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RESEARCH

Genetic Improvement in Resistance to *Striga* in Tropical Maize Hybrids

Abebe Menkir,* and Silvestro Meseka

ABSTRACT

Striga hermonthica (Del.) Benth parasitizes maize (*Zea mays* L.) in sub-Saharan Africa, causing yield losses of up to 100% under severe infestation. Hybrid maize breeding for polygenic resistance to *Striga* has been undertaken at the International Institute of Tropical Agriculture (IITA) since the 1980s. This study was conducted to estimate genetic gain in grain yield and associated traits in a set of 32 maize hybrids developed over three breeding periods under artificial *Striga*-infested and noninfested conditions for 4 yr. The results of regression analyses showed a linear annual yield gain of 3.2% with a mean increase of 93.7 kg ha^{-1} yr^{-1} under *Striga* infestation, much of which was primarily associated with significant reductions of 2.6% yr^{-1} in *Striga* damage symptoms and 5.5% yr^{-1} in the number of emerged parasites at 10 wk after planting. Other traits associated with grain yield including plant height and number of ears per plant increased, whereas silking days, ear aspect, and anthesis–silking interval decreased over time. On average, hybrids developed after the 1990s yielded 64% more and displayed 61% less parasite emergence and 30% less parasite damage at 10 wk after planting compared with hybrids developed before the 1990s. These improvements were achieved with increases in grain yield, early silking, reduced anthesis–silking interval, and resistance to ear rot under noninfested conditions. The trends in breeding progress achieved during this time period appear to be in the right direction, highlighting the potential that exists to further reduce yield losses to *S. hermonthica* in hybrids.

International Institute of Tropical Agriculture, PMB 5320, Oyo Road, 20001, Ibadan, Oyo State, Nigeria. Received 13 Dec. 2018. Accepted 10 July 2019. *Corresponding author (A.Menkir@cgiar.org). A. Menkir ORCID iD: 0000-0002-5907-9177. Assigned to Associate Editor Timothy Beissinger.

Abbreviations: BLUE, best linear unbiased estimate; IITA, International Institute of Tropical Agriculture; PC, principal component; RI, Striga resistance index; WAP, weeks after planting.

Maize (*Zea mays* L.) and other cereals like sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R. Br.] are the major staple food crops for millions of people in sub-Saharan Africa. *Striga hermonthica* (Del.) Benth has been recognized as one of the most destructive parasitic weeds, with its haustorial cells penetrating roots of maize and the other cereals to derive the resources for its growth and development (Parker and Riches, 1993). Since the 1980s, maize production in West and Central Africa has expanded considerably into the savannas, which are high-production zones, where this endemic obligate root hemiparasite poses a serious threat to maize cultivation (Ejeta, 2007). The area infested with *S. hermonthica* and its negative impact continue to increase because of diverse parasite seed dispersal mechanisms, including contaminated crop seeds, animals, farm implements, wind, and surface water (Berner et al., 1995; Ejeta, 2007). Climate change may further increase the geographic distribution and invasive potential of *S. hermonthica*, as habitats suitable for its growth might expand (Mohamed et al., 2007). Growth and yields of maize are adversely affected by the withdrawal of water, nutrients, and assimilates by this root parasite from the host to sustain its development (Gurney et al., 1999), causing yield losses that can reportedly reach up to 100% in severely infested smallholder farmer fields in Africa (Kim et al., 2002; Ejeta, 2007).

Many control methods, including hand pulling, crop rotation, trap and catch crops, and the use of herbicides and N fertilizer,

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have been recommended to minimize the destructive effects of the parasite (Gressel et al., 2004). Nevertheless, limited success has been achieved in controlling *Striga* on smallholder farmers' fields in Africa, primarily because of the parasite's (i) highly specialized life cycle synchronized with host growth, (ii) breeding behavior that maintains enormous genetic variability, (iii) ability to parasitize a broad host range, (iv) seed longevity in the soil, and (v) capacity to inflict most of the damage to the host before emerging aboveground (Ejeta, 2007; Hearne, 2009). An integrated management strategy involving several control methods acting at the different stages of the parasite's life cycle is therefore necessary to achieve effective *Striga* control. Maize cultivars with broad-spectrum resistance can be a critical component of an integrated control strategy to minimize yield losses in farmers' fields (Kim, 1996; Kling et al., 2000; Menkir et al., 2007). Maize breeders at the International Institute of Tropical Agriculture (IITA) have therefore considered breeding for polygenic resistance to *S. hermonthica* as a viable approach to provide durable protection to the crop against diverse parasite populations.

Breeding for resistance to *S. hermonthica* was initiated at IITA with the belief that heritable genetic variation in polygenic resistance against the parasitic could occur at varying frequencies in adapted maize germplasm that had not been subjected to selection against the parasite in the course of its development (Kim, 1996). As the susceptible maize cultivars at that time could suffer up to 100% yield losses under severe *S. hermonthica* infestation, the early breeding effort had specifically emphasized selection for less parasite-induced leaf scorching, better host plant growth, good ear development, and high grain yield (Kim, 1991). Several adapted maize inbred lines and hybrids with temperate and tropical genetic backgrounds were then screened under natural field infestation in Nigeria, which led to the identification and use of *Striga*-tolerant maize inbred lines to develop maize hybrids with moderate to high levels of tolerance to the parasite (Kim, 1991). However, the uneven distribution of *S. hermonthica* seeds in the soil under field conditions hampered rapid genetic advance from selection. A field infestation technique, involving a large number of *Striga* seeds for inoculation, coupled with suboptimal application of N and planting on ridges, was developed to expose maize plants to an optimal parasite density, whereby escapes were prevented and only the most susceptible maize genotypes were affected by *S. hermonthica* (Kim, 1996; Kling et al., 2000). This screening technique enabled maize breeders to make a significant shift in emphasis towards the selection of resistant maize genotypes that supported a reduced number of emerged parasites. In contrast with tolerant cultivars, the development and deployment of *Striga*-resistant cultivars supporting fewer emerged parasites can contribute to reduced production of *Striga* seeds that attack maize and other crops in subsequent years (Haussmann et al., 2000). Using this approach, excellent sources of polygenic resistance were identified from among late-maturing, elite breeding materials, landraces, and wild relatives of maize and used to create broad-based populations (Kling et al., 2000). These populations were subjected to recurrent selection not only for reduced visible *Striga* damage and increased grain yields but also for reduced number of emerged *Striga* plants using a base index. Screening of lines derived from the improved populations at each inbreeding stage under artificial *S. hermonthica* infestation across locations and seasons led to the development of late-maturing maize inbred lines with consistent expression of resistance to the parasite (Berner et al., 1995; Kim, 1996; Kling et al., 2000; Menkir, 2006).

Since 1983, late-maturing *Striga*-tolerant and *Striga*-resistant hybrids developed across the years were repeatedly evaluated through successive stages, with and without artificial *Striga* infestation across locations and seasons, until promising tolerant or resistant hybrids were identified for dissemination to partners (Kim, 1996; Kling et al., 2000; Menkir et al., 2007). These hybrids encapsulate the history of decades of maize breeding efforts that improved polygenic resistance to *S. hermonthica* and are thus suitable for assessing the progress of the breeding program. Evaluating such genetic gains is extremely important to generate critical information for identifying defensive traits that may require increased attention by breeders in the future, improve selection criteria, design alternative breeding strategies, and guide breeders in the best use of existing resistant germplasm to further enhance polygenic resistance against this noxious parasitic weed.

