Table 1. Pedigree and mean lysine, tryptophan and protein contents of QPM inbred lines used

Inbred lines	Code	Lysine (%)	Tryptophan (%)	Zein crude (µg/ml)	Crude protein (%)	Zein in dry matter (%)
TZEEQI 10	P1	3.12	0.86	122.02	10.21	1.72
TZEEQI 9	P2	3.38	0.95	116.70	8.25	0.96
TZEEQI 5	P3	3.38	0.95	100.03	8.25	0.97
TZEEQI 8	P4	3.36	0.94	117.43	8.40	1.02
TZEEQI 2	P5	2.99	0.82	124.44	11.20	2.10
TZEEQI 12	P6	3.05	0.84	139.66	10.74	1.93
TZEEQI 7	P7	3.16	0.88	120.09	9.89	1.60
TZEEQI 16	P8	2.99	0.82	126.37	11.20	2.10
TZEEQI 6	P9	3.14	0.87	121.29	10.06	1.67
TZEEQI 3	P10	2.90	0.79	129.51	11.87	2.36

Laboratory chemical analysis

Endosperm modification was determined at the Maize Improvement Programme, IAR&T., Ibadan to confirm the presence of modified hard endosperm in the kernels of quality protein maize inbreds and hybrids. Thus, a random 100 whole and intact kernel sample were drawn from each of the sib-mated ten quality protein inbreds to give a total of 1000 kernels. The kernels were viewed under light box for endosperm modification. The maize kernels' embryo axis was placed against the light table while, kernels were visually assessed and assigned the scores ranging from 1 – 5 [(1 = completely modified (translucent with no opaqueness, normal phenotype); 2 = 25% modified; 3 = 50% modified; 4 = 75% modified; 5 = 100% completely opaque)] (PIXLEY and BJARNASON, 2002; OLAKOJO *et al.*, 2007; KRIVANEK *et al.*, 2007; VIVEK *et al.*, 2008). Kernels with score 2 to 3 were selected as quality protein maize grain among the inbreds as recommended by VIVEK *et al.* (2008), because kernels with scores of 2 to 3, contain significant modified hard endosperm with adequate amount of lysine and tryptophan than other groups, so they were selected as QPM grain for this study. A random of 20-50 modified kernel were selected based on endosperm modification. Zein crude, zein in dry matter, lysine and tryptophan contents were determined using turbidimetric rapid method described by DROCHIOIU *et al.* (2002) and modified by OLAKOJO *et al.* (2007). Also, crude protein was estimated from percentage of nitrogen in each sample and conversion factor for maize (6.25) using standard micro-Kjeldahl procedure (AOAC, 2006).

Data analyses

Analysis of variance (ANOVA) for lysine, tryptophan and protein contents (crude protein, zein crude and zein in dry matter) at three locations and across locations were carried out with parents being considered as fixed effects and replications and blocks within replications as random effects. Combining ability of different cross combinations was estimated per location and across locations by the procedure developed by GRIFFINS (1956) linear, Method II using Plant Breeding Tool software (Version 1.2, 2013). Relative contribution of GCA and SCA on progeny performance was estimated, based on Baker's predictability ratio (BAKER, 1978) cited

by OLAKOJO and OLAOYE (2005). Heterosis was computed using Microsoft excel (FEHR, 1987) as follow:

$$\text{Heterosis over mid-parent (relative heterosis) (MPH)} = \frac{F_1 - MP}{MP} \times 100$$

$$\text{Heterosis over better parent (BPH)} = \frac{F_1 - BP}{BP} \times 100$$

$$\text{Heterosis over check (standard heterosis) (SH)} = \frac{F1 - CC}{CC} x100$$

Where: where F_1 was the performance of a hybrid with respect to a character, $MP = (P_1 + P_2) \div 2$ in which P_1 and P_2 were the performance of a given pair of inbred parents and BP was the yield of the better parent with respect to a character. CC = mean performance of the commercial check. Pearson correlation coefficient analysis was performed on grain yield of quality protein hybrids obtained in the previous study (unpublished) with lysine, tryptophan and protein contents at three locations and across locations in this study using Statistical Tool for Agricultural Research (STAR, Version: 2.0.1).

RESULTS

Combining ability for lysine, tryptophan and other protein contents of hybrids across locations

Analysis of variance (ANOVA) of genotype (main effect) and location as well as interaction between main effect and locations were highly significant ($P<0.01$) for all the traits such as lysine, tryptophan, zein crude, crude protein, zein in dry matter, across three locations (Table 2). General and specific combining ability (GCA and SCA) effects were highly significant for all traits in Ibadan and Ile-Ife, whereas only SCA effect was highly significant for all the traits in Kishi, but GCA effect was non-significant for all the traits in Kishi. However, across locations, GCA and SCA were not significant for all of the traits while GCA × location and SCA × location interactions were highly significant for all the traits. GCA mean squares were larger than SCA mean squares for all traits in Ibadan and Ile-Ife, whereas SCA mean squares were larger than GCA mean squares for all traits in Kishi (Table 2). Also, progeny performance revealed high predictability values (>0.7) in Ibadan, Ile-Ife and across location for all traits, except for lysine in across locations, whereas, the values were less than or equal to 0.5 (≤ 0.5) for all traits in Kishi (Table 2).

Table 3 revealed that lysine and tryptophan contents of the QPM hybrids ranged from 2.71% and 0.73% (Kishi) to 3.41% and 0.96% (Ibadan), respectively, whereas other protein contents such as crude protein, zein in crude form and zein in dry matter were highest in Kishi with least values recorded in Ibadan. Also, most of the hybrids had higher percentage lysine and tryptophan contents than the two checks at three locations and across locations. On the other hand, QPM hybrids had higher lysine (3.12%) and tryptophan (0.86%) contents than QPM check with mean values of 2.99% and 0.82% for lysine and tryptophan, respectively, across locations.

Table 2. Mean squares for lysine, tryptophan and other protein contents in quality protein maize in Ibadan, Ile-Ife, Kishi and across locations

Source	Df	Lysine (%)	Tryptophan (%)	Zein (µg/ml)	Crude Protein (%)	Zein in Dry matter (%)
			Ibadan			
Hybrids	54	0.16**	0.02**	661.07**	9.06**	1.35**
GCA	9	0.13**	0.014**	520.18**	7.13**	1.06**
SCA	45	0.04**	0.0043**	160.39**	2.00**	0.33**
Error	110	0.0001	0.0001	0.18	0.01	0.001
PR		0.75	0.77	0.76	0.78	0.76
			Ile-Ife			
Hybrids	54	0.56**	0.06**	3290.76**	31.05**	4.64**
GCA	9	0.40**	0.043*	2650.10**	22.25*	3.39*
SCA	45	0.14**	0.016**	786.28**	7.97**	1.18**
Error	110	0.004	0.0004	0.18	0.21	0.006
PR		0.74	0.73	0.77	0.74	0.74
			Kishi			
Hybrids	54	0.62**	0.62**	3777.94**	34.82**	5.18**
GCA	9	0.16	0.017	1000.45	9.02	1.34
SCA	45	0.22**	0.023**	1311.08**	12.12**	1.81**
Error	110	0.0001	0.0001	0.0005	0.003	0.0001
PR		0.48	0.43	0.43	0.43	0.43
			Across			
Location(L)	2	16.04**	1.74**	82375.65**	894.23**	132.93**
Hybrids(H)	54	0.38	0.041	2086.13	21.06	3.09
GCA	9	0.5	0.054	3792.92	27.98	4.12
SCA	45	0.83	0.038	1744.77	19.68	2.89
H × L	108	0.48**	0.052**	2821.82**	26.94**	4.04**
GCA × L	18	0.78**	0.08**	4359.63**	43.62**	6.64**
SCA × L	90	0.42**	0.05**	2414.26**	23.60**	3.52**
PR		0.38	0.59	0.68	0.59	0.59
Error	330	0.0037	0.0004	0.0053	0.22	0.0073
Mean		3.12	0.86	121.11	4.55	1.72
Minimum		2.17	0.55	87.22	2.91	0.07
Maximum		4.10	1.18	189.45	17.34	4.47
SE(0.05)		0.02	0.01	1.54	0.16	0.06
CV%		1.99	2.37	0.59	10.2	4.95

