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ORIGINAL PAPER

Relative changes in genetic variability and correlations in an early-maturing maize population during recurrent selection

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Abstract Four cycles of S_1 family recurrent selection to improve grain yield and resistance to *Striga hermonthica* have been completed in TZE-Y Pop STR C_0. In order to determine whether or not to continue with the recurrent scheme, it was desirable to evaluate the amount of residual genetic variance and associated parameters in the population. The objective of this study was to characterize the relative changes in the levels of the genetic variances, heritability estimates and genetic correlation coefficients, and to predict future gains from selection for grain yield, *Striga* resistance and other agronomic traits. Fifty S_1 families, derived from each cycle, were evaluated under *Striga*-infested and *Striga*-free conditions at Mokwa, Ikenne and Abuja, Nigeria, in 2005 and 2007. Under *Striga* infestation, genetic variances for grain yield, days to anthesis, plant height and *Striga* damage generally increased in the advanced cycles of selection. In contrast, the genetic variances for days to silk, anthesis–silking interval, ears per plant, ear aspect and number of emerged *Striga* plants decreased with selection. The advanced cycles of selection significantly out-yielded the original cycle in both research environments. Heritabilities for grain yield, *Striga* damage and number of emerged *Striga* plants were significantly greater than zero. The realized gains from selection for grain yield under *Striga* infestation (52 kg ha^{-1} cycle^{-1}) and *Striga*-free conditions (130 kg ha^{-1} cycle^{-1}) were remarkably lower than the predicted gains (350 and 250 kg ha^{-1} cycle^{-1}, respectively). Adequate genetic variability exists in cycle 4 of the scheme to ensure future gains from selection.

Introduction

Maize (*Zea mays* L.) occupies a strategic position in the food, feed and agro-industrial economy of West African countries. In recent years, there has been more awareness than ever of the potential of this crop species among the governments of the sub-region. For example, the Nigerian government, apparently in an effort to increase total grain production, challenged all the stakeholders in the maize sector in 2006 to double maize grain production in the country within 2 years. Therefore, it has become urgently necessary to develop maize cultivars that are highly productive to meet the demand for maize grain in the sub-region.

Maize production and productivity in West Africa are highly constrained by several abiotic and biotic factors, especially in the savannas which are the most productive maize ecologies in the sub-region. Parasitism by *Striga hermonthica* (Del.) Benth is one of the major biotic stresses constraining maize production and productivity. *Striga* spp. are parasitic flowering plants indigenous to Africa and pose a major threat to the rapid spread of maize and hence to increased production and productivity in the region. The incidence and severity of the parasite are particularly high in the savannas of West Africa (Berner et al. 1996) where it is estimated to severely infest 40 million ha of cereal production, while nearly 70 million ha have moderate levels of infestation (Lagoke et al. 1991). As of 1986,

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estimated annual cereal yield losses due to *Striga* in Africa amounted to about 4.1 million megagrams of grain, worth about US $7 billion (Lagoke 1998). Yield losses may range from 10 to 100 % depending on the variety and the environmental conditions (Kroschel 1999; Lagoke 1998). The *Striga* problem in WA may be attributed to the use of cereal monocropping with little or no fallow or rotations with non-host crops, leading to a decline in soil fertility. This has resulted in a rapid increase in the extent and intensity of *Striga* infestations and is still posing a serious threat to food production (Vogt et al. 1991).

Several methods are available for the control of *Striga* in maize; however, host plant resistance is considered the most practical, sustainable and effective *(*Kim 1991, 1994; Parkinson et al. 1989; Badu-Apraku et al. 2004) and this has been the major control strategy adopted at the International Institute of Tropical Agriculture (IITA) for about three decades. Over the years, scientists on the programme have relied mainly on field selection for multiple traits under both *S. hermonthica*-infested and non-infested conditions. Sources of moderate resistance have been identified and reliable artificial field infestation techniques have been developed and standardized. At the initial stages of the programme, researchers were faced with the problem of quantifying *Striga* resistance in maize. *Striga* plants thrive on the host, but much damage would have been done underground before the parasitic plants appear on top of the soil around the maize plant. Therefore, two types of defence mechanisms by the maize plant were identified: that is, resistance and tolerance (Kim 1994). In *Striga* research, tolerance is used to describe the ability of the host plant to withstand the effects of the parasitic plants that are already attached, regardless of their number. It is quantified by a host damage rating score. Resistance refers to the ability of the host plant to prevent the parasite from attaching itself to the roots (Kim 1994). This is quantified by the number of emerged *Striga* plants around the base of the maize plant. Kim (1994) established that host damage score and *Striga* emergence were quantitatively inherited. The two traits, along with high grain yield under *Striga* infestation, were considered the most appropriate to use in breeding for *Striga* tolerance/resistance (Kim 1991, 1994; Badu-Apraku et al. 1999). The traits are controlled predominantly by additive gene action, although nonadditive gene action could also be important (Kim 1994; Kling et al. 2000; Badu-Apraku and Fakorede 2001). The heritabilities of host damage score and yield under *S. hermonthica* infestation are moderate, but heritability for *Striga* emergence is low (Kling et al. 2000; Badu-Apraku 2007). Akanvou et al. (1997) reported narrow-sense heritability estimates of 0.33 for host plant damage, 0.14 for the number of emerged *Striga* plants and 0.32 for grain yield in a tropical maize population under *Striga* infestation.

In an effort to identify *Striga*-resistant/*Striga*-tolerant varieties, breeders at IITA screened the available maize germplasm, including OPVs, hybrids and inbred lines. Those that were resistant or tolerant were used in backcross breeding to incorporate *Striga* resistance in agronomically acceptable varieties. The solution to the maize production and productivity constraints in much of the savannah ecology was not so straightforward. In addition to the *Striga* problem, varieties that would fit the relatively short rainy season were urgently needed. In 1980, IITA started breeding specific varieties for this agroecology and developed several early-maturing varieties and incorporated *Striga* resistance into some of the varieties in collaboration with the NARS through the West and Central Africa Collaborative Maize Research Network (Badu-Apraku and Fakorede 2001). Among the outputs of the programme is TZE-Y Pop DT STR, a yellow source population with stable and durable polygenic resistance to *Striga* and the major important diseases in West and Central Africa (Badu-Apraku et al. 2008).