Studies examining responses to long-term recurrent selection in broad-based populations of maize (Menkir and Kling, 2007; Badu-Apraku et al., 2008) and pearl millet (Kountche et al., 2013) found significant increases in grain yield, coupled with reductions in parasite-induced damage symptoms, and number of emerged parasites. Genetic gain studies involving 50 early (Badu-Apraku et al., 2013) and 56 extra-early (Badu-Apraku et al., 2016) maturity open-pollinated maize cultivars also reported grain yield increases of 41 and 42 kg ha^{-1} yr^{-1} under artificial *Striga* infestation, respectively. Other studies evaluating temperate maize hybrids developed during different eras concluded that much of the genetic gains in grain yield had resulted from improvements in adaptation to increased inputs and stresses applied by intensive management systems (Tollenaar, 1991; Tollenaar and Wu, 1999; Duvick, 2005). A 30-yr genetic gain study of a wheat improvement program detected an annual yield increase of 0.48% in plots protected with a fungicide and 2.21% in plots that were not treated with fungicides but protected through incorporation of genes that conferred slow leaf rusting resistance (Sayre et al., 1998). To the best of our knowledge, there is no published study that has examined genetic gain for polygenic resistance to *S. hermonthica* in late-maturing tropical maize hybrids developed across several decades. The present study was therefore conducted (i) to examine the genetic improvements in grain yield and other traits of *S. hermonthica*-resistant maize hybrids developed during three breeding periods under artificial *Striga* infested and noninfested conditions, and (ii) to identify the most important traits that contributed to the improvement in productivity with and without parasite pressure.

MATERIALS AND METHODS

Genetic Materials

These hybrids were grouped into three breeding periods (Table 1). Period 1 (1982–1990) includes hybrids H01 to H09 developed from pairs of *Striga*-tolerant maize inbred lines and their improved versions. Period 2 (1991–2000) includes hybrids H10 to H14 that were crosses of *Striga*-resistant maize inbred lines derived from different improved source populations with selected *Striga*-tolerant maize inbred lines. Period 3 (2001–2010) includes hybrids H15 to H30 formed from pairs of *Striga*-resistant maize inbred lines derived from improved source populations. Details on the development of *Striga*-tolerant elite inbred lines and their further improvement for increased tolerance to the parasite are presented by Kim (1991, 1996). Also, the genetic backgrounds of tropical source populations, synthetics, and a backcross containing *Zea diploperennis* Iltis, Doebley & Guzman as a resistance donor, and their improvement under artificial *Striga* infestation before inbred lines were developed, have been extensively described by Kling et al. (2000).

Experimental Design and Field Infestation with *Striga hermonthica*

A trial consisting of the 32 hybrids was conducted with and without artificial *S. hermonthica* infestation at Kubwa and Mokwa in Nigeria in 2011, 2012, 2013, and 2014. The testing sites are located 340 km apart and represent different growing conditions. Kubwa is located near Abuja (9°14′ N, 7°35′ E; 445 m asl), has a ferric luvisol Plinthustalf soil containing 81% sand, 12% silt, and 7% clay, has an average annual temperature of 25.7°C, and receives annual rainfall of ∼1389 mm. At Kubwa, the growing season starts in May and ends in October. Mokwa is situated in Niger state (9°29′ N, 5°05′ E; 210 m asl), has a Tropeptic Haplustox soil that is fine and kaolinitic in nature, has a mean annual temperature of 27.6°C, and receives 1150 mm of rainfall. The growing season at Mokwa starts at the end of June and ends in October.

At each location, the 32 hybrids were arranged in an eight-by-four α-lattice design, with three replications and planted in a crisscross arrangement (Pearce, 1976). Each hybrid was planted in adjacent infested and noninfested strips, which were located opposite to each other and separated by a 1.5-m alley. Within each strip, a hybrid was planted in a 5-m-long row with an inter-row spacing of 0.75 m and an intra-row spacing

Table 1. List of *Striga*-tolerant and -resistant hybrids developed and disseminated to partners from 1982 to 2010.

Hybrid	Pedigree	Year of dissemination	Hybrid	Pedigree	Year of dissemination
H01	TZi3/TZi15	1983	H17	ZDiploBC4-472-2-2-1-2-3-B-1-BBB/ TZLComp1(TC87)-2-$^{\#}$-4-1-4-B-1-BBB	2002
H02	Oba Super 2 (commercial hybrid)	1986	H18	ZdiploBC4-290/POP43SRS5-3-1-1-1-1-1-B*5	2003
H03	TZi25/TZi18	1984	H19	ZdiploBC4-472/ZdiploBC4-551	2003
H04	TZi3STR/TZi12STR	1990	H20	ACR97SYN-Y-S1-38-BB/ZDiploBC4-467-4-1-2-1-1-B-1-B*5	2004
H05	TZi35STR/TZi18STR	1990	H21	ACR97SYN-Y-S1-79-B*4/ZDiploBC4-467-4-1-2-1-1-B-1-B*5	2004
H06	TZi3STR/TZi15STR	1990	H22	Oba Super 7 (Commercial hybrid)	2005
H07	TZi3/TZi12	1983	H23	Oba Super 9 (Commercial hybrid)	2005
H08	TZi18STR/TZi35	1990	H24	ZdiploBC4-472-2-3-4-3-B-3-BB/ TZLCompIC4S1-37-5-BB	2006
H09	Oba Super 1 (Commercial hybrid)	1983	H25	STRSyn-Y(43-2)-1-1-5-1-BB/ZDiploBC4-467-4-1-2-1-1-B-1-B*6	2006
H10	STRSyn-Y(43-2)-1-1-5-1-B/TZi25	1999	H26	ACR97TZL-CCOMP1-Y-S3-33-6-BBB/ ACR97SYN-Y-S1-79-B*4/ZDiploBC4-467-4-1-2-1-1-B-1-B*5	2007
H11	STRSyn-Y(43-2)-1-1-5-1-B/MMB90	1999	H27	ACR97SYN-Y-S1-79-B*4/ZDiploBC4-467-4-1-2-1-1-B-1-B*5/ACR97TZL-CCOMP1-Y-S3-56-1-BB	2007
H12	STRSyn-Y(43-2)-1-1-5-2-B/TZi25	1999	H28	ACRSYN-W-S2-173-B*4/TZLCompIC4S1-37-1-B*4	2008
H13	TZLCOMP1-(TC87)-2-$^{\#}$-5-1-5-BB/TZi3	2000	H29	ZDiploBC4-19-4-1-$^{\#}$-3-1-B-1-B*4/ TZLCompIC4S1-37-5-BBB	2008
H14	ZdiploBC4-472-2-2-1-6-4-BB/TZi12	2000	H30	ACRSYN-W-S2-173-B*4/TZLCompIC4S1-37-5-BBB	2008
H15	ZDiploBC4-282-5-2-2-1-B-1-BBB/ZDiploBC4-472-2-2-1-2-3-B-1-BBB	2002	H31	9022-13	1990
H16	ZDiploBC4-290-4-2-1-1-B-1-BBB/ZDiploBC4-472-2-2-1-2-3-B-1-BBB	2002	H32	8338-1	1983

of 0.25 m. The infested row of a hybrid was planted directly opposite to the noninfested row to obtain precise estimates of yield loss attributable to *S. hermonthica* damage (Kling et al., 2000). The noninfested rows were treated with ethylene 2 wk before planting to eliminate any potential *S. hermonthica* seeds present in the soil. The *S. hermonthica* seeds used for the trial conducted every year were collected in the previous year from farmers' sorghum fields around Abuja and Mokwa. *Striga hermonthica* infestation was performed by injecting 8.5 g of sand mixed with *S. hermonthica* seed inoculum into holes of about 6-cm depth and 10-cm width. The estimated number of germinable seeds per hill was 3000. Two maize seeds were placed into the holes infested with sand-mixed *S. hermonthica* seeds and covered with soil. One plant was manually removed from each hill 2 wk after planting to attain a population density of 53,333 plants ha^{-1}. Nitrogen was applied at the rate of 30 kg ha^{-1} at planting and an additional 30 kg N ha^{-1} was applied 4 wk later. Additionally, 60 kg ha^{-1} each of P_2O_5 and K_2O were applied at planting. Weeds other than *S. hermonthica* were manually removed throughout the cropping season.