*Significant at p=0.05, **significant at p=0.01. GCA and SCA= general and specific combining ability, respectively; CV and SE are coefficient of variation, and standard error of the mean, respectively. PR implies relative contribution of GCA and SCA on progeny performance

Table 3. Means and coefficient of variation for lysine, tryptophan and protein contents of hybrids at Ibadan, Ile-Ife and Kishi in Southwestern Nigeria

	Lysine (%)	Tryptophan (%)	Zein DM (%)	Crude protein (%)	Zein crude (µg/ml)
		Ibadan			
Grand mean	3.41	0.96	0.9	8.08	97.59
Mean for QPM hybrids	3.44	0.97	0.82	7.87	95.38
Mean for QPM check	3.31	0.92	1.19	8.84	100.99
Mean for non-QPM check	2.2	0.56	4.37	17.08	193.07
CV(%)	0.51	0.59	0.73	1.59	4.73
		Ile-Ife			
Grand mean	3.16	0.88	1.62	9.91	119.9
Mean for QPM hybrids	3.19	0.89	1.54	9.69	122.46
Mean for QPM check	2.83	0.77	2.56	12.39	118.33
Mean for non-QPM check	2.16	0.55	4.5	17.4	198.15
CV(%)	3.6	4.28	0.63	8.58	9.04
		Kishi			
Grand mean	2.71	0.73	2.9	13.25	149.55
Mean for QPM hybrids	2.8	0.73	2.87	13.18	149.2
Mean for QPM check	2.82	0.77	2.57	12.4	112.35
Mean for non-QPM check	2.13	0.54	4.56	17.56	202.5
CV(%)	0.49	0.6	0.5	0.75	1.32
		Across			
Grand mean	3.10	0.86	1.78	10.34	122.24
Mean for QPM hybrids	3.12	0.86	1.72	10.2	121.11
Mean for QPM check	2.99	0.82	2.11	11.21	108.57
Mean for non-QPM check	2.17	0.54	4.48	17.35	197.9
P value	**	**	**	**	**
SE(0.05)	0.02	0.01	1.56	0.06	0.16
CV(%)	2.16	2.58	0.6	5.03	4.8

CV and SE are coefficient of variation, and standard error of the mean, respectively

Table 4. General combining ability (GCA) for protein contents, lysine and tryptophan of inbreds at Ibadan, Ile-Ife and Kishi in southwestern Nigeria

Inbreds	Lysine (%)	Trypto Phan (%)	Zein Crude (µg/ml)	Crude Protein (%)	Zein dry matter (%)	Lysine (%)	Trypto phan (%)	Zein Crude (µg/ml)	Crude Protein (%)	Zein dry matter (%)	Lysine (%)	Trypto phan (%)	Zein Crude (µg/ml)	Crude Protein (%)	Zein dry matter (%)
			Ibadan					**Ile-Ife**					**Kishi**		
TZEEQI10	0.01	0.00	-7.02	-0.06	-0.02	0.24	0.08	-23.41	-1.83	-0.72	0.09	0.03	-6.05	-0.65	-0.25
TZEEQI9	-0.25	-0.08	14.25	1.88	0.72	0.21	0.07	-15.07	-1.55	-0.61	0.07	0.02	-5.69	-0.52	-0.20
TZEEQI5	0.06	0.02	-5.21	-0.48	-0.19	0.22	0.07	-17.30	-1.61	-0.63	-0.19	-0.06	14.24	1.41	0.54
TZEEQI8	0.03	0.01	5.91	-0.25	-0.10	0.08	0.03	-0.51	-0.57	-0.17	0.23	0.08	-19.16	-1.71	-0.66
TZEEQI2	0.02	0.01	-2.67	-0.16	-0.06	-0.02	-0.01	0.04	0.13	0.04	-0.04	-0.01	1.86	0.31	0.12
TZEEQI12	0.07	0.02	5.24	-0.49	-0.18	-0.23	-0.07	20.21	1.70	0.70	-0.02	-0.01	1.98	0.14	0.05
TZEEQI7	0.07	0.02	-4.24	-0.50	-0.19	-0.27	-0.09	19.49	2.00	0.76	0.02	0.01	-0.13	-0.13	-0.05
TZEEQI16	-0.05	-0.02	-1.40	0.37	0.14	-0.09	-0.03	7.53	0.64	0.23	0.03	0.01	-1.10	-0.20	-0.08
TZEEQI6	0.11	0.04	-4.60	-0.80	-0.31	-0.04	-0.01	0.82	0.28	0.10	-0.12	-0.04	8.39	0.88	0.34
TZEEQI3	-0.06	-0.02	-0.25	0.47	0.19	-0.11	-0.04	8.19	0.81	0.30	-0.06	-0.02	5.67	0.46	0.18
SE(gi-gj)	0.00	0.00	0.17	0.03	0.01	0.02	0.01	0.17	0.19	0.03	0.00	0.00	0.17	0.02	0.01
LSD(0.05)	0.01	0.00	0.34	0.05	0.02	0.05	0.02	0.34	0.37	0.06	0.01	0.00	0.34	0.05	0.02

LSD: Least significant difference at P= 0.05; SE: Standard error of g_i and g_j general combining ability of i^{th} and j^{th} parent respectively

GCA effects showed that seven inbreds TZEEQI10, TZEEQI5, TZEEQI8, TZEEQI2, TZEEQI12, TZEEQI7 and TZEEQI6 expressed positive GCA effect for lysine and tryptophan in Ibadan, whereas, only four inbreds TZEEQI10, TZEEQI9, TZEEQI5 and TZEEQI8 had positive GCA effect for these traits in Ile-Ife and five inbreds TZEEQI10, TZEEQI9, TZEEQI8, TZEEQI7 and TZEEQI16 displayed positive GCA effect for these traits in Kishi (Table 4). Across, locations, four inbreds TZEEQI10, TZEEQI9, TZEEQI8 and TZEEQI5 exhibited positive GCA effect for for lysine and tryptophan (Table 4b). Two inbreds TZEEQ 12 and TZEEQI3 exhibited positive GCA effect for crude proein, zein crude and zein in dry matter in Ile-Ife, Kishi and across locations (Table 5).

SCA effects revealed that some inbreds such as TZEEQI8, TZEEQI3, TZEEQI10, TZEEQI2 possessed good combining ability in hybrid combinations for lysine and tryptophan. For instance, inbreds TZEEQI8 and TZEEQI3 featured in 6 crosses while inbreds TZEEQI10 and TZEEQI2 had 5 appearances in hybrid combination for lysine and tryptophan across locations (Table 4a). Moreover, 28 and 29 hybrids exhibited positive SCA effect for lysine and tryptophan, respectively, which ranged from -0.58 for TZEEQI9 × TZEEQI2 to 0.28 for TZEEQI10 × TZEEQI9, TZEEQI2 × TZEEQI16 for lysine and -0.19 for TZEEQI9 × TZEEQI2 to 0.09 for TZEEQI10 × TZEEQI9, TZEEQI2 × TZEEQI16, TZEEQI2 × TZEEQI3 for tryptophan in Ibadan. Also, 26 hybrids manifesting positive SCA effect for lysine and tryptophan with a range of -0.81 for TZEEQI5 × TZEEQI8 to 0.58 for TZEEQI2 × TZEEQI6 for lysine and -0.27 for TZEEQI5 × TZEEQI8 to 0.19 for TZEEQI2 × TZEEQI6 for tryptophan in Ile-Ife. In addition, 17 showed positive SCA effect with a range of -0.71 for TZEEQI8 × TZEEQI2 to 0.59 for TZEEQI9 × TZEEQI5 for lysine and -0.23 for TZEEQI8 × TZEEQI2 to 0.20 for TZEEQI9 × TZEEQI5 for tryptophan in Kishi (Table 6).

