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Genetic variability, heritability and genetic advance in *shrunken-2* super-sweet corn (*Zea mays* L. *saccharata*) populations

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Inbred line development requires information on the nature and magnitude of genetic variability and transmissibility of desired trait in source populations. In this study, the level of genetic variability, heritability and genetic advance of thirteen agronomic and fresh yield traits among twelve *shrunken*-2 super-sweet corn populations were evaluated. Field experiments were conducted for two years in Ibadan, Nigeria using a randomised complete block design with three replicates. Estimates of genetic variability components, broad-sense heritability and genetic advance were computed for each trait. All the traits exhibited significant genotypic differences. Genotypic variance was significant for number of marketable cobs, yield of cobs, number of cobs, number of kernel rows, husk cover, ear height and days to anthesis, while environmental variance was significant for all the traits. Phenotypic coefficients of variation were higher than the corresponding genotypic coefficients of variation for all traits. Broad-sense heritability ranged from 22.2% for anthesis-silking interval to 85.1% for husk cover. The genetic advance was high (32.7%) for husk cover, medium (12.0%) for yield of cobs and low for other traits. Genetic variability was present among the *shrunken*-2 super-sweet corn populations. Opportunities abound for further improvement of the populations and extraction of lines for hybrid seed production.

Key words: Broad-sense heritability, genotypic coefficient of variation, husk cover score, sweet corn, yield of marketable cobs.

INTRODUCTION

Maize is the most widely cultivated staple food crop in sub-Saharan Africa, where it contributes up to 70% of the daily caloric intake (Martin et al., 2000; FAO, 2007). It is a highly diverse grain crop with multiple applications and consists of different types, generally classified by kernel endosperm characteristics. The most common types of maize are flint, dent, flour, pop, pod, waxy and sweet. The physical appearance of each kernel type is determined by the endosperm pattern, quantity and quality. Cultivated maize varieties in West and Central Africa are mostly of the flint and dent types which have largely been improved by the use of both temperate and tropical exotic germplasm (Kim et al., 1987; Kim and Ajala, 1996).

Sweet corn (*Zea mays* L. var *saccharata*) is a highly perishable vegetable maize crop, harvested exclusively

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for fresh human consumption when the grains are at the milk stage with approximately 75% moisture content. It is a type of maize with kernels that are sweet as a result of high sugar content which when consumed in the immature stage, has high levels of total sugars than normal field maize, rich in fibre, minerals and certain vitamins (Tracy, 1997; Lertrat and Pulam, 2007). It has also been reported to possess significant antioxidant properties which reduce the possibilities of developing cancer and inflammations in humans (Dewanto et al., 2002). Because of these qualities, sweet corn could play a significant role in the nutrition of the peoples of West and Central Africa (Adetimirin, 2008) where fresh green maize is an important component of human diet. The difference between sweet corn and field maize arises from a mutation that influences carbohydrate biosynthesis in the endosperm. In the genome of sweet corn, at least one of the eight mutant monogenic and recessive genes preventing the conversion of sugars to starch is present (Tracy et al., 2006; Qi et al., 2009; Santos et al., 2014) resulting in the characteristic sugary taste. Of these mutants, the four most useful are *shrunken-2* (*sh2*), *brittle-2* (*bt2*), *sugary-1* (*su1*), and *sugary enhancer* (*se*). While *sh2* and *bt2*, classified as class 1 mutants (super-sweet corn), are involved in large reductions in starch and large increase in sugar, *su1* and *se* referred to as class 2 mutants (sweet corn) occur later in the starch biosynthesis pathway and influence the types and proportion of polysaccharides stored in the endosperm (Boyer and Shannon, 1984; Tracy, 1997). The grain of matured normal field maize is known to contain about 3% sugar, while sweet and super-sweet corns contain 9 to 14% and 15 to 30% sugar, respectively (Creech, 1965; Teixeira et al., 2013). The *sh2* (Yousef and Juvik, 2002) and *bt2* (Brewbaker, 1977) types of sweet corn have the greatest commercial value.