Trait Measurements

Data recorded in each plot under both *Striga*-infested and noninfested conditions included plant stand, anthesis and silking days, anthesis–silking interval, plant height, ear aspect, and grain yield. Plant stand was counted as the total number of plants per plot obtained immediately after thinning. Days to anthesis and silking were recorded as the number of days from planting to when 50% of the plants in a plot had anthers shedding pollen and showing emerged silks, respectively. Anthesis–silking interval was calculated as the interval in days between dates of silking and anthesis. Plant height was measured in centimeters as the distance from the base of the plant to the height of the first tassel branch. Ear aspect was scored on a scale of 1 to 9, where 1 = clean, uniform, and large ears, and 9 = rotten, variable, and small ears. All ears harvested from each plot were shelled to determine percent moisture, which was used to determine grain yield adjusted to 15% moisture under both infested and noninfested conditions. Host plant damage symptoms were visually rated in each infested row at 8 and 10 wk after planting (WAP) using a scale of 1 to 9, where 1 = no visible host plant damage symptom, and 9 = all leaves completely scorched, resulting in premature death (Kim, 1994). Also, the emerged *S. hermonthica* plants were counted in each infested row at 8 and 10 WAP and were divided by the corresponding plant stand to obtain the number of emerged parasites per plant in each row. The total number of plants and ears were determined in each *Striga*-infested plot at the time of harvest and used to calculate the number of ears per plant. Ear height was measured in centimeters in the noninfested row as the distance from the base of the plant to the height of the node bearing the upper ear. Husk cover was rated on a scale from 1 to 5 under noninfested conditions, where 1 = husks tightly arranged and extended beyond the ear tip, and 5 = ear tips exposed. Plant aspect was rated on a scale of 1 to 9 in noninfested plots, where 1 = excellent plant type with large and similar ears, low ear placement, shorter plants, resistance to foliar diseases, and little stalk and root lodging, and 9 = plants with small and variable ears, high ear placement, tall plants, susceptibility to foliar diseases, and stalk and root lodging. Also, ear rot was rated on a scale of 1 to 5, where 1 = little or no visible rotting of the ears, and 5 = extensive visible rotting of the ears.

Statistical Analysis

Analyses of variance combined across eight year–location combinations, which are hereafter referred to as environments, were conducted for all traits measured under infested and noninfested conditions based on mixed-model analysis with the restricted maximum likelihood procedure of SAS (Vargas et al., 2013). Separate analyses were conducted for traits measured under infested and noninfested conditions because *Striga* damage, *Striga* emergence, and number of ears per plant were measured only in the *Striga*-infested block, whereas husk cover, plant aspect, and ear aspect were measured only in the noninfested block. In these analyses, environments, replication (environments), and block (replication × environments) were considered random effects, whereas developing periods and hybrids (period) were regarded as fixed effects. The mixed model analysis generated best linear unbiased estimates (BLUEs) for hybrids, LSD, and repeatability estimates (Vargas et al., 2013). All pairwise differences between means of the three periods were tested using LSMEANS/PDIFF option in SAS (SAS Institute, 2010).

A nonparametric statistic, which is insensitive to outliers and robust in providing protection against violations of assumptions associated with the distribution of variables recorded in multienvironment trials was used to assess consistency of the three major *Striga* resistance-related traits of hybrids across the eight environments (Madden et al., 2007). In each environment, BLUEs for grain yield of the hybrids and the checks were ranked using PROC RANK in SAS (SAS Institute, 2010). Kendall's coefficient of concordance (W) was calculated to assess the similarity of rank order of the 32 hybrids across eight environments, each under infested and noninfested conditions. A *Striga* resistance index (RI) was calculated using the formula described by Johnson (1975) as: RI = (hybrid mean grain yield under *Striga* infestation/mean yield under noninfested condition) × 100. A linear regression coefficient (b) was used as an estimate of genetic gain over a period of 26 yr, with year of hybrid development and dissemination to partners being an independent variable and hybrid mean for each trait being a dependent variable. Percent gain per cycle was obtained by dividing the linear regression coefficient by the intercept multiplied by 100.

The combinations of traits that contributed significantly to yield gains and RI of hybrids developed in different periods were identified using separate principal component analysis for infested and noninfested conditions based on the correlation matrix of all traits, excluding yield. Correlation coefficients between the original traits and their corresponding principal component axis scores were calculated to identify important traits in each particular axis. The relationship of principal component axis score with year of hybrid development and dissemination to partners was calculated for both *Striga*-infested and noninfested conditions using PROC CORR in SAS (SAS Institute, 2010). Correlation analyses of mean grain yields recorded under infested and noninfested conditions with the corresponding first two principal component (PC1 and PC2) axes scores were conducted to examine the relationships of multiple traits with host productivity. Also, the correlations of RI with PC1 and PC2 axes scores were computed to assess whether resistance in hybrids was related to multiple traits recorded under the two growing conditions.

RESULTS

Genetic Improvement under *Striga* Infestation

On average, yield reduction resulting from *Striga* damage was 77% for the susceptible (8338-1) and 26% for the tolerant (9022-13) benchmark hybrids. In the combined ANOVA for the infested condition, environment had significantly affected all measured traits, except grain yield and anthesis–silking interval (Table 2). The breeding periods, hybrids (breeding periods), and their interactions with environments had significant effects on most or all traits recorded under infestation (Table 2). Further assessment of the W of hybrid ranks across environments were significant ($P < 0.001$) for each of the three major *Striga* resistance-related traits, including grain yield under infestation ($W = 0.64$), *Striga* damage rating at 8 ($W = 0.80$) and 10 WAP ($W = 0.79$), and the number of emerged *Striga* per plant at 8 ($W = 0.78$) and 10 WAP ($W = 0.80$). Furthermore, repeatability estimates for these three and other traits recorded under infestation were high, varying from 0.69 to 0.94 (Table 2).

We determined progress in *Striga* resistance and other traits by comparing the performance of the hybrids developed in different breeding periods relative to the performance of the susceptible (8338-1) and tolerant (9022-13) benchmark hybrids. Even though the mean grain yield of 8338-1 did not differ significantly from that of 9022-13 under noninfested conditions, 9022-13 produced 268% more grain yield than 8338-1 under *Striga* infestation (Tables 3 and 4). The hybrids in Period 1 yielded significantly more, showed fewer *Striga* damage symptoms, and supported as many emerged *Striga* per plant as 8338-1 at both 8 and 10 WAP (Table 3). Six of the nine hybrids in Period 1 were found to be as high yielding as the tolerant benchmark hybrid 9022-13 (Supplemental Table S1). On the other hand, all hybrids in Period 2 and Period 3 yielded significantly better and showed significantly lower *Striga* damage symptoms at both 8 and 10 WAP than 8338-1 (Table 3, Supplemental Table S1). Also, four of the five hybrids in Period 2 and all hybrids in Period 3 supported significantly fewer emerged *Striga* per plant than 8338-1 at both 8 and 10 WAP. Furthermore, a hybrid in Period 2 and nine hybrids in Period 3 yielded significantly better than 9022-13, whereas the rest of the hybrids in the two periods had yield potential comparable with that of 9022-13 (Supplemental Table S1). Although eight of the nine hybrids in Period 1 produced 14 to 40% lower mean grain yields compared with 9022-13, most of the hybrids in Period 2 and Period 3 had yield

