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Gains in Genetic Enhancement of Early Maturing Maize Hybrids Developed during Three Breeding Periods under *Striga*-Infested and *Striga*-Free Environments

Baffour Badu-Apraku [1,*], Gloria B. Adu [2], Abdoul-Madjidou Yacoubou [3], Johnson Toyinbo [1] and Samuel Adewale [1]

1 International Institute of Tropical Agriculture (IITA), Ibadan 200001, Nigeria; o.toyinbo@cgiar.org (J.T.); s.adewale@cgiar.org (S.A.)
2 Council for Scientific and Industrial Research (CSIR)—Savanna Agricultural Research Institute, Tamale 00233, Ghana; gloriaboakyewaa@yahoo.com
3 Crop Breeding Department, National Institute of Agricultural Research of Benin/CRA, Cotonou 01BP884, Benin; abdoulmadjidou.yacoubou@yahoo.com
* Correspondence: b.badu-apraku@cgiar.org; Tel.: +234-810-848-2590

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Abstract: *Striga hermonthica* is a major maize production constraint in West and Central Africa (WCA). Fifty-four early maturing maize hybrids of three breeding periods: 2008–2011, 2012–2013, 2014–2015, were evaluated under *Striga*-infested and non-infested environments in WCA. The study aimed at assessing genetic improvement in grain yield of the hybrids, identifying traits associated with yield gain during the breeding periods, and grain yield and stability of the hybrids in *Striga* infested and non-infested environments. Annual increase in grain yield of 101 kg ha^{-1} (4.82 %) and 61 kg ha^{-1} (1.24%) were recorded in *Striga*-infested and non-infested environments, respectively. The gains in grain yield from period 1 to period 3 under *Striga*-infested environments were associated with reduced anthesis-silking interval, reduced *Striga* damage, number of emerged *Striga* plants, improved ear aspect, and increased ears per plant. Ear aspect, ears per plant, and *Striga* damage at 8 and 10 weeks after planting (WAP) were significantly correlated with yield in *Striga*-infested environments, whereas ears per plant and plant and ear aspects had significant correlations with yield in non-infested environments. Hybrids TZdEI 352 × TZEI 355, TZdEI 378 × TZdEI 173, and TZdEI 173 × TZdEI 352 were outstanding in grain yield and stability in *Striga*-infested environments, whereas TZEI 326 × TZdEI 352, TZEI 495 × ENT 13, and TZdEI 268 × TZdEI 131 were superior in non-stress environments. These hybrids should be further tested extensively and commercialized. Significant genetic gains have been made in breeding for resistance to *Striga hermonthica* in early maturing maize hybrids.

Keywords: genetic gains; maize; breeding period; *Striga*; hybrids

1. Introduction

Maize (*Zea mays* L.) is an important staple food crop in sub-Saharan Africa (SSA). Its prominence has increased in SSA owing to its use as a cheap energy source in both human and livestock diets. The high insolation, cold night, and minimal occurrence of pest and diseases that characterize the savanna agroecology of SSA make it an ideal environment for maize production [1]. The early maturing maize varieties that are often available in July during the food deficit period, when other food reserves have been exhausted due to the extended hunger period, have helped to alleviate starvation in the savannas of SSA [2]. The availability and wide adoption of early maturing maize cultivars have resulted in tremendous increase in productivity and production of maize, leading to improved farmers' incomes. However, low-soil nitrogen, moisture stress, and infestation by *Striga hermonthica* constitute major limitations to the maize production capacity of SSA [3].

About two-thirds of the arable land in the savannas of SSA is endemic to *Striga hermonthica*, which often compels famers to abandon their farmlands. Continuous cropping and short fallow resulting from the rising human population pressure on available land area have aggravated the *Striga* menace [4]. *Striga* parasitism causes about 50−100% yield loss in maize depending on the variety, severity of infestation, soil fertility level, and prevailing environmental conditions [5,6]. Several control methods such as hand pulling, application of high fertilizer doses, crop rotation, and fallowing of land have been proposed but have proved inadequate and unsustainable [7]. There is a consensus that genetic control via *Striga* resistance is the most reliable and economically viable approach for mitigating effects of the parasitic weed [8–10]. *Striga* resistance is defined as the capacity of a host plant to disallow the germination and prevent the parasite from attaching to its roots, leading to the emergence of few *Striga* plants, while tolerance describes a host plant's capacity to produce substantial yield despite attachment of the parasitic weeds [11,12]. Amusan et al. [13] in a study of the mechanism of resistance to *Striga* in maize inbreds demonstrated differences in the root morphology of resistant and susceptible lines. *Striga* ingress into the root of a resistant line was usually impeded at the endodermis, and parasites which penetrate the xylem cells of the resistant host had delayed haustorial growth compared to those infesting roots of susceptible lines. They reported that resistant genotypes had less attached *Striga* plants, delayed *Striga* development, and more death of attached parasitic plants, relative to susceptible genotypes.

Striga infestation causes tremendous economic losses resulting in immense reduction of the potential of maize for combating food insecurity and alleviating poverty in SSA. Consequently, since 1980, improvement of maize for *Striga* resistance has become a major goal of National Maize Programs in WCA and the Maize Improvement Program of the International Institute of Tropical Agriculture (IITA-MIP). The germplasm exploited were obtained from a wide range of sources, selected following extensive testing for many years in multiple locations in WCA. These included introduced resistant germplasm from the temperate region, selected resistant African landraces, local and exotic germplasm, and backcross progenies derived from crosses involving the wild maize, *Zea diploperennis* [14]. Using existing germplasm and methods such as inbreeding, hybridization, and recurrent selection, the IITA-MIP during the last three to four decades developed numerous early maturing inbred lines, high-yielding open-pollinated populations, and hybrids possessing *Striga* resistance alleles.

Periodic assessment of genetic gains realized over time in a breeding program is helpful for evaluating the effectiveness of breeding methodologies and devising new strategies. Several studies comparing yield performance of maize varieties generated during different breeding periods have been carried out to document yield gain from selection [15–18]. Badu-Apraku et al. [2] studied the yield gains of early maturing open-pollinated maize varieties (OPVs) of three breeding periods under *Striga*-infested and non-infested environments from 2010 to 2011. Yield gains of 0.86, 2.07, and 2.11% were reported for periods 1, 2 and 3, respectively. Also, in a genetic gain study involving 32 late/intermediate maize hybrids, Menkir and Meseka [18] reported an annual yield gain of 3.2 and <1%, which corresponded to an annual gain of 93.7 and 29.3 kg ha^{-1} under *Striga*-infested and non-infested environments, respectively. However, information is unavailable on how genetic improvement for *Striga* resistance has affected agronomic characteristics of early maturing maize hybrids, including grain yield. Furthermore, identification of reliable secondary traits is critical for progress in genetic enhancement of early maturing hybrids for improved resistance to *Striga*. The present study aimed to (i) investigate gains in yield of 52 early maturing maize hybrids developed in the course of three breeding periods (period 1, 2008–2010: period 2, 2011–2013; and period 3, 2014–2016) in *Striga*-infested and *Striga*-free environments, (ii) identify traits linked with genetic gains from selection for grain yield and other agronomic characters during the periods in both research environments, and (iii) evaluate grain yield and stability of performance of the hybrids across test environments.

2. Results

2.1. Analysis of Variance for Grain Yield and Other Measured Characters

Results of the combined analysis of variance (ANOVA) of the 54 maize hybrids under *Striga*-infested and non-infested environments showed that environment, period, hybrid (period), hybrid (period) × environment interaction, and environment × period interaction effects were significant for yield and several other measured characters (Table 1). However, period effect for ear rot in *Striga*-infested environment were not significant. Similarly, period effect for days to 50% anthesis, husk cover, ears per plant, hybrid (period) × environment interaction effect for ears per plant, and period *x* environment interaction effect for days to 50% anthesis, days to silking, anthesis-silking interval in non-infested environments were not significant. Estimates of repeatability varied from 0.45 for root lodging to 0.85 for days to 50% anthesis in *Striga*-infested environments, and from 0.39 for anthesis-silking interval to 0.71 for days to 50% anthesis and plant aspect in *Striga*-free environments.

Table 1. Mean squares for grain yield and other measured traits for early maize hybrids of three breeding periods, evaluated under *Striga*-infested in seven environments and non-infested conditions in four environments from 2017 to 2019.

