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Pattern analysis of genotype × environment interaction for striga resistance and grain yield in African sorghum trials

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Summary

The parasitic weed *Striga hermonthica* (Del.) Benth. seriously limits sorghum [*Sorghum bicolor* (L.) Moench] production in Sub-Saharan Africa. As an outbreeder, *S. hermonthica* is highly variable with an extraordinary capacity to adapt to different hosts and environments, thereby complicating resistance breeding. To study genotype × environment (G×E) interaction for striga resistance and grain yield, nine sorghum lines, 36 F_2 populations and five local checks were grown under striga infestation at two locations in both Mali and Kenya. Mean squares due to genotypes and G×E interaction were highly significant for both sorghum grain yield and area under striga severity progress curve (ASVPC, a measure of striga emergence and vigor throughout the season). For grain yield, the entry × location-within-country interaction explained most of the total G×E while for ASVPC, entry × country and entry × location-within-country interactions were equally important. Pattern analysis (classification and ordination techniques) was applied to the environment-standardized matrix of entry × environment means. The classification clearly distinguished Malian from Kenyan locations for ASVPC, but not for grain yield. Performance plots for different entry groups showed differing patterns of adaptation. The ordination biplot underlined the importance of entry × country interaction for ASVPC. The F_2 derived from the cross of the striga-resistant line Framida with the striga-tolerant cultivar Seredo was the superior entry for both grain yield and ASVPC, underlining the importance of combining resistance with tolerance in striga resistance breeding. The observed entry × country interaction for ASVPC may be due to the entries' different reactions to climatic conditions and putative differences in striga virulence in Mali and Kenya.

Abbreviations: ASVPC – area under striga severity progress curve; G×E – genotype × environment interaction

Introduction

Parasitic weeds of the genus *Striga* (Scrophulariaceae) are widely distributed in the savanna regions of Sub-Saharan Africa. *Striga hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze parasitize staple crops including maize (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench], pearl millet [*Pennisetum glaucum* (L.) Leeke] and rice (*Oryza sativa* L.). Striga may infest an area of 21 million ha in Africa, making it one of the worst biotic constraints to African subsistence agriculture (Sauerborn, 1991). In periods of drought, severe striga infestations can lead to total crop loss.

There is evidence that *S. hermonthica* originated in Sudan and Ethiopia, regions postulated to be the center of diversity for sorghum. Therefore, the natural distribution of striga may be congruent with that of

sorghum (Sauerborn, 1999). The parasite's life cycle is finely attuned to that of its host. Developmental stages for which there is evidence or supposition of control via host-derived chemical signals include seed germination, haustorial initiation, differentiation into shoot tissue, and growth of shoots (Butler, 1995). Host plant resistance is central to an integrated approach to striga control, and is the most practical and economical means for reducing crop losses due to striga.

As an obligate outbreeder, *S. hermonthica* is a highly