Recurrent selection is a breeding procedure designed to improve population performance and maintain genetic variability to ensure continued progress from selection (Sprague and Eberhart 1977; Hallauer and Miranda 1988). The procedure has been used successfully to improve grain yield and other agronomic traits in several crops, especially in maize (Sprague and Eberhart 1977; Hallauer and Miranda 1988; Lamkey 1992; Weyhrich et al. 1998; and Menkir and Kling 1999). However, the use of recurrent selection for improvement of resistance to parasitic plants in maize is limited. IITA has conducted recurrent selection in several maize populations with varying genetic backgrounds, maturities and grain colours under artificial infestation with *Striga* (Menkir and Kling 2007; Badu-Apraku 2007; Badu-Apraku et al. 2008). One type of recurrent selection uses the S_1 family as the selection unit and is, therefore, called S_1 family recurrent selection. This procedure is designed to improve population performance and allows alleles to be fixed rapidly, with deleterious, homozygous alleles exposed and eliminated early in the selection programme (Weyhrich et al. 1998). In the absence of overdominance, the S_1 or S_2 family selection method is considered to be superior to other recurrent selection methods for the improvement of the population per se (Lamkey 1992). The S_1 recurrent selection method capitalizes on additive gene action and has been used in combination with an effective and reliable artificial *Striga* infestation method to screen segregating families of maize at IITA. Along with several other populations, TZE-Y Pop STR has been subjected to four cycles of S_1 family recurrent selection to upgrade the level of *Striga* resistance and improve the grain yield performance under *Striga*-infested as well as *Striga*-free environments (Badu-Apraku

2007; Badu-Apraku et al. 2008, 2009). It was of interest to re-examine the changes in genetic variability, heritabilities and genetic correlations in the cycles of selection. Badu-Apraku (2007) investigated the type of gene action and the extent of genetic variability available in the population after three cycles of S_1 recurrent selection. The results showed that the estimates for dominance variance were larger than additive genetic variance for grain yield, plant height, ear height, number of ears at harvest and *Striga* damage rating at 8 weeks after planting. Heritability estimates were generally low for most traits (<0.40). However, moderate-to-large additive genetic variances and wide ranges for mean values were observed for most traits, indicating that adequate genetic variability was present in the population to allow further significant progress from selection. So far, no study has been conducted in maize to characterize the relative changes in genetic variances, the heritability of *Striga* resistance traits (*Striga* damage, *Striga* emergence ears/plant [EPP]) and the genetic correlations among traits during cycles of recurrent selection.

The objectives of this study, therefore, were to (i) characterize the relative changes in the levels of the genetic variances, heritabilities and genetic correlations for grain yield and other agronomic traits in the early yellow population during four cycles of S_1 family recurrent selection and (ii) predict possible future gains from selection. This information is needed for a decision on whether or not to continue with the selection programme and in determining the necessary modifications for more efficient and effective progress from selection.

Materials and methods

Genetic materials

A drought-tolerant and *Striga*-resistant early-maturing yellow population, TZE-Y Pop STR C_0, was used for this study. The population was developed following one cycle of half-sib recombination of the drought-tolerant yellow germplasm sources, DR-Y Pool BC_2F_2, KU 1414 and 9499. The resultant early yellow population was designated TZE-Y Pop as shown in chart 1. The *Striga*-resistant/-tolerant IITA inbred line 9450 STR (Kim et al. 1987) was incorporated into TZE-Y Pop to upgrade the level of *Striga* resistance/tolerance. This was followed by two backcrosses, the generation of S_1 progenies, the selection of *Striga*-resistant S_1 lines from the population and two cycles of random mating under artificial *Striga* infestation and induced moisture stress to form TZE-Y Pop DT STR C_0. Details on the various strategies adopted for screening for *Striga* resistance/tolerance as well as water stress management for drought tolerance selection during the development of the population at the different screening sites have been described by Badu-Apraku (2007). Briefly, the S_1 family selection programme was initiated in the source population for *Striga* resistance in 1996 and since then the population has undergone four cycles of S_1 recurrent selection. Progenies of each cycle of improvement were screened under artificial infestation with *S. hermonthica* and non-infested conditions at Ferkessedougou (hereafter called Ferké) in Côte d'Ivoire from 1996 to 2001 and at Abuja and Mokwa in Nigeria in 2003. Genotypes were evaluated using lattice designs with two replications. The number of progenies screened in each cycle ranged from 196 to 256. Based on the data across locations, 25–30 % of the top ranking S_1 families of the population were selected using a base index that involved grain yield, *Striga* emergence counts, *Striga* damage syndrome rating and number of ears per plant measured under infested and/or non-infested conditions (MIP 1996; Menkir and Kling 2007). The means of the selected traits were expressed in standard deviation units and the index scores computed as $I = (2.0YLI + 1.0YLN + 1.0EHV - 1.0SDR8 - 1.0SDR10 - 1.0ESP8 - 1.0ESP10)$, where YLI was yield of *Striga*-infested plots, YLN was yield of the *Striga*-free plots, EHV was the number of ears per plant at harvest in the *Striga*-infested plots, SDR8 and SDR10 were *Striga* damage ratings at 8 and 10 weeks after planting (WAP), and ESP8 and ESP10 were number of emerged *Striga* plants at 8 and 10 WAP. The remnant seeds of the selected S_1 families were recombined using the half-sib method to form a new, improved population for the next cycle of selection. The seeds of each of the cycles of selection were produced in the same nursery. A minimum of three seasons were required per cycle of selection and four cycles had been completed in each population by the time the experiment reported herein was initiated in 2005 (Fig. 1).

Experimental protocol

Fifty S_1 families each were extracted by selfing non-inbred (S_0) plants from C_0, C_2, C_3 and C_4 of TZE-Y Pop STR. The fifty S_1 progenies from each cycle were divided into ten sets containing five S_1 lines each and were laid out in a 10 × 5 rectangular lattice in a randomized incomplete block design with block-in-replicate arrangement. The resulting 200 S_1 families from the source populations were evaluated during the planting seasons of 2005 and 2007 for yield potential and tolerance or resistance to *Striga* under artificial infestation of *S. hermonthica* at Abuja (9°16′N, 7°20′E, 300 m asl, and 1,500 mm annual rainfall) and Mokwa (9°18′N, 5°4′E, 457 m asl, 1,100 mm annual rainfall). *Striga* is endemic at both sites, which are located in the southern Guinea savanna agro-ecological zone. The S_1 lines were also evaluated under *Striga*-free conditions in Mokwa and Ikenne (6°53′N, 3°42′E, 60 m asl, 1,200 mm

