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Variability for resistance to the pink stem borer (*Sesamia calamistis* Hampson) and the sugarcane borer (*Eldana saccharina* Walker) in two tropical maize populations

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Abstract

A set of 100 S_1 plants were selected from a white and yellow maize population to generate both full-sib and half-sib progenies using North Carolina Design II (NCD II) mating scheme. The 250 progenies generated in each population were evaluated under artificial infestation with two borer species (*Sesamia calamistis* and *Eldana saccharina*) at two locations in two seasons to determine levels of genetic variability for improvement purposes.
There were wide ranges for most of the traits studied in both maize populations. Plant height and grain yield were significantly reduced with mean grain yield loss being between 25 and 30%. In the white population, additive variance was larger than dominance variance for grain yield, days to 50% silking, stalk breakage and ear per plant, but for the yellow counterpart, additive variance was larger for plant height, ear per plant, leaf feeding and cob damage. None of the gene actions was important for dead heart. Narrow-sense heritability was low to moderate for the resistance parameters. It ranged from 1.45% for leaf feeding to 40.6% for stalk breakage in the white population, and from 3.80% for leaf feeding to 40.1% for cob damage in the yellow population. Heritability for grain yield was 37.6% in the white population but much lower (10.5%) in the yellow population.
Although, heritability was low to moderate for the traits studied, the wide ranges and moderate additive variances obtained suggest that substantial genetic variability exist in the two maize populations for reasonable improvement to be made. Breeding scheme that capitalizes on both additive and dominance gene action would be effective for improving the populations for stem borer resistance and grain yield.

Keywords: stem borers, plant resistance, genetic variance, heritability, maize population

Introduction

Stem borers are the most important insect pest of maize in Africa. Three stem borer species namely the pink stem borer (*Sesamia calamistis*), the sugarcane borer (*Eldana saccharina*), and the African stem borer (*Busseola fusca*) are of economic importance to maize in West and Central Africa. However, *S. calamistis* and *E. saccharina* are the most damaging and widespread in the sub-region (Bosque-Perez and Mareck, 1990; Polaszek, 1998). Yield loss due to stem borer attack was estimated to be between 20 and 70% depending on the severity and stage of plant development when attacked (Ajala et al, 2001; De Groote et al, 2001; Odiyi, 2006). Total crop failure has also been reported in some instances (Girling, 1980; Bosque-Perez and Mareck, 1991; Gounou et al, 1994; Schulthess and Ajala, 1999) especially in the second planting season in the south of the sub-region.

Various measures have been employed to control stem borers. Lawani (1982) did a review on the complex nature of cultural and chemical control methods for stem borers while Ampofo (1986) noted that chemical application may not be effective when the insect has bored into the stem. Ande et al (2010)

also reported on the repetitive and serial application of biochemical for stem borer control which makes it tedious and almost impracticable. All the authors noted that breeding for resistance is therefore the most viable option for the control of stem borers because it is cheap, safe and compatible with other control measures.

The choice of efficient breeding procedure requires information about the magnitude of genetic variances. Several studies on genetic variability and resistance to different pests of maize exist in the literature but very few have reported on genetic variability and resistance to the African stem borer complex, the few being on the *Chilo partellus* (Ajala, 1992; Pathak and Othieno, 1990; Ajala et al, 1995) and *Sesamia nonagrioides* (Butron et al, 1999; Butron et al, 2006), with none being on either *S. calamistis* or *E. saccharina*, or resistance to both. This study was therefore carried out to determine the extent of genetic variability for resistance to both the pink stem borer (*S. calamistis*) and the sugarcane borer (*E. saccharina*) in two adapted maize populations.

Materials and Methods

Development and evaluation of progenies

Two tropically adapted early-maturing maize populations, one yellow-grained (DMR ESR-Y) and the other white-grained (DMR ESR-W), both resistant to downy mildew and the maize streak virus diseases, were used in this study. Both populations were developed by intermating downy mildew resistant (DMR) sources from the Philippines with TZSR (Tropical Zea Streak Resistance) from IITA (Fajemisin et al, 1985). About 300 S_1 progenies were generated from each of the populations. Thereafter, 100 S_1s with well filled cobs that were representative of the population by being predominantly dent, were then selected from each population and used to generate both full- and half-sib progenies using the North Carolina Design II (NCD II) mating scheme of Comstock and Robinson (1952). To generate the full- and half-sib progenies, the selected S_1s from each population were grouped into 10 sets, with each set having 10 lines. Five lines from each set were designated as males while the other five were females. Each male line was then used to cross all the five females in the set to produce five units of half-sib and consequently, 25 full-sib families within the set. Therefore, a total of 250 progenies were generated altogether across all the sets in each population. However, only 225 progenies were obtained for the white population due to problem of flowering date synchrony between males and females in one set.

