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Full Length Research Paper

Genetic Control of Total Phenolic Content and some Kernel Compositional Traits in Purple Maize

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Abstract

Purple maize kernels are rich in phytochemicals and nutrients which can be exploited to promote human health. A better understanding of the genetic mechanisms controlling these qualities, which could also be dependent on the choice of parents and their role in the cross, is important for their improvement. This study was conducted to: investigate the nature and relative importance of gene effects involved in the inheritance of total phenolic content (TPC) and proximate composition in reciprocal crosses between two maize lines (UIp01 and TZi3) with purple and white kernels, respectively using generation mean analysis. Kernels of F_1, F_2 and backcross generations derived from UIp01 × TZi3 and TZi3 × UIp01 and the parents were assessed for TPC and proximate composition following standard procedures. Analysis of variance revealed that the populations differed significantly for all traits, except moisture content. Reciprocal differences were observed only for TPC indicating the influence of maternal parent in its inheritance. Heritability estimates were moderate (0.4-0.5) to high (0.7-0.9) for most traits. Results showed the importance of non-additive effects over additive effects for starch and fat contents, and varying levels of additive and non-additive effects for TPC, moisture, protein, ash and fiber contents.

Keywords: Gene action, heritability, purple maize, reciprocal effects, total phenolic contents.

1.0 INTRODUCTION

Chronic diseases such as cancer, cardiovascular diseases (CVDs), diabetes and obesity are on a yearly increase, causing approximately 71% of deaths globally (WHO, 2021). High intake of foods rich in phytochemicals, such as anthocyanins and other phenolic compounds have been shown to help prevent the occurrence of these diseases (Peng *et al*., 2011; Tsuda, 2012). Purple maize (*Zea mays* L.), like every other maize type, can be used as food, feed and raw materials. However, it differs from the conventional white and yellow types due to its content of anthocyanins and phenolic compounds which are known to possess antioxidant properties beneficial to human health (Lao and Giusti, 2016; Lao *et al*., 2017). It is indigenous to the Andes region of South America, and consumed mainly in Peru, Ecuador, Bolivia and Argentina (FAO, 2013). As a result of its distinct color and antioxidant contents, it is utilized as a natural functional food colorant in South America, Asia and Europe in substitution of unhealthy synthetic dyes (Lao *et al*., 2017). Reports from previous studies (Prior *et al*., 1998; Cevallos-Casals and Cisneros-Zevallos, 2003; Kim *et al*., 2013) showed that the total phenolic contents in purple maize kernels (1756 mg 100 g^{-1} GAE) are considerably higher than popularly known phenolic-rich blueberries (138 to 672 mg 100 g^{-1} GAE). It has also been shown that extracts of purple maize at a

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dose of 0.525µg/mL can significantly reduce the proliferation of cancerous cell lines *in vitro* (Zhao *et al*., 2009, Long *et al*., 2013). In another finding, mice fed high fat diet containing phenolic extracts from black rice, black soybean and purple maize for 12 weeks had less body weight gain and fat accumulation than rats fed diets without the extracts (Tsuda *et al*., 2003; Wu *et al*., 2017). The awareness of the use and value of purple maize in Africa is however, still very low.

In maize, studies are being conducted to increase the contents of phytochemicals in purple and red maize. Also, due to the association of these colors with important phytochemicals and minerals, several efforts are being directed to the transfer of purple and red colors to adapted commercial varieties. One important aspect of plant breeding is the investigation of mechanisms of inheritance of traits. Findings from such studies provide information on the type of gene effects and heritability estimates that can facilitate successful selection of parents and the development of promising hybrids (Khamphasan *et al*., 2018). Generation mean analysis was developed by Hayman (1958) as a biometrical method useful in determining genetic influences such as additive, dominance and most importantly, non-allelic (epistatic) interactions on quantitatively inherited traits (Singh and Singh, 1992; Said, 2014). In maize, generation mean analysis have been used to assess genetic effects on major agronomic traits (Wahba *et al*., 2015; Wannows *et al*., 2015), minerals (Chakraborti *et al*., 2010) and phytochemicals (Harakotr *et al*., 2016). There have been several investigations on the quantification of phenolic compounds (Montilla *et al*., 2011;Salinas-Moreno *et al*., 2017; Navarro *et al*., 2018) and proximate contents (Nascimento *et al*., 2014; Ai and Jane, 2016; Feng *et al*., 2020) of purple maize kernels, but little is known about the genetic basis for their inheritance.

There is the need to develop and promote purple maize as a specialty corn with high contents of phenolic compounds and nutritional quality. Knowledge of the genetic factors underlying the expression of these traits is required to achieve this goal. In this study, generation mean analysis was employed to provide information on estimates of relative genetic effects on these traits. Broad and narrow-sense heritability, heterosis and potence ratio values were estimated. The existence or otherwise of reciprocal effects on the inheritance of the traits was also investigated.