Nigeria produces about 40% of the maize production in West and Central Africa (FAO, 2016). Maize is grown throughout Nigeria from the high rainfall forest of the southeast to the low rainfall Sudan Savanna of the north. Widening food preferences have resulted in increased importation of canned sweet corn to Nigeria. Great potential therefore exists for the production and commercialisation of super-sweet corn. However, sweet corn cultivars are virtually nonexistent in Nigeria. To bridge the gap created by this challenge, a broad-base temperate super-sweet *sh2* maize population was introduced into the country and adapted to the prevailing tropical environmental conditions by four cycles of mass selection (Adetimirin, 2008). This adapted population was meant to serve both as an open pollinated variety, as well as, basis for inbred line development.

Super-sweet corn has a narrow genetic base (Tracy, 2001; Teixeira et al., 2013; Mahato et al., 2018) and possesses some undesirable characteristics, such as poor field emergence and seedling vigour and susceptibility to diseases and pests. In addition, tropical climatic conditions are characterized by high disease incidence, pest attack, short day length, and high temperatures. One way to improve the performance of this tropicalised population and broaden it genetic base is by crossing the *sh2* maize with the more adapted field maize germplasm, which could be sources of favourable alleles for enhanced agronomic performance, as well as, increased disease and pest resistance. Previous studies (Tracy, 2001; Cartea et al., 1996; Malvar et al., 1997, 2001; Butrón et al., 2008; Entringer et al., 2017) have shown the utility of field corn in the improvement of agronomic performance of sweet corn. These studies have also indicated that field maize genotypes could differ in their ability to improve the agronomic performance and quality of sweet corn.

In order to develop hybrids, the source populations from which inbred lines are extracted for hybrid seed production should have superior qualities (Hallauer, 1990). One of such source populations are the open-pollinated varieties (Sleper and Poehlman, 2006; Hallauer et al., 2010). In this study, the estimates of variance components, heritability and genetic advance for measured traits in *sh2* super-sweet corn populations derived from crosses between a tropicalised *sh2* super-sweet corn population and tropical field maize genotypes were reported.

MATERIALS AND METHODS

Experimental site

The study was conducted at the experimental field of the Department of Agronomy, Faculty of Agriculture, along Parry road, University of Ibadan (7°26' N, 3°54' E), Ibadan, Nigeria.

Experimental design and layout

Twelve *sh2* populations, eleven of which were derived from crosses between tropical field maize genotypes and a tropicalised *sh2* donor population were evaluated over two years in a randomised complete block design with four replicates. The soil at the experimental site is sandy-loam with 20.3 g kg^{-1} organic carbon, 0.90 g kg^{-1} total nitrogen, 17.90 mg kg^{-1} available P (Bray-1), 0.28 cmol kg^{-1} K and a pH (H_2O) of 6.2. The populations in each block were planted in four 5.0 m long rows spaced at 0.75 m apart. Seeds were sown at 0.50 m apart within the row. Four seeds were sown per hill and later thinned to two to give a plant population of approximately 53,333 plants per hectare. At two weeks after planting (WAP), NPK 15-15-15 fertilizer was applied at the rate of 45 kg N ha^{-1}. This was top-dressed at 4 WAP using urea at the rate of 25 kg N ha^{-1}. Hand weeding was done as necessary to keep the plots weed free.

All agronomic and fresh ear yield data excluding flowering data collected on the two middle rows of each plot. Data on days to anthesis (DA) and days to silking (DS) were recorded as number of days from planting to when 50% of the plants in a plot shed pollen or have emerged silks, respectively. Anthesis-silking interval (ASI) was calculated as the difference between DS and DA. Plant height (PH) and ear height (EH) measured in meters were taken at fresh ear yield harvest on all plants in the two middle rows of a plot, as the average distance from the soil level to the collar of the