The 225 progenies of the white with three checks and 250 progenies of the yellow population with six checks were subsequently evaluated in both early and late seasons of 2008 and 2009 at Ibadan (Lat 7°22N, Long 03°58E) and Ikenne (Lat 6°54N, Long 03°42E), both locations in southwest Nigeria. A randomized incomplete block design with two replications was used for evaluation in each location. For evaluations in Ibadan, a single row plot of 7m long was used, but each row was separated into two half-row plots of 3m each with 1m in the middle. The first 3m was artificially infested with egg masses of stem borers raised on artificial diet in laboratory, while the other half was left as control. However, a single un-infested 5m row plot was used at Ikenne. For both locations, plant spacing of 75 cm x 25 cm was used and two seeds were planted per hole but thinned to one plant per hill at three weeks after planting (WAP) just before infestation to get a maximum of 13 plants per sub-plot at Ibadan and 21 plants per row at Ikenne resulting in a plant density of 53,333 plants/ha. An egg mass of both *S. calamistis* and *E. saccharina* containing 30-40 eggs at black head stage was inserted in-between the stem and leaf sheath at three WAP and in-between the forming cob and the stem at silking, respectively. Other cultural practices included pre-emergence spray of gramozone and primextra for weed control supplemented with hand weeding as necessary during the season. Fertilizer was also split-applied using N-P-K 15:15:15 at 10 days after planting (DAP) at the rate of 30 kg N/ha and top dressed with urea six WAP at the same rate.

Data collected from both Ibadan and Ikenne trials included days to silking estimated as days from planting to the day when half of the plants in a plot had silk extrusion, plant height measured from five competitive plants per plot as distance from base of the plant to base of the tassel, plant aspect rated per plot after anthesis on a scale 1-9 with 1 representing vigorous and appealing plants without leaf defoliation, disease symptoms, or lodging, and carrying their first ear at the middle of the plant, while 9 represents lodged, diseased and defoliated plants with their first ear closer to the soil surface or to the tassel. Ear per plant was calculated as ear at harvest divided by plant at harvest per plot. Data on leaf feeding, dead heart, stalk breakage, cob damage count and stem tunneling were collected per plot from the Ibadan trials on infested plots. Leaf feeding was scored at three weeks after infestation (WAI) based on a visual rating on a scale of 1-9 with 1 = clean un-defoliated leaves and 9 = 80-100% defoliation of the entire leaf area. Dead heart was counted at four WAI as number of plants with their growing points destroyed, and expressed as the percentage of plant stand. Stalk breakage was taken as number of broken plants and expressed as percentage of plant stand. Number of damaged cobs was expressed as percentage of ear at harvest, while stem tunneling was taken after harvesting by splitting five stalks longitudinally and measuring the length tunneled by stem borer larvae then expressed as percentage of plant height. Grain yield (t/ha) was obtained as ear weight adjusted to 14% moisture content.

Data analyses

Data from each population were analysed separately. Data on dead heart, stalk breakage and cob damage were normalized using arcsine transformation before analysis. Analysis of variance for North Carolina Design II was performed for individual character studied for both infested and non infested plots using PROC GLM of SAS (Version 9.2). Random model was assumed for the analysis. The statistical model (for Design II) for producing number of sets (n1 x n2 progenies) tested in a replicated trial was followed as:

$$Y_{ijkln} = \mu + s_i + b_{ij} - m_{ik} + f_{il} + (mxf)_{jk,l} + e_{ijkln}$$

where μ = general mean, s_i = the effect of ith set, b_{ij} = the effect of jth replication in i^{th} set, m_{ik} = the effect of kth male in i^{th} set, f^{il} = the effect of lth female in i^{th} set, $(mxf)_{jk,l}$ = the male x female effect in i^{th} set, e_{ijkln} = the error associated with each observation.