2.0 MATERIALSAND METHODS

2.1 Plant Materials

Two inbred lines: TZi3 and UIp01differing in kernel color were used as genetic materials in this study. Line TZi3 (formerly 1368) is a white-kernelled flint maize inbred developed by the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. It is one of the parental lines for the commercial white-kernelled hybrid Oba Super-1. Line UIp01 is a purple-kernelled flint maize line developed at the Department of Crop and Horticultural Sciences, University of Ibadan. The purple kernelled maize was originally identified and collected from an open pollinated yellow-kernelled maize field and subjected to cycles of selfing and selection for purple kernels. Six basic populations(P_1, P_2, F_1, F_2, BC_1 and BC_2) were generated from the parental cross of UIp01 × TZi3 and its reciprocal TZi3 × UIp01.

2.2 Field Experiment

The F_1 and RF_1 hybrids were produced in the nursery at the experimental field of the Department of Crop and Horticultural Sciences, University of Ibadan between September 2019 and January 2020. In other to produce the kernels of all generations in a planting season, seeds of the inbred parents, their F_1 and RF_1 were planted in randomized complete block design with two replicates in 5 m rows. In a block, each parent was planted in 11 rows, while the F_1 and RF_1 hybrids had 7 rows each. Three seeds were sown per hill at a spacing of 0.75 m between rows and 0.50 m within a row, and later thinned to two. The maize lines were planted during the main cropping season of 2020 between May and August. The parental lines were sib-mated and crossed to produce P_1, P_2, F_1 and RF_1 kernels, while the F_1 and RF_1 were self-pollinated to produce the respective F_2 and RF_2 kernels, and equally backcrossed to both parental lines to generate the backcross populations. Kernels of parental lines, F_1, RF_1, F_2,RF_2 and all backcross populations were evaluated in this study. Pollination was controlled and by hand. Standard agronomic practices for maize production in southwest Nigeria were adopted.

Ears of generated P_1, P_2, F_1, RF_1, F_2, RF_2, BC_1 and BC_2 populations were harvested separately at physiological maturity, about 35 days after pollination (DAP). All ears were air dried to about 12% moisture content and bagged for further analysis.

2.3 Sample Preparation

Ten ears were randomly taken from each replicate of P_1, P_2, F_1, RF_1, BC_1, RBC_1, BC_2 and RBC_2 generations. Due to the observed pattern of segregation of the F_2 and RF_2 ears, 10 ears each of the segregated (white and yellow) and non-segregated (purple) ears were randomly selected from each replicate. All ears of each generation in each replication were shelled, cleaned and thoroughly mixed. A 200 g sub-sample was ground into flour and analyzed for total phenolic contents and proximate composition.

2.3.1 Determination of Total Phenolic Contents

The total phenolic contents in each sample were extracted according to the method described by Burgos *et al*. (2013). A 2.5 g of maize flour for each sample was loaded into a conical flask containing 20 mL of the extracting solvent (methanolic HCL). The solution was homogenized with a multi stirrer at 200 rpm for 1 hour and the samples filtered with Whatman No 1 filter paper. The extraction process was repeated three more times on the residue. Finally, the filtrates were evaporated in a rotary evaporator to reduce the volume from 80 mL to 20 mL. The total phenolic content of each sample was determined using the Folin-Ciocalteu method as described by Hu and Xu (2011). A 0.5 mL of the plant extract was added to 2.5 mL of distilled water in a test tube. The solution was further oxidized with 0.5 mL of Folin-Ciocalteu reagent and neutralized with 1.5 mL of Na_2CO_3 after 5 minutes. The resulting solution was allowed to stand for 90 minutes and the absorbance of the resulting blue color was measured with a UV-visible spectrophotometer at 765 nm. The total phenolic content was determined by means of a calibration curve prepared with gallic acid. Total phenolic content was expressed as mg gallic acid equivalents (GAE) per g of dry weight of samples (mg GAE g^{-1} DW). Measurements were done in duplicates.

2.3.2 Determination of Kernel Proximate Composition

The moisture, carbohydrate, lipids, protein, fiber and ash contents were determined by the methods described by the Association of Official Analytical Chemists (AOAC, 2000), FOSS (2003) and AACC (2005). The nitrogen content of the samples was determined by the Kjeldhal technique using Kjeltec^{TM} model 8400, as described in FOSS manual (FOSS, 2003). The crude protein content (%) was determined by multiplying the nitrogen content by 6.25. Total carbohydrate (TC) was estimated using the formula:

TC (%) = 100 – (moisture content + crude fat + crude fiber + crude protein + ash).

All measurements were done in duplicates.

2.4 Data Analyses

The data recorded were subjected to individual analysis of variance (ANOVA) for randomized complete block design with four replicates using the proc GLM procedure in SAS (SAS Institute, 2003). Means of the generations were compared using Duncan's multiple range test at 5% level of probability.