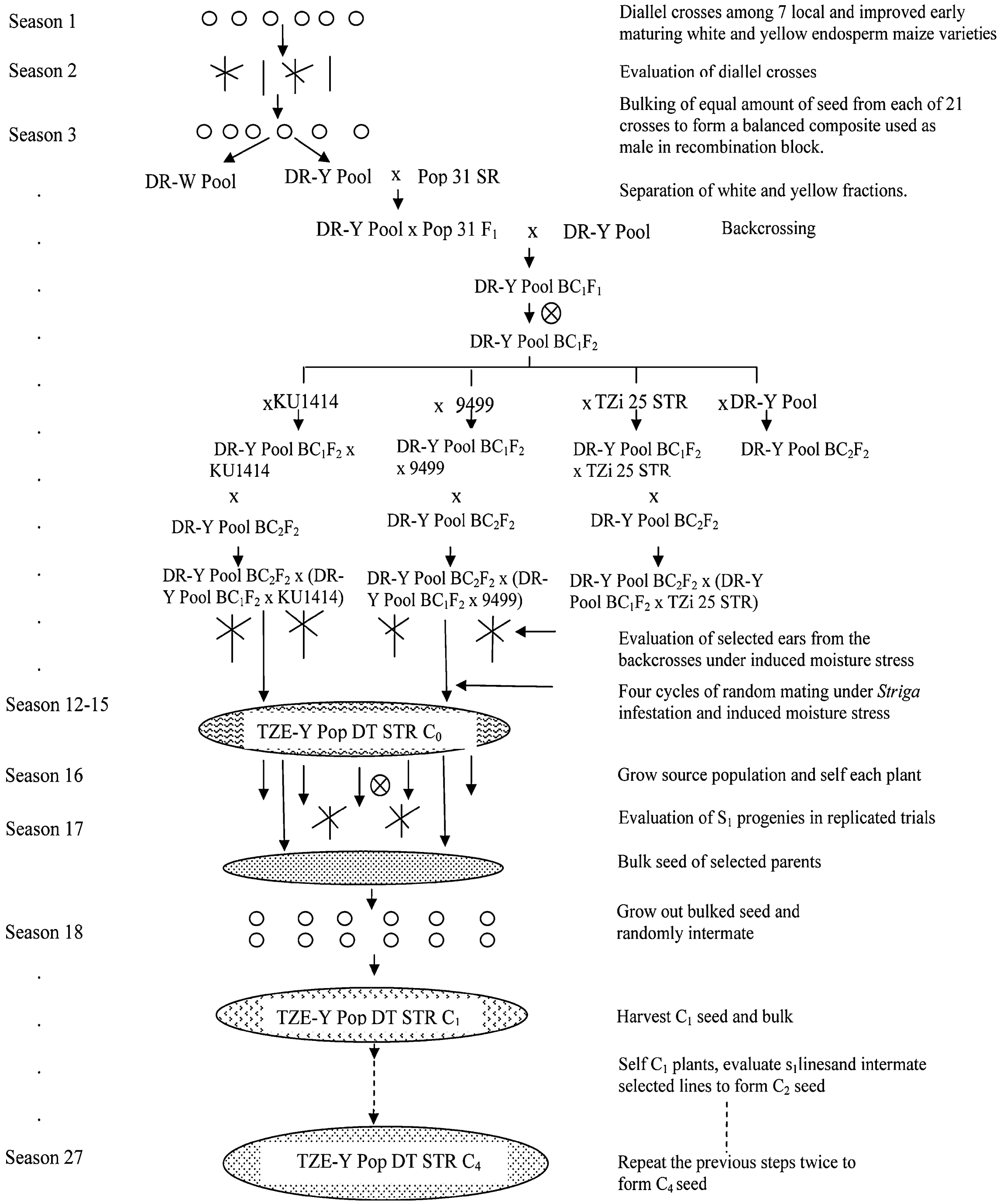

Fig. 1 Procedure for the development of *Striga*-resistant and drought-tolerant early-maturing yellow maize population and S_1 progeny test

annual rainfall) in 2005 and 2007 to determine their yield potential and disease reaction in the savanna and forest zones of Nigeria. There were two replications for each test environment (location–year combinations). In the *Striga*-infested environments at Abuja and Mokwa, the S_1 progenies were planted into one-row plots. The field layout in the *Striga*-free environments at Mokwa and Ikenne was similar, except that there was no artificial *Striga* infestation of the plots. In all locations, rows were ridges, 4 m long, spaced 0.75 m apart, with planting hills spaced 0.4 m within the row. Three seeds were planted in each planting hill. The *S. hermonthica* seeds for infestation were mixed with finely sieved sand in the ratio of 1:99 by weight and about 5,000 germinable seeds were placed in each planting hill on the ridges, as described by the IITA Maize Programme (Kim 1991). About 7 days before the S_1 progenies were planted at Mokwa and Abuja in the *Striga*-infested experiments, the field was fumigated with ethylene gas to induce suicidal germination of volunteer *Striga* seeds in the soil. The maize plants in both the infested and *Striga*-free experiments were later thinned to two per hill about 2 weeks after emergence, to give a population density of 66,000 plants ha^{-1}. For the *Striga*-infested plots, a fertilizer (15-15-15N-P-K) was applied twice to give a total rate of 30 kg ha^{-1} each of N, P_2O_5 and K_2O. The first application was at planting, followed by the second dose at 30 days after planting. Fertilizer was applied to the *Striga*-free treatments at Mokwa and Ikenne at the rate of 60 kg N, 60 kg P_2O_5 and 60 kg K_2O ha^{-1} at sowing. An additional 60 kg N ha^{-1} was top-dressed at 4 WAP. A mixture of Grammoxone® (Paraquat) and Primextra® was sprayed at 2 DAP to control weeds in all locations. Subsequently, weeds other than *Striga* were handpicked on a regular basis. Apart from the *Striga* infestation and fertilizer rates, all other management practices for the *Striga*-free environments were the same as those of the *Striga* infestation.

Data collection

Traits

For both *Striga*-free and *Striga*-infested plots, data were recorded for days to anthesis as the number of days from planting to when 50 % of the plants had shed pollen, and days to silking as the number of days when 50 % had emerged silks. The anthesis–silking interval (ASI) was computed as the interval in days between anthesis and silking. Plant and ear heights were calculated as the average measurements on 20 competitive plants per plot and were measured after anthesis from the base of a plant to the node bearing the upper ear for ear height and to the base of the tassel for plant height. Ratings for ear aspect were on a scale of 1–9, where 1 = clean, uniform, large and well-filled ears and 9 = rotten, variable, small and partially filled ears. Data were obtained for grain yield, grain moisture at harvest, number of ears at harvest, EPP, root lodging (percentage of plants leaning more than 30° from the vertical) and stalk lodging (percentage of plants broken at or below highest ear node). A shelling percentage of 80 % was assumed for all S_1 families and grain yield (obtained from ear weight and converted to kg ha^{-1}) was adjusted to 15 % moisture. In addition, data were collected on the number of emerged *Striga* plants and the host plant damage syndrome rating in the infested plots at 8 and 10 WAP. The *Striga* damage syndrome was scored per plot using the modified scale of 1–9 (Kim 1991) where 1 = no damage, indicating normal plant growth and high level of tolerance, and 9 = complete collapse or death of the maize plant; i.e. highly sensitive/intolerant (DeVries 2000; Badu-Apraku and Akinwale 2011).