Source of Variation	df	Grain Yield	Days to Anthesis	Days to Silk	Anthesis-Silking Interval	Plant Height	Ear Height	Root Lodging	Stalk Lodging	Husk Cover	Ear Rot	Ears/Plant	Ear Aspect	Plant Aspect	*Striga* Damage (8 WAP)	*Striga* Damage (10 WAP)	Emerged *Striga* Plants (8 WAP)	Emerged *Striga* Plants (10 WAP)
***Striga*-infested Environments**																		
Environment (E)	6	187,179,984 **	971.12 **	1010.09 **	81.24 **	119,621.59 **	51,861.01 **	3393.36 **	13,735.25 **	211.27 **	3916.82 **	1.14 **	123.81 **	-	148.82 **	113.93 **	55,858.52 **	59,034.27 **
Block (E × replicate)	105	2996,086 **	4.26 **	7.89 **	1.96 **	486.59 **	250.53 **	114.30 **	122.48 **	1.03 **	19.10 **	0.04 **	2.99 **	-	1.61 **	1.66 **	468.98 **	696.12 **
Replicate	14	4,479,624 **	11.57 **	15.90 **	2.91 **	870.12 **	353.07 **	347.63 **	120.57	1.80 **	74.25 **	0.13 **	1.62 *	-	4.71 **	6.80 **	2395.68 **	2999.63 **
Period	2	39,614,625 **	36.55 **	172.88 **	46.73 **	10,900.78 **	1263.82 **	40.50 **	1239.94 **	10.83 **	0.10	0.78 **	35.95 **	-	38.29 **	39.47 **	1955.59 **	2139.52 **
Hybrid (period)	51	7,169,598 **	33.15 **	37.97 **	3.44 **	1833.61 **	583.06 **	116.50 **	337.46 **	6.97 **	69.23 **	0.17 **	4.84 **	-	6.60 **	8.27 **	2033.06 **	1770.50 **
E × hybrid (period)	306	1,392,259 **	4.69 **	6.68 **	1.56 **	425.87 **	173.60 **	67.55 **	125.96 **	1.14 **	32.72 **	0.04 **	1.67 **	-	1.50 **	1.55 **	601.41 **	714.33 **
E × period	12	3,344,381 **	17.27 **	22.70 **	4.55 **	1017.00 **	576.26 **	56.63 **	235.93 **	5.98 **	135.72 **	0.12 **	6.39 **	-	4.89 **	5.74 **	1302.86 **	1627.54 **
Error	637	612,970	2.01	3.23	1.13	216.60	112.35	37.68	83.41	0.43	7.49	0.02	0.77	-	0.58	0.57	299.07	426.30
Repeatability		0.83	0.85	0.84	0.70	0.80	0.70	0.45	0.63	0.82	0.47	0.60	0.70	-	0.79	0.82	0.70	0.60
Non-infested Environments																		
Environment (E)	3	433,095,265 **	1741.90 **	1802.59 **	55.12 **	125,385.49 **	32,753.19 **	7169.99 **	695.24 **	255.28 **	1042.30 **	0.27 **	50.38 **	14.88 **	-	-	-	-
Block (E × replicate)	60	2,267,835 **	4.16 **	4.42 **	0.33	530.60 **	190.60 **	97.16 **	7.74	0.31	7.17 **	0.02 **	0.76 **	0.90 **	-	-	-	-
Replicate	8	9,778,028 **	4.74 *	7.04 **	0.71	1076.04 **	873.76 **	20.53	13.69	1.34 **	70.12 **	0.02	6.63 **	2.27 **	-	-	-	-
Period	2	8,761,734 **	1.53	9.72 **	5.71 **	3346.92 **	712.33 **	165.06 **	70.12 **	0.13	16.74 *	0.03	21.95 **	15.20 **	-	-	-	-
Hybrid (period)	51	3,897,210 **	13.12 **	15.17 **	0.98 **	1102.54 **	381.12 **	96.02 **	16.54 **	1.41 **	13.19 **	0.02 **	2.77 **	2.00 **	-	-	-	-
E × hybrid (period)	153	2,108,184 **	3.95 **	4.74 **	0.69 **	474.11 **	181.24 **	62.05 **	12.07 **	0.70 **	8.29 **	0.01	1.25 **	0.70 **	-	-	-	-
E × period	6	4,555,138 **	2.79	3.08	0.52	1106.49 **	657.64 **	134.75 **	31.37 **	1.60 **	10.22 *	0.04 **	2.68 **	1.10 *	-	-	-	-
Error	364	613,212	1.86	1.98	0.44	237.01	107.79	32.80	9.39	0.34	4.14	0.01	0.41	0.41	-	-	-	-
Repeatability		0.46	0.71	0.70	0.39	0.59	0.50	0.35	0.30	0.46	0.40	0.33	0.63	0.71	-	-	-	-

*, ** significant at 0.05 and 0.01 probability levels, respectively; WAP—weeks after planting.

2.2. Genetic Gains in Grain Yield of Early Maturing Hybrids in Striga-Infested and Non-Infested Environments

In *Striga*-infested environments, grain yield ranged between 2248 and 2917 kg ha^{-1} for hybrids of period 1 and period 3, respectively, resulting in the equivalent of 4.82% annual yield gain (Tables 2 and 3). Contrarily, in *Striga*-free environments, yield varied from 5016 kg ha^{-1} for hybrids of period 1 to 5442 kg ha^{-1} for those of period 3, which corresponded to an annual yield gain of 1.24%. Grain yield increased by 101 and 61 kg ha^{-1} year^{-1} in *Striga*-infested and *Striga*-free environments, respectively. The significant gain from selection for grain yield between periods 1 and 3 observed in *Striga*-infested environments was associated with reduced anthesis-silking interval, increased plant and ear heights, and improved ear aspect. Other characters included reduced *Striga* damage at 8 and 10 weeks after planting (WAP), fewer number of emerged *Striga* plants at 10 WAP, and increased ears per plant. Additionally, significant positive *b* estimates were observed for yield, plant, and ear heights, while significant negative *b* values were obtained for husk cover, ear aspect, days to 50% anthesis and silking, number of emerged *Striga* plants, and *Striga* damage at 8 and 10 WAP under *Striga*-infested conditions (Table 3). Under non-infested conditions, however, only plant aspect and stalk lodging had significant *b* values.

Regression analysis of yield of the maize hybrids in *Striga*-free environments on yield under *Striga*-infested conditions, distinctly grouped hybrids into three breeding periods (Figure 1). Despite overlaps in performance of the hybrids of the three periods, those of period 3 were the best in terms of grain yield in both research environments.

Table 2. Means ± standard error for grain and other agronomic traits for early maturing maize hybrids of three breeding periods evaluated under *Striga*-infested conditions in seven environments and non-infested conditions in four environments from 2017 to 2019.

Trait	Period	Number of Hybrids	*Striga*-Infested Conditions	Optimal Conditions
Grain yield (kg ha^{-1})	2008–2010	18	2247.53 ± 76.98	5016.46 ± 131.43
	2011–2013	18	2632.09 ± 77.23	5162.61 ± 129.61
	2014–2016	18	2917.13 ± 91.99	5441.79 ± 129.32
Days to anthesis	2008–2010	18	55.44 ± 0.17	55.58 ± 0.24
	2011–2013	18	55.24 ± 0.16	55.58 ± 0.22
	2014–2016	18	54.79 ± 0.16	55.51 ± 0.25
Days to silking	2008–2010	18	57.84 ± 0.18	57.17 ± 0.24
	2011–2013	18	57.38 ± 0.18	57.06 ± 0.22
	2014–2016	18	56.42 ± 0.18	56.72 ± 0.26
Anthesis-silking interval	2008–2010	18	2.44 ± 0.08	1.60 ± 0.06
	2011–2013	18	2.15 ± 0.07	1.48 ± 0.06
	2014–2016	18	1.68 ± 0.06	1.26 ± 0.06
Plant height (cm)	2008–2010	18	129.29 ± 1.69	155.13 ± 2.26
	2011–2013	18	138.41 ± 1.71	160.50 ± 2.13
	2014–2016	18	140.74 ± 1.61	162.99 ± 2.06
Ear height (cm)	2008–2010	18	59.38 ± 1.08	73.80 ± 1.35
	2011–2013	18	63.71 ± 1.17	76.75 ± 1.20
	2014–2016	18	63.69 ± 1.05	76.86 ± 1.11
Root lodging %	2008–2010	18	2.65 ± 0.18	2.28 ± 0.23
	2011–2013	18	2.44 ± 0.15	2.83 ± 0.32
	2014–2016	18	2.55 ± 0.19	2.40 ± 0.28
Stalk lodging %	2008–2010	18	4.05 ± 0.25	0.93 ± 0.06
	2011–2013	18	3.72 ± 0.24	1.29 ± 0.14
	2014–2016	18	5.27 ± 0.34	1.13 ± 0.09
Husk cover	2008–2010	18	3.63 ± 0.08	2.98 ± 0.09
	2011–2013	18	3.31 ± 0.07	3.00 ± 0.09
	2014–2016	18	3.57 ± 0.08	2.92 ± 0.09