Combined ANOVA was done for each population across all environments. Variance due to entry was sub-divided into variance due to male (sets), female (sets), and female x male (sets). Variance due to entry by environment interaction was also partitioned into males/sets x environment, females/sets x environment, and males x females/sets x environment. Variances of males within sets and females within

sets were tested by variances due to environment by males in sets and environment by females in sets respectively. The variances of male by females within sets interaction, environment by males in sets, and environment by females in sets interaction were tested using variance due to environment by males by females in sets in situations where the second order interactions were significant. Since variances due to males in sets and females in set have the same degree of freedom, the sum of square of male in set and female in set were pooled to estimate additive variance. Similarly, the male in set by environment and female in set by environment sum of squares were pooled to estimate the additive x environment interaction according to Hallauer and Miranda (1988).

Additive genetic variance (σ^2_a), dominance variance $\sigma^2 d$) and their interaction with environment $\sigma^2 ae$ and $\sigma^2 de$) were estimated from the mean squares of ANOVA as:

$\sigma^2_m = (MS_M - MS_{MF} - MS_{ME} + MS_{EMF})/ref$
$\sigma^2_a = 4\sigma^2_m = 4\sigma^2_f$
$\sigma^2_{mf} = (MS_{MF} - MS_{EMF})/re = 1/4\sigma^2_d$
$\sigma^2_d = 4\sigma^2_{mf}$
$\sigma^2_{me} = (MS_{ME} - MS_{EMF})/rf$
$\sigma^2_{ae} = 4\sigma^2_{me}$
$\sigma^2_{mfe} = (MS_{EMF} - MS_E)/r$
$\sigma^2_{de} = 4\sigma^2_{mfe}$
$\sigma^2_e = MS_E/er$

The standard errors for the variance estimates and narrow-sense heritability were calculated as described by (Hallauer and Miranda, 1988). Narrow-sense heritability (h^2) was estimated as:

$h_n^2 = 4\sigma^2 m/ [\sigma^2/er + 4\sigma2_{me}/e + 4\sigma2_{mfe}/e + 4\sigma2_{mf} + 4\sigma2_m]$

Dominance ratio was also estimated as σ^2_d/σ^2_a.

Results

Performance of progenies of DMR ESR-W and DMR ESR-Y

Means and ranges of traits studied under infested (IC) and non-infested condition (NIC) in the two maize populations are shown in Tables 1 and 2. Plant height and grain yield were significantly reduced under IC relative to NIC in both maize populations. In DMRESR-W, average grain yield of 3.5 t/ha was obtained under IC and 4.6 t/ha under NIC (Table 1), therefore grain yield reduction in the white population was 23.9%. For DMR ESR-Y, the yellow maize population, the mean grain yield was 3.2 t/ha under IC and 4.6 t/ha under NIC (Table 2) thus reflecting a relatively higher grain yield reduction of 30.4% when compared with the white population. Proportion of dead heart was low in both populations being 2% for the white and 0.4% for the yellow. However, values obtained for other damage parameters were high. Leaf feeding was 5.3 for the white and 4.7 for the yellow population. Stalk breakage and cob damage were also high, up to 25% and 31% for the white, and 20% and 44% for the yellow population, respectively. Generally, there were wide ranges for most of the traits studied in both maize populations. CVs for most of the traits were moderate except for dead heart, stalk breakage, cob damage and stem tunneling, where the standard error of means were also large.

Variance estimates of progenies of DMR ESR-W and DMR ESR-Y

Partitioning the sum of square of entries (data not shown) revealed that GCA accounted for 50.0% of the total variation among entries for grain yield, 35.1% for stem tunneling, 38.4% for leaf feeding, 37.6% for cob damage count, 29.8% for dead heart, and 53.0% for stalk breakage for DMR ESR-W population under infested condition. But for DMR ESR-Y under the same infested condition, it accounted for 38.6% of the total variation for grain yield, 42.2% for stem tunneling, 34.2% for leaf feeding, 47.7% for cob damage count, 34.8% for dead heart and 48.7% for stalk breakage. Dominance variance was greater than additive variance for plant height, leaf feeding, stem tunneling and cob damage count while additive variance was larger than dominance variance for grain yield, days to silking, stalk breakage and ear per plant under infested condition in DMR ESR-W. None of the gene actions was important for dead heart in the same population

Table 1 - Mean ± SE and ranges for agronomic and resistance traits among progenies of DMR ESR-W maize population evaluated under stem borer infested condition in Ibadan and non-infested condition in Ibadan and Ikenne during 2008 and 2009 seasons.