Generation mean analysis (GMA) was separately conducted for each trait to determine the mode of gene action governing their expression. Scaling tests A, B, C and D as described by Hayman and Mather (1955) was used to test the adequacy of the additive-dominance model and determine the presence of epistatic effects. Significance of either one or more of the scales indicated the presence of epistasis. Thus, the six-parameter genetic models were estimated as outlined by Kearsey and Pooni (1996):

$$m = 0.5\overline{P_1} + 0.5\overline{P_2} + 4\overline{F_2} - 2\overline{BC_1} - 2\overline{BC_2}$$
$$d = 0.5\overline{P_1} - 0.5\overline{P_2}$$
$$h = 6\overline{BC_1} + 6\overline{BC_2} - \overline{F_1} - 8\overline{F_2} - 1.5\overline{P_1} - 1.5\overline{P_2}$$
$$i = 2\overline{BC_1} + 2\overline{BC_2} - 4\overline{F_2}$$
$$j = 2\overline{BC_1} - 2\overline{BC_2} - \overline{P_1} + \overline{P_2}$$
$$l = \overline{P_1} + \overline{P_2} + 2\overline{F_1} + 4\overline{F_2} - 4\overline{BC_1} - 4\overline{BC_2}$$

Where, *m*- mean effect, *d*- additive effect, *h*- dominance effect, *i*- additive × additive gene interaction,*j*- additive × dominance gene interaction, *l*- dominance × dominance gene interaction. $\overline{P_1}$, $\overline{P_2}$, $\overline{F_1}$, $\overline{F_2}$, $\overline{BC_1}$ and $\overline{BC_2}$ are the means of P_1, P_2, F_1, F_2, BC_1 and BC_2, respectively.

Broad-sense (H^2) and narrow-sense (h^2) heritability for each trait were estimated according to Warner (1952) and Kearsey and Pooni (1996) using: $H^2 = \frac{\sigma_G^2}{\sigma_P^2}$and

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

Where, σ_G^2, σ_A^2 and σ_P^2 are the genotypic, additive and phenotypic variances, respectively. Heritability values were classified as high (> 0.6), moderate (0.3 - 0.6) and low (< 0.3) as described by Robinson *et al*. (1949). Also, due to the shortcomings of the models used to estimate the variance components, negative variances derived were rounded to zero.

Estimate of potence ratio (P) for each trait was calculated to determine the degree of dominance according to Smith (1952) using:$P = \frac{F_1 - MP}{0.5\ (P_2 - P_1)}$

Where, *P*: relative potency, F_1: first generation mean, P_1: the mean of lower parent, P_2: the mean of higher parent and MP: mid parent value = $(P_1 + P_2)/2$. Values of +1 or –1 indicated complete dominance, values greater than +1 or –1 indicated over dominance, values ranging from –1 to +1 suggested partial/ incomplete dominance, while a potence ratio of zero (0) indicated the absence of dominance.

Heterosis was computed as the mean performance of the F_1 hybrids over the mid-parent and better parent. Mid-Parent Heterosis (MPH) and Better-Parent Heterosis (BPH) values, expressed as percentage were calculated using the formulae of Singh and Chaudhary (1977):

$$MPH = \frac{(\overline{F_1} - \overline{MP})}{\overline{MP}} \times 100$$
$$BPH = \frac{(\overline{F_1} - \overline{BP})}{\overline{BP}} \times 100$$

Where, $\overline{F_1}$: first generation mean, $\overline{F_2}$: second generation mean, $\overline{MP}$: the mean of mid-parent value and $\overline{BP}$: the mean of the better-parent.

3.0 RESULTSAND DISCUSSION

Variability among generation means for the studied traits

Total phenolic contents (TPC) differed significantly among the generations of cross UIp01 × TZi3 (Table 1). The TPC (1.8 mg GAE g^{-1})of the purple parent, UIp01 (P_1) was significantly higher (1.4 mg GAE g^{-1}) than that recorded for the white parent, TZi3 (P_2). The TPC (1.7 mg GAE g^{-1})of the F_1 generation was 6.2% higher than the value of the mid-parent (1.6 mg GAE g^{-1}), while the TPC of F_2 generation was similar to the mid parental value. The backcross to the white kernelled parent (BC_2) had the highest TPC (2.0 mg GAE g^{-1}), which was similar to that of BC_1, but significantly higher than the values recorded for the other generations. These results indicated that in the cross UIp01 × TZi3, partial dominance towards the high parent (P_1), as well as varying additive effects in the inheritance of TPC existed in purple maize kernel. Similar results were observed by Harakotr *et al*. (2016), who reported a greater degree of additive effects than dominance effect for the inheritance of TPC in purple maize kernel. In the reciprocal cross TZi3 × UIp01, significant difference among the generations was only observed between the purple parent, UIp01 and the F_1 (Table 2). These results suggest dominance towards the maternal parent and the importance of maternal effect on the concentration of total phenolic content in maize kernels.