Statistical analysis

The statistical model corresponding to the experimental layout is:

$$y_{ijklm} = \mu + E_i + R/E_{j(i)} + B/R \times E_{k(ij)} + C_l + G/C_{m(l)} + \mathrm{EC}_{il} + \mathrm{EG}/C_{im(l)} + \in_{ijklm}$$

In this model, Y_{ijklm} is the observed value for the *m*th progeny within the *l*th cycle, in the *i*th environment, *j*th replication within the *i*th environment, and *k*th incomplete block; μ is the overall mean; E_i is the effect of the *i*th environment; $B/R \times E_{k(ij)}$ is the effect of block within replicate by environment interaction; $R/E_{j(j)}$ is the effect of the *j*th replicates within the *i*th environment; C_l is the cycle effect; $G/C_{m(l)}$ is the *m*th progeny within the *l*th cycle; EC_{il} is the cycle by environment interaction effect; $\mathrm{EG}/C_{im(l)}$ is the interaction of the *m*th progeny with the *j*th environment and ε_{ijklm} is residual effects.

The location–year combinations were considered as environments in the combined ANOVA for each trait. In the above model, the effects of environment, replication, incomplete block, environment by cycle interaction and environment by genotype within cycle interaction were considered random effects; cycle and genotype within cycle effects were considered fixed when estimating means and standard errors per cycle, and were considered random when estimating variance components. The analyses were performed separately for the stressed (*Striga*-infested) and non-stressed (*Striga*-free) conditions using the MIXED procedure from Statistical Analysis System (SAS 2001).

Genetic variance and covariance component estimates were obtained for each cycle of selection from the combined ANOVA by the restricted maximum likelihood (REML) method. Broad-sense heritability was computed as the ratio of the genetic variance to the phenotypic variance on a progeny-mean basis as follows:

$$H = \frac{\sigma_{\mathrm{g}}^2}{\sigma_{\mathrm{g}}^2 + \frac{\sigma_{\mathrm{ge}}^2}{e} + \sigma^2/er}$$

where *r* is the number of replications per environment; *e* is the number of environments; σ_{g}^2 represents the component of variance estimate due to genotypes; σ_{ge}^2 is the component of variance due to genotype × environment interactions; and σ^2 represents the estimate of experimental error variance.

Standard errors for genetic variance and heritability estimates were calculated using the method of Hallauer and Miranda (1988). Changes in the variances and heritability estimates among S1 families were tested for significance by pairwise comparison of estimates using their standard errors.

The predicted gain from selection based on C_4 alone was estimated according to the method of Hallauer and Miranda (1988) as follows:

$$G_s = k\sigma_g^2/\sigma_p$$

where k represents the standardized selection differential for S_1 families (20 % selection intensity was used in this case, which is $k = 1.3998$), σ_g^2 is the genetic variance, and σ_p denotes the square root of the phenotypic variance. The predicted gains may be biased upwards depending on the contribution of nonadditive genetic variances to σ_g^2. Means for each cycle were tested for significant differences using twice the standard error, and the difference between the means of C_4 and C_0 provided an estimate of observed gain from selection. For each trait, entry means of the cycles across environments were regressed as dependent variables on cycle numbers (independent variable) to obtain estimates of realized gain per cycle of selection. The coefficient of linear regression (b-value) provided an estimate of the gain per cycle, which was divided by the intercept and multiplied by 100 to obtain the percent response per cycle. The significance of the slope b was tested using orthogonal polynomial contrasts in the mixed model considering cycle number as fixed effect. The test was based on the linear degree of polynomial coefficients for comparison among four treatments with unequal intervals according to Gomez and Gomez (1984). Specifically, the comparisons made were C_0 versus others, C_0 versus C_4, C_2 versus $C_3 + C_4$, C_2 versus C_4, and C_3 versus C_4.

Genotypic correlation coefficients among agronomic traits and their standard errors were computed with the REML method (Holland 2006) using procedures MIXED and IML of the SAS system (SAS 2001). The correlation was calculated using the following formula

$$r_{gij} = \frac{\sigma_{gij}}{\sqrt{\sigma_{gi}^2 + \sigma_{gj}^2}}$$

where r_g^2 is the correlation coefficient, σ_{gij} is the genotypic covariance between traits i and j, and σ_{gi}^2 and σ_{gj}^2 are variances of the two traits. Standard errors were obtained using the Delta method as described by Holland (2006). A genetic correlation larger than twice its standard error was considered statistically significant. Also, two times the standard error was used to test for significant difference among the four cycles.

Results

The combined analyses of variances revealed highly significant genotypic variance (σ_g^2) for all traits under both research environments except plant height, ear aspect and EPP when *Striga* free (Table 1). Also, G × E interactions were significant for all traits except number of ears per plant under both research environments. The environment (E) constituted the major component of the total variation for days to anthesis and silking, number of ears per plant, ear aspect and emerged *Striga* plants at 8 and 10 weeks after planting under *Striga* infestation. Genotype and environment contributed approximately equal proportions for *Striga* damage at 8 weeks after planting, while the contributions of E were about 25 % higher than G for grain yield and ASI when *Striga* infested (Table 2). The contribution of G × E interactions to the total variation ranged from 3.3 % for days to anthesis to 11.3 % for ASI. Under *Striga*-free conditions, the contributions of E (26.3 %) were relatively higher (about twice) than that of the G × E interactions (11.4 %) for grain yield. Environment constituted the greatest proportion of the variance for grain yield, days to silking, days to anthesis, ASI, number of ears per plant and ear aspect; G × E interactions made the highest contribution to the sum of squares for plant height. In general, the contribution of G × E interaction to the total variation for most measured traits was smaller than those of E and G. The percentage contribution of the error variance to the total variation was remarkably high for grain yield, ASI, plant height, number of ears per plant, ear aspect and *Striga* damage at 8 and 10 weeks after planting under both research conditions except for ear aspect when *Striga* free.