Traits	Infested			Non infested		
	Mean ± SE	CV (%)	Range	Mean ± SE	CV (%)	Range
Days to silking	50.0±1.34	3.8	46.2 - 56.5	51.0±1.20	3.3	47.0 - 57.0
Plant aspect	5.3±0.80	21.3	3.0 - 7.0	3.1±0.48	22.1	1.9 - 4.7
Plant height (cm)	144.6±0.09	7.9	112.4 - 177.3	162.6±9.66	8.4	137.8 - 183.8
Ear per plant	0.8±0.09	17.3	0.5 - 1.1	1.0±0.11	16.3	0.7 - 1.3
Grain Yield (t/ha)	3.5±0.60	24.3	1.7 - 5.2	4.6±0.79	24.5	1.6 - 6.3
Dead heart (%)	2.0±5.30	366.4	0.0 - 27.8	-	-	-
Leaf feeding	5.3±0.86	23.1	3.1 - 6.9	-	-	-
Stalk breakage (%)	25.1±12.14	68.5	0.8 - 59.7	-	-	-
Cob damage count (%)	30.6±7.70	81.9	0.0- 78.4	-	-	-
Stem tunneling (%)	15.9±6.42	57.3	4.4 - 33.3	-	-	-

SE - Standard error; CV - Coefficient of variation

Table 2 - Mean ± SE and ranges for agronomic and resistance traits among progenies of DMR ESR-Y maize population evaluated under stem borer infested condition in Ibadan and non-infested condition in Ibadan and Ikenne during 2008 and 2009 seasons.

Traits	Infested			Non infested		
	Mean ± SE	CV (%)	Range	Mean ± SE	CV (%)	Range
Days to silking	49.8±0.95	2.7	46.0 - 55.0	51.3± 1.02	2.8	48.0 - 56.0
Plant aspect	4.5±0.73	23.0	3.1 - 6.4	3.1± 0.43	19.9	1.8 - 4.1
Plant height (cm)	175.4±8.28	6.7	146.7 - 204.5	186.6±10.46	7.9	155.9 - 214.5
Ear per plant	0.7±0.09	16.9	0.5 - 1.0	0.9± 0.10	15.5	0.8 - 1.2
Grain Yield (t/ha)	3.2±0.61	27.0	1.9 - 5.5	4.6± 0.93	28.4	3.2 - 8.3
Dead heart (%)	0.4±1.28	406.2	0 - 6.1	-	-	-
Leaf feeding	4.7±0.91	27.6	3.1 - 6.5	-	-	-
Stalk breakage (%)	19.9±10.75	76.5	0 - 56.9	-	-	-
Cob damage count (%)	43.9±14.88	47.9	15.4 - 89.1	-	-	-
Stem tunneling (%)	4.4±2.46	78.6	0.4 - 9.9	-	-	-

SE - Standard error; CV - Coefficient of variation

(Table 3). However, for DMR ESR-Y, additive variance was larger than dominance variance for plant height, ear per plant, leaf feeding and cob damage count while both additive and dominance variances were equally important for days to 50% silking and stalk breakage but neither of the two gene actions was important for dead heart (Table 4). Estimates of variance components were at least twice their corresponding standard error for days to 50% silking and plant height for the two populations.

Generally, environmental or error variances were low to moderate, but larger than genetic variances for plant aspect, ear per plant, leaf feeding and stem tunneling. Also, estimates of additive by environment interaction variance were lower than that of dominance by environment interaction for most of the traits studied in the two maize populations (Table 3 and 4). Dominance ratio (σ^2_d / σ^2_a) was above unity for some traits in the two maize populations. The ratio was strikingly high for leaf feeding and cob damage count in the white population (Table 3), and for grain yield and stem tunneling in the yellow maize population (Table 4). Complete dominance was observed for days to 50% silking in the yellow population while partial dominance was observed for days to 50% silking and grain yield in the white population, and plant height and stalk breakage in the yellow counterpart.

Narrow-sense heritability estimate was low to moderate under infested condition in both maize populations. It ranged from 1.45 % for leaf feeding to 42.3 % for days to 50% silking in DMR ESR-W, and 3.55% for ears/plant to 45.3% for plant height in DMR ESR-Y (Table 3). Heritability estimate for grain yield in the white population was 37.6% but was rather low for the yellow population with a value of 10.5%. Among the resistance parameters, stalk breakage had highest heritability estimate of 40.6% for the white population while cob damage count had highest value of 40.1% for the yellow population. Leaf feeding had the least in both populations (Tables 3 and 4).