There were no significant differences for moisture content among the generations of crosses UIp01 × TZi3 and TZi3 × UIp01 (Tables 1 and 2). This result indicated the importance of additive gene action for the inheritance of moisture. This finding is contrary to those reported for moisture content by Afful *et al*. (2019) in eggplant and Pfeiffer and Rooney (2016) in sorghum. The authors reported the existence of genetic variability for moisture content among the populations studied.

Fat content differed significantly among the different generations of both crosses (Tables 1 and 2). The fat content of the purple parent, UIp01 (4.4%) was not significantly different from the white parent TZi3 (4.0%). In the cross UIp01 × TZi3, the BC_2 generation had the highest fat content which was similar to those of the P_1 and F_2 generation. In the reciprocal cross TZi3 × UIp01, fat content was highest in the backcross to the white-kernelled parent(4.6%), and least (3.5%) in the backcross to the purple-kernelled parent. However, the fat content of both theF_1 (4.0%, 3.9%) and F_2(4.3%, 4.2%) generations were similar to the parental values. These results indicate the important role of additive gene effect in the inheritance of fat content in the plant materials used in this study.

There were no significant differences among the generations of cross UIp01 × TZi3 for ash content (Table 1). However, for cross TZi3 × UIp01, the ash content of the F_1 generation was significantly less than the other generations (Table 2). This result indicates greater importance of additive effects for the inheritance of ash content.

In both crosses, protein content differed significantly among the generations (Tables 1 and 2). Protein content of the white parent (TZi3) was significantly higher than the purple parent (UIp01). In the cross UIp01 × TZi3, the protein content of the F_1 generation was 2.8% and 8.4% higher than those of the mid-parent and purple parent (UIp01), respectively. The protein content of the F_2 generation were significantly lower than the F_1 generation, white kernelled parent (P_2), and the backcross to the white parent (BC_2). In the cross TZi3 × UIp01, similar trend was observed. The F_1 was 4.6 % and 10% higher than the mid-parental and purple parental (UIp01) values, respectively. These results suggest dominance towards the better parent irrespective of the parent used as the maternal or paternal parent.

Fiber contents differed significantly among the generations of crosses UIp01 × TZi3 and TZi3 × UIp01 (Tables 1 and 2). The fiber content of the purple kernelled parent (4.8%) was not significantly different from the white kernelled parent (5.13%). The fiber contents of the F_1 generations (3.8% and 4.3%) were lower than the parental values in both crosses. However, the F_2 generations had similar fiber contents with the parents. These results suggest overdominance towards the lower parent (UIp01) as well as additive effect in the inheritance of fiber content. Pfeiffer and Rooney (2016) reported similar findings for fiber contents in black sorghum. In both crosses, the backcross to the white kernelled parent (TZi3) resulted in the highest fiber contents (5.9% and 6.2%). These results indicated that recurrent selection may be helpful in improving the fiber contents of plant materials used in this study.

Significant differences were observed among the generations of both crosses (Tables 1 and 2) for starch content. The starch contents of the purple parent UIp01 (70.3%) was significantly higher than that of the white parent, TZi3 (68.6%). The starch contents of the F_1 generations (70.4% and 70.1%) were not significantly different from that of the purple parent (UIp01) in both crosses. The starch content of the F_2 generations were lower but not significantly different from their respective F_1 generations. In both crosses, the backcross to the purple parent had higher starch contents than the backcross to the white parent. These results indicate dominance effects towards the high parent (UIp01) as well as additive gene effects for the inheritance of starch contents in purple maize kernels.

Reciprocal Differences

Significant genotypic differences were found among the

Table 1. Generation means of total phenolic contents and proximate composition of maize populations originating from cross UIp01 × TZi3.

Traits	P_1 (UIp01)	P_2 (TZi3)	Mid-parent	Generations F_1	F_2	BC_1	BC_2	Mean
TPC (mg GAE g^{-1})	1.84b	1.47d	1.66	1.77bc	1.61cd	1.94ab	2.05a	1.78
MC (%)	8.15	8.62	8.39	8.46	8.26	8.37	8.37	8.37
Fat (%)	4.43ab	4.03b	4.23	4.00b	4.28ab	4.13b	4.73a	4.27
Ash (%)	1.35	1.32	1.34	1.37	1.28	1.36	1.42	1.35
Protein (%)	10.95b	12.26a	11.61	11.95a	11.17b	11.00b	12.07a	11.57
Fiber (%)	4.85b	5.13ab	4.99	3.80c	4.63bc	4.88b	5.99a	4.88
Starch (%)	70.27a	68.64b	69.45	70.43a	70.37a	70.26a	67.41b	69.56

Values followed by the letter along a row are not significantly different by Duncan's multiple range test. TPC = Total phenolic contents; MC = Moisture content.

Table 2. Generation means of total phenolic contents and proximate composition of maize populations originating from cross TZi3 × UIp01.