Progress from selection in *Striga*-infested and *Striga*-free environments

Linear contrasts revealed significant ($P < 0.05$) differences in the cycles of selection for grain yield and all other traits except days to silk, ASI, *Striga* emergence count at 8 and 10 weeks after planting when *Striga* infested and days to silk and anthesis when *Striga* free (Table 2). The advanced cycles of selection significantly ($P < 0.01$) out-yielded their original cycles of selection in both research environments (*Striga*-infested and *Striga*-free environments). The yield gain from C_0 to C_4 was 52.5 kg ha^{-1} cycle^{-1} (14.18 % cycle^{-1}) when *Striga* infested and 130 kg ha^{-1} cycle^{-1} (10.02 % cycle^{-1}) when *Striga* free. The yield gain when *Striga* infested was associated with an increase in days to anthesis, plant height, number of ears per plant, improved ear aspect and decreased *Striga* damage. When *Striga* free, the yield gain was accompanied by improved ear aspect, a decrease in ASI, and an increase in plant and ear heights and number of ears per plant. The predicted gain cycle^{-1} was 350.41 kg ha^{-1} for grain yield when *Striga* infested and 250 kg ha^{-1} when *Striga* free. The high predicted gains from selection for grain yield were associated with a reduced number of emerged *Striga* plants at 8 and 10 weeks after planting (17 and 19 plants cyle^{-1}),

Table 1 Estimates of genetic variance (±SE) and broad-sense heritability (±SE), of measured traits of S_1 lines derived from four cycles of selection in the early yellow maize population tested under artificial *Striga* infestation at Mokwa and Abuja, and *Striga*-free conditions at Ikenne and Mokwa, Nigeria in 2005 and 2007

	Genetic variance s^2				Broad-sense heritability (H^2, %)			
	C_0	C_2	C_3	C_4	C_0	C_2	C_3	C_4
Striga-infested environment								
Yield, kg/ha	12810 ± 4184*	7439 ± 5075	2459 ± 5153	48817 ± 12709**	49.88 ± 0.16	28.93 ± 0.20	10.28 ± 0.22	62.88 ± 0.16
Days to silking	4.66 ± 1.06**	4.82 ± 1.25**	3.54 ± 1.12**	4.37 ± 1.17**	69.20 ± 0.16	70.89 ± 0.18	59.30 ± 0.19	70.70 ± 0.19
Days to anthesis	1.90 ± 0.46**	2.97 ± 0.68**	1.25 ± 0.42**	2.76 ± 0.59**	69.53 ± 0.17	80.20 ± 0.18	57.26 ± 0.19	78.75 ± 0.17
Anthesis–silking interval	3.13 ± 0.69**	2.26 ± 0.69**	2.24 ± 0.70**	2.31 ± 0.70**	72.11 ± 0.16	59.82 ± 0.18	60.10 ± 0.19	60.17 ± 0.18
Plant height, cm	59.60 ± 22.07*	21.74 ± 13.21	38.39 ± 18.61*	89.72 ± 25.93**	50.44 ± 0.19	33.04 ± 0.20	38.80 ± 0.19	58.97 ± 0.17
Ear per plant	0.0062 ± 0.0022*	0.0152 ± 0.0034**	0.0029 ± 0.0017	0.011 ± 0.003**	50.94 ± 0.18	76.31 ± 0.17	29.32 ± 0.18	68.14 ± 0.18
Ear aspect	0.083 ± 0.034*	0.085 ± 0.043	0.089 ± 0.041*	0.135 ± 0.046*	41.08 ± 0.17	37.53 ± 0.19	42.02 ± 0.19	49.20 ± 0.17
Striga rating at 8 WAP	0.174 ± 0.05**	0.23 ± 0.070**	0.116 ± 0.048*	0.39 ± 0.10**	59.46 ± 0.18	61.62 ± 0.19	44.480 ± 0.18	71.28 ± 0.18
Striga rating at 10 WAP	0.143 ± 0.048*	0.115 ± 0.055	0.040 ± 0.048	0.261 ± 0.082**	51.89 ± 0.18	39.94 ± 0.19	16.71 ± 0.20	55.15 ± 0.17
Striga count at 8 WAP	172.91 ± 35.67**	154.92 ± 40.01**	148.74 ± 36.17**	108.74 ± 27.45**	74.92 ± 0.18	65.60 ± 0.17	69.80 ± 0.17	64.96 ± 0.16
Striga count at 10 WAP	291.61 ± 58.91**	195.29 ± 49.00**	227.34 ± 54.68**	137.74 ± 35.54**	76.74 ± 0.16	69.10 ± 0.17	69.80 ± 0.17	64.90 ± 0.17
Striga-free environment								
Yield, Kg/ha	43430 ± 12566**	37996 ± 17614*	4270 ± 11314	36139 ± 5673**	58.92 ± 0.17	35.64 ± 0.17	7.50 ± 0.20	43.23 ± 0.19
Days to anthesis	0.94 ± 0.27**	0.83 ± 0.31*	0.41 ± 0.23	0.13 ± 0.13	54.08 ± 0.16	40.68 ± 0.15	30.82 ± 0.17	17.49 ± 0.17
Days to silking	1.16 ± 0.32*	1.09 ± 0.35*	0.49 ± 0.29	0.31 ± 0.17	52.65 ± 0.15	49.48 ± 0.16	31.02 ± 0.17	29.53 ± 0.16
Anthesis–silking interval	0.06 ± 0.06	0.02 ± 0.10	0.11 ± 0.03*	$^{+}$	18.75 ± 0.17	3.96 ± 0.25	50.79 ± 0.14	$^{++}$
Plant height, cm	8.86 ± 10.71	$^{+}$	44.29 ± 14.69**	25.24 ± 15.37	14.31 ± 0.17	0	48.12 ± 0.16	32.85 ± 0.20
Ear height, cm	3.36 ± 5.00	29.01 ± 9.02*	5.36 ± 5.99	14.72 ± 7.70	12.52 ± 0.19	54.36 ± 0.17	17.27 ± 0.19	37.57 ± 0.20
Ear per plant	$^{+}$	0.003 ± 0.003	0.004 ± 0.002*	0.004 ± 0.02	$^{++}$	24.82 ± 0.21	36.48 ± 0.20	4.80 ± 0.22
Stalk lodging, %	$^{+}$	0^{+}	0.05 ± 0.15	0.23 ± 0.15	$^{++}$	$^{++}$	6.83 ± 0.20	31.06 ± 0.20
Plant aspect	0.014 ± 0.006*	0.014 ± 0.007*	0.007 ± 0.006	0.007 ± 0.006	13.12 ± 0.20	32.46 ± 0.17	19.58 ± 0.17	27.08 ± 0.22
Ear aspect	0.01 ± 0.01	0.007 ± 0.01	0.02 ± 0.02	0.005 ± 0.01*	21.13 ± 0.19	14.32 ± 0.22	21.48 ± 0.19	7.86 ± 0.19