Table 2. Mean squares from the combined ANOVA for traits of hybrids recorded under artificial *Striga* infestation at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

Source	df	Grain yield	Anthesis days	Silking days	Plant height	*Striga* damage rating 8 wk	*Striga* damage rating 10 wk	Emerged *Striga* per plant 8 wk	Emerged *Striga* per plant 10 wk	Ear aspect	Ears per plant	Anthesis–silking interval
		kg ha^{-1}	d	d	cm	wk	wk	wk	wk	1–9†	no.	d
Environment (ENV)	7	19,184,121	2,008****	1,948****	22,993****	32.0**	51.5***	75.8***	114.9***	60.3****	0.36*	6.7
Replication (ENV)	16	4,184,262***	20****	23***	1,064**	2.1***	5.0***	7.4****	10.8****	0.8**	0.04	1.1
Block (ENV × replication)	120	1,062,628***	4****	5****	316****	0.5****	1.2****	1.1***	1.8***	0.3***	0.03*	0.8***
Period	2	153,878,907****	32*	73**	9,619****	128.1****	297.3****	120.5***	177.5***	45.9****	2.37****	20.3**
ENV × period	14	7,123,702****	5*	11***	278	4.0****	4.4***	7.6****	10.5****	1.7****	0.07**	2.6****
Hybrid (period)	29	5,206,959****	10****	12****	929****	5.7****	7.7****	3.1****	4.1****	1.5****	0.16****	1.5**
ENV × hybrid (Period)	200	1,349,790****	2.7****	4****	169*	0.7****	1.5****	1.2****	1.6***	0.4****	0.03***	0.8****
Repeatability		0.90	0.80	0.79	0.90	0.94	0.94	0.87	0.89	0.90	0.90	0.69

*, **, ***, **** Significant at the 0.05, 0.01, 0.001, and 0.0001 probability levels, respectively.

† Ear aspect (1–9): 1 = clean, uniform, large, and well-filled ears, and 9 = rotten, variable, and small ears.

advantages of 9 to 71% over 9022-13 (Supplemental Table S1). The RI was 23% for the susceptible benchmark hybrid and 74% for the tolerant benchmark hybrid (Table 3). The RI values of the hybrids developed and disseminated to partners varied from 40 to 64% in Period 1, from 67 to 84% in Period 2, and from 71 to 98% in Period 3.

All pairwise differences in grain yield between developing periods were significant ($P < 0.01$), demonstrating consistent increases in host plant productivity over a 26-yr period (analysis not sown). On average, the hybrids included in Period 2 and Period 3 produced 818 and 1555 kg ha^{-1} more grain, respectively, than those in Period 1 (Table 3). These improvements in grain yield over time were accompanied by a <15% increase in plant height and number of ears per plant, but a reduction of 33% in anthesis–silking interval, 17 to 33% lower *Striga* damage rating at 8 and 10 WAP, and a 48 to 71% decrease in emerged *Striga* per plant at 8 and 10 WAP (Table 3). The observed changes from Period 1 to Period 2 and from Period 1 to Period 3 in anthesis and silking days, as well as in ear aspect score, were very small. Changes in the average annual rate of genetic gain were further assessed by linear regression analysis of hybrid means on years of hybrid development and dissemination to partners, which were found to be significant and positive for grain yield, plant height, and ears per plant but were significant and negative for almost all other traits (Table 4).

The average genetic gain was 93.7 kg ha^{-1} yr^{-1} for grain yield, representing a relative genetic gain of 3.2% yr^{-1}. The annual gain was <1.50% for plant height and ears per plant. In contrast, the linear changes in silking days, *Striga* damage rating, emerged *Striga* per plant, ear aspect, and anthesis–silking interval were significant and negative, varying from less than −1% yr^{-1} for silking days

Table 3. Minimum, maximum, and mean values for grain yield and other traits of hybrids representing three breeding periods recorded under artificial *Striga* infestation at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

	Period 1 (1982–1990)			Period 2 (1991–2000)			Period 3 (2001–2010)			Mean		LSD
Trait	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Tolerant	Susceptible	(0.05)
Grain yield (kg ha^{-1})	1567	2881	2103	2308	3494	2921	2848	4467	3658	2617	712	818
Resistance index	40	64	54	67	84	77	71	98	86	74	23	
Anthesis (d)	59	62	60	60	62	61	58	61	60	61	60	1.0
Silking (d)	62	64	63	62	64	63	61	64	62	64	64	1.2
Plant height (cm)	148	160	155	160	185	168	150	174	165	149	150	8
Striga damage rating at 8 WAP†	4	5	4	3	4	3	3	3	3	4	6	0.6
Striga damage rating at 10 WAP†	5	7	6	4	6	5	3	5	4	6	8	0.8
Emerged *Striga* per plant at 8 WAP‡	1.3	3.2	2.1	0.7	1.5	1.0	0.2	1.1	0.6	2.0	2.3	0.8
Emerged *Striga* per plant at 10 WAP‡	1.8	3.9	2.7	0.9	2.2	1.4	0.4	1.7	0.9	2.9	2.8	0.9
Ear aspect§	3	4	3	3	3	3	2	3	3	3	4	0.4
Ears per plant (no.)	0.7	0.9	0.8	0.8	1.0	0.9	0.9	1.0	0.9	0.8	0.4	0.1
Anthesis–silking interval (d)	2	4	3	2	3	2	2	3	2	3	3	0.6

† *Striga* damage rating (1–9): 1 = no damage symptoms, and 9 = severe damage symptoms due to *Striga*. WAP, weeks after planting

‡ Number of emerged *Striga* seedlings counted in 3.75 m^{-1}.

§ Ear aspect (1–9): 1 = clean, uniform, large, and well-filled ears, and 9 = rotten, variable, and small ears.

Table 4. Observed genetic gains for grain yield and other traits of hybrids representing three breeding and dissemination periods recorded under artificial *Striga* infestation at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

Trait	Gain per year	*P* value	R^2	Regression intercept	Gain per year
					%
Grain yield (kg ha^{-1})	93.69	<0.0001	0.77	2958	3.17
Anthesis (d)	−0.02	0.2203	0.05	60	−0.03
Silking (d)	−0.05	0.0264	0.15	63	−0.08
Plant height (cm)	0.65	0.0004	0.34	162	0.40
Striga damage rating at 8 WAP†	−0.08	<0.0001	0.71	4	−2.00
Striga damage rating at 10 WAP†	−0.13	<0.0001	0.72	5	−2.60
Emerged *Striga* per plant at 8 WAP‡	−0.08	<0.0001	0.72	1.19	−6.72
Emerged *Striga* per plant at 10 WAP‡	−0.09	<0.0001	0.68	1.64	−5.49
Ear aspect§	−0.05	<0.0001	0.76	3	−1.67
Ears per plant (no.)	0.01	<0.0001	0.55	0.9	1.11
Anthesis–-silking interval (d)	−0.03	<0.0001	0.49	3	−1.00

† *Striga* damage rating (1–9): 1 = no damage symptoms, and 9 = severe damage symptoms due to *Striga*. WAP, weeks after planting.

‡ Number of emerged *Striga* seedlings counted in 3.75 m^{-1}.