Table 5. General combining ability (GCA) for protein contents, lysine and tryptophan of inbreds across locations in southwestern Nigeria

Inbreds	Lysine (%)	Tryptophan (%)	Zein Crude (µg/ml)	Crude Protein (%)	Zein dry matter (%)
TZEEQI10	0.11	0.04	-12.16	-0.85	-0.33
TZEEQI9	0.01	0.00	-2.17	-0.06	-0.03
TZEEQI5	0.03	0.01	-2.76	-0.23	-0.09
TZEEQI8	0.11	0.04	-4.59	-0.84	-0.31
TZEEQI2	-0.01	0.00	-0.26	0.09	0.03
TZEEQI12	-0.06	-0.02	9.15	0.45	0.19
TZEEQI7	-0.06	-0.02	5.04	0.46	0.17
TZEEQI16	-0.04	-0.01	1.68	0.27	0.10
TZEEQI6	-0.02	-0.01	1.53	0.12	0.04
TZEEQI3	-0.08	-0.03	4.54	0.58	0.22
SE(gi-gj)	0.01	0.00	0.10	0.06	0.01
LSD(0.05)	0.02	0.01	0.19	0.12	0.02

LSD: Least significant difference at P= 0.05; SE: Standard error of g_i and g_j general combining ability of i^{th} and j^{th} parent respectively

Table 6. Effects of specific combining ability (SCA) for lysine and tryptophan among some selected hybrids at Ibadan, Ile-Ife, Kishi and across locations

Hybrids	Ibadan		Ile-Ife		Kishi		Across	
	Lysine (%)	Tryptophan (%)	Lysine (%)	Tryptophan (%)	Lysine (%)	Tryptophan (%)	Lysine (%)	Tryptophan(%)
P1 × P2	0.28	0.09	-0.74	-0.24	0.32	0.10	-0.05	-0.02
P1 × P3	-0.10	-0.03	-0.22	-0.07	-0.09	-0.03	-0.14	-0.04
P1 × P6	-0.07	-0.02	0.37	0.12	0.41	0.13	0.24	0.08
P1 × P7	-0.07	-0.02	0.48	0.16	0.37	0.12	0.26	0.09
P1 × P9	-0.17	-0.06	-0.03	-0.01	0.48	0.16	0.09	0.03
P1 × P10	0.00	0.00	0.10	0.03	0.48	0.16	0.20	0.06
P2 × P3	0.07	0.02	-0.27	-0.09	0.59	0.20	0.13	0.04
P2 × P5	-0.58	-0.19	0.05	0.02	-0.38	-0.13	-0.29	-0.10
P3 × P4	-0.03	-0.01	-0.81	-0.27	-0.60	-0.20	-0.48	-0.16
P3 × P8	0.11	0.04	0.29	0.10	0.00	0.00	0.14	0.04
P3 × P9	-0.07	-0.02	0.06	0.02	-0.28	-0.09	-0.10	-0.03
P4 × P5	0.07	0.02	0.33	0.11	-0.71	-0.23	-0.10	-0.03
P4 × P6	0.06	0.02	0.20	0.07	0.33	0.11	0.20	0.06
P4 × P8	0.05	0.02	0.43	0.14	0.37	0.12	0.29	0.09
P5 ×P 6	0.10	0.03	0.58	0.19	0.51	0.17	0.40	0.13
P5 × P7	0.07	0.02	-0.29	-0.10	0.53	0.17	0.10	0.03
P5 × P8	0.28	0.09	-0.45	-0.15	0.52	0.17	0.12	0.04
P5 × P9	0.12	0.04	0.42	0.14	-0.40	-0.13	0.05	0.02
P5 × P10	0.27	0.09	0.46	0.15	-0.48	-0.16	0.08	0.03
P6 × P10	0.23	0.08	-0.55	-0.18	-0.17	-0.06	-0.16	-0.05
P8 × P9	-0.37	0.02	0.45	0.15	-0.46	-0.15	0.02	0.01
P8 × P10	-0.37	-0.12	-0.26	-0.09	-0.22	-0.07	-0.28	-0.09
P9 × P10	0.15	0.05	0.57	0.19	-0.01	0.00	0.23	0.08
SE(Sii-jj)	0.01	0.00	0.07	0.02	0.01	0.00	0.02	0.01
LSD(0.05)	0.02	0.01	0.14	0.05	0.02	0.01	0.05	0.02

SE(Sii-jj): Standard error of s_i and s_j specific combining ability of the hybridization between ith and jth parents; LSD: Least significant difference at p=0.05; P1: TZEEQI 10; P2: TZEEQI 9; P3: TZEEQI 5; P4: TZEEQI 8; P5: TZEEQI 2; P6: TZEEQI 12; P7: TZEEQI 7; P8: TZEEQI 16; P9: TZEEQI 6 and P10: TZEEQ 3

Across locations, 24 displayed positive SCA effect, with a range of -0.48 for TZEEQI5 × TZEEQI8 to 0.40 for TZEEQI2 × TZEEQI12 for lysine. Also, percentage tryptophan ranged from -0.16 for TZEEQI5 × TZEEQI8 to 0.13 for TZEEQI2 × TZEEQI12 (Table 5a). The best top five specific combiners for these same traits were TZEEQI2 × TZEEQI12, TZEEQI8 × TZEEQI16, TZEEQI10 × TZEEQI7, TZEEQI10 × TZEEQI12 and TZEEQI6 × TZEEQI3 across locations (Table 6). SCA effects for crude protein, zein crude and zein in dry matter are presented in Table 7, where TZEEQI5 × TZEEQI8 was the best combiner for these same traits across locations.

Table 7. Specific combining ability (SCA) for protein contents (Zein crude, crude protein and zein in dry matter) among some selected hybrid