Discussion

Knowledge of genetic variability is important in determining breeding method to adopt and gains from selection. The wide ranges and reasonable level of variance estimates for most of the traits measured is an indication of substantial genetic variability in the two maize populations to allow good progress from selection for grain yield and resistance to the two borer species. When maize plant is infested by stem borer larvae, photosynthetic parts are reduced and the vascular tissues destroyed as the larvae feed on the leaves and bore into the stem. This leads to stunt-

Table 3 - Components of genetic variance* and narrow sense heritability estimates of agronomic and resistance traits among progenies of DMR ESR-W maize population under stem borer infested condition in Ibadan in 2008 and 2009.

Trait	σ^2_a ± SE	σ^2_d ± SE	σ^2_{ae}	σ^2_{de}	σ^2_e	σ^2_d / σ^2_a	σ^2_{ph}	h²(%) ± SE
Days to silking	2.18 ± 0.77	1.71 ± 0.75	0.00	1.10	0.76	0.78	5.16	42.29 ± 0.15
Plant aspect	0.10 ± 0.10	0.12 ± 0.23	0.00	0.47	0.27	1.15	0.67	15.53 ± 0.15
Plant height (cm)	59.83 ± 25.21	90.72 ± 26.53	9.42	12.73	25.29	1.52	186.92	32.01 ± 0.13
Ear per plant	0.001 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	†	0.01	18.30 ± 0.23
Grain Yield (t/ha)	0.15 ± 0.08	0.01 ± 0.12	0.00	0.20	0.15	0.08	0.41	37.56 ± 0.19
Dead heart (%)	0.00 ± 0.00	0.00± 0.00	0.00	0.00	0.01	1.46	0.00	†
Leaf feeding	0.01 ± 0.11	0.17 ± 0.21	0.12	0.00	0.33	30.33	0.38	1.45 ± 0.28
Stalk breakage (%)	0.01 ± 0.01	0.00 ± 0.01	0.01	0.04	0.02	†	0.03	40.59 ± 0.29
Cob damage count (%)	0.01± 0.02	0.23 ± 0.03	0.00	0.00	0.04	22.25	0.16	6.36 ± 0.10
Stem tunneling (%)	0.00 ± 0.00	0.002 ± 0.00	0.001	0.00	0.00	†	0.00	†

*σ^2_e =environmental variance; σ^2_a = additive variance; σ^2_{de}=dominance x environment interaction variance; σ^2_{ae}=additive x environment interaction variance; σ^2_d =dominance variance; σ^2_{ph} = phenotypic variance; h² = narrow-sense heritability; SE = standard error; † not estimated because of negative additive and dominance variance

Table 4 - Components of genetic variance* and narrow sense heritability estimates of agronomic and resistance traits among progenies of DMR ESR-Y maize population under stem borer infested condition in Ibadan in 2008 and 2009.

Trait	$\sigma^2_a \pm SE$	$\sigma^2_d \pm SE$	σ^2_{ae}	σ^2_{de}	σ^2_e	σ^2_d / σ^2_a	σ^2_{ph}	$h^2(\%) \pm SE$
Days to silking	1.25 ± 0.43	1.25 ± 0.39	0.00	0.13	0.43	1.00	2.96	42.37 ± 0.15
Plant aspect	0.04 ± 0.10	0.06 ± 0.17	0.11	0.21	0.24	1.65	0.50	7.57 ± 0.20
Plant height (cm)	98.93 ± 36.22	78.52 ± 26.49	24.48	0.00	31.81	0.79	218.46	45.28 ± 0.17
Ear per plant	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	†	0.01	3.55 ± 0.27
Grain Yield (t/ha)	0.06 ± 0.08	0.28 ± 0.15	0.00	0.24	0.17	4.34	0.62	10.47 ± 0.12
Dead heart (%)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	†	0.00	4.09 ± 0.17
Leaf feeding	0.01 ± 0.12	0.00 ± 0.25	0.00	0.28	0.39	†	0.34	3.80 ± 0.34
Stalk breakage (%)	0.01 ± 0.01	0.01 ± 0.01	0.00	0.02	0.01	0.94	0.05	26.18 ± 0.15
Cob damage count (%)	0.01 ± 0.01	0.00 ± 0.01	0.00	0.01	0.02	†	0.02	40.10 ± 0.29
Stem tunneling (%)	0.00 ± 0.00	0.003 ± 0.00	0.001	0.00	0.00	8.86	0.00	8.12 ± 0.18

*σ^2_e =environmental variance; σ^2_a = additive variance; σ^2_{de}=dominance x environment interaction variance; σ^2_{ae}=additive x environment interaction variance; σ^2_d =dominance variance; σ^2_{ph} = phenotypic variance; h^2 = narrow-sense heritability; SE = standard error; † not estimated because of negative additive and dominance variance

ed growth, poor plant appeal and eventually, yield reduction. The reduction in plant height and grain yield under infested condition in the two maize populations is a direct result of infestation by stem borers as observed by Ajala (1994) for *Chilo partellus*. Percentage yield reduction recorded in this study also falls within the range of loss recorded by previous workers (Ajala et al, 2001; De Groote et al, 2001; Odiyi, 2006) for various stem borers.