Table 2. *Cont.*

Trait	Period	Number of Hybrids	*Striga*-Infested Conditions	Optimal Conditions
Plant aspect	2008–2010	18	-	4.79 ± 0.06
	2011–2013	18	-	4.48 ± 0.06
	2014–2016	18	-	4.16 ± 0.06
Ear aspect	2008–2010	18	5.01 ± 0.08	4.74 ± 0.07
	2011–2013	18	4.49 ± 0.07	4.33 ± 0.08
	2014–2016	18	4.44 ± 0.07	4.03 ± 0.08
Ear rot	2008–2010	18	5.75 ± 0.34	4.39 ± 0.24
	2011–2013	18	5.58 ± 0.33	4.12 ± 0.24
	2014–2016	18	5.61 ± 0.32	4.01 ± 0.23
Ears per plant	2008–2010	18	0.73 ± 0.01	0.90 ± 0.01
	2011–2013	18	0.81 ± 0.01	0.92 ± 0.01
	2014–2016	18	0.83 ± 0.01	0.93 ± 0.01
Striga damage (8 WAP)	2008–2010	18	4.75 ± 0.07	-
	2011–2013	18	4.23 ± 0.07	-
	2014–2016	18	4.14 ± 0.07	-
Striga damage (10 WAP)	2008–2010	18	5.33 ± 0.07	-
	2011–2013	18	4.79 ± 0.08	-
	2014–2016	18	4.67 ± 0.08	-
Emerged *Striga* plants (8 WAP)	2008–2010	18	3.43 ± 0.05	-
	2011–2013	18	3.23 ± 0.05	-
	2014–2016	18	3.38 ± 0.04	-
Emerged *Striga* count (10 WAP)	2008–2010	18	3.69 ± 0.04	-
	2011–2013	18	3.55 ± 0.05	-
	2014–2016	18	3.60 ± 0.04	-

Table 3. Relative genetic gain, coefficient of determination (R^2), slope (A), and regression coefficient (B) of grain yield, and other traits of early maize hybrids of three breeding periods evaluated under *Striga* infested conditions in seven environments and non-infested conditions in four environments from 2017 to 2019.

Trait	Relative Gain (% per year)	R^2	A	B
***Striga*-infested Environments**				
Grain yield (kg ha^{-1})	4.82	0.143	2088.00	100.69 **
Days to anthesis	−0.10	0.012	55.45	−0.06
Days to silk	−0.33	0.104	58.20	−0.19
Anthesis silking interval	−4.82	0.421	2.77	−0.13 **
Plant height (cm)	1.47	0.184	126.68	1.87 **
Ear height (cm)	0.96	0.061	59.37	0.57 **
Root lodging	−0.79	0.004	7.96	−0.06
Stalk lodging	1.80	0.013	11.16	0.20
Husk cover	−0.42	0.004	3.58	−0.01 **
Ear aspect	−1.89	0.182	5.15	−0.10 **
Ear rot	0.19	0.001	5.59	0.01
Striga damage (8 WAP)	−2.14	0.169	4.91	−0.11 **
Striga damage (10 WAP)	−1.95	0.143	5.48	−0.11 **
Emerged *Striga* plants (8 WAP)	−0.86	0.007	41.23	−0.36 **
Emerged *Striga* plants (10 WAP)	−0.94	0.014	49.58	−0.47 *
Ears/plant	1.90	0.120	0.72	0.01 **

Table 3. *Cont.*

Trait	Relative Gain (% per year)	R^2	A	B
Non-infested Environments				
Grain yield (kg ha^{-1})	1.24	0.062	4897.7	60.954
Days to anthesis	0.07	0.008	55.368	0.038
Days to silk	−0.05	0.004	57.129	−0.028
Anthesis silking interval	−3.33	0.204	1.7455	−0.058
Plant height (cm)	0.93	0.115	152.36	1.416
Ear height (cm)	0.90	0.074	72.494	0.653
Root lodging	1.10	0.004	6.6741	0.073
Stalk lodging	3.59	0.039	2.9326	0.105 **
Husk cover	−0.24	0.003	3.0023	−0.007
Plant aspect	−1.84	0.219	4.9075	−0.090 **
Ear aspect	−2.12	0.219	4.8964	−0.104
Ear rot	−2.11	0.047	4.6782	−0.099
Ears/plant	0.38	0.040	0.90	0.003

*, ** significant at 0.05 and 0.01 probability levels, respectively.

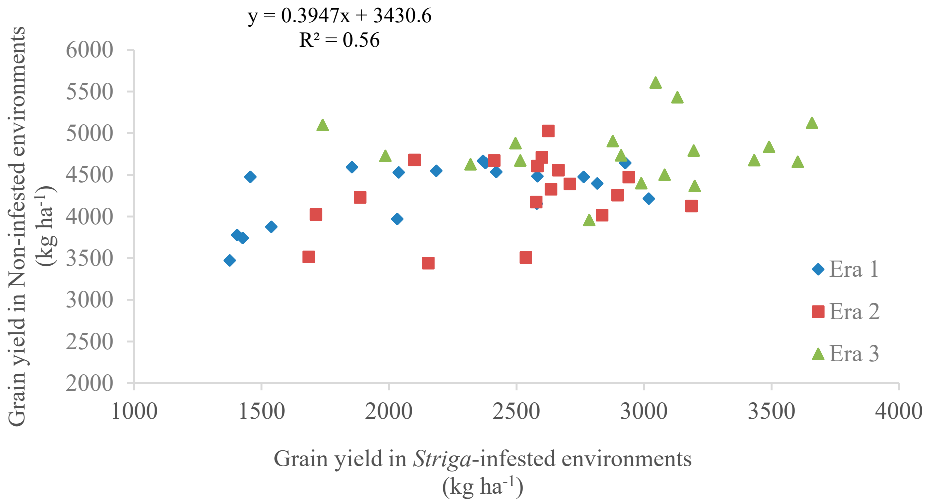

Figure 1. Regression of grain yield of early maturing maize hybrids of three breeding periods in non-infested environments on grain yield in *Striga*-infested environments.

2.3. Interrelationships among Measured Traits

Of the possible 55 correlation coefficients recorded under artificial *Striga* environments, 47 were statistically significant while 16 out of the 28 correlation coefficients identified in *Striga*-free environments were significant (Figures 2 and 3). Under *Striga* infestation, grain yield displayed positive and significant associations with ears per plant and plant and ear heights, but negative correlations with anthesis-silking interval, husk cover, ear aspect, *Striga* damage, and number of emerged *Striga* plants at 8 and 10 WAP (Figure 2). Similarly, *Striga* damage at 8 and 10 WAP recorded positive and significant correlations with anthesis-silking interval, husk cover, ear aspect, and number of emerged *Striga* plants at 8 and 10 WAP. In *Striga*-free environments, grain yield displayed positive and significant correlations with ears per plant and plant and ear heights, while negative and significant correlations were found between yield and plant aspect, as well as ear aspect (Figure 3). Additionally, plant aspect had positive and significant associations with ear aspect, husk cover, and anthesis-silking interval, but had significant and negative association with plant and ear heights in *Striga*-free environments.