	Ibadan			Ile-Ife			Kishi			Across		
Hybrids	Zein Crude (µg/ml)	Crude Protein(%)	Zein dry matter(%)	Zein Crude (µg/ml)	Crude protein(%)	Zein dry matter(%)	Zein Crude (µg/ml)	Crude Protein(%)	Zein dry Matter(%)	Zein Crude (µg/ml)	Crude Protein (%)	Zein dry matter(%)
P1 × P2	-14.36	-2.09	-0.81	24.74	5.49	2.13	-25.57	-2.38	-0.92	-5.06	0.34	0.14
P1 × P3	2.20	0.72	0.28	16.82	1.66	0.65	12.49	0.67	0.26	10.50	1.02	0.40
P1 × P6	-8.26	0.50	0.19	-27.95	-2.80	-1.13	-26.72	-3.04	-1.17	-20.97	-1.78	-0.70
P1 × P7	0.51	0.51	0.20	-25.05	-3.56	-1.36	-26.06	-2.77	-1.07	-16.87	-1.94	-0.74
P1 × P9	8.12	1.26	0.49	3.05	0.21	0.09	-35.30	-3.56	-1.38	-8.04	-0.70	-0.27
P1 × P10	0.87	-0.01	-0.01	-5.77	-0.77	-0.29	-34.03	-3.59	-1.39	-12.98	-1.46	-0.56
P2 × P3	-10.37	-0.54	-0.21	15.74	2.04	0.80	-52.40	-4.44	-1.71	-15.68	-0.98	-0.37
P2 × P5	5.94	4.34	1.68	-4.50	-0.38	-0.13	25.24	2.54	0.98	8.89	2.17	0.84
P3 × P4	3.77	0.23	0.09	59.18	6.04	2.28	45.18	4.45	1.72	36.04	3.57	1.36
P3 × P8	-1.97	-0.85	-0.33	-17.74	-2.19	-0.83	10.44	0.00	0.00	-3.09	-1.01	-0.39
P3 × P9	2.68	0.55	0.21	-14.65	-0.47	-0.17	18.35	2.09	0.81	2.13	0.72	0.28
P4 × P5	-11.09	-0.54	-0.21	-27.76	-2.49	-1.01	57.56	5.32	2.05	6.23	0.76	0.28
P4 × P6	-19.73	-0.44	-0.17	18.76	-1.50	0.04	-24.49	-2.44	-0.94	-8.49	-1.46	-0.36
P4 × P8	-8.74	-0.40	-0.15	-28.73	-3.23	-1.30	-25.75	-2.78	-1.07	-21.07	-2.13	-0.84
P5 × P6	-5.36	-0.76	-0.30	-45.59	-4.30	-1.71	-46.96	-3.78	-1.46	-32.63	-2.95	-1.16
P5 × P7	5.58	-0.53	-0.20	22.56	2.19	0.86	-39.05	-3.96	-1.53	-3.63	-0.76	-0.29
P5 × P8	-4.51	-2.07	-0.80	35.98	3.33	1.30	-39.53	-3.89	-1.50	-2.69	-0.88	-0.34
P5 × P9	3.04	-0.90	-0.35	-29.82	-3.11	-1.19	31.46	2.95	1.14	1.56	-0.35	-0.13
P5 × P10	-1.31	-1.98	-0.77	-35.01	-3.41	-1.31	35.63	3.61	1.39	-0.23	-0.60	-0.23
P6 × P10	-8.50	-1.73	-0.63	29.63	4.08	1.52	14.48	1.28	0.49	11.87	1.21	0.46
P8 × P9	-1.13	-0.53	-0.20	-32.24	-3.39	-1.30	29.35	3.46	1.34	-1.34	-0.15	-0.06
P8 × P10	10.47	2.73	1.05	28.54	1.97	0.77	16.84	1.62	-0.08	18.62	2.11	0.82
P9 × P10	-2.27	-1.08	-0.42	-34.35	-4.24	-1.63	5.90	0.08	0.03	-10.24	-1.75	-0.67
SE(Sii-jj)	0.48	0.08	0.03	0.48	0.52	0.09	0.48	0.07	0.03	0.28	0.18	0.03
LSD(0.05)	0.96	0.17	0.05	0.96	1.04	0.18	0.10	0.13	0.05	0.55	0.35	0.06

P1: TZEEQI 10; P2: TZEEQI 9; P3: TZEEQI 5; P4: TZEEQI 8; P5: TZEEQI 2; P6: TZEEQI 12; P7: TZEEQI 7; P8: TZEEQI 16; P9: TZEEQI 6 and P10: TZEEQ 3

Heterosis estimates for lysine, tryptophan and protein contents for the QPM hybrids at three locations

The selected hybrids were those having best and least mean percentage mid-parent heterosis (MPH), better-parent heterosis (BPH) and standard heterosis (SH) for lysine and tryptophan at each location and across locations (Table 8,9,10,11). Ibadan had highest proportion of hybrids exhibiting significant and positive heterosis over MPH, BPH and SH, followed by Ile-Ife and Kishi for lysine and tryptophan. For instance, hybrid TZEEQI9 × TZEEQI2 had least MPH (-20.02%, -23.66%), while TZEEQI12 × TZEEQI3 had highest MPH (19.31%, 23.09%).

Table 8. Estimates of heterosis for lysine, tryptophan and protein contents among some selected hybrids in Ibadan

	Lysine			Tryptophan			Zein in dry matter			Crude Protein			Zein Crude		
Hybrids	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH
P5 × P8	11.54**	11.03**	10.93**	13.61**	13.00**	12.88**	-87.94	-88.35	-87.42	-31.56	-32.41	-30.53	-8.13	-10.12	-10.77
P5 × P9	7.09**	3.42**	10.93**	8.30**	3.98**	12.88**	-82.36	-87.50	-87.42	-22.79	-30.69	-30.53	0.77	-1.51	-6.46
P6 × P9	8.04**	3.42**	10.93**	9.43**	3.98**	12.88**	-83.99	-89.08	-87.42	-24.92	-34.04	-30.53	-24.88	-39.56	-10.05
P6 × P10	19.31**	12.61**	10.46**	23.09**	14.91**	12.33**	-87.25	-82.38	-79.70	-21.30	-32.79	-29.21	-27.58	-36.66	-5.74
P5 × P10	17.82**	10.25**	10.16**	21.27**	12.09**	11.97**	-87.64	-81.33	-81.21	-18.03	-28.53	-28.36	-9.39	-16.10	-6.46
P5 × P6	10.21**	9.20**	9.11**	12.05**	10.85**	10.74**	-74.84	-76.43	-72.84	-27.45	-29.21	-25.44	-22.08	-36.18	-5.03
P6 × P7	5.32**	0.00	9.11**	6.23**	0.00	10.74**	-61.86	-76.43	-72.84	-17.10	-29.21	-25.44	-24.43	-39.56	-10.05
P9 × P10	12.29**	1.72**	9.11**	14.56**	2.01**	10.74**	-77.85	-86.64	-72.84	-3.34	-6.47	-25.44	-10.30	-18.67	-9.33
P3 × P7	0.97**	-0.73	8.32**	1.13**	-0.84	9.80**	-19.92	-40.72	-66.49	-3.65	2.97	-23.22	1.18	-0.77	-7.90
P4 × P6	9.79**	9.29**	8.20**	11.57**	10.97**	9.66**	-69.13	-68.08	-65.54	-25.89	-24.98	-22.89	-40.47	-40.89	-10.77
P4 × P9	4.91**	0.87**	8.20**	5.76**	1.02**	9.66**	-54.03	-68.08	-65.54	-15.50	-24.98	-22.89	-21.39	-37.09	-5.03
P4 × P10	16.29**	9.29**	8.20**	19.46**	10.97**	9.66**	-77.86	-83.05	-65.54	-13.04	-24.98	-22.89	-28.17	-37.57	-5.74
P5 × P7	3.53**	-0.83	8.20**	4.13**	-0.97	9.66**	-46.09	-65.77	-65.54	-11.77	-23.07	-22.89	4.68	1.51	-3.59
P6 × P8	9.79**	9.29**	8.20**	11.57**	10.97**	9.66**	-69.13	-70.10	-65.54	-25.89	-26.79	-22.89	-23.44	-36.18	-5.03
P7 × P9	-0.85	-1.69	7.26**	-0.99	-1.97	8.56**	21.39**	0.00	-58.06	3.34	0.00	-20.28	3.99	3.17	-6.46
P2 × P10	6.47**	0.94**	-1.91	7.75**	1.11	-2.25	-29.26	-5.95	15.26**	15.47**	-2.36	5.33**	-25.57	-36.06	-0.72
P8 × P10	-4.45	-10.21	-11.10	-5.32	-12.05	-13.08	21.27**	-7.17	88.75**	47.73**	27.45	31.00**	1.02	-4.51	6.46
P2 × P7	-17.37	-21.89	-14.77	-20.36	-25.42	-17.41	191.40**	78.00**	118.12**	54.85**	30.94	41.25**	-8.22	-27.74	12.20**
P2 × P8	-13.12	-13.92	-14.77	-15.51	-16.43	-17.41	89.26**	78.00**	118.12**	34.11**	30.94**	41.25**	-13.54	-29.13	10.05**
P2 × P5	-20.02	-21.12	-21.18	-23.66	-24.89	-24.96	141.34**	119.81**	169.36**	52.94**	47.53**	59.14**	-8.03	-25.89	15.08**

*Significant at p=0.05, **significant at p=0.01. MPH, BPH and SH indicate mid-parent, better parent and standard heterosis, respectively