§ Ear aspect (1–9): 1 = clean, uniform, large, and well-filled ears, and 9 = rotten, variable, and small ears.

to −6.72% yr^{-1} for emerged *Striga* per plant at 8 WAP (Table 4). The coefficient of determination (R^2) for grain yield, *Striga* damage rating, and emerged *Striga* per plant and ear aspect varied from 68 to 77%, indicating that a large proportion of the variation for these important *Striga* resistance-related parameters in maize was associated with the variation in years of hybrid development and dissemination to partners (Table 4). The variation in other traits represented 15 to 55% of the variance in years of hybrid development and dissemination to partners.

Genetic Improvement under Noninfested Conditions

In the combined ANOVA (Table 5), environment had a significant effect on all measured traits, except on anthesis–silking interval. The mean squares for breeding periods, hybrids (breeding period), and their interactions with environment were significant for most or all traits recorded under noninfested conditions. The variances for the interactions of developing period or hybrid (breeding period) with environment were always considerably smaller than those of the corresponding developing period and hybrid (breeding period) main effects for most or all traits (Table 5). The repeatability estimates were also high for all traits, except for anthesis–silking interval, suggesting that genotypic effects were strong on traits recorded under noninfested conditions.

The susceptible (8338-1) and tolerant (9022-13) benchmark hybrids did not differ significantly from each other in grain yield under noninfested conditions (Table 6), demonstrating that the observed difference between these hybrids under *Striga* infestation was not associated with differences in their yield potential. Two hybrids in Period 1, one hybrid in Period 2, and nine hybrids in Period 3 produced significantly higher grain yields than 9022-13, with the remaining hybrids in all three periods having similar yield potential to 9022-13 (Table 5). Yield advantages of four hybrids in Period 1, one hybrid in Period 2, and 12 hybrids in Period 3 over 9022-13 varied from 10 to 43% (Supplemental Table S2). Although the average grain yield of the hybrids in Period 3 was higher than those in Period 1 and Period 2, all pairwise differences between developing periods were not significant for this trait, nor for ear height, husk cover, and ear rot (Table 6). On average, the hybrids in Period 3 differed significantly from those in Period 1, Period 2, or both for other traits. The rate of genetic gain over time was significant and positive for grain yield but was significant and negative for silking days, plant aspect, ear aspect, anthesis–silking interval, and ear rot score (Table 7). The average yield gain per year was 29.3 kg ha^{-1}, representing a relative genetic gain of <1% yr^{-1}. Also, the significant average annual gain for other traits was <1%. The R^2 values showed that grain yield and associated traits of hybrids accounted for 13 to

Table 5. Mean squares from the combined ANOVA for traits of hybrids recorded under noninfested condition at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

Source	df	Grain yield	Anthesis days	Silking days	Plant height	Ear height	Husk cover	Plant aspect	Ear aspect	Anthesis–silking interval	Ear rot score
		kg ha^{-1}	d		cm		1–5†	1–9‡	1–9§	d	1–5¶
Environment (ENV)	7	40,985,918**	2,284****	2,368****	24,878****	13,224****	7.8****	11.5***	41.6****	8.2	11.3****
Replication (ENV)	16	5,261,695**	18****	15***	1,030**	556*	0.5	1.1***	0.9***	1.4**	0.5*
Block (ENV × replication)	120	1,561,517****	4****	4****	309****	199****	0.5***	0.2	0.2	0.4	0.2
Period	2	18,043,193*	57**	38**	2,668****	275*	0.7	11.0***	5.1**	5.1	1.5
ENV × period	14	3,439,739*	8**	5*	117	64	0.3	0.6**	0.6*	2.3****	0.5*
Hybrid (period)	29	4,773,963****	11****	9****	746****	630****	1.4****	1.0****	1.0****	0.8	0.6***
ENV × hybrid (period)	200	1,675,192****	3****	2****	187***	121	0.5****	0.2	0.3****	0.6****	0.3****
Repeatability		0.72	0.82	0.81	0.84	0.85	0.75	0.86	0.75	0.42	0.65

*, **, ***, **** Significant at the 0.05, 0.01, 0.001, and 0.0001 probability levels, respectively.

† Husk cover (1–5): 1 = husks tightly arranged and extended beyond the ear tip, and 5 = ear tips exposed.

‡ Plant aspect (1–9): 1 = excellent plant type with large and similar ears, low ear placement, shorter plants, resistance to foliar diseases, and little stalk and root lodging, and 9 = plants with small and variable ears, high ear placement, tall plants, susceptibility to foliar diseases, and stalk and root lodging.

§ Ear aspect (1–9): 1 = clean, uniform, large, and well-filled ears, and 9 = rotten, variable, and small ears.

¶ Ear rot (1–5): 1 = little or no visible rotting of the ears, and 5 = extensive visible rotting of the ears.

49% of the total variation in years of hybrid development and dissemination to partners.

Changes in Multiple Traits Associated with Improvement in Grain Yield

Among the traits recorded under *Striga* infestation, silking days, plant height, *Striga* damage rating at 8 and 10 WAP, emerged *Striga* per plant at 8 and 10 WAP, ear aspect, ears per plant, and anthesis–silking interval had significant ($P < 0.01–0.0001$) and linear associations with grain yield of the hybrids developed over the 26-yr period. These traits represented 23 to 87% of the total variation in yield gain over time. As multiple traits could be biologically correlated due to pleiotropy or linkage, further examination of their combined effects on genetic gains in grain yields was performed using principal component analysis. Both PC1 and PC2 explained 82% of the total variation in multiple traits recorded under *Striga* infestation. The first PC alone accounted for 66% of the total variation, and its large scores were characterized by a significant delay in silking, high *Striga* damage symptom rating, more emerged *Striga* per plant, poor ear aspect scores, longer anthesis–silking interval, and fewer ears per plant (Table 8). The second PC represented 16% of the total variation in multiple traits, and its scores were mainly associated with increases in anthesis and silking days. The correlation of axis scores with year of hybrid development and dissemination to partners was significant and negative for PC1, but not for PC2 (Table 8). Regression analysis of the PC1 axis scores on hybrid mean grain yields accounted for 82% of the total variation in multiple traits measured under *Striga* infestation (Fig. 1). This analysis showed that for every unit increase in PC1 axis score, grain yield decreased by 310 kg ha^{-1}. The relationships of the reaction patterns of

Table 6. Minimum, maximum, and mean values for grain yield and other traits of hybrids representing three breeding and dissemination periods recorded under noninfested condition at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

	Period 1 (1982–1990)			Period 2 (1991–2000)			Period 3 (2001–2010)			Mean		
Trait	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Tolerant	Susceptible	LSD (0.5)
Grain yield (kg ha^{-1})	3556	4505	3891	3426	4686	3821	3268	5044	4290	3536	3155	797
Anthesis (d)	59	61	60	59	61	60	58	61	60	61	60	0.9
Silking (d)	61	63	62	61	64	63	60	63	62	63	63	1.1
Plant height (cm)	170	182	176	175	198	184	168	193	181	170	182	7.9
Ear height (cm)	75	89	81	77	99	83	67	92	81	83	75	6.4
Husk cover (1–5)†	3	3	3	2	3	3	2	3	3	3	3	0.4
Plant aspect (1–9)‡	3	4	3	3	3	3	3	3	3	4	4	0.4
Ear aspect (1–9)§	3	3	3	3	3	3	2	3	3	3	4	0.3
Anthesis–silking interval (d)	2	3	2	2	3	2	2	3	2	2	3	0.5
Ear rot (1–5)¶	2	2	2	2	2	2	2	2	2	2	2	0.3

† Husk cover: 1 = husks tightly arranged and extended beyond the ear tip, and 5 = ear tips exposed.

‡ Plant aspect: 1 = excellent plant type with large and similar ears, low ear placement, shorter plants, resistance to foliar diseases, and little stalk and root lodging, and 9 = with small and variable ears, high ear placement, tall plants, susceptibility to foliar diseases, and stalk and root lodging.