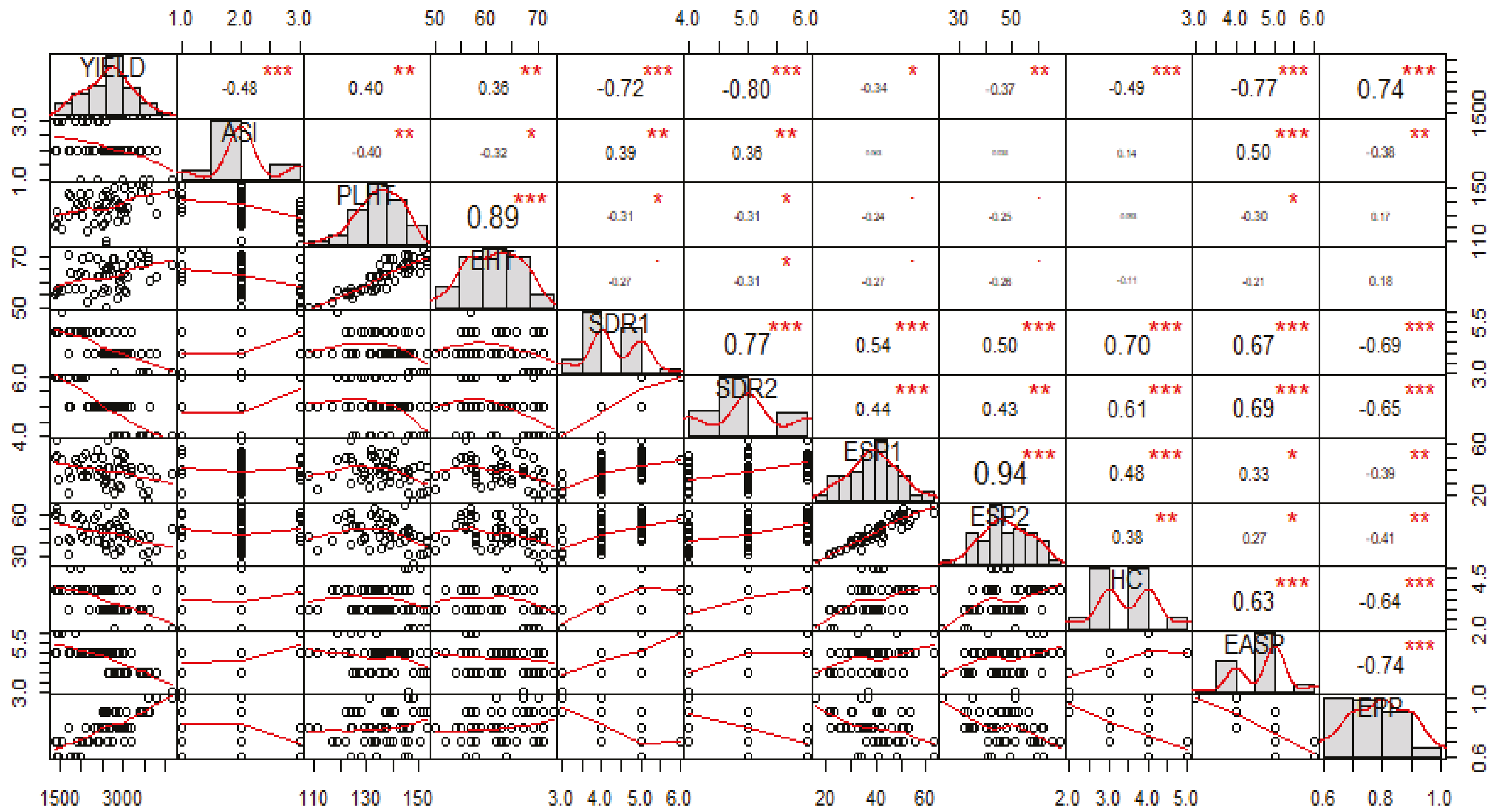

Figure 2. Correlation coefficients of grain yield and other agronomic traits of early maize hybrids of three breeding periods evaluated under *Striga*-infested environments in West Africa between 2017 and 2019. YIELD = grain yield, ASI = anthesis-silking interval, PLHT = plant height, EHT = ear height, EASP = ear aspect, EPP = ears per plant, HC = husk cover, SDR1 and SDR2 = *Striga* damage at 8 and 10 WAP, ESP1 and ESP2 = emerged *Striga* plants at 8 and 10 WAP, *, **, *** significant at 0.05, 0.01 and 0.0001 probability levels, respectively.

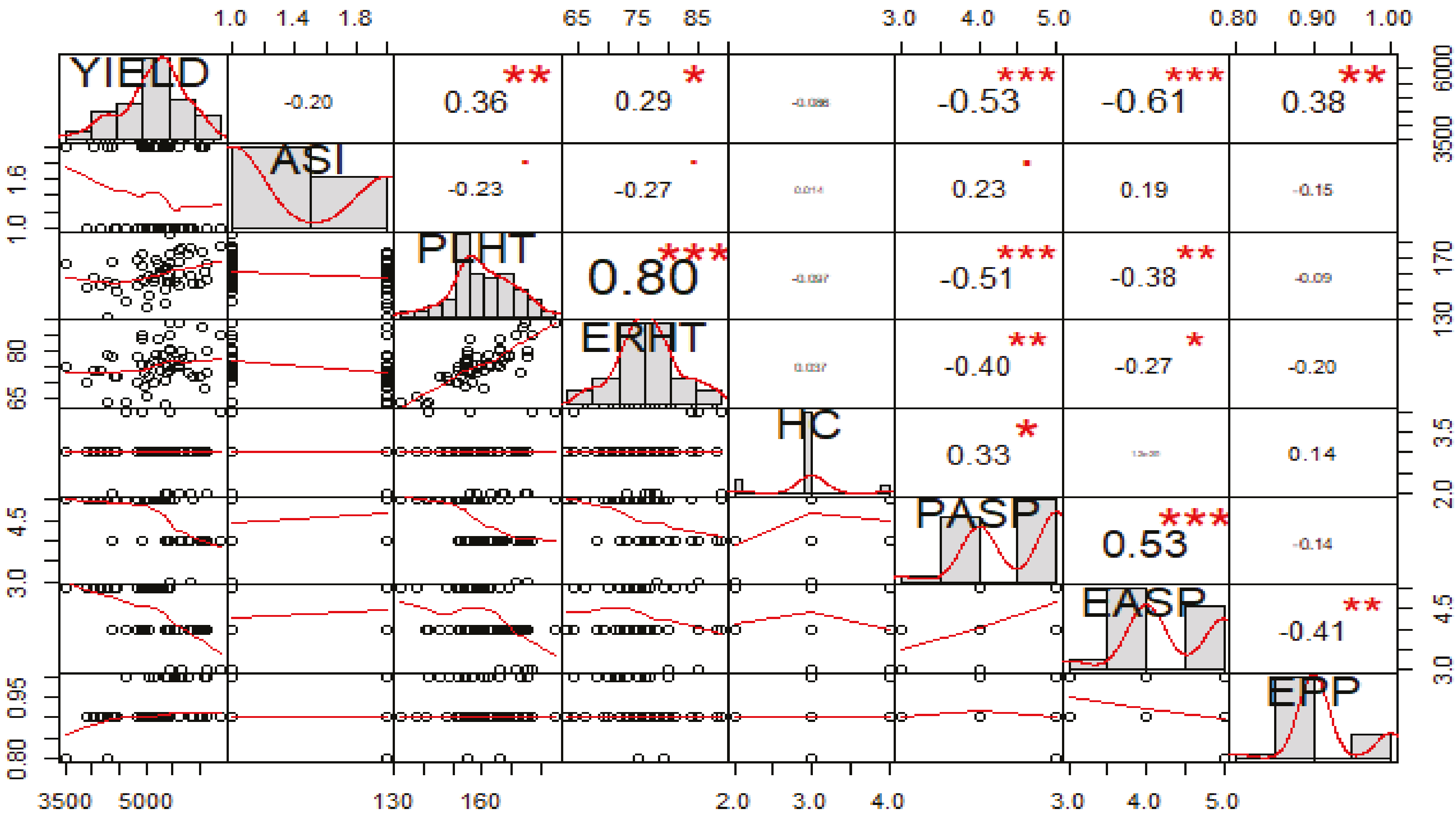

Figure 3. Correlation coefficients of grain yield and other agronomic traits of early maize hybrids of three breeding periods evaluated under *Striga*-free environments in West Africa between 2017 and 2019. YIELD = grain yield, ASI = anthesis-silking interval, PLHT = plant height, EHT = ear height, EASP = ear aspect, EPP = ears per plant, HC = husk cover, *, **, *** significant at 0.05, 0.01 and 0.0001 probability levels, respectively.