×: crosses between two parents; TZEEQI10(P1); TZEEQI9 (P2); TZEEQI5 (P3); TZEEQI8 (P4); TZEEQI2 (P5); TZEEQI12 (P6); TZEEQI7 (P7); TZEEQI16 (P8); TZEEQI6 (P9) and TZEEQI3 (P10)

Table 9. Estimates of heterosis for lysine, tryptophan and protein contents among some selected hybrids in Ile-Ife

	Lysine			Tryptophan			Zein in dry matter			Crude Protein			Zein Crude		
Hybrids	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH
P1 × P7	16.49**	0.00	27.43**	19.67**	0.00	33.32**	-81.97	-90.09	-87.36	-36.65	-53.64	-46.80	-27.79	-43.75	-17.85
P3 × P8	16.29**	0.87	26.37**	19.46**	1.02	32.03**	-77.86	-87.21	-83.97	-35.44	-51.55	-44.98	-25.60	-42.10	-16.56
P4 × P8	15.71**	0.00	26.37**	18.75**	0.00	32.03**	-77.32	-87.21	-83.97	-34.72	-51.55	-44.98	-20.54	-38.51	-11.40
P9 × P10	37.27**	35.71**	26.37**	46.12**	44.08**	32.03**	-87.20	-87.54	-83.97	-51.54	-52.30	-44.98	-41.02	-41.79	-14.63
P1 × P6	14.15**	-1.69	25.27**	16.87**	-1.97	30.70**	-71.71	-84.43	-80.49	-31.77	-49.90	-43.11	-29.09	-44.58	-19.79
P2 × P10	14.70**	-1.69	25.27**	17.54**	-1.97	30.70**	-72.38	-84.83	-80.49	-32.50	-50.68	-43.11	-25.59	-41.79	-14.63
P3 × P7	15.66**	0.00	25.27**	18.71**	0.00	30.70**	-73.46	-84.70	-80.49	-33.71	-50.43	-43.11	-22.25	-39.77	-12.05
P4 × P5	17.01**	-0.87	25.27**	20.37**	-1.01	30.70**	-74.82	-85.96	-80.49	-35.32	-52.94	-43.11	-27.23	-44.29	-17.21
P1 × P5	15.44**	-2.53	24.21**	18.47**	-2.94	29.41**	-69.79	-83.52	-77.10	-32.55	-51.43	-41.30	-29.16	-45.16	-18.50
P2 × P9	12.64**	-2.53	24.21**	15.05**	-2.94	29.41**	-65.96	-81.21	-77.10	-28.82	-47.46	-41.30	-23.74	-39.76	-13.98
P3 × P10	14.86**	-0.85	24.21**	17.76**	-0.99	29.41**	-69.08	-82.20	-77.10	-31.83	-49.10	-41.30	-25.88	-42.67	-15.92
P5 × P9	37.34**	33.39**	24.21**	46.41**	41.22**	29.41**	-82.44	-83.52	-77.10	-49.53	-51.43	-41.30	-43.62	-44.72	-17.85
P5 × P6	36.96**	33.77**	23.14**	46.02**	41.81**	28.12**	-80.10	-81.08	-73.70	-48.37	-49.93	-39.48	-41.79	-42.55	-14.63
P5 × P10	37.77**	35.31**	23.14**	47.08**	43.83**	28.12**	-80.35	-81.08	-73.70	-48.76	-49.93	-39.48	-43.05	-43.42	-15.92
P8 × P9	33.01**	32.25**	23.14**	40.80**	39.81**	28.12**	-78.73	-79.02	-73.70	-46.28	-46.70	-39.48	-39.59	-39.86	-13.34
P6 × P8	-1.16	-1.16	-9.01	-1.43	-1.43	-10.95	2.70	2.70	28.70**	1.60	1.60	15.37**	6.03	5.80	53.13**
P5 × P7	1.56	-0.43	-9.04	1.94	-0.54	-10.99	-3.35	-7.32	28.79**	-2.03	-4.51	15.42**	-1.31	-2.17	45.39**
P7 × P9	-6.03	-6.92	-13.33	-7.46	-8.54	-16.19	14.21**	11.69**	42.45**	8.96**	8.09**	22.74**	1.56	0.44	46.68**
P6 × P10	-12.32	-12.82	-19.75	-15.26	-15.86	-23.98	28.28**	26.62**	62.88**	16.80**	15.90**	33.68**	9.52**	8.80**	59.58**
P6 × P7	-13.65	-13.98	-20.82	-16.91	-17.30	-25.29	31.53**	30.37**	66.29**	18.70**	19.33**	35.51**	10.21**	10.70**	60.23**
P3 × P4	-25.99	-26.31	-6.88	-30.24	-30.60	-8.37	586.0**	524.7**	21.92	99.7**	96.4**	11.74	81.9**	80.4**	44.7**

*Significant at p=0.05, **significant at p=0.01. MPH, BPH and SH indicate mid-parent, better parent and standard heterosis, respectively

×: crosses between two parents; TZEEQI10(P1); TZEEQI9 (P2); TZEEQI5 (P3); TZEEQI8 (P4); TZEEQI2 (P5); TZEEQI12 (P6); TZEEQI7 (P7); TZEEQI16 (P8); TZEEQI6 (P9) and TZEEQI3 (P10)

TZEEQI9 × TZEEQI7 had least BPH (-21.89%, 25.42), whereas TZEEQI12 × TZEEQI3 had highest BPH (12.61%, 14.91%). Also, TZEEQI9 × TZEEQI2 had least SH (-21.18%, -24.96%) while TZEEQI2 × TZEEQI16 had highest SH (10.93%, 12.88%) for lysine and tryptophan, respectively in Ibadan (Table 8). Also, in Ile-Ife, TZEEQI5 × TZEEQI8 recorded least MPH (-25.99%, -30.24%), while highest MPH (37.77%, 47.08%) was obtained from TZEEQI2 × TZEEQI3 for lysine and tryptophan, respectively. Hybrid TZEEQI5 × TZEEQI8 recorded least BPH (-26.31%, -30.60%) while TZEEQI6 × TZEEQI3 had the highest BPH (35.71%, 44.08%) (Table 9).

Highest SH (27.43%, 33.32%) was obtained from TZEEQI10 × TZEEQI7 whereas, least percentage SH (-20.82%, -25.29%) was obtained from TZEEQI12 × TZEEQI7 for lysine and tryptophan, respectively (Table 8). In addition, in Kishi, hybrid TZEEQI12 × TZEEQI7 had the least MPH (-32.14%, -37.88) for lysine and tryptophan, respectively while hybrid TZEEQI10 × TZEEQI16 had highest MPH (25.32%, 31.25%) for the same traits (Table 8). TZEEQI12 × TZEEQI7 had the least BPH (-32.14%, -37.88%) for lysine and tryptophan, respectively while TZEEQI10 × TZEEQI16 had highest BPH (6.85%, 8.18%) for the same traits. TZEEQI8 × TZEEQI16 had highest SH (21.09%, 25.63%) for the same traits in Kishi whereas, least SH (-21.84%, -26.53%) was obtained from TZEEQI2 × TZEEQI3 for the same traits in Kishi (Table 10).