§ Ear aspect: 1 = clean, uniform, large, and well-filled ears, and 9 = rotten, variable, small, and partially filled ears.

¶ Ear rot: 1 = little or no visible rotting of the ears, and 5 = extensive visible rotting of the ears.

Table 7. Observed genetic gains for grain yield and other traits of hybrids representing three breeding and dissemination periods recorded under noninfested condition at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

Trait	Gain per year	*P* value	R^2	Regression intercept	Gain per year
					%
Grain yield (kg ha^{-1})	29.31	0.01	0.2	4036	0.73
Anthesis (d)	−0.02	0.39	0.03	60	−0.03
Silking (d)	−0.04	0.04	0.13	62	−0.06
Plant height (cm)	0.31	0.06	0.12	180	0.17
Ear height (cm)	0.13	0.37	0.03	81	0.16
Husk cover (1–5)†	−0.01	0.26	0.04	3	−0.33
Plant aspect (1–9)‡	−0.03	<0.0001	0.49	3	−1.00
Ear aspect (1–9)§	−0.02	<0.0001	0.45	3	−0.67
Anthesis–silking interval (d)	−0.02	0.0008	0.33	2	−1.00
Ear rot (1–5)¶	−0.01	0.01	0.22	2	−0.50

† Husk cover: 1 = husks tightly arranged and extended beyond the ear tip, and 5 = ear tips exposed.

‡ Plant aspect: 1 = excellent plant type with large and similar ears, low ear placement, shorter plants, resistance to foliar diseases, and little stalk and root lodging, and 9 = with small and variable ears, high ear placement, tall plants, susceptibility to foliar diseases, and stalk and root lodging.

§ Ear aspect: 1 = clean, uniform, large, and well-filled ears, and 9 = rotten, variable, small, and partially filled ears.

¶ Ear rot: 1 = little or no visible rotting of the ears, and 5 = extensive visible rotting of the ears.

Table 8. Correlations of the first two principal component axis (PC1 and PC2) scores with mean traits of hybrids recorded under *Striga* infestation and noninfested conditions at Abuja and Mokwa in Nigeria in 2011, 2012, 2013, and 2014.

	Infested			Noninfested	
Trait	Correlation with PC1	Correlation with PC2	Trait	Correlation with PC1	Correlation with PC2
Anthesis (d)	0.64****	0.69****	Anthesis (d)	0.42*	0.86****
Silking (d)	0.33	0.90****	Silking (d)	0.28	0.88****
Plant height (cm)	−0.63***	0.45	Plant height (cm)	−0.47**	0.45**
Striga damage rating at 8 WAP†	0.92****	−0.09	Ear height (cm)	−0.54**	0.31
Striga damage rating at 10 WAP	0.95****	−0.15	Husk cover (1–5)	0.55**	−0.49**
Emerged *Striga* count at 8 WAP	0.93****	0.01	Plant aspect (1–9)	0.89****	0
Emerged *Striga* count at 10 WAP	0.90****	0.03	Ear aspect (1–9)	0.95****	−0.02
Ear aspect (1–9)	0.95****	−0.08	Anthesis–silking interval (d)	0.62***	0.54**
Ears per plant (no.)	−0.88****	0.16	Ear rot (1–5)	0.80****	−0.34
Anthesis–silking interval (d)	0.80****	−0.06	Variance	0.42	0.27
Variance	0.66	0.16	Correlation with year	−0.67***	−0.13
Correlation with year	−0.89****	0.13			

*, **, ***, **** Significant at the 0.05, 0.01, 0.001, and 0.0001 probability levels, respectively.

† WAP, weeks after planting.

the hybrids under *Striga* infestation with multiple traits were further examined using a scatterplot of the PC1 and PC2 axis scores along with RI values presented in Fig. 2. The hybrids in Period 2 and Period 3 combined high RI with low or negative PC1 axis scores, and they were clearly separated from those in Period 1 and the tolerant and susceptible benchmark hybrids.

Regression analyses did not find a significant relationship of grain yield recorded under noninfested conditions with anthesis days, silking days, anthesis–silking interval, or plant height. However, ear height, plant aspect, ear aspect, and ear rot scores were found to be associated with grain yield, accounting for 15 to 59% of the total yield gain under noninfested conditions. Principal component analysis showed that PC1 and PC2 together accounted for 74% of the total variation in multiple traits of hybrids measured under noninfested conditions (Table 8). The PC1 axis scores were described by a significant delay in silking, reductions in plant and ear heights, poor husk cover, undesirable plant and ear aspects, more susceptibility to ear rot, and longer anthesis–silking interval. The PC2 axis scores were significantly associated with increases in anthesis and silking days, as well as longer anthesis–silking interval, but with better husk cover. Again, year of hybrid development and dissemination to partners was significantly

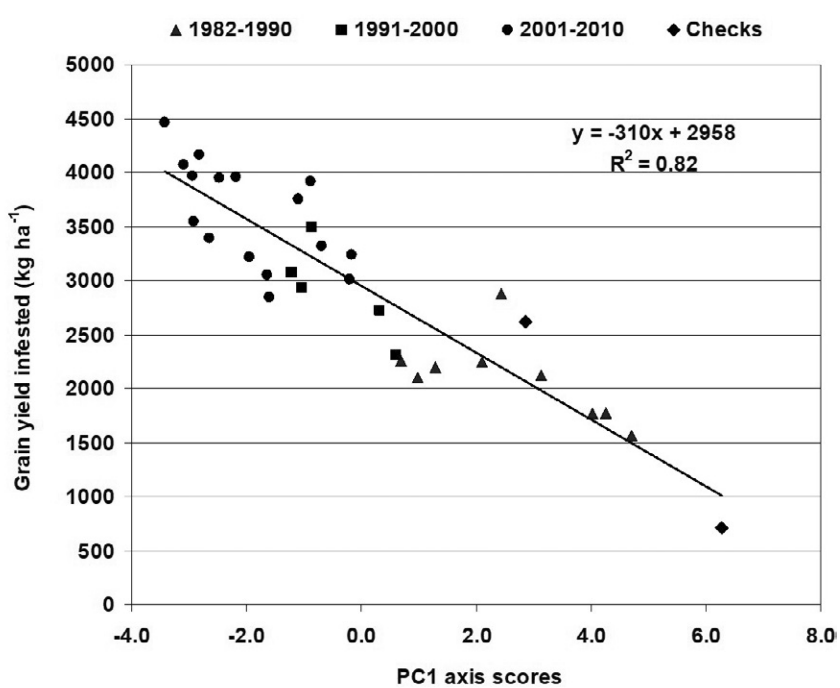

Fig. 1. Scatterplot of hybrid mean grain yields and the first principal component (PC1) axis scores of other traits recorded under artificial *Striga* infestation for 4 yr.