uppermost leaf and collar of the leaf bearing the uppermost ear, respectively. Husk cover (HC) was scored on a scale of 1 to 9 (1 = husk tightly covers ear tip and extends beyond it; 9 = poor husk cover with ear tip clearly exposed). Harvesting of fresh ears was done three weeks after silking. Fresh ear yield data included: number of cobs (NC; fresh ears with husk removed) harvested per plot expressed per hectare; yield of cobs (YC; fresh ears with husks removed) recorded as total weight of cobs harvested per plot expressed in tonnes per hectare; number of marketable cobs (NMC; cobs with approximately 250 filled edible kernels) per plot expressed per hectare; yield of marketable cobs (YMC) recorded as total weight of marketable cobs per plot expressed in tonnes per hectare; number of kernel rows (KR) recorded as the average number of kernel rows of 10 top cobs; cob length (CL) measured in cm as the average length of 10 top cobs; cob diameter (CD) measured in mm using an electronic 6 in. digital calliper (Pittsburgh®, Item #47257), as the average diameter of 10 top cobs taken at the middle portion of the cob.

Data analyses

The PROC MIXED procedure in SAS (SAS version 9.1.3, SAS Institute, 2003) was used to compute variance components for all traits. In the model, populations and the interaction of populations by environment were considered random, while environments and replications within environments were fixed. Each year was considered a separate environment.

Genotypic (GCV) and phenotypic (PCV) coefficients of variation were computed for all traits according to Singh and Chaudhary (2004) using the equations:

$$GCV\ (\%) = \{(\sqrt{\sigma^2_g})\ /x\} \times 100$$

$$PCV\ (\%) = \{(\sqrt{\sigma^2_p})\ /\ x\} \times 100$$

where σ^2_g = genotypic variance, σ^2_p = phenotypic variance and x = grand mean for the trait.

The GCV and PCV were considered low when less than 10%, moderate when 10 to 20% and high when greater than 20% as explained by Deshmukh et al. (1986).

Broad-sense heritability and their standard errors were estimated using variance ratios as explained by Hallauer et al. (2010) using the following equations:

$$H^2 = \{\sigma^2_g/\ (\sigma^2_g + \sigma^2_{ge}/e + \sigma^2/re)\} \times 100$$

$$SE\ (H^2) = SE\sigma^2_g/\ (\sigma^2_g + \sigma^2_{ge}/e + \sigma^2/re)$$

where σ^2_g = genotypic variance, σ^2 = environmental variance, σ^2_{ge} = variance due to genotype by environment interaction, σ^2_p = phenotypic variance = $\sigma^2_g + \sigma^2_{ge} + \sigma^2$, r = number of replicates, e = number of environments and SE = standard error.

Heritability estimates were categorized into low (less than 40%), medium (40-59%), moderately high (60-79%) and very high (80% and above) as described by Singh (2001).

Genetic advance (GA) was estimated using the formula by Singh and Chaudhary (2004):

$$GA = i\ \sigma_p\ h^2$$

where i = 1.40 (selection intensity at 20.0%), σ_p = phenotypic standard deviation, h^2 = broad-sense heritability.

Genetic advance expressed as percentage of the mean was estimated as described by Souza et al. (2009) as follows:

$$GA\ (\%) = GA/x \times 100$$

where x = grand mean of all hybrids for the trait.

The GA was considered low (less than 10%), moderate (10-20%) and high (above 20%) according to Johnson et al. (1955).

RESULTS AND DISCUSSION

Mean performance of populations

Selection of genetically superior genotypes as well as inbred lines for hybrid seed production requires sufficient genetic variability and high heritability in the base population. The populations evaluated in this study exhibited a wide range in values for all the traits assessed (Table 1). This indicates that a sufficient range of variability in all the traits exists among the populations. The presence of variability could be a consequence of the differences in the ability of the field maize genotypes involved in the development of derived *sh2* populations to improve the donor *sh2* population (Butrón et al., 2008; Entringer et al., 2017) as well as a reflection of the influence of environment on the expression of the traits.