+, negative genetic variances were equated to zero; ++, heritability was not computed because of negative genetic variances

*,** Significantly different at 0.05 and 0.01 levels of probability

Table 2 Trait means, linear response per cycle and predicted gain per cycle of S_1 families derived from four cycles of selection in early yellow maize population evaluated under artificial *Striga* infestation + and *Striga*-free ++ conditions in 2005 and 2007

Cycle	Grain yield, kg ha^{-1}	Days to silk	Days to anthesis	Anthesis–silking interval	Plant height, cm	Ears per plant	Ear Aspect	*Striga* damage rating at 8 WAP	*Striga* damage rating at 10 WAP	*Striga* emergence count at 8 WAP	*Striga* emergence count at 10 WAP
Artificial *Striga* infestation											
C_0	375.6	59.4	54.1	5.3	105	0.45	6.4	6.0	6.3	33.1	38.4
C_2	498.3	59.3	54.1	5.2	109	0.49	6.2	5.7	6.0	36.4	43.5
C_3	461.7	59.8	54.0	5.8	107	0.46	6.1	5.9	6.2	34.4	40.1
C_4	618.8	59.6	54.8	4.8	114	0.53	5.9	5.5	5.7	32.2	37.5
GRAND MEAN	488.6	59.5	54.2	5.3	109	0.5	6.2	5.8	6.0	34.0	39.9
SE	104.53	2.22	2.62	1.27	6.27	0.10	0.40	0.32	0.33	12.78	14.75
Gain cycle-^{1}	52.5	0.07	0.13	−0.06	1.93	0.02	−0.12	−0.09	−0.11	−0.16	−0.17
% response cycle^{-1}	14.18	0.11	0.24	−1.11	1.85	3.33	−1.79	−1.50	−1.75	−0.47	−0.43
R^2	79	27	35	6.9	70	49	91	57	0.61	2.2	1.7
Significance of test	**	ns	*	ns	**	*	**	**	**	ns	ns
Predicted gain cycle^{-1}	350.41	3.52	2.95	2.36	14.55	0.17	0.51	1.06	0.76	16.81	18.91
Striga-free environments											
C_0	1266	56	54	1.6	152	0.77	3.74				
C_2	1650	55	54	1.3	157	0.83	3.50				
C_3	1633	55	54	1.1	154	0.84	3.51				
C_4	1815	55	54	1.2	162	0.92	3.34				
Mean	1591	55	54	1	156	1	4				
SE	222.7	1.80	1.82	0.3	3.2	0.1	0.4				
Gain cycle^{-1}	130	−0.26	−0.09	−0.14	2.55	0.05	−0.12				
% response cycle^{-1}	10.02	−0.46	−0.17	−8.70	1.70	6.94	−3.16				
R^2	92	95	44	72	67	93	88				
Significance of test	**	ns	ns	*	**	**	**				
Predicted gain cycle^{-1}	249.98	0.94	0.3	0	5.76	0.03	0.04				

*, ** Significant differences in the contrast *T* test ($P \leq 0.05$ and $P \leq 0.01$, respectively)

reduced *Striga* damage rating at 8 and 10 weeks after planting (1.06 and 0.76, respectively), increased number of ears per plant, improved ear aspect and increased days to silking, days to anthesis, ASI and plant height.

Genetic variance, heritability and genetic correlation estimates

Most of the genetic variances of each trait in the different cycles of selection were significantly greater than zero, as revealed by the standard errors. Under *Striga* infestation, the genetic variances for grain yield, plant height and *Striga* damage at 8 and 10 weeks after planting were significantly larger in cycle 1–4 than in the other cycles (Table 1). In contrast, the genetic variances for days to silk, anthesis-to-silking interval, number of ears per plant, ear aspect and number of emerged *Striga* plants at 8 and 10 weeks after planting decreased with selection. Under *Striga*-free conditions, the genetic variances for grain yield, days to anthesis, days to silking, ASI and ear aspect generally decreased as selection progressed. On the other hand, increases were generally detected for plant height, number of ears per plant and stalk lodging. However, not all the genetic variances of the traits in the different cycles of selection were significantly greater than zero. Genetic variances for measured traits were generally higher when *Striga* infested than when *Striga* free.

Changes in the broad-sense heritability for grain yield and other traits with selection followed trends similar to that of the genetic variances and were all significantly greater than zero in both research environments (Table 1). The heritability estimates for *Striga* damage and emerged *Striga* plants were strikingly high. In general, heritability estimates of measured traits were higher when *Striga* infested than when *Striga* free. Genetic correlation between grain yield and all other traits were not significant under

Striga-free conditions, except for grain yield and ear height of C_4, EASP of C_2 and C_4, and EPP of C_2 (Table 3). Also, correlations between plant height and ear height were not significant in the different cycles except in C_2. The genetic correlation between other pairs of traits was low and not significant (data not shown). On the other hand, under *Striga* infestation, grain yield had highly significant genetic correlation with the number of ears per plant, ear aspect and *Striga* damage at 8 and 10 weeks after planting for all or most cycles of selection. Grain yield had significant genetic correlation with only the ASI of C_3. Strong genotypic correlations were also obtained between *Striga* damage syndrome rating at 8 and 10 weeks after planting, and number of emerged *Striga* plants at 8 and 10 weeks after planting, *Striga* damage rating at 8 weeks after planting and EASP, *Striga d*amage rating at 10 weeks after planting, and number of emerged *Striga* plants at 8 weeks after planting for C_2 and C_4, as well as anthesis-silking interval and *Striga* damage at 8 weeks after planting for C_0. The genetic correlations between other pairs of traits were not significant. It is striking to note the lack of significant genotypic correlation between grain yield and number of emerged *Striga* plants at 8 and 10 weeks after planting, *Striga* damage at 8 and 10 weeks after planting and the number of emerged *Striga* plants at 8 and 10 weeks after planting for most cycles of selection.