Traits	P_1 (TZi3)	P_2 (UIp01)	Mid-parent	Generations F_1	F_2	BC_1	BC_2	Mean
TPC (mg GAE g^{-1})	1.47ab	1.84a	1.66	1.42b	1.63ab	1.76ab	1.73ab	1.64
MC (%)	8.62	8.15	8.39	8.39	8.41	8.55	8.12	8.37
Fat (%)	4.03abc	4.43ab	4.23	3.95bc	4.19abc	4.63a	3.55c	4.13
Ash (%)	1.32a	1.35a	1.34	1.09b	1.32a	1.30a	1.41a	1.30
Protein (%)	12.26a	10.95b	11.61	12.17a	11.15b	11.81a	11.01b	11.56
Fiber (%)	5.13b	4.85bc	4.99	4.27d	4.88bc	6.24a	4.69c	5.01
Starch (%)	68.64bc	70.27a	69.45	70.13ab	70.06ab	67.47c	71.21a	69.63

Values followed by the letter along a row are not significantly different by Duncan's multiple range test. TPC = Total phenolic contents; MC = Moisture content.

populations for all the traits, except MC and ash content (Table 3). The parents (UIp01 and TZi3) differed significantly for TPC, protein and starch contents (Table 3). The purple parental line UIp01 was significantly higher in TPC and starch, content, while the white parental line TZi3 was significantly higher in protein contents. The differences between the purple and white kernelled lines could be attributed to differences in their kernel color or genotype.

Except for TPC, no differences were observed between the F_1 (UIp01 × TZi3) and RF_1 (TZi3 × UIp01) for the traits. The TPC in the F_1 hybrid was significantly higher than in the RF_1 hybrid. The observed differences between the F_1 and RF_1 hybrids indicated the existence of reciprocal effects attributable to maternal effect. This suggests the inheritance of TPC could be dependent on the direction of the cross. The F_2 and reciprocal F_2 hybrids were not significantly different for all the traits. Irrespective of the direction of cross, significant differences were observed among the backcrosses for protein, fiber and starch contents. Backcrosses to the purple parent had similar values for protein, fiber and starch contents, while the compositions of the same nutrients in backcrosses to the white parent were also similar. Backcrosses to the purple parent were significantly higher in starch content than backcrosses to the white parent, while backcrosses to the white parent were significantly higher in their content of protein and fiber. The observed results among the backcrosses for protein, fiber and starch suggest that backcross selection may prove useful for the improvement of these traits in the studied materials. Similar observation was reported for protein by Pollmer *et al*. (1979), who found no significant differences between the original and reciprocal maize hybrids. Additionally, the findings on the starch content agrees with the report of Santos *et al*. (2017),

Table 3. Total phenolic contents and proximate composition of ten maize populations originating from a reciprocal cross between purple and white kernelled maize.

Generations	TPC (mg GAE g^{-1})	MC (%)	Fat (%)	Ash (%)	Protein (%)	Fiber (%)	Starch (%)
UIp01	1.84^{ab}	8.15	4.43^{abc}	1.35	10.95^{b}	4.85^{bc}	70.27^{a}
TZi3	1.47^{cd}	8.62	4.03^{bcd}	1.32	12.26^{a}	5.13^{b}	68.64^{bc}
UIp01 × TZi3 (F$_1$)	1.77^{abc}	8.46	4.00^{cd}	1.37	11.95^{a}	3.80^{d}	70.43^{a}
TZi3 × UIp01 (RF$_1$)	1.42^{d}	8.39	3.95^{cd}	1.09	12.17^{a}	4.27^{cd}	70.13^{a}
F$_1$ × F$_1$ (F$_2$)	1.61^{bcd}	8.26	4.28^{abc}	1.28	11.17^{b}	4.63^{bc}	70.37^{a}
RF$_1$ × RF$_1$ (RF$_2$)	1.63^{bcd}	8..41	4.19^{abc}	1.32	11.15^{b}	4.88^{bc}	70.06^{ab}
UIp01 × F$_1$	1.94^{ab}	8.37	4.13^{a-d}	1.36	11.00^{b}	4.88^{bc}	70.26^{a}
TZi3 × RF$_1$	1.76^{abc}	8.55	4.63^{ab}	1.3	11.81^{a}	6.24^{a}	67.47^{c}
TZi3 × F$_1$	2.05^{a}	8.37	4.73^{a}	1.42	12.07^{a}	5.99^{a}	67.41^{c}
UIp01 × RF$_1$	1.73^{a-d}	8.12	3.55^{d}	1.41	11.01^{b}	4.69^{bc}	71.21^{a}
Mean	1.72	8.37	4.19	1.32	11.55	4.94	69.63
CV (%)	13.62	5.28	9.96	10.3	2.87	10.96	1.41

Means with the same letters within a column are not significantly different by Duncan's multiple range test. TPC = Total phenolic contents; MC = Moisture content.

who reported no significant differences in the kernel sucrose content of maize hybrids derived from a reciprocal cross.