Estimates of variance components, heritability and genetic advance

Estimates of genetic variance (σ^2_g) were significant only for YC, NC KR, HC, EH and DA, while estimates of environmental variance (σ^2_e) were significant for all variables (Table 2). The estimates of genetic variances were higher than the corresponding environmental variances for all traits except PH and ASI. The EH had the highest significant genetic and environmental variances. The observed differences among the genotypes for most of the traits were therefore more due to genetic than environmental causes. The PCV estimates in this study were higher than the corresponding GCV for all traits, although the differences between values were low except for ASI. The PCV and GCV were high for HC, whereas only PCV was high for ASI. The GCV and PCV estimate for YC, as well as GCV for ASI and PCV for YMC were moderate. All other traits manifested low GCV and PCV values. The range in values of GCV and PCV were 1.43 (DS) to 26.50 (HC) and 1.75 (DS) to 30.05 (HC), respectively (Table 2). The slightly higher PCV than GCV for all traits in this study indicates that the expressions of the traits were influenced, though to a limited extent, by the environment and there is the possibility of improvement using phenotypic selection. Similar results indicating higher PCV than GCV for all traits were reported by Saleh et al. (2002), Alan et al. (2013) and Niji et al. (2018) in sweet corn as well as Maphumulo et al. (2015), Sesay et al. (2016) and Jilo et al. (2018) in field maize. The PCV for ASI was more than twice the GCV, an indication of limited chance for selection for the trait in the populations studied. Jilo et al. (2018) reported similar results for ASI. The high GCV exhibited by HC shows that the trait is less affected by environmental fluctuations, which guarantees

Table 1. Mean performance, standard deviation, range and coefficient of variation for selected agronomic and yield traits of 12 *sh-2* super-sweet maize populations evaluated for two years in Ibadan.

Trait	Mean ± SE†	SD	Range	CV (%)
Yield of marketable cobs (t ha^{-1})	6.8±0.1	0.79	5.2 - 8.9	11.6
Number of marketable cobs	39,946.6±371.4	3,151.7	34,594.0 - 47,059.0	7.9
Yield of cobs (t ha^{-1})	7.2±0.1	0.9	4.2 - 9.3	12.7
Number of cobs	48,098.7±426.1	3,615.5	39,215.0 - 53,333.0	7.5
Number of kernel rows	14.2±0.1	0.8	13.0 - 16.0	5.5
Cob length (cm)	15.7±0.1	0.7	13.8 - 16.8	4.6
Cob diameter (mm)	45.2±0.2	1.6	40.8 - 48.9	3.6
Husk cover	4.2±0.2	1.2	2.0 - 7.0	29.6
Plant height (cm)	199.2±1.0	8.5	172.6 - 225.1	4.3
Ear height (cm)	100.6±1.2	9.8	75.9 - 141.1	9.8
Days to anthesis	55.2±0.1	1.1	53.0 - 57.0	2.0
Days to silking	57.8±0.1	1.1	55.0 - 60.0	1.9
Anthesis-silking interval	2.6±0.1	0.8	1.0 - 5.0	31.7

†SE = Standard error; SD = standard deviation; CV = coefficient of variation.

selection progress for the trait. High GCV estimates are indicative of low amenability of the trait to environmental changes (Hefny, 2011). Emphasis on HC is therefore important in the development of cultivars from the present genetic materials. In sweet corns, good husk covering is one of the most important quality characteristics (Tracy, 1997) as complete husk covering shields of the ears from earworm attack (Lynch et al., 1999; Gardner et al., 2000). Consistent with the results of the present study, Alan et al. (2013) and Niji et al. (2018) reported low PCV and GCV estimates for DA, DS, PH, CL and CD in sweet corn.

Estimates of broad-sense heritability ranged from 22.2% for ASI to 85.1% for DA. The heritability estimates were low for ASI, medium for PH, moderately high for YMC, NMC, YC, NC, KR, CL, CD, HC, EH and DS, and very high for DA (Table 2). Genetic advance expressed as a percentage of the mean ranged from 1.7 (DS) to 32.7 (HC). The YC and HC exhibited medium and high GA, respectively, while the estimates for all other variables were low (Table 2). In this study, heritability estimates were moderately high to very high for the traits considered, except PH and ASI. However, the GA expressed as a percentage of the mean accompanying these estimates were low, except for YC with medium GA and HC with high GA. This suggests that genetic control of the traits was predominantly non-additive. Johnson et al. (1955) and Jilo et al. (2018) had previously suggested the simultaneous consideration of heritability estimates and GA because high heritability may not always be associated with high GA. These traits may respond to phenotypic selection and could be improved through heterosis breeding (Bello et al., 2012; Nzuve et al. 2014). The moderately high heritability estimate for HC in this study coupled with high GA indicated that husk covering is a quality trait exhibiting additive gene action and selection for the trait would be effective. However, HC manifested high PCV suggesting a strong influence of environment on its expression.