Discussion

An effective recurrent selection programme should improve the population performance and maintain genetic variability to ensure continued genetic gain in future cycles of selection. In this study, the advanced cycles of selection of TZE-Y Pop DT STR significantly out-yielded their original cycles of selection in both *Striga*-infested and *Striga*-free environments. Significant increases were observed in the genetic variances for grain yield, DA, ASI, plant height and number of emerged *Striga* plants at 8 and 10 WAP in the advanced cycles of selection of the population under *Striga* infestation. The heritability estimates for the principal traits associated with *Striga* resistance (*Striga* damage and number of emerged *Striga* plants) were significantly greater than zero. The realized gain from selection for grain yield from C_0 to C_4 was 52 kg ha^{-1} cycle^{-1} when *Striga* infested and 130 kg ha^{-1} cycle^{-1} when *Striga* free. These results indicate that the S_1 family selection method adopted in our breeding programme has been effective and that there is still adequate genetic variability in the source population to ensure significant gain from selection. Similar findings were reported by Badu-Apraku et al. (2008) for TZE-Y Pop DT STR. However, the realized yield gains were remarkably lower than the predicted gains cycle^{-1} of 350.41 kg ha^{-1} when *Striga* infested and 250 kg ha^{-1} when *Striga* free. The predicted gain is highly theoretical with many underlying assumptions that may or may not be valid in actual field situations. For example, the predicted gain is normally based on parameter estimates obtained from the base population and is strictly supposed to be for one cycle of selection, whereas realized gains are estimated over several cycles of selection. Also, the estimated parameters, especially the genetic, phenotypic and environmental variances are assumed to remain constant throughout the selection cycles being evaluated, whereas this is hardly possible under actual field conditions. This has been clearly demonstrated in the present study where the estimated variances varied from one cycle to another, including the heritability estimates. The important conclusion to draw from the results of this study is that four cycles of recurrent selection has improved the grain yield potential of TZE-Y Pop DT STR by about 85 % under *Striga* infestation and 60 % under *Striga*-free conditions. In an earlier study evaluating the four cycles of S_1 family selection in the same population, Badu-Apraku et al. (2008) reported yield gains cycle^{-1} of 13 % when *Striga* infested and 5 % in *Striga*-free environments, both of which were lower than gains obtained in the present study as well as those reported by Menkir and Kling (2007) for some other maize populations. The yield gain obtained in the present study compare favourably with the results of Menkir and Kling (2007) who reported a yield gain of 24 % cycle^{-1} for the late-maturing population, TZL COMP1-W under *Striga* infestation after six cycles of combined selfed progeny and full-sib family selection. The relatively large yield gain from selection under *Striga* infestation in the present study corroborates the findings of a similar study by Badu-Apraku (2007). Both studies involved the estimation of gains using S_1 progenies rather than the improved cycles of selection which contained S_0 plants, as in the study by Badu-Apraku et al. (2008). Badu-Apraku (2007) reported generally low heritability estimates for grain yield and most measured traits in TZE-Y Pop DT STR C_3, but moderate-to-large additive genetic variances, high means and wide ranges, and concluded that there was adequate genetic variation for improving *Striga* resistance and grain yield in the population. Obviously, parameter estimates based on a relatively large sample size (50 S_1 families in this case, a total of 1,300 plants per cycle) are more reliable than those based on a population (104 pants only) derived from the selection program.

In studies involving estimation of genetic variances, it is important to examine the relative contribution of the components of phenotypic variance to the total observed variation in the study. It is desirable that the genotypic variation (σ_g^2) contributes the largest proportion of the total

Table 3 Genetic correlation between selected pairs of traits of S_1 lines derived from four cycles of selection in TZE-Y Pop STR evaluated under *Striga*-free environments at Ikenne and Mokwa in 2005 and 2007

Trait	Genetic correlation			
	C_0	C_2	C_3	C_4
Striga-free environment				
Grain yield versus days to silk	ns	ns	ns	ns
Grain yield versus plant height	+	ns	ns	0.52
Grain yield versus ear height	ns	ns	ns	0.73*
Grain yield versus plant Aspect	ns	−0.88*	ns	−0.57*
Grain yield versus EPP	ns	0.87*	ns	ns
Grain yield versus ear aspect	ns	ns	ns	−1.00
Plant height versus ear height	ns	0.83**	ns	ns
Striga-infested environment				
Grain yield versus days to silk	ns	ns	ns	ns
Grain yield versus plant height	ns	ns	ns	ns
Grain yield versus *Striga* rating at 8 WAP	−0.64**	−0.79**	−0.56**	−1.00**
Grain yield versus *Striga* rating at 10 WAP	−0.78**	−0.81**	ns	−0.99**
Grain yield versus *Striga* count at 8 WAP	ns	ns	ns	ns
Grain yield versus *Striga* count at 10 WAP	ns	ns	ns	ns
Grain yield versus ears per plant	0.66**	1.00**	ns	0.93**
Grain yield versus ear aspect	−0.93**	−0.99**	−0.79**	−0.89**
Grain yield versus ASI	ns	ns	−0.79*	ns
Ears per plant versus plant height	ns	ns	ns	ns
Ears per plant versus *Striga* rating at 8 WAP	ns	−0.96**	−1.00*	−0.73**
Ears per plant versus *Striga* rating at 10 WAP	+	+	−0.54**	−0.88**
Ears per plant versus *Striga* count at 8 WAP	ns	ns	+	ns
Ears per plant versus *Striga* count at 10 WAP	ns	ns	+	ns
Striga rating at 8 WAP versus *Striga* rating at 10 WAP	0.89**	1.00**	1.00**	0.95**
Striga rating at 8 WAP versus *Striga* count at 8 WAP	ns	ns	ns	0.42**
Striga rating at 8 WAP versus *Striga* count at 10 WAP	ns	ns	ns	ns
Striga count at 8 WAP versus *Striga* count at 10 WAP	1.00**	1.00**	0.98**	1.00**
Striga rating at 10 WAP versus *Striga* count at 8 WAP	ns	0.51*	ns	0.49*
Striga rating at 10 WAP versus *Striga* count at 10 WAP	ns	ns	ns	ns
Ear aspect versus *Striga* rating at 8 WAP	0.89**	0.76**	ns	1**
Ear aspect versus *Striga* rating at 10 WAP	1.00**	0.66*	ns	0.92*
ASI versus *Striga* rating at 8 WAP	0.47*	ns	ns	ns
ASI versus *Striga* rating at 10 WAP	ns	ns	ns	ns

ns non-significant; + correlations not estimable because one or both variances involved were estimated to be zero

*, ** Significantly different at 0.05 and 0.01 levels of probability

variation. The larger the contribution of G, the more reliable are the parameter estimates for predicting future progress from selection in the population under study. In the present study, significant increases in the genetic relative to phenotypic variances were observed in cycle 4 for grain yield, days to anthesis, plant height, *Striga* damage at 8 and 10 weeks after planting, the number of ears per plant and ear aspect under *Striga* infestation. Similarly, there were significant increases in the genetic variances for plant height, number of ears per plant, stalk lodging and ear aspect under *Striga*-free conditions. Perhaps the random mating that took place during the recombination of selected lines allowed linkage blocks to be broken, thereby generating more genetic variability for some traits in the advanced cycles of selection. Another plausible explanation is that favourable alleles might have been at very low frequencies initially in the population for these traits and, if that was the case, then effective selection would have increased the genetic variance. This result seems to confirm the hypothesis of Badu-Apraku et al. (2009) that the S_1 family selection method could induce greater genetic variation than was available in the original population.