Genetic Effects

The test for adequacy of the additive-dominance model using scaling tests A, B, C and D for each trait, and the results of the six-parameter model are presented in Table 4. Either one or more of the scales was significant for the studied traits, except moisture content. This indicated the presence of epistatic gene effect in the inheritance of these traits. The mean (*m*) effect was highly significant for all the traits in both crosses, indicating the effect of common genes and environment.

For TPC, the additive (*d*), dominance (*h*), additive × additive (*i*), additive × dominance (*j*) and dominance× dominance (*l*)gene effects were non-significant in both crosses. Contrary to this finding, Harakotr *et al*. (2016) reported the adequacy of the additive-dominance model to explain the inheritance of TPC in purple maize. Similarly, Pfeiffer and Rooney (2016) found that additive, additive × dominance and dominance × dominance gene effects were important for the inheritance of total phenols in black sorghum. Although dominance (*h*) and dominance × dominance (*l*) gene effects were non-significant in this study; the associated opposite signs of the effects indicate interaction between the dominant alleles in both parents.

In the case of fat content, the additive-dominance model was inadequate to explain the inheritance the trait in both crosses (Table 4). Although no significant epistatic interaction was detected in cross UIp01 × TZi3 for fat content, significant additive × dominance (*j*) interaction was detected for its inheritance in the cross TZi3 × UIp01. Pfeiffer and Rooney (2016) reported that dominance and dominance × dominance epistatic interaction were important for the inheritance of fat in black sorghum, while Singkham *et al*. (2012) observed additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) epistatic interactions for the inheritance of oil in peanut kernels. Saxena and Bisen (2018) reported additive × additive (*i*) and additive × dominance (*j*) genetic effects for the inheritance of oil content in four out of five sesame crosses. In the same report, Saxena and Bisen observed additive × dominance (*j*) genetic effect in only one of the five crosses, consistent with the findings in this study.

The additive-dominance model was adequate to explain the inheritance of ash contents in the cross UIp01 × TZi3, however, the B scaling test was found to be significant in the cross TZi3 × UIp01, indicating the inadequacy of the additive-dominance model in this cross (Table 4). Thus,

Table 4. Scaling test and six parameter model estimates and their standard errors for total phenolic contents and proximate composition of maize kernels derived from six generations of a reciprocal cross.

Genetic Parameters	TPC (mg GAE g^{-1})	MC (%)	Fat (%)	Ash (%)	Protein (%)	Fiber (%)	Starch (%)
	Cross UIp01 × TZi3						
Scaling test							
A	0.26±0.47	0.14±0.46	-0.18±0.75	-0.00±0.07	-0.90±0.73	1.12±1.38	-0.17±1.57
B	0.84±0.39*	-0.34±0.42	1.43±0.49*	0.16±0.28	-0.06±0.32	3.06±0.82**	-4.25±1.26**
C	-0.41±0.98	-0.64±1.57	0.68±0.77	-0.28±0.24	-2.42±0.73**	0.96±3.30	1.70±3.35
D	-0.76±0.50	-0.22±0.77	-0.29±0.37	-0.22±0.18	-0.73±0.48	-1.61±1.62	3.06±1.69
Genetic effects							
Mean (*m*)	1.61±1.01**	7.95±1.55**	3.65±0.76**	0.90±0.36*	10.15±0.96**	4.63±0.76**	75.58±3.44**
Additive (*d*)	0.18±0.12	-0.23±0.11	0.20±0.17	0.01±0.04	-0.66±0.12**	-0.14±0.51	0.82±0.60
Dominance (*h*)	4.26±2.32	0.75±3.29	2.18±2.23	1.06±0.96	2.29±2.53	9.42±7.12	-15.70±7.79
Additive × additive (*i*)	1.52±1.00	0.44±1.55	0.58±0.74	0.44±0.36	1.46±0.95	3.22±3.24	-6.13±3.38
Additive × dominance (*j*)	-0.58±0.54	0.48±0.52	-1.61±0.78	-0.16±0.29	-0.84±0.77	-1.94±1.50	4.08±1.93
Dominance × dominance (*l*)	-2.63±1.39	-0.24±1.82	-1.83±1.59	-0.60±0.60	-0.49±1.63	-7.40±3.98	10.56±4.52*
	Cross TZi3 × UIp01						
Scaling test							
A	0.63±0.18**	0.07±0.21	1.29±0.46*	0.19±0.18	-0.81±0.49	3.07±1.31*	-3.82±1.43*
B	0.21±0.42	-0.30±0.48	-1.27±0.41*	0.38±0.14*	-1.10±0.75	0.26±1.57	2.02±1.42
C	0.36±0.48	0.07±1.96	0.39±1.68	0.44±0.26	-2.96±0.69**	0.99±3.03	1.07±4.42
D	-0.24±0.24	0.15±0.99	0.18±0.75	-0.06±0.07	-0.53±0.46	-1.18±1.39	1.43±2.01
Genetic effects							
Mean (*m*)	1.18±0.49**	8.69±1.98**	4.60±1.50**	1.21±0.14**	10.55±0.92**	4.88±0.60**	72.32±4.07**
Additive (*d*)	-0.18±0.12	0.23±0.11	-0.20±0.17	-0.01±0.04	0.66±0.12**	0.14±0.51	-0.82±0.60
Dominance (*h*)	1.55±1.29	-0.82±4.10	-1.00±3.06	0.58±0.43	0.77±2.59	7.33±6.60	-6.86±8.62
Additive × additive (*i*)	0.48±0.48	-0.30±1.98	-0.37±1.49	0.13±0.14	1.05±0.91	2.35±2.78	-2.87±4.02
Additive × dominance (*j*)	0.42±0.42	0.37±0.49	2.56±0.36**	-0.19±0.14	0.29±0.83	2.81±1.73	-5.84±1.60**
Dominance × dominance (*l*)	-1.31±0.85	0.52±2.15	0.34±1.70	-0.70±0.36	0.85±1.74	-5.69±4.12	4.67±4.90