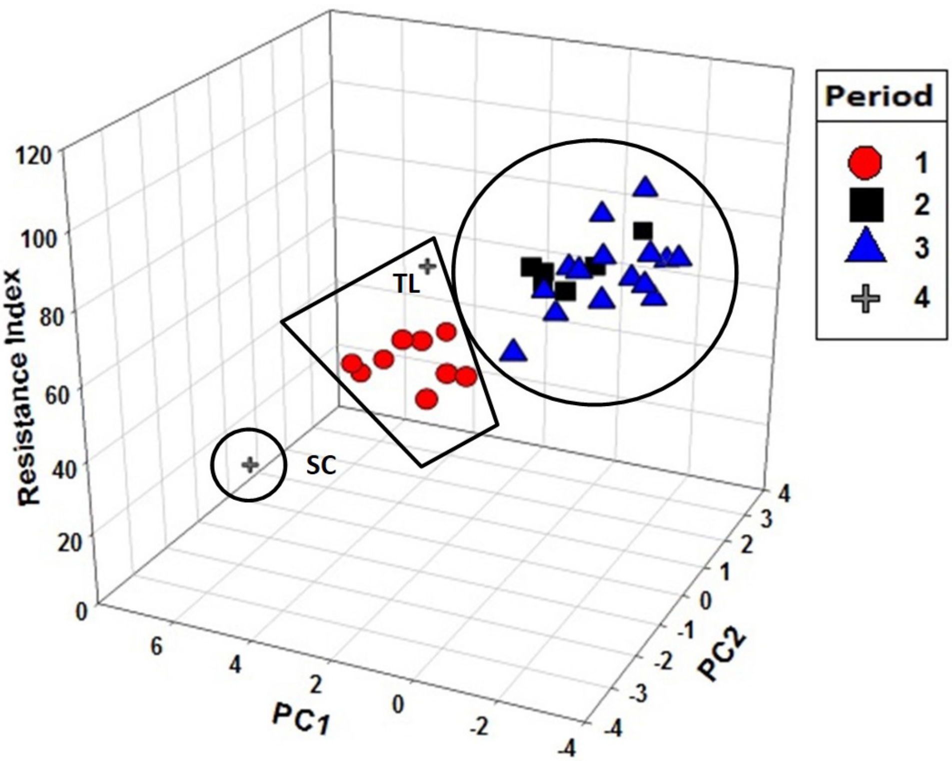

Fig. 2. Scatterplot of resistance indices of hybrids and their corresponding principal component (PC1 and PC2) axis scores computed from multiple traits recorded under artificial *Striga* infestation +TL refers to the tolerant benchmark hybrid, whereas +SC refers to the susceptible benchmark hybrid.

and negatively correlated with PC1 axis scores, but not with PC2 axis scores. The regression of PC1 axis scores on hybrid mean grain yields accounted for 50% of the total variation in multiple traits measured under noninfested conditions (Fig. 3). This analysis found a 192-kg ha^{-1} decrease in grain yield for every unit increase in PC1 axis score. A scatterplot of PC1 and PC2 axes scores along with RI values (Fig. 4) showed a clear separation of most of the hybrids in Period 2 and Period 3 from those in Period 1 and the tolerant and susceptible benchmark hybrids, indicating that high RI was associated with desirable combination of multiple traits even under noninfested conditions.

Correlation analyses were computed to examine the relationship of hybrid performance under *Striga* infested and noninfested conditions. Grain yield under *Striga* infestation was significantly and positively correlated with grain yield ($r = 0.70$, $P < 0.0001$) and negatively correlated with PC1 axis scores ($r = -0.86$, $P < 0.0001$) under noninfested conditions. Also, grain yield under noninfested conditions was significantly correlated with PC1 axis scores ($r = -0.47$, $P < 0.0064$) under *Striga* infestation. The correlation of PC1 and PC2 axes scores under *Striga* infestation with the corresponding PC1 ($r = 0.81$) and PC2 ($r = 0.84$) axes scores under noninfested conditions were significant ($P < 0.0001$). The RI was significantly ($P < 0.0001$) correlated only with PC1 axis scores under both infested ($r = -0.91$) and noninfested ($r = -0.68$) conditions.

DISCUSSION

Hybrids developed for polygenic resistance to *S. hermonthica* and disseminated to partners for a 26-yr period were evaluated in a trial under both *Striga*-infested and noninfested conditions. The highest yield loss was recorded in the susceptible benchmark hybrid, indicating the presence of high level of parasite infection during evaluations of this trial. The significant environmental effects and environment × period and environment × hybrids (period) interactions observed for most traits recorded under *Striga* infestation in this study could arise from a combination of factors experienced during evaluations of the hybrids (King and Zummo, 1977; Kim, 1996). As the trial was planted in different fields every year at each location with different soil characteristics, pH, and nutrient levels, their effects on inducing maize hybrids to release varying amounts of strigolactone may result in irregular germination of *Striga* seeds and their attachment to host roots (Jamil et al., 2012). Seasonal differences in temperature, humidity, the amount and distribution of rainfall, and the length of the growing period could also elicit varying levels of *Striga* infection in the present study (Kim, 1996; Menkir et al., 2012). It is thus reasonable to postulate that the interactions among these factors modulated varying levels of aggressiveness of *S. hermonthica* eliciting the differential performance of the breeding periods and hybrids. Nonetheless, the relatively high repeatability values of all measured traits under both *Striga*-infested and noninfested conditions

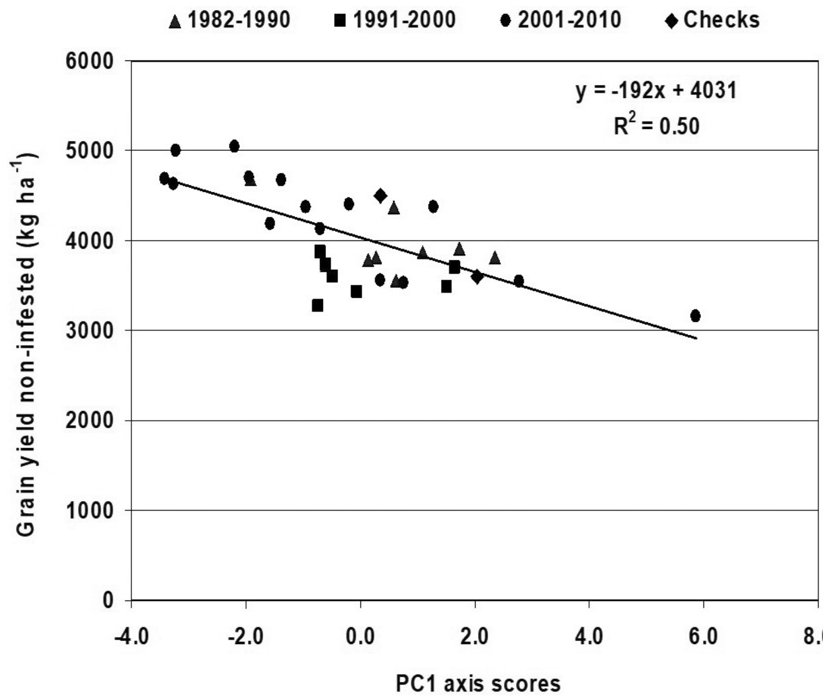

Fig. 3. Scatterplot of hybrid mean grain yields and the first principal component (PC1) axis scores of other traits recorded under noninfested conditions for 4 yr.