2.4. Performance Assessment of Grain Yield Stability of Early Maturing Maize Hybrids Developed during Three Breeding Periods

Presented in Table 4 are the grain yield and other assayed agronomic characters of the 20 highest-yielding and 5 lowest-yielding maize hybrids identified by utilizing the IITA selection index for *Striga* resistance and the corresponding mean performance of different traits under optimal test environments. The values of the selection index ranged from −11.1 for the double-cross hybrid, (TZEI 59 × TZEI 108) × (TZEI 63 × TZEI 87) to 10.9 for TZdEI 352 × TZEI 383. Grain yield of the hybrids varied between 1426 kg ha^{-1} for (TZEI 59 × TZEI 108) × (TZEI 63 × TZEI 87) and 4186 kg ha^{-1} for TZdEI 352 × TZEI 355 across *Striga*-infested environments. Furthermore, grain yield of the hybrids across *Striga*-free environments ranged from 3506 kg ha^{-1} for TZEI 352 × TZdEI 352 to 6379 kg ha^{-1} for TZdEI 173 × TZdEI 280. Hybrids that possessed positive selection indices produced grain yields above 4200 and 2400 kg ha^{-1} in *Striga*-free and *Striga*-infested test environments, respectively.

The average reduction in grain yield caused by the parasitic weed was about 50%. Top performing hybrids identified using the *Striga* selection index were characterized by reduced yield losses under *Striga* infestation. The best five hybrids recorded yield losses varying from 24.5 to 37.6%. These losses were low compared to those of the five worst hybrids, which varied from 64 to 70%. The significant yield loss in the susceptible genotypes was associated with increased anthesis-silking interval, reduced ear and plant heights, fewer ears per plant, increased *Striga* damage, and number of emerged *Striga* plants at 8 and 10 WAP under artificial *Striga* infestation.

The significance of hybrid and hybrid × environment interaction for yield in the two research environments necessitated the use of the genotype main effect plus genotype × environment interaction (GGE) biplot analysis to partition the hybrid × environment interaction for better understanding of the yield performance and the stability of the hybrids in each test environment. The grain yield "stability vs. mean performance" GGE biplots of the hybrids under both research environments in West Africa between 2017 and 2019 are presented in Figures 4 and 5. Under *Striga*-infestation, the first (PRC1) and second (PRC2) principal component axes explained 61.2 and 11.6% of the overall variation, respectively; therefore, both principal component axes jointly explained about 73% of the overall variation in the yield of the hybrids. The PRC1 of the maize hybrids evaluated in four optimal test environments captured 38.7% of the overall variation, while PRC2 explained 35.9% of the overall variation. Thus, the two PRC axes captured about 75% of the overall variation in yield of the hybrids, an indication of adequate approximation of the environment-centered data. Furthermore, the average-tester coordinate (ATC; double-arrow line) y-axis of GGE biplot separates genotypes with yield above the mean on the right side of the line, distinguishing them from genotypes characterized by grain yield below the mean.

Table 4. Grain yield and other agronomic traits of hybrids (the best 20 and the worst 5, based on the *Striga* base index) evaluated under *Striga*-infested and *Striga*-free environments in West Africa between 2017 and 2019.

Hybrid	YIELD		Yield Reduction	DYSK		ASI		PLHT		EHT		SDR1	SDR2	ESP1	ESP2	EASP		EPP		BI
	SI	SF		SI	SF	SI	SF	SI	SF	SI	SF	SI				SI	SF	SI	SF	
	kg ha^{-1}		%					cm		cm										
TZdEI 352 × TZEI 383	3582	5616	36.2	59	58	1.7	1.2	148	175	70	89	3.1	3.6	15.8	24.1	3.7	3.9	0.97	0.91	10.9
TZdEI 352 × TZEI 355	4186	6138	31.8	57	57	1.2	1.2	146	166	67	80	3.1	3.6	36.9	51.1	3.0	3.4	0.95	0.99	10.2
TZdEI 173 × TZdEI 352	3603	5343	32.6	58	58	1.9	1.3	153	163	68	76	3.4	3.8	22.6	33.0	3.6	4.2	0.94	0.92	9.2
TZdEI 157 × TZdEI 352	3490	5591	37.6	59	59	1.5	1.4	152	167	73	77	3.3	3.8	21.5	31.9	3.8	4.1	0.92	0.94	9.0
TZEI 16 × TZEI 8	3816	5052	24.5	55	56	2.0	1.7	131	146	62	72	3.9	4.5	34.1	35.4	4.0	4.2	0.97	1.00	7.7
TZdEI 352 × TZdEI 441	2785	4361	36.1	61	61	2.3	2.3	151	168	69	78	3.3	3.5	21.8	31.8	4.2	4.4	0.93	0.88	7.4
TZEI 326 × TZdEI 352	3412	5832	41.5	58	58	1.9	1.2	153	176	71	78	3.4	4.1	29.6	41.8	3.6	3.9	0.88	0.95	6.8
TZdEI 378 × TZdEI 173	3658	6015	39.2	56	56	1.6	1.1	141	153	61	72	3.9	4.5	40.2	45.3	3.8	4.1	0.94	0.92	6.1
TZdEI 268 × TZdEI 131	3432	5794	40.8	57	57	1.6	1.3	148	173	67	73	3.7	4.1	41.6	46.0	3.8	4.3	0.86	0.95	5.4
TZdEI 21 × TZEI 23	3081	5150	40.2	56	56	1.5	1.1	126	155	56	77	3.7	4.4	40.9	52.4	4.3	4.8	0.89	0.92	3.9
TZEI 474 × TZEI 10	2940	5359	45.1	56	56	2.2	1.8	131	149	59	71	4.3	4.6	25.8	34.2	4.4	4.3	0.83	0.96	3.3
TZEI 14 × TZEI 25	2926	5416	46.0	58	58	2.2	1.3	136	158	61	73	4.0	4.5	27.7	36.1	4.5	4.7	0.77	0.86	3.2
TZdEI 479 × TZdEI 124	3198	5456	41.4	55	54	1.6	0.7	153	185	67	89	4.2	4.6	41.7	40.5	4.6	3.9	0.82	0.85	3.1
TZEI 470 × ENT 13	2896	5140	43.7	57	57	2.2	2.1	137	157	63	70	3.7	4.5	41.8	49.5	4.5	4.9	0.85	0.95	2.8
TZEI 486 × TZEI 23	2536	4264	40.5	56	56	2.4	1.6	124	132	58	64	4.0	4.7	29.7	37.6	5.1	5.1	0.89	0.89	2.7
TZdEI 173 × TZdEI 492	3131	6134	49.0	57	57	2.0	1.3	135	156	62	73	4.3	4.6	36.9	44.4	4.2	4.0	0.78	0.92	2.3
TZEI 24 × TZEI 17	2581	5343	51.7	57	57	2.3	1.5	111	141	50	63	4.2	4.6	25.0	34.5	4.5	4.3	0.81	0.91	2.3
TZdEI 17 × TZEI 17	2877	5841	50.7	58	57	1.6	1.0	125	158	54	78	3.9	4.2	46.1	53.8	4.4	4.5	0.82	0.93	2.2
TZE-Y Pop DT C5 STR C5 × TZEI 10	2577	4838	46.7	58	58	2.5	1.4	139	169	63	78	4.2	4.6	30.8	38.5	4.6	4.1	0.85	0.87	2.1
ENT 12 × TZEI 48	3018	6083	50.4	58	58	1.7	1.6	132	161	57	68	3.9	4.5	50.6	60.7	4.1	4.1	0.85	0.96	2.0
TZEI 31 × TZEI 18	1375	4160	67.0	59	57	2.1	1.4	122	152	55	74	5.1	5.8	48.6	59.8	5.4	5.4	0.73	0.87	−7.8
TZEI 5 × TZEI 98	1456	4847	70.0	60	58	2.7	1.5	128	152	58	70	5.5	6.3	32.8	40.6	5.5	5.0	0.62	0.95	−8.2
TZEI 31 × TZEI 63	1404	3909	64.1	59	58	2.1	1.4	133	151	57	70	5.4	6.2	51.0	64.9	5.4	4.6	0.68	0.86	−9.5
(TZEI 63 × TZEI 59) × TZEI 87	1538	4273	64.0	57	57	3.0	2.2	119	155	57	79	5.7	6.5	48.4	57.1	5.6	5.0	0.67	0.83	−9.6
(TZEI 63 × TZEI 87) × (TZEI 59 × TZEI 108)	1426	4042	64.7	58	57	3.3	1.9	124	157	56	74	5.5	6.4	62.7	61.8	5.6	5.0	0.59	0.90	−11.1
Mean	2599	5207	50.1	571	57	2.1	1.5	136	160	62	76	4.3	4.9	39.4	47.2	4.6	4.4	0.79	0.92	
SED	385	625		1	1	0.4	0.4	7	9	4	6	0.4	0.4	8.1	8.7	0.4	0.5	0.07	0.05	

YIELD = grain yield, ASI = anthesis-silking interval, PLHT = plant height, DYSK—days to silking, EHT = ear height, EASP = ear aspect, EPP = ears per plant, HC = husk cover, SDR1 and SDR2 = *Striga* damage ratings at 8 and 10 WAP, ESP1 and ESP2 = emerged *Striga* plants at 8 and 10 WAP, SI—*Striga*-infested, SF—*Striga*-free, BI—*Striga* base index.