The low values for dead heart recorded in this study suggest limited migration of larvae of the pink stem borer to the growing tip of maize and it is an indication that the pink stem borers rarely cause dead heart. Dead heart occurs when the feeding larva migrate to the meristematic region to feed thus damaging the growing point. Coefficients of variability (CV) for especially the resistance traits under infested condition were high. A similar observation was reported by Odiyi (2006) under stem borer infestation and by Badu-Apraku et al (2005) under drought stress suggesting that CVs are usually high under stressed conditions. However, CVs for traits derived from other traits are usually higher than the ones measured directly (Ajala et al, 2009). Data on dead heart, stalks breakage, and stem tunneling were based on proportions and could necessitate the high CVs observed.

In general, both additive and dominance genetic variances were very low for leaf feeding and deadheart in the two populations. Deadheart as a parameter was not influenced by either of the two gene actions. Additive gene action controlling leaf feeding and dominance gene action controlling stem tunneling, with dead heart not being conditioned by either type of gene action in DMR ESR-Y is similar to the finding of Ajala (1992). Dominance gene action controlling leaf feeding in DMR ESR-W is also in agreement with report of Odiyi (2006). However, heritability estimates for stalk breakage and cob damage, two other resistance parameters, were moderate. Furthermore, low heritability estimate obtained for stem tunneling in DMRESR-Y suggests that resistance to the two borer species is under genetic control but progress from recurrent selection will be slow. Rounding-off variance component values resulted in

seemingly very low variance estimates, although the original values were used to calculate heritability estimates that gave low to moderate values observed for most traits. However, since partial inbreds were used to generate both full- and half sib progenies for evaluation, values obtained for both additive and non-additive variances in this study may be biased. Gardner (1963) had noted that values of additive variance will change depending on levels of inbreeding. The low additive variance for plant height and grain yield is not unconnected with the high error variance for these traits. Both environmental and dominance by environment variance for leaf feeding and stalk breakage were larger than estimate of additive variance. The implication of this is that environmental forces have a strong influence on the expression of the two traits and that they may not be very reliable traits for selection for higher levels of resistance to the stem borers used in this study despite the significant differences among entries under stem borer infestation obtained from the analyses of variance.

The strikingly high dominance ratio (above unity) for leaf feeding and cob damage in DMR ESR-W, and grain yield and stem tunneling in DMR ESR-Y suggests that the non-additive variance may include not only dominance and epistatic variances but also some portion of genotype by environment interaction variance. It also suggests possible occurrence of over-dominance at some loci. An explanation for build-up of dominance variance was given by Badu et al (2007) that in the presence of overdominance, heterozygote is favoured, and both favourable and unfavourable alleles are retained in the population and as a result, gene frequency move towards equilibrium. The genetic variance resulting from their segregation contributes to the dominance variance components.

The low estimates of heritability observed for some of the resistance traits in this study was also observed by Odiyi (2006). Low heritability may be due to poor precision in the field experiment or low initial frequency of resistance genes in tropical maize populations (Kling et al, 2000). It may also be due to influence of environment on the traits concerned (Falconer, 1989) or due to the few environments used

for evaluation. Silva et al (2004) got higher heritability values for grain yield when progenies were evaluated in six environments with two replications per environment which have reduced considerably, the genotype by environment and error variances. Negative heritability for some traits is due to high dominance effects of such traits (Ajala et al, 2009) or high environmental variance. Diversifying the genetic background can enhance heritability values but, high heritability alone is not enough to aid significant improvement in a selection program, but should be accompanied by substantial amount of genetic advance, which is a function of selection intensity, phenotypic variance and heritability (Badu-Apraku, 2006). The low to moderate heritability values observed for resistance traits in both maize populations suggests that those traits are under genetic control. But although improvement will be made, progress from selection will be slow using either of the traits as selection criteria.

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