*, ** Significant at p <0.05 and 0.01, respectively. MC = Moisture content.

Table 5. Heritability, potence ratio and heterosis estimates for all studied traits in the two crosses UIp01 × TZi3 and TZi3 × UIp01.

	Cross UIp01 × TZi3					**Cross TZi3 × UIp01**				
				Heterosis (%)					**Heterosis (%)**	
TRAITS	**H^2**	**h^2**	**P**	**MPH**	**BPH**	**H^2**	**h^2**	**P**	**MPH**	**BPH**
TPC (mg GAE g^{-1})	0.53	0.53	0.09	7.20	-3.36	0.00	0.00	-0.17	-14.38	-22.82
Protein (%)	0.75	0.00	0.91	2.99	-2.54	0.00	0.00	1.5	4.90	-0.73
MC (%)	0.86	0.86	0.06	0.80	-1.95	0.95	0.95	0.00	0.03	-2.69
Fat (%)	0.38	0.00	-0.19	-5.55	-9.83	0.77	0.77	-0.23	-6.73	-10.96
Ash (%)	0.89	0.00	0.00	2.17	1.08	0.00	0.00	-0.01	-18.74	-19.61
Fiber (%)	0.68	0.68	-0.66	-23.85	-25.91	0.30	0.30	-0.40	-14.33	-16.65
Starch (%)	0.52	0.52	3.20	1.41	0.24	0.69	0.69	2.22	0.98	-0.20

H^2 = Broad-sense heritability; h^2 = Narrow-sense heritability; P = Potence ratio; MPH = Mid-parent heterosis; BPH = Better-parent heterosis; Zero values of H^2 and h^2 due to negative estimates of dominant genetic variance and/ or additive genetic variance, while identical values due to the negative estimates of dominant genetic variance.

the six-parameter model was adopted to test the epistatic interactions. No significant epistatic interaction was detected for the inheritance of ash contents in both crosses. This report is contrary to that of Pfeiffer and Rooney (2016),who reported significant additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) epistatic interactions for the inheritance of ash content in sorghum.

Epistatic interaction effect was not significant for the inheritance of protein content in both crosses. However, additive (*d*) effect was highly significant. These results indicated the importance of additive gene effects over non-additive effect in the inheritance of protein contents in the plant materials studied. This finding agrees with the reported higher values of additive effect over non-additive effects in the inheritance of protein content in black sorghum by Pfeiffer and Rooney (2016). However, in a similar study in eggplant, Afful *et al*. (2019) reported the predominance of dominant gene effect in the inheritance of protein content. The opposite signs of the additive effects for the inheritance of protein content in the two crosses reveals the important role of the maternal parent in the inheritance of protein in the genetic materials used (Edwards *et al*., 1975; Cukadar-Olmedo and Miller, 1997).

In this study, the inheritance of fiber content could not be explained using the additive-dominance model. Furthermore, the results of the six-parameter model did not indicate significant epistatic effects for its inheritance in both crosses. This finding is in agreement with the report of Afful *et al*. (2019) who observed no significant epistatic interaction for fiber in egg plant. In contrast, Pfeiffer and Rooney (2016) reported significant additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) epistatic interactions for fiber in sorghum.

Positive and significant dominance × dominance (*l*) interaction influenced the inheritance of starch content in the cross UIp01 × TZi3, while in the reciprocal cross TZi3 × UIp01, the inheritance was influenced by significant negative additive × dominance interaction. The significant negative estimates of additive × dominance (*j*) gene effect for the inheritance of starch in the cross TZi3 × UIp01 indicates duplicate epistasis between additive- and dominance-increasing alleles (Sharmila *et al*., 2007). This report is contrary to that of Pfeiffer and Rooney (2016), who reported complementary epistatic effects for starch contents in black sorghum. Bano *et al*. (2017) observed significant duplicate epistatic interaction for amylose (a type of starch) in basmati rice.