Table 10. Estimates of heterosis for lysine, tryptophan and protein contents among some selected hybrids in Kishi

	Lysine			Tryptophan			Zein in dry matter			Crude Protein			Zein Crude		
Hybrids	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH
P4 × P8	8.13**	5.60**	21.09**	9.66**	6.63**	25.63**	-46.62	-53.06	-66.92	-19.47	-23.83	-35.89	-14.62	-16.74	-13.34
P4 × P6	1.87**	0.94**	17.89**	2.20**	1.11	21.74**	-13.70	-19.16	-56.78	-5.03	-7.32	-30.45	-6.34	-8.48	-9.46
P4 × P9	2.82**	2.82**	17.89**	3.33**	3.33**	21.74**	-19.16	-19.16	-56.78	-7.32	-7.32	-30.45	-13.98	-14.26	-14.63
P4 × P10	2.82**	2.82**	17.89**	3.33**	3.33**	21.74**	-19.16	-19.16	-56.78	-7.32	-7.32	-30.45	-7.83	-7.83	-8.82
P1 × P8	25.32**	6.85**	16.80**	31.25**	8.18**	20.40**	-61.58	-72.95	-53.30	-35.99	-48.62	-28.59	-31.99	-44.17	-9.46
P1 × P10	21.82**	1.86**	16.80**	26.75**	2.20**	20.40**	-58.70	-72.95	-53.30	-33.26	-48.62	-28.59	-25.70	-40.19	-3.01
P5 × P7	1.87**	0.00	16.80**	2.21**	0.00	20.40**	-12.73	-22.58	-53.30	-4.87	-9.28	-28.59	-2.01	-3.94	-5.59
P5 × P8	5.31**	3.82**	16.80**	6.32**	4.52**	20.40**	-28.58	-33.72	-53.30	-12.31	-15.15	-28.59	-7.97	-5.25	-6.88
P1 × P2	18.71**	-1.83	15.73**	22.86**	-2.16	19.11**	-53.60	-71.00	-49.92	-29.77	-47.31	-26.77	-24.90	-41.78	-5.59
P1 ×P 6	19.38**	-0.91	15.73**	23.71**	-1.07	19.11**	-54.34	-71.00	-49.92	-30.39	-47.31	-26.77	-21.88	-38.20	0.22
P1 × P7	19.38**	-0.91	15.73**	23.71**	-1.07	19.11**	-54.34	-71.00	-49.92	-30.39	-47.31	-26.77	-22.89	-39.00	-1.08
P2 × P3	1.40**	-1.83	15.73**	1.66**	-2.16	19.11**	-9.20	-25.35	-49.92	-3.58	-11.07	-26.77	-8.04	-14.35	-11.40
P4 × P7	0.00	-0.91	15.73**	0.00	-1.07	19.11**	0.00	-6.33	-49.92	0.00	-2.42	-26.77	-9.01	-11.09	-12.05
P1 × P9	19.59**	0.00	14.66**	24.03**	0.00	17.82**	-52.71	-69.04	-46.53	-29.87	-46.01	-24.96	-24.90	-39.40	-1.72
P2 × P4	-1.39	-2.74	14.66**	-1.64	-3.22	17.82**	10.60**	0.00	-46.53	3.80	0.00	-24.96	-6.52	-11.09	-12.05
P6 × P7	-32.14	-32.14	-20.75	-37.88	-37.88	-25.21	255.04**	255.04**	65.82**	89.46**	89.46**	35.30**	77.92**	77.92**	67.97**
P6 × P9	-31.52	-32.14	-20.75	-37.21	-37.88	-25.21	231.07**	210.13**	65.82**	84.77**	80.30**	35.30**	69.86**	65.46**	64.74**
P8 × P9	-29.23	-30.88	-20.75	-34.71	-36.52	-25.21	167.59**	135.31**	65.82**	69.97**	60.77**	35.30**	57.35**	53.94**	60.23**
P3 × P9	-30.54	-31.84	-21.84	-36.23	-37.64	-26.53	180.86**	152.35**	69.30**	74.30**	66.57**	37.17**	61.67**	58.64**	64.10**
P5 × P10	-31.19	-31.84	-21.84	-36.94	-37.64	-26.53	197.55**	180.64**	69.30**	78.41**	74.25**	37.17**	68.39**	67.84**	66.04**

*Significant at p=0.05, **significant at p=0.01. MPH, BPH and SH indicate mid-parent, better parent and standard heterosis, respectively
×: crosses between two parents; TZEEQI 10(P1); TZEEQI 9 (P2); TZEEQI 5 (P3); TZEEQI 8 (P4); TZEEQI 2 (P5); TZEEQI 12 (P6); TZEEQI 7 (P7); TZEEQI 16 (P8); TZEEQI 6 (P9) and TZEEQI 3 (P10)

Across locations, hybrid TZEEQI2 × TZEEQI12 had highest positive MPH (14.08%, 16.87%) and BPH (12.94%, 15.48%) for lysine and tryptophan, respectively while hybrid TZEEQI5 × TZEEQI8 expressed the least MPH (-17.39%, -20.41%) and BPH (-17.63%, -20.69%) whereas, hybrid TZEEQI8 × TZEEQI16 displayed highest positive SH (16.65%, 20.00%) whereas TZEEQI12 × TZEEQI7 showed least SH (-9.76%, -11.71%) for lysine and tryptophan, respectively (Table 8). Furthermore, some inbreds such as TZEEQI10, TZEEQI8, TZEEQI2, TZEEQI3 were good combiners for standard heterosis (SH) in hybrids combination for lysine and tryptophan. For instance, inbred TZEEQI10, TZEEQI8, TZEEQI2 and TZEEQI3 featured in 9, 8, 7 and 6 crosses, respectively in hybrid combination for lysine and tryptophan across locations (Table 11).

On the other hand, Kishi had highest proportion of hybrids displaying significant and positive heterosis over MPH, BPH and SH for crude zein, crude protein and zein in dry matter than the other locations followed by Ile-Ife and least were obtained in Ibadan (Table 5, 6, 7, 8). Some hybrids such as TZEEQI9 × TZEEQI7, TZEEQI9 × TZEEQI2 in Ibadan; TZEEQI5 × TZEEQI8, TZEEQI12 × TZEEQI7 in Ile-Ife; TZEEQI12 × TZEEQI7, TZEEQI5 × TZEEQI6, TZEEQI2 × TZEEQI3 in Kishi; TZEEQI5 × TZEEQI8, TZEEQI12 × TZEEQI7 across locations exhibited highest positive MPH, BPH and SH for crude zein, crude protein and zein in dry matter (Table 8, 9, 10, 11).

Table 11. Estimates of heterosis for lysine, tryptophan and protein contents among some selected hybrids across location