The mean performance of a hybrid is measured by the projection of the hybrid's marker on the abscissa, whereas the smaller the absolute length of a genotype on the ATC, the more stable it is [19]. Hybrids 37 (TZdEI 352 × TZEI 355), 26 (TZdEI 378 × TZdEI 173), and 19 (TZdEI 173 × TZdEI 352) were the top performing and most stable across *Striga*-infested research environments. These were therefore identified as ideal hybrids across test environments, while hybrids 2 [(TZEI 59 × TZEI 108) × (TZEI 63 × TZEI 87)] and 13 (TZEI 31 × TZEI 63), which recorded the lowest grain yield, were highly stable (Figure 5). Additionally, hybrids 21 (TZdEI 173 × TZdEI 280) and 24 (TZdEI 173 × TZdEI 492) were productive but unstable across the *Striga*-infested environments, while hybrids 39 (TZEI 352 × TZdEI 352) and 40 (TZEI 355 × TZdEI 425), in addition to being low yielding, were among the least stable hybrids. Across *Striga*-free environments, hybrids 25 (TZdEI 268 × TZdEI 131), 41 (TZEI 326 × TZdEI 352), and 46 (TZEI 495 × ENT 13) displayed superior grain yield and had short projections onto the ATC y-axis (stable) across non-stress environments. Contrarily, hybrids 39 (TZEI 352 × TZdEI 352) and 13 (TZEI 31 × TZEI 63), which produced yield far below the average grain yield and had long projections onto the ATC y-axis, were the lowest yielding and most unstable. Hybrids 15 (TZEI 14 × TZEI 25), 32 (TZdEI 17 × TZEI 17), 30 (TZdEI 479 × TZdEI 124), 22 (TZdEI 124 × TZdEI 268), and 21 (TZdEI 173 × TZdEI 280) were the least stable under optimal conditions.

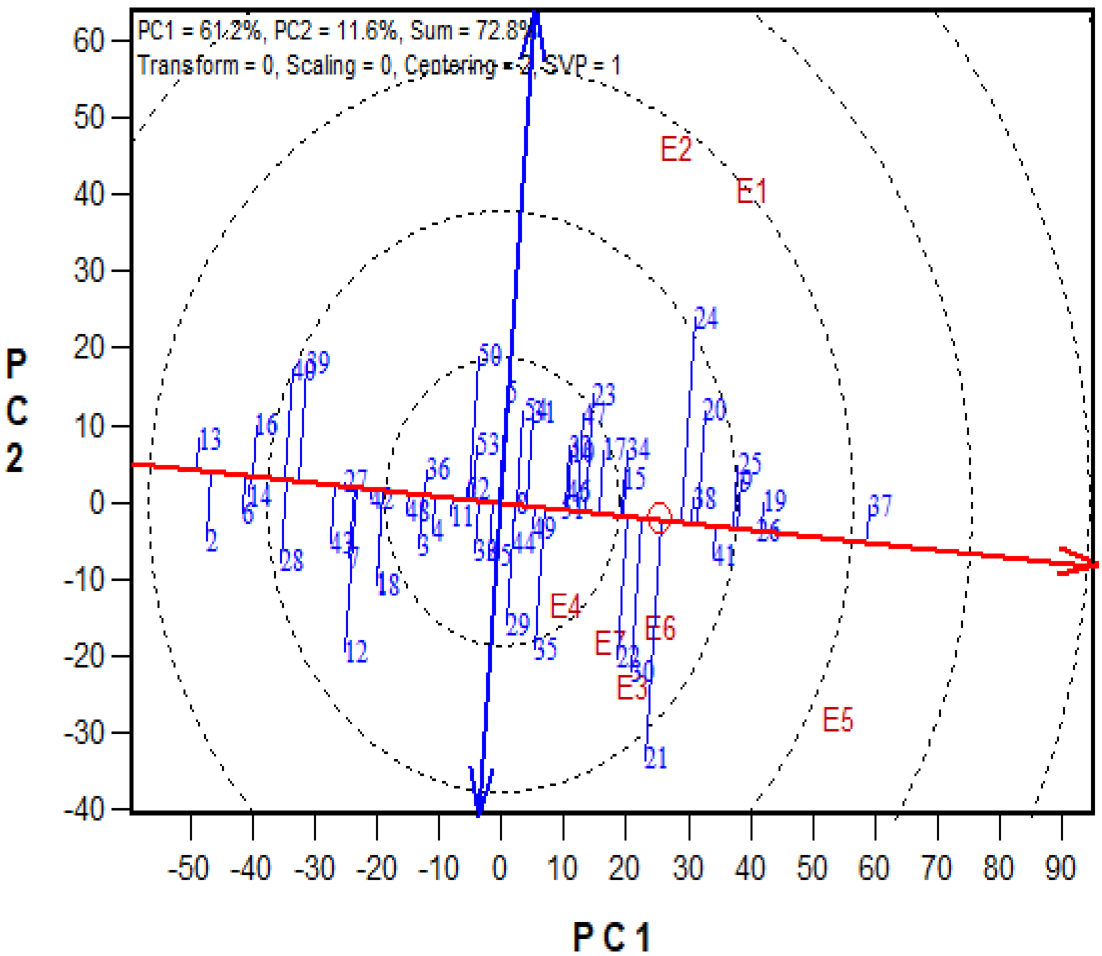

Figure 4. The "mean vs. stability" view of the genotype main effect plus genotype × environment interaction (GGE) biplot based on a genotype × environment yield data of 54 early maturing maize hybrids evaluated under *Striga*-infestation at 7 environments in West Africa between 2017 and 2019. PRC 1 and PRC 2 explained 72.8% variation in grain yield.