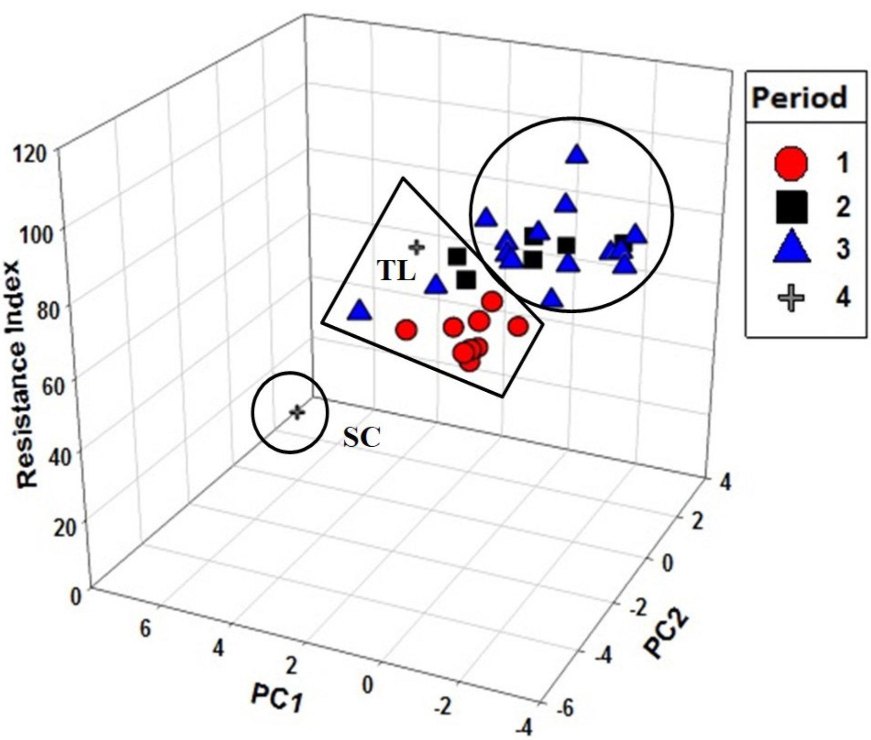

Fig. 4. Scatterplot of resistance indices of hybrids and their corresponding principal component (PC1 and PC2) axis scores computed from multiple traits recorded under noninfested conditions. +TL refers to the tolerant benchmark hybrid, whereas +SC refers to the susceptible benchmark hybrid.

indicated that trait variations were largely determined by the genetic backgrounds of the hybrids rather than by environmental effects (Falconer and Mackay, 1996). Additionally, these hybrids had consistent ranking for grain yield, *Striga* damage symptoms, and parasite emergence across environments that were in line with the findings in other studies (Kling et al., 2000; Gethi and Smith, 2004; Menkir et al., 2007). These results underscore the importance of using a stringent field screening technique that leads to a more intense exposure of parental lines to parasite populations with varying levels of aggressiveness to develop hybrids with stable performance and to attain further genetic gains under different parasite pressure, which are commonly encountered in farmers' fields.

The observed average yield gain of 3.2% yr^{-1} under *Striga* infestation in our study was greater than the gains reported for 50 early- and 56 extra-early-maturing open-pollinated maize varieties (Badu-Apraku et al., 2013, 2016). This yield gain was accompanied by marked decrease in both parasite damage and emergence, leading to more dry matter accumulation in the resistant hybrids through a minimal rate of nutrient transfer from the host to the parasite and maintenance of higher rates of photosynthesis and metabolism under parasite pressure (Gurney et al., 1995; Olivier, 1996; Gurney et al., 2002). In a study on rice (*Oryza sativa* L.), Cissoko et al. (2011) found negative correlation between aboveground biomass of the cultivars and the amount of parasite biomass measured on their roots, highlighting the potential that exists to further reduce parasite damage and emergence for attaining much greater productivity gains in maize hybrids targeted to areas infested with *S. hermonthica*. Our results also show that the linear increase in grain yield over time under *Striga* infestation was achieved without compromising the yield potential and other agronomic traits of hybrids under noninfested conditions.

Among the multiple traits recorded under infestation, *Striga* damage rating and the number of emerged *Striga* per plant were the most strongly related to the yield gain in hybrids, consistent with the results documented in other studies (Menkir and Kling, 2007; Badu-Apraku et al., 2008, 2013, 2016; Kountche et al., 2013). The scatterplot of PC1 and PC2 axis scores, along with RI values, provided clearly separated hybrid groups representing two breeding episodes of improvements in different defense mechanisms against the parasite. The first episode involved tolerant maize hybrids developed in Period 1 that were superior to the susceptible benchmark hybrid in yield potential while showing significantly fewer *Striga* damage symptoms and supporting as many parasites as the susceptible hybrid. These results highlight the success of the pioneering breeding work of Kim (1991, 1996) who extensively used host plant damage symptom rating as a major trait for developing maize genotypes tolerant to *S. hermonthica*.

The second breeding episode occurred when breeders at IITA placed more emphasis on selection for less emerged parasitic plants coupled with further reduction in *Striga*-induced damage symptoms and increased grain yield under infestation (Kling et al., 2000; Menkir et al., 2007). This change in emphasis led to yield increases of 195 to 527% in hybrids developed in Period 2 and Period 3 over the susceptible benchmark hybrid while at the same time showing drastic reductions in parasite damage and emergence, resulting from the use of appropriate weights assigned to the three major *Striga* resistance-related traits in a selection index during evaluation of lines at each inbreeding stage under artificial field infestation. As the ultimate number of emerged *Striga* plants is an indicator of attempts made by the parasite to overcome a sequence of defense reactions used by the maize crop, screening maize germplasm for fewer emerged parasites may serve as a selection agent shaping changes in underground defense mechanisms operating during parasite germination, attachment, and growth (Gurney et al., 2006; Amusan et al., 2008; Scholes and Press, 2008; Cissoko et al., 2011; Jamil et al., 2011; Rodenburg et al., 2015; Samejima et al., 2016, Rodenburg et al., 2017). Combining multiple resistance mechanisms that reduce parasite emergence is particularly important to increase further productivity gains for the farmers and reduce reproduction of parasite seed that attack other crops planted in the same field in subsequent growing seasons.

Even though different sets of traits defined the performance of hybrids under *Striga*-infested and noninfested conditions, the results of correlation analyses found that the highest yielding hybrids had desirable combinations of traits, whereas the lowest yielding hybrids had undesirable combinations of traits, irrespective of whether they were infected with the parasite or not. These results coupled with the observed strong and positive correlation of grain yields of the hybrids recorded under *Striga*-infested and noninfested conditions implied that the advances made in breeding hybrids for resistance to *S. hermonthica* was achieved without undesirable changes in hybrid performance in the absence of the parasite.

In conclusion, the results of the present study showed that the hybrids developed in three breeding periods and disseminated to partners had linear reductions in parasite damage and emergence and increases in productivity. Although none of the maize hybrids exhibited immunity to the parasite in the present study, several hybrids had marked reductions in parasite emergence and damage symptoms and produced higher grain yields under *Striga* infestation. These results clearly showed that selection for multiple traits using a stringent field infestation method coupled with appropriate weights assigned to traits in the selection index were effective in identifying maize inbred lines and hybrids with higher levels of field resistance to *S. hermonthica* without compromising the yield potential and other traits under noninfested conditions. The findings of our study provide evidence for further improvement in polygenic resistance to *S. hermonthica* to reduce yield loss to insignificant levels. As indicated by Wilkins (1975), the level of resistance conferred by polygenes can be very high in some instances and may not be distinguishable from major gene resistance. Given that maize genotypes rely on multiple defense mechanisms, each providing reductions in severity of parasite infection and damage, understanding the underlying mechanisms conditioning field resistance of parental lines of the hybrids evaluated in the present study and their molecular basis constitutes important research that can lead to stacking of diverse defensive mechanisms to develop more productive maize hybrids with consistently high levels of field resistance to the different ecotypes of *S. hermonthica* and meet the needs of farmers.

Supplemental Material

Supplemental materials for this article include two tables (Supplemental Tables S1 and S2) mentioned in the results section. Supplemental Tables S1 and S2 provide information on mean grain yields and other traits of hybrids recorded under artificial *Striga* infestation and noninfested conditions at two locations for 4 yr, respectively.

Conflict of Interest

The authors declare that there is no conflict of interest.

Author Contributions

The first author, A. Menkir, designed the crosses and the experiment and wrote the manuscript. S. Meseka assisted in conducting the experiment and recording the data at the two locations. Both authors read and approved the manuscript.

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