	Lysine			Tryptophan			Zein in dry matter			Crude Protein			Zein Crude		
Hybrids	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH
P4 × P8	9.71**	3.61**	16.65**	11.54**	4.25**	20.00**	-56.90	-67.96	-68.04	-23.50	-33.05	-33.13	-20.32	-23.14	-10.54
P5 × P6	14.08**	12.94**	15.30**	16.87**	15.48**	18.36**	-60.79	-62.42	-62.50	-28.92	-27.42	-30.43	-26.26	-30.28	-10.31
P1 × P7	9.27**	8.52**	14.95**	11.02**	10.11**	17.95**	-50.60	-52.42	-61.09	-21.65	-22.90	-29.74	-19.76	-20.40	-10.54
P1 × P6	10.65**	9.39**	14.27**	12.70**	11.17**	17.13**	-51.86	-54.41	-58.30	-23.40	-25.29	-28.39	-25.77	-30.45	-10.54
P4 × P6	5.12**	0.22	12.83**	6.07**	0.25	15.41**	-15.57	-35.37	-40.88	-12.80	-22.31	-25.53	-8.84	-16.09	7.94
P1 × P 8	10.09**	7.77**	12.58**	12.06**	9.24**	15.10**	-46.45	-51.28	-51.39	-21.49	-24.94	-25.02	-21.60	-22.95	-10.31
P4 × P10	7.11**	-0.30	12.25**	8.45**	-0.35	14.71**	-37.86	-55.48	-50.06	-16.38	-28.61	-24.37	-16.64	-20.53	-5.19
P1 × P10	11.42**	7.45**	12.24**	13.68**	8.86**	14.70**	-48.46	-55.44	-50.02	-23.23	-28.59	-24.35	-20.08	-22.39	-7.42
P1 × P9	5.82**	5.48**	10.89**	6.92**	6.52**	13.08**	-31.00	-32.16	-44.52	-13.42	-14.05	-21.68	-15.79	-16.04	-5.64
P9 × P10	8.04**	3.87**	9.20**	9.63**	4.60**	11.06**	-34.75	-44.39	-37.61	-16.53	-22.89	-18.31	-6.75	-9.70	7.72**
P5 × P8	6.76**	6.77**	6.82**	8.13**	8.12**	8.20**	-27.72	-27.73	-27.88	-13.48	-13.47	-13.57	-4.43	-5.16	10.39**
P1 × P5	3.81**	1.62	6.15**	4.56**	1.93	7.39**	-17.53	-24.98	-25.13	-8.12	-12.15	-12.24	-6.86	-7.77	5.71
P5 × P7	2.41	-0.43	5.47**	2.88	-0.51	6.57**	-11.54	-22.18	-22.34	-5.24	1.04	-10.88	0.00	-1.75	12.61**
P5 × P9	2.48	0.00	5.13**	2.96	0.00	6.17**	-11.61	-20.80	-20.97	-5.33	-10.12	-10.21	0.89	-0.39	14.17**
P5 × P10	5.71**	4.11**	4.16**	6.89**	4.95**	5.01**	-21.70	-16.84	-17.01	-10.88	-13.42	-8.28	-1.43	-3.36	15.29**
P2 × P6	-4.88	-9.58	2.42	-5.77	-11.23	2.92	31.28**	-1.50	-9.90	12.34**	-0.70	-4.82	-1.04	-9.17	16.84**
P3 × P9	-6.83	-10.17	1.74	-8.06	-11.92	2.10	48.79**	17.53**	-7.12	18.15	7.51	-3.46	10.26	0.60	12.39**
P2 × P7	-10.25	-13.16	-1.64	-12.10	-15.44	-1.97	75.56**	40.82	6.70	27.64	17.07	3.26	7.55	6.04	17.29**
P2 × P8	-8.42	-13.76	-2.32	-9.99	-16.15	-2.79	50.46**	9.76	9.49	20.61	4.74	4.62	3.78	-0.19	16.18**
P6 × P9	-8.33	-9.66	-5.02	-9.93	-11.49	-6.03	41.37**	31.76	20.52	18.50**	14.76**	9.99**	14.08**	6.58**	37.10**
P2 × P5	-11.27	-16.44	-5.36	-13.36	-19.29	-6.43	67.47**	22.15**	21.89**	27.56**	10.77**	10.66**	5.81**	2.52	17.51**
P7 × P10	-7.40	-11.30	-6.04	-8.87	-13.42	-7.25	32.67**	11.15**	24.68**	15.40**	5.75**	12.02**	16.94**	12.69**	34.43**
P3 × P4	-17.39	-17.63	-6.71	-20.41	-20.69	-8.06	170.00**	162.35**	27.43**	52.59**	51.23**	13.36**	37.79**	27.58**	37.99**
P7 × P9	-12.75	-13.08	-7.93	-15.16	-15.54	-9.53	71.04	67.52**	32.39**	30.08**	28.94**	15.77**	21.93**	21.32**	35.54**
P6 × P7	-13.23	-14.80	-9.76	-15.76	-17.58	-11.71	67.27	52.91**	39.87**	29.76**	24.59**	19.42**	17.96**	9.69**	41.11**

*Significant at p=0.05, **significant at p=0.01. MPH, BPH and SH indicate mid-parent, better parent and standard heterosis, respectively
×: crosses between two parents; TZEEQI10(P1); TZEEQI9 (P2); TZEEQI5 (P3); TZEEQI8 (P4); TZEEQI2 (P5); TZEEQI12 (P6); TZEEQI7 (P7); TZEEQI16 (P8); TZEEQI6 (P9) and TZEEQI3 (P10

Correlation of grain yield with lysine, tryptophan and other protein contents at three locations and across locations

Table 12. Pearson coefficient of correlation between pairs of grain yield with lysine, tryptophan and other protein contents among quality protein maize hybrids in across locations

	Grain yield	Lysine (%)	Tryptophan (%)	Zein Crude (µg/ml)	Crude Protein (%)	Zein dry matter (%)
				Ibadan		
Grain yield		-0.28*	-0.28*	0.19	0.31*	0.28*
Lysine (%)			1.00**	-0.70**	-0.94**	-1.00**
Tryptophan (%)				-0.70**	-0.94**	-1.00**
Zein crude(µg/ml)					0.69**	0.70**
Crude Protein(%)						0.94**
Zein dry matter(%)				Ile-Ife		
Grain yield		-0.12	-0.11	0.04	0.11	0.11
Lysine (%)			1.00**	-0.94**	-1.00**	-1.00**
Tryptophan (%)				-0.94**	-1.00**	-1.00**
Zein crude(µg/ml)					0.94**	0.95**
%Crude protein						1.00**
Zein dry matter				Kishi		
Grain yield		-0.18	-0.18	0.17	0.18	0.18
Lysine (%)			1.00**	-0.99**	-1.00**	-1.00**
Tryptophan (%)				-0.99**	-1.00**	-1.00**
Zein crude(µg/ml)					0.99**	0.99**
Crude protein						1.00**
Zein dry matter				Across	locations	
Grain yield		-0.34*	-0.34*	0.24	0.34*	0.34**
Lysine (%)			1.00**	-0.93**	-1.00**	-1.00**
Tryptophan (%)				-0.93**	-1.00**	-1.00**
Zein crude (µg/ml)					0.93**	0.93**
Crude Protein(%)						1.00**
Zein dry matter(%)						

*Significant at p=0.05, **significant at p=0.01

Correlation between pair of grain yield with lysine, tryptophan and other protein contents at each location and across locations showed that significant and negative association existed between grain yield with lysine in Ibadan and across locations with correlation coefficient (r) values of -0.28* and -0.34*, respectively (Table 12). Similarly, grain yield was

negatively nd significantly associated with tryptophan in Ibadan (r= -0.28*) and across locations (r= -0.34*). However, grain yield was significantly and positively correlated with crude protein with r= 0.31* in Ibadan and r= 0.34* across locations. Positive and significant relationship was recorded between grain yield and zein in dry matter in Ibadan (r= 0.28*) and across locations (r= 0.34*). In addition, positive and highly significant association existed between lysine and tryptophan (r= 1.00**), whereas pair of lysine and tryptophan had highly significant and negative association with zein in crude form, crude protein and zein in dry matter at the three location and across locations with a range of r= -0.70** to -1.00**. Positive and significant relationship was also recorded in zein in crude form with crude protein and zein in dry matter at the three location and across locations with range of r= 0.69** to 1.00** (Table 10).

DISCUSSION

Maize is a staple food of sub-Saharan African (SSA) populace but deficient in protein. Quality protein maize has been developed to contain essential amino acids including lysine and tryptophan to alleviate malnutrition in SSA. Significant differences observed among the quality protein maize hybrids for lysine, tryptophan and other protein contents at the three locations in this study, depicts an existence of variability for lysine, tryptophan and protein contents under different environments, which would facilitate effective selection in quality protein maize improvement. These findings corroborate the work of some other scientists (HADJI, 2004; VIVEK *et al.,* 2008; MUSILA *et al.,* 2010; WEGARY *et al.,* 2013; ANNOR and BADU-APRAKU, 2016). For instance, QPM hybrids had higher percentage lysine and tryptophan than two checks, which were within the threshold of 2.7 - 4.5% for lysine and 0.5 - 1.1% for tryptophan in QPM (VASAL, 2001; CIMMYT, 2002; VIVEK *et al.,* 2008). This could be due to genetic factor over the expression of gene controlling lysine and tryptophan as earlier reported by SENTAYEHU (2008). QPM hybrids evaluated had relative stability over those of commercial checks for lysine and tryptophan in this study. The identified hybrids with high percent lysine and tryptophan could be incorporated into the breeding programs to cater for daily nutritional requirements of increasing population in SSA, especially among children, pregnant women, nursing mothers, sick adults and in weaning diet in baby foods.