Conclusions

Super-sweet corn has a narrow genetic base and poorly adapted to tropical environmental conditions. The performance of super-sweet corns under tropical conditions could be enhanced by crossing super-sweet corn cultivars with adapted tropical field maize germplasm. However, field maize genotypes could differ in their ability to improve the agronomic performance and quality of super-sweet corn. In this study, 11 *sh2* super-sweet corn populations (developed by backcrossing between a *sh2* donor population and 11 adapted field maize genotypes) along with the donor parent *sh2* population were assessed to determine the nature and extent of genetic variability and transmissibility of desired trait within them. This study revealed the existence of a wide range of genetic variability in the *sh2* populations for the traits studied, which could be exploited for specific breeding objectives. The range of variability for most of the traits indicated that the field corn genotypes varied in their ability for sweet corn production. The higher estimates of genetic variances than the corresponding environmental variances for most of the traits indicated that the observed differences among the genotypes for most of the traits were more due to genetic than environmental causes. The conversion of the field corn genotypes to *sh2* super-sweet corn offer great promise for the development of super-sweet corn adapted to the growing conditions of Nigeria. Opportunities abound for further improvement of the populations and extraction of lines for hybrid seed production.

Table 2. Estimates of genetic parameters for selected agronomic and yield traits of 12 *sh-2* super-sweet maize populations evaluated for two years in Ibadan.

Trait	σ^2_g ± SE	σ^2_e ± SE	σ^2_p	GCV	PCV	H^2 (%)	GA (%)
Yield of marketable cobs (t ha^{-1})	0.33 ± 0.19	0.16 ± 0.03	0.49	8.36	10.24	66.71 ± 0.88	9.56
Number of marketable cobs	5,162,076.00 ± 2,014,192.00	3,116,633.00 ± 644,686.00	82,878,709.00	5.69	7.20	62.35 ± 0.21	6.29
Yield of cobs (t ha^{-1})	0.55 ± 0.26	0.25 ± 0.05	0.80	10.34	12.47	68.69 ± 0.64	11.99
Number of cobs	9,521,966.00 ± 4,358,537.00	3,632,024.00 ± 774,350.00	13,153,990.00	6.42	7.54	72.39 ± 0.16	7.64
Number of kernel rows	0.43 ± 0.21	0.12 ± 0.03	0.55	4.60	5.22	77.60 ± 0.84	5.68
Cob length (cm)	0.27 ± 0.16	0.13 ± 0.03	0.40	3.29	4.01	67.20 ± 1.00	3.77
Cob diameter (mm)	1.41 ± 0.78	0.72 ± 0.15	2.13	2.63	3.23	66.09 ± 0.41	2.99
Husk cover	1.23 ± 0.56	0.35 ± 0.07	1.58	26.50	30.05	77.76 ± 0.47	32.72
Plant height (cm)	25.37 ± 17.31	27.62 ± 5.89	52.99	2.53	3.65	47.87 ± 0.08	2.45
Ear height (cm)	59.31 ± 27.80	30.69 ± 6.54	90.00	7.65	9.43	65.90 ± 0.06	8.70
Days to anthesis	1.03 ± 0.47	0.18 ± 0.04	1.21	1.83	1.99	85.14 ± 0.57	2.37
Days to silking	0.69 ± 0.37	0.33 ± 0.07	1.02	1.43	1.75	67.41 ± 0.60	1.65
Anthesis-silking interval	0.10 ± 0.14	0.34 ± 0.07	0.44	12.04	25.54	22.24 ± 0.86	7.95

†SE = Standard error; SD = standard deviation; CV = coefficient of variation; σ^2_g = genotypic variance; σ^2_e = environmental variance; σ^2_p = phenotypic variance; GCV = genotypic coefficient of variation; PCV = phenotypic coefficient of variation; H^2 = broad-sense heritability; GA = genetic advance.

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