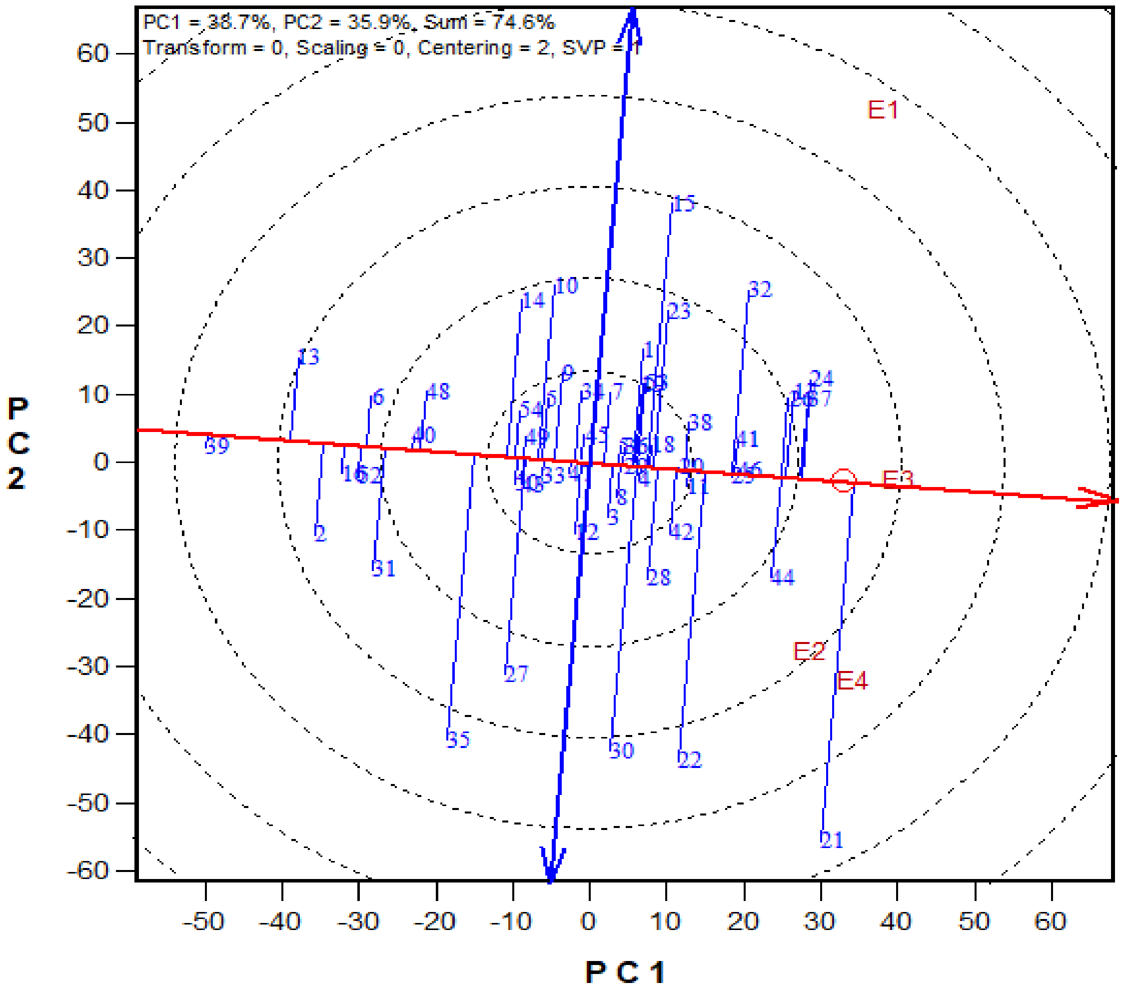

Figure 5. The "mean vs. stability" view of the genotype main effect plus genotype × environment interaction (GGE) biplot based on a genotype × environment yield data of 54 early maturing maize hybrids evaluated at 4 *Striga*-free environments in West Africa between 2017 and 2019. PRC 1 and PRC 2 explained 74.6% variation in grain yield.

3. Discussion

The significance of environment, period, and hybrid effects recorded for most traits including grain yield under both research environments signified the uniqueness of the test environments and the significant variability among the hybrids of the three periods.

This facilitated the identification and selection of promising maize hybrids of early maturity in the test environments.

The significance of hybrid × environment interaction as well as period × environment interaction effects for most measured traits, including grain yield in both *Striga*-infested and optimal research environments, signified contrasting performance of the hybrids under the research conditions. This result emphasized the importance of testing genotypes in multiple environments, in years, and locations prior to recommendations for commercialization [20]. The high estimates of repeatability recorded for several traits in both research environments implied that the hybrids would be consistent in the expression of the measured traits in the research environments.

The significance of period and hybrid effects for most agronomic traits including grain yield necessitated the analysis of the genetic gains in order to evaluate the progress that was achieved in developing superior early maturing maize hybrids possessing durable *Striga* resistance. The 4.82% yield gain per year with an increase of 101 kg ha^{-1} in *Striga*-infested environments across the three breeding periods obtained in this study was considerably higher than the 3.28, 2.56, and 2.25% reported for a set of extra-early maturing OPVs under moisture deficit, *Striga*-infested, and optimal conditions, respectively [21]. Furthermore, the yield gain per year realized in the present study is also higher than the 1.93 and 1.0% reported for early maturing OPVs under *Striga* infestation and non-infested environments by Badu-Apraku et al. [2] and 3.2% yield gain per year in *Striga*-infested environments reported by Menkir and Meseka [18] for intermediate maturing hybrids. The implications of these results are that early maturing hybrids responded better to selection for improved resistance to *Striga*, as well as high grain yield relative to the extra-early and early varieties as well as intermediate hybrids. Also, the non-significant gains from selection for grain yield of the early maturing hybrids under optimal conditions confirmed that greater attention of the IITA maize breeders has been on improving *Striga* resistance under infested conditions rather than enhanced performance of the hybrids in *Striga*-free environments. In this study, the significant genetic gain in yield of the hybrids under *Striga*-infested environments was associated with increased plant and ear heights, decreased days to 50% anthesis and silking, as well as reduced anthesis-silking interval. Other traits associated with the genetic gain of the hybrids included improved ear aspect, increased ears per plant, reduced *Striga* damage, and decreased emerged *Striga* plants at 8 and 10 WAP.

Regression of the yield of the early hybrids in non-infested environments over the yield in *Striga*-infested environments clearly classified hybrids of the three breeding periods into three groups with a few hybrids of different periods overlapping in performance. This result confirmed the superior performance of hybrids of period 3 over those of periods 1 and 2 in both research environments. This implied that significant progress has been achieved in developing productive hybrids possessing enhanced resistance to *Striga hermonthica* parasitism during the three breeding periods.

Information on trait association is important for designing effective breeding programs for maize genetic enhancement [22]. The significant and negative correlations obtained for grain yield and *Striga* damage and number of emerged *Striga* plants at 8 and 10 WAP implied that these characters were important for yield improvement under *Striga* infestation. This was a justification for the need to integrate the characters into the multiple-trait selection index for enhanced genetic gain from selection for grain yield under *Striga*-infested environments. Our findings corroborated those of Badu-Apraku et al. [4], Kim et al. [6], and Karaya et al. [23]. Significant positive associations detected between grain yield and ears per plant and plant height under both research environments were earlier reported by Badu-Apraku et al. [17]. Hybrid TZdEI 352 × TZEI 355 developed in period 3 was the highest-yielding and most stable across *Striga*-infested environments, and one of the outstanding hybrids under optimal environments. This suggested that this hybrid is widely adapted to *Striga* endemic and optimal growing regions in WCA. Our results further justified the need for testing extensively outstanding hybrids at multiple locations and on-farm trials for commercialization in SSA. It is striking that of the 20 top performing hybrids identified using the *Striga* selection index, only hybrids TZdEI 352 × TZEI 355, TZdEI 378 × TZdEI 173, and TZdEI 173 × TZdEI 352 across *Striga*-infested environments and TZEI 326 × TZdEI 352, TZEI 495 × ENT 13, and TZdEI 268 × TZdEI 131 across *Striga*-free conditions were selected by the GGE biplot as productive and stable in performance. This was anticipated as GGE biplot analysis was conducted using the yield data only, compared to the *Striga* selection index which took into consideration yield and other important yield-related characters. The outstanding maize hybrids identified thus have the potential to combat hunger and alleviate poverty in *Striga* prone environments in SSA.

4. Materials and Methods

4.1. Development of Striga Resistant Early Maturing Maize Hybrids

A major objective of the IITA-MIP is to develop early maturing hybrids with outstanding grain yield under multiple stresses, viz., drought, low-soil nitrogen, and *S. hermonthica* parasitism. Towards this end, the IITA-MIP started a breeding program for *Striga* resistance in 1992 with the objective of combating the menace of *Striga hermonthica* in the savannas of SSA. By 1994, the IITA-MIP had developed several populations and OPVs with early maturity and had initiated inbred and a hybrid development program in maize. The early maturing inbreds were derived from several broad-based maize populations possessing resistance to maize streak virus (MSV) and resistance/tolerance to *Striga* formed from four diverse germplasm sources, which included TZE-W Pop × 1368 STR C_0, TZE Comp 5-Y C_6, TZE-Y Pop DT STR C_0, and TZE-W Pop DT STR C_0 [24]. S_1 lines extracted from each population were evaluated under artificial *Striga*-infested conditions at Ferkessedougou and non-infested conditions at Sinematiali in Côte d'Ivoire in the 1997 cropping season. Superior S_1 lines from each of the populations were advanced through repeated cycles of selfing and selection under *Striga*-infested environments and managed drought. At the S_4 stage of inbreeding, 250−300 inbreds extracted from each of the populations were crossed to a tester that was the corresponding source population. The testcrosses as well as the S_4 lines were screened under artificial *Striga* infestation and non-infested conditions at Ferkessedougou and Sinematiali, respectively. The grain yield and the combining abilities of the lines for traits such as grain yield, *Striga* damage syndrome rating, *Striga* emergence counts, number of ears per plant, and plant and ear aspects across the two contrasting research environments served as criteria for selecting 90–100 S_4 lines for advancement to the S_6 stage. Selection for *Striga* resistance was based on an index of traits which included *Striga* damage, ears per plant, and grain yield. Through this program, several S_6 inbreds and OPVs were developed from the populations. Even though considerable progress had been made in developing *Striga* resistant OPVs, inbreds, hybrids, and several of the OPVs extracted from the populations still supported significant number of the parasitic weeds, which could flower and produce seeds, resulting in increased *Striga* seed bank in the soil. It was, therefore, desirable to enhance resistance levels of the populations. Therefore, in addition to the exploitation of the genetic variation available in domestic maize, *Striga* resistance alleles from the wild maize, perennial teosinte *Zea diploperennis* were introgressed into the breeding populations using the backcross breeding method. Badu-Apraku et al. [2] described in detail the strategies and procedures adopted in screening the early maize populations for *Striga* resistance. Additionally, the levels of tolerance to moisture stress in the populations were not very high. Consequently, a program was started in 2007 to enhance drought tolerance in the populations using the S_1 recurrent selection method. Also, *Striga*, low-N, and drought-tolerant lines identified in the program were employed as sources of drought tolerance alleles and were incorporated into each population. Subsequent genetic enhancement of the populations under managed drought employing the S_1 family selection scheme led to the development of a new generation of superior early maturing multiple-stress tolerant populations from which were derived inbreds, hybrids, and OPVs with combined high levels of low-N tolerance and improved levels of *Striga* resistance/tolerance, as well as drought tolerance. Multiple-stress tolerant inbreds selected based on outstanding performance were used in hybrid combinations to obtain the early hybrids used for the genetic gain study under *Striga hermonthica* infestation.