Lysine (3.4%) and tryptophan (1.0%) were highest in Ibadan, where severe rain cessation was experienced during reproductive stage, while least lysine (2.8%) and tryptophan (0.7%) contents were recorded in Kishi, whereas other protein contents such as crude protein, zein in crude form and zein in dry matter were highest in Kishi with least values recorded in Ibadan. These genotypic variations may be attributed to the varied rainfall distribution of the test locations which resulted to significant variations in synthesis of grain protein, lysine and tryptophan at three locations. The result obtained agrees with findings of IGNJATOVIC-MICIC *et al.* (2020) who reported higher percent tryptophan under drought prone environment than in optimum environment. Also, NGABOYISONGA *et al.* (2012) obtained increased in percent tryptophan and decreased in protein content under low nitrogen and drought stress environments in maize. This phenomenon suggests that action of *o2*-endosperm modifiers genes tend to be silent or suppressed under stressed conditions, which triggers *opaque 2* (*o2*) gene to confer higher lysine and tryptophan among QPM genotypes (NGABOYISONGA *et al.,* 2012). Thus, endosperm modifiers genes tend to alter the expression of other genes at different loci.

In addition, tryptophan and lysine had been implicated to play vital role in the response of plants against stress and regulating plant growth and development (GALILI *et al.*, 2001; WANG *et al.*, 2019). Therefore, expression of *opaque 2* (*o2*) gene that confers high percent lysine and tryptophan in QPM was dependent on the environmental factors (IGNJATOVIC-MICIC *et al.*, 2013). It is now advisable for seed companies and other stakeholders in maize value chain to select QPM under moisture stressed environments for higher lysine and tryptophan contents. Nevertheless, plant breeders, crop physiologist and agronomist may need to collaborate to decipher factors that are responsible for varied quality of protein in maize in different environments. This will provide basic information for stable nutritional quality of maize in all environments where they may be grown if such factor(s) does not include rainfall distribution, soil fertility or mineral variations.

The SCA was significant for lysine and tryptophan in all locations, while GCA was significant in Ibadan and Ile-Ife suggest inheritance of lysine and tryptophan was dependent on location. This agrees with findings of NGABOYISONGA *et al.* (2008) and WEGARY *et al.* (2011) in QPM. The magnitude of GCA for lysine, tryptophan and protein contents were higher than those of SCA in most locations showing preponderance of additive gene action in the control of these traits. The relative stable performance of lysine, tryptophan and protein contents due to non-significant GCA and SCA across locations; justify the rationale for evaluating the inbreds in a diallel mating scheme to identify the best tester(s) with a consistent performance across locations conferring high percent lysine and tryptophan among the inbreds.

Progeny performance showed a higher predictability ratio for lysine, tryptophan and other protein contents across locations, elucidates the fact that progeny performance can adequately be predicted on the basis of parental performance (GCA) for these traits as reported by BAKER (1978). For instance, inbreds TZEEQI3, TZEEQI10, TZEEQI2, TZEEQI12, TZEEQI8 possessed good combining ability and heterosis in hybrids combination for lysine and tryptophan across locations. The top 5 hybrids that expressed significant and positive heterosis over standard heterosis for lysine and tryptophan were TZEEQI8 × TZEEQI16, TZEEQI2 × TZEEQI12, TZEEQI10 × TZEEQI7, TZEEQI10 × TZEEQI12 and TZEEQI8 × TZEEQI12 across locations. Standard heterosis (SH) obtained in this study for lysine and tryptophan is higher than the one reported by BISEN *et al.* (2017) among quality protein maize varieties for lysine and tryptophan, but very close to the range obtained by NEPIR *et al.* (2015) for SH. These findings therefore confirm the reliability of methodology and data generated from this study, and that information is useful in maize research especially breeding for quality protein maize.

Negative and significant correlation obtained between grain yield with lysine and tryptophan across locations in this study, is undesirable, but there is need for careful monitoring of breeding stages and selection for QPM genotypes with high lysine and tryptophan contents as well as high yielding genotypes at the same time. The result obtained agrees with the findings of other scientists (LOVATTO *et al.*, 2006; BELLO *et al.*, 2012; ALVES and CARGNELUTTI-FILHO, 2017). This observation accentuates the importance of monitoring protein quality traits levels throughout the breeding stages. Positive and significant relationship obtained between lysine and tryptophan with very high magnitude in this study had already been established by others (DROCHIOIU *et al.*, 2002; OLAKOJO *et al.*, 2007). Positive and significant correlation obtained between protein contents corroborated by the work of some scientists (OLAKOJO *et al.*, 2007;

BELLO *et al.*, 2012). HABBEN *et al.* (1993) suggested that homozygous recessive *o2* gene restricts synthesis of zein and pleiotropic increases the non-zein content that contains high lysine and tryptophan levels in the QPM endosperm. Therefore, there is need for monitoring protein contents, tryptophan and lysine while breeding or selecting for QPM genotypes.

CONCLUSION

Gene actions for expression of lysine and tryptophan varied with location. Additive gene action was preponderance in inheritance of lysine and tryptophan in Ibadan and Ile-Ife, whereas non-additive gene action was involved in inheritance of lysine and tryptophan in Kishi. It is now advisable for seed companies and other stakeholders in maize value chain to select QPM from moisture stressed environments for higher lysine and tryptophan contents. The relationship between grain yield with lysine and tryptophan was negative and significant across locations. Hence, breeding for high yielding QPM genotypes with high lysine and tryptophan contents at the same time, requires careful monitoring of lysine and tryptophan contents in the laboratory.

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DELOVANJE GENA I HETEROZA ZA SVOJSTVA KVALITETA HIBRIDA KUKURUZA U VLAŽNIM AGRO-EKOLOGIJAMA NIGERIJE

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Izvod

Kukuruz je osnovna hrana stanovništva podsaharske Afrike (SSA), ali mu nedostaje proteina. Kvalitetni proteinski kukuruz (*QPM*) je razvijen da sadrži esencijalne aminokiseline, uključujući lizin i triptofan, kako bi se ublažila pothranjenost kod SSA. Ova studija je sprovedena da bi se procenili efekti opšte i specifične kombinacione sposobnosti (GCA i SCA), delovanja gena i heterozisa među *QPM* hibrida za lizin i triptofan na tri lokacije u vlažnim agroekologijama Nigerije. Zrna iz punih srodnika deset linija, 45 hibrida dobijenih poludialelom i dve provere analizirana su na lizin i triptofan. Rezultati su pokazali da se sadržaj lizina i triptofana kretao od 2,71% - 0,73% (Kishi) do 3,41% - 0,96% (Ibadan). Akcije gena za ekspresiju lizina i triptofana varirale su u zavisnosti od lokacije; prema tome, aditivno delovanje gena je preovladavalo u nasleđivanju lizina i triptofana u Ibadanu i Ile-Ifeu, dok je neaditivno delovanje gena bilo uključeno u nasleđivanje ovih osobina kod Kišija. Inbri TZEEKI-8, TZEEKI3, TZEEKI-10, TZEEKI-12, TZEEKI-2 su bili najbolji kombinatori za lizin i triptofan. Hibridi TZEEKI-8×TZEEKI-16, TZEEKI-2×TZEEKI-12, TZEEKI 10×TZEEKI-7, TZEEKI-10×TZEEKI-12 i TZEEKI-8×TZEEKI-12 bili su ocenjeni kao pet top hibrida, sa pozitivnim i značajnim heterozisom u odnosu na standard sa rasponom od 12,8%-16,7% za lizin i 15,4%-20,0% za triptofan u odnosu na standard na različitim lokacijama. Veza između prinosa zrna sa lizinom i triptofanom bila je negativna i značajna na različitim lokacijama. Stoga, oplemenivanje za visoko prinosne *QPM* genotipove sa visokim sadržajem lizina i triptofana u isto vreme, zahteva pažljivo praćenje sadržaja lizina i triptofana u laboratoriji.

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