In the present study, epistatic gene effects were not significant for most of the traits. However, the opposite signs associated with the estimates of additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) interactions indicated a complex mode of inheritance for most of the traits. Improvement for these traits could be delayed due to possibility of biases in the interpretation of genetic effects (Falconer and Mackay, 1996).

Heritability, Heterosis and Potence Ratio

Estimates of broad-sense (H^2) and narrow-sense (h^2) heritability for the measured traits are presented in Table 5. In a number of cases, identical estimates were observed for both types of heritability owing to the negative estimates of the dominance variance. The estimates of heritability for total phenolic contents were identical and moderate in cross UIp01 × TZi3 but low in cross TZi3 × UIp01. Mahan *et al*. (2013) had earlier reported high narrow-sense heritability (0.80) for total phenolics in red, blue and purple maize kernels. Also, Carvalho *et al*. (2016) reported high broad sense heritability (0.62) and low narrow-sense heritability (0.14) for total phenols in maize kernels. Estimates of heritability for moisture content were high, both in the broad-sense and narrow sense in both crosses. Pfeiffer and Rooney (2016) had previously reported moderate heritability (H^2 = 0.57) for moisture content in sorghum. Protein and ash had high broad sense heritability in cross UIp01 × TZi3, but the estimates were negligible in cross TZi3 × UIp01. Heritability estimates for fiber content were high in cross UIp01 × TZi3, but moderate to low in crossTZi3 × UIp01, which was contrary to Pfeiffer and Rooney (2016), who reported low broad-sense and narrow-sense heritability for fiber content in sorghum. In both crosses, starch was moderately to highly heritable. The heritability estimates for fat were low to moderate in cross UIp01 × TZi3,but high in cross TZi3 × UIp01.These results were similar to those reported by Pfeiffer and Rooney (2016) for starch (H^2 = 0.69), protein (H^2 = 0.8) and fat (H^2 = 0.69). Likewise, Bekele and Rao (2014) reported high heritability estimates for protein (0.96) but low heritability for oil (0.11) in maize.

Estimates of potence ratio indicated varying degrees of dominance effects for the traits (Table 5). Over dominance towards the higher parent was observed for starch in both crosses, and protein in the cross TZi3 × UIp01. Partial dominance toward the higher parent was detected in the cross UIp01 × TZi3 for TPC, protein, and moisture content, while partial dominance towards the low parent was detected for fat and fiber contents. In crossTZi3 × UIp01, partial dominance towards the low parent was detected for most of the traits except protein and starch content. Potence ratio of zero, indicating zero dominance was observed for moisture and ash contents in both crosses.

Positive, as well as negative heterosis over mid- and better- parents were observed for the different traits (Table 5). The significance of estimating heterosis is to detect whether or not the traits under observation are influenced by non-additive genetic effect (Wannows *et al*., 2015). In cross UIp01 × TZ$_{i}$3,the F_1 hybrids exhibited positive mid- and better-parent heterosis for ash and starch, while negative mid- and better-parent heterosis were observed for fat and fiber. Positive mid-parent heterosis and negative better-parent heterosis were recorded for TPC, protein and moisture contents. These results implied that the F_1 hybrids performed better than both parental lines for ash and starch. In cross TZ$_{i}$3 × UIp01, positive mid-parent heterosis was recorded for protein, moisture content and ash. However, better-parent heterosis was negative for all the traits in this cross. These results indicate that dominance was in the direction of the respective low parents and the F_1 hybrids performed lowly for most of the studied traits, except protein, moisture content and starch. This finding is in accordance with Netravati *et al*. (2013), who reported better-parent heterosis ranging from -40.4 to 27.7% and -36.6 to 32.4% for starch and protein contents, respectively in hybrids from 91 maize crosses. Similarly, Patel *et al*. (2016) reported better-parent heterosis ranging from -11.1 to 11.1% for protein content in pearl millet.

CONCLUSION

In this study, the genetic effects controlling the inheritance of total phenolic contents (TPC) and proximate composition traits were investigated in the six basic generations arising from a cross between purple and white maize. Additive effect was more important for TPC, MC, ash, protein and fiber suggesting that selection in the early generations would be effective for these traits. Non-additive effect was predominant for the inheritance of starch, and fat in the cross TZi3 × UIp01.Due to the duplicate type of epistasis observed for the inheritance of fat and starch, combination of different breeding methods that guarantees the accumulation and fixation of desirable alleles such as recurrent selection and selection from the early generations through to the advanced generation would be necessary for the improvement of the traits. The reciprocal differences observed between the F_1hybrid and its reciprocal for TPC, indicated the importance of maternal effect in the control of its inheritance. It will be more effective to use purple maize inbred as the maternal parent when increasing the TPC in maize hybrids. The findings of this study will be useful to maize breeders interested in improving populations or developing hybrids with increased contents of total phenolic compounds and proximate composition traits.

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Conflict of interest

The authors declare no conflict of interest.

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