Despite the increases in genetic variances in advanced cycles of selection, the contribution of the residual SS for some traits, especially those with values $\geq$40 %, were sufficiently large to be of concern to the breeder. Although the analysis of variance model was highly significant in most cases, the residual SS of these traits were sufficiently large to mask an accurate estimation of gains from selection. This result suggests that we should be more concerned with reducing the environmental variance for maximum progress from selection in the population. To achieve this, more effort should be devoted to reducing the environmental variance by using more uniform fields, uniform artificial *Striga* infestation, and probably more replications and locations for testing.

The results of this study revealed that relatively small improvement in the *Striga* resistance indices led to rather large increase in grain yield. As shown in Table 3, for example, *Striga* rating 8 and 10 weeks after planting reduced by only 0.5 and 0.6 units in C_4 relative to C_0, which served as the reference check, whereas grain yield increased by about 60 % at C_4 from about 400 kg ha^{-1} at C_0. This dramatic yield increase under *Striga* infestation was associated with increased number of days to silk, plant height and EPP, and improved EASP. It is interesting to note that the increased grain yield in the advanced cycles of selection in the population was associated with significant increases in EPP in both research environments. This finding corroborates the results of Badu-Apraku et al. (2004, 2008) and suggests that a major improvement in grain yield resulting from recurrent selection under *Striga* infestation was a reduction in the frequency of alleles that confer barrenness under *Striga* infestation. Another plausible explanation is that a reduction in the number of *Striga* plants parasitizing the maize plant makes more photosynthate available for grain filling, thus increasing ears per plant. The results of this study confirm the previous findings that ears per plant was a major yield determinant under *Striga* infestation and justifies its inclusion in the selection index for grain yield improvement in *Striga*-prone environments, as previously reported (Adetimirin et al. 2000; Badu-Apraku et al. 2004, 2008). The increase in plant height, DS, DA and ASI associated with the gain cycle^{-1} in grain yield was not expected since a base index which deliberately penalized any tendency towards increased plant height, later maturity, and a large ASI was used in selecting S_1 progenies for recombination. The base index was effective in increasing grain yield and EPP, improving EASP and in reducing *Striga* damage traits, but not the other traits.

These results suggest the need to re-examine the base index used in our programme to ensure that plant height, DS and DA remain constant at the level of C_0, while increasing grain yield in future cycles. The strong negative genetic correlations between grain yield and *Striga* damage at 8 and 10 weeks after planting in this population confirm the reliability of the traits for selection for improvement of grain yield and *Striga* resistance. This finding is consistent with the results of earlier studies (Kim 1991, 1994; Efron 1993; Kim and Adetimirin 1997; Badu-Apraku et al. 2004) and confirms that *Striga* damage is an appropriate trait for the assessment of resistance under *Striga* infestation. The finding also supports the hypothesis that simultaneous improvement in grain yield and *Striga* damage rating can easily be achieved in the population. In contrast, the low and non-significant genetic correlations between grain yield and number of emerged *Striga* plants at 8 and 10 WAP confirm the results of several researchers (Kim 1991; Kim and Adetimirin 1997; Akanvou et al. 1997; Badu-Apraku et al. 2004, 2006, 2008) and the conclusion that *Striga* emergence count is not a reliable selection criterion for improving *Striga* resistance. However, this result could also be interpreted to mean that grain yield and *Striga* emergence count were genetically independent (no linkage or pleitropy) and could be effectively selected for simultaneously using an appropriate base index (Kim 1991, Badu-Apraku et al. 2004, 2006). The strong genotypic correlations obtained between *Striga* damage syndrome rating at 8 and 10 weeks after planting on one hand, and the number of emerged *Striga* plants at 8 and 10 weeks after planting, on the other, suggest that either of these traits may serve as a selection parameter for the evaluation of genotypes for *Striga* resistance without a great loss in precision. Howeve*r, Striga* emergence count alone is not reliable for the evaluation of resistance, especially when genotypes are highly susceptible, because such materials suffer more damage even when few *Striga* plants are attached to the roots of the host plant (Kim et al. 1998). Therefore, for maximum gain from selection for *Striga* resistance and increased grain yield, it would be desirable to use a combination of host damage syndrome rating and *Striga* emergence counts to improve both traits simultaneously. Similar findings were reported by Efron (1993); Kim (1991, 1994); Kim and Adetimirin (1997); Badu-Apraku (2007); Badu-Apraku et al. (2004). The negative genetic correlations between grain yield and flowering traits, plant height, ear aspect, *Striga* damage scores and number of emerged *Striga* plants were expected, since *Striga* affects the physiology and yield of infested plants. In general, the correlation coefficients between grain yield and flowering traits as well as plant height have a positive sign under stress-free conditions (Badu-Apraku et al. 2004). The negative correlations of grain yield with these traits could be due to the severe stress on the progenies from high, artificial infestation. It is not uncommon for the flowering traits to have negative correlations with grain yield under severe stress (Badu-Apraku 2007; Badu-Apraku et al. 2004).

The presence of significant genotype × environment interaction for all traits under both research environments except for stalk lodging and EPP when *Striga* free and emerged *Striga* plants at 10 WAP under artificial *Striga* infestation indicates that the genotypes responded differently to *Striga* infestation in the different years. The significant G × E interactions may be attributed to large differences in environmental factors such as soil type, temperature, amount of rainfall and disease pressure at the test locations Abuja, Mokwa and Ikenne. This finding corroborates the results of Badu-Apraku et al. (2008). However, in contrast to these results, Berner et al. (1996) attributed the significant G × E interactions for grain yield and other traits to the presence of different biotypes of the parasite at the different locations.

In summary, recurrent selection is an effective method for improving quantitative traits with low and intermediate heritability. Four cycles of S_1 recurrent selection resulted in a significant improvement in grain yield and *Striga* resistance/tolerance without exhausting the genetic variability of the base population, TZE-Y Pop DT STR under *Striga*-infested and *Striga*-free environments. Therefore, further selection for the improvement of these traits is warranted. However, for faster progress from selection, there is a need for refinements in the selection index as well as the field design under which both selection and evaluation of progress from selection are done in future cycles.

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