The hybrids were categorized into three breeding periods (2008–2010, 2011–2013, and 2014–2016) with each period of development comprising 18 hybrids. Pedigree information, period, and year of development of the hybrids are presented in Supplementary Table S1.

4.2. Trial Establishment and Agronomic Management

The set of 54 hybrids used in this study was evaluated in 2017, 2018, and 2019 under artificial *Striga* infestation in West Africa. In Nigeria, the hybrids were evaluated at Mokwa (9°18′ N, 5°4′ E, 457 m above sea level, 1.1 m annual precipitation) and Abuja (9°16′ N, 7°20′ E, 300 m above sea level, 1.5 m annual precipitation) from June to October, 2017–2019; both experimental sites are *Striga* endemic locations in the Southern Guinea Savanna of Nigeria. Additionally, the 54 hybrids were tested at Nyankpala (9°25′ N, 0°58′ W, 183 m above sea level, and 1000 mm annual precipitation) in Ghana and at Ina (9°30′ N and 2°62′ E, 119 m above sea level, 1500 mm annual precipitation) in the northern part of Benin Republic in 2017. The trial was laid in a 9 × 6 lattice design with three replicates while an experimental plot was 4 m long, spaced at 0.75 m between and 0.4 m within rows. Each plot at all locations was artificially infested with *Striga* seeds following the IITA Maize Breeding Unit infestation method [11]. The *Striga* seeds utilized for infestation in the present study were collected during the previous cropping season from neighboring sorghum farmlands near each experimental site. At about two weeks before planting, the *Striga* experimental fields were sterilized by injecting ethylene gas (a synthetic germination stimulant) directly into the soil to initiate self-destructive germination of *Striga* seeds in the soil. The suicidal germination strategy helped to reduce the existing *Striga* seed in the soil. Infestation was done by infusing an 8500 mg mixture of finely sieved sand and *S. hermonthica* seed inoculum (containing an estimated number of 5000 viable *Striga* seeds) in the same hill as the maize seeds. Fertilizer application on the maize plots was deferred until about 21 to 24 days after planting (DAP) when 30 kg ha^{-1} each of N, P, and K was applied. The decreased fertilizer dose and delay were to stress the maize plants to stimulate production of strigolactones, a hormone which facilitates the germination of seeds of the parasitic weed and the attachment of the emerging parasitic plants to the roots of maize plants in *Striga* infested plots [11]. Other weeds apart from *Striga* were controlled manually.

Furthermore, the trials were conducted under *Striga*-free conditions during the 2017, 2018, and 2019 growing seasons in Nigeria (Abuja in 2017 and 2018, Mokwa in 2019) and at Ina, Benin, in 2017. All trials under non-infested conditions received 60 kg ha^{-1} each of nitrogen, phosphorus, and potassium during planting, followed by topdressing with an additional 60 kg ha^{-1} of nitrogen at 4 WAP, with the exception of *Striga*-free plots which received 30 kg ha^{-1} each of nitrogen, phosphorus, and potassium as NPK 15–15–15 at 25 DAP. Herbicides supplemented with manual weeding were employed for the weed control in the non-infested plots.

4.3. Trait Measurements

Data were recorded for grain yield in both *Striga*-infested and *Striga*-free trials. Yield (kg ha^{-1}) was measured in both trials based on 80% (800 g grain per kilogram ear weight) shelling percentage and adjusted to 150 g grain kg^{-1} moisture content. *Striga*-infested trials were assessed for *Striga* damage and number of emerged *Striga* plants [25] at 8 and 10 WAP. *Striga* damage in each plot was rated on a scale of 1 to 9 (1 = no damage, indicating high resistance; 9 = severe damage or death of the maize plant, i.e., high susceptibility). Data on plant aspect were recorded only on the *Striga*-free plots on a scale of 1 to 9, where 1 = excellent plant type and 9 = poor plant type. Data on other measured traits, which included days to 50% anthesis, days to 50% silking, anthesis-silking interval, ear aspect, ears per plant, and plant and ear heights, as well as root and stalk lodging, were recorded as described in detail by Badu-Apraku et al. [17].

4.4. Analysis of Data

The data were analyzed for variances across the seven *Striga*-infested and three *Striga*-free research environments on plot means of each trait with PROC GLM in SAS 9.3 utilizing a RANDOM statement with the TEST option [26]. In the analyses, the test environments (location × year combinations), the breeding periods, replications, blocks, and hybrid × environment interactions for each experiment were considered as random factors and hybrids as fixed effects.

Repeatability (H) estimates of all measured traits were computed for each research environment as:

$$H = \frac{\sigma_g^2}{\left(\sigma_g^2 + \sigma_{g\times e}^2/e + \sigma_e^2/re\right)} \tag{1}$$

where σ_g^2 represents hybrid variance, $\sigma_{g\times e}^2$ the variance due hybrid × environment interaction, σ_e^2 the error variance, e the number of test environments, and r the number of replications in a test environment.

The gain in yield of the 54 maize hybrids over the eight-year period of development was estimated by linear regression. The genetic gain representing the regression coefficient (b-value) was obtained by regressing hybrid means (dependent variable, *y*) of yield and other agronomic characters on the year of development (independent variable, *x*) under both infested and non-infested environments using SAS. Relative genetic gain per year was obtained by dividing the genetic gain (*b* value) by the intercept and multiplying by 100 [21]. Additionally, the relationship between grain yield under *Striga* infestation and optimal environments was determined for each breeding period. Employing the Microsoft Excel software for the regression analysis, the regression line was obtained.

The package "PerformanceAnalytics" in the R software [27] was used to compute the correlation coefficients between grain yield and other characters of the maize hybrids under *Striga* infestation and *Striga*-free test environments. The early maturing maize hybrids were characterized as either resistant or susceptible to *Striga* using a selection index that involved grain yield, ears per plant, *Striga* damage, and number of emerged *Striga* plants [14]. The means of the hybrids adjusted for block effects were standardized (using 1 and 0 as standard deviation and mean, respectively) to reduce the effects of varying scales. Hence, hybrids with *Striga* base index (BI) values greater than 0 were considered resistant to *Striga* whereas those with BI values less than 0 were rated as susceptible.

In order to identify outstanding hybrids in terms of high grain and stability under *Striga* infestation and *Striga*-free environments, yield across replications were analyzed using the genotype main effect plus genotype × environment interaction (GGE) biplot statistical tool to partition significant hybrid × environment interaction [21,28].

5. Conclusions

The annual yield gain of 4.82% of the hybrids studied under *Striga*-infestation revealed that considerable progress had been achieved in developing superior multiple stress tolerant early maturing maize hybrids for SSA. Improved ear aspect, reduced anthesis-silking interval, reduced *Striga* damage syndrome rating combined with fewer emerged *Striga* plants, and increased ears per plant were associated with the yield gain of the early hybrids. Ear aspect and ears per plant were identified as invaluable selection indices for achieving rapid gain in yield under *Striga* infestation and optimal research environments. The superior early maturing hybrids selected in this study should be extensively evaluated in on-farm trials and commercialized to combat food insecurity as well as contribute to alleviation of poverty in SSA.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/10/8/1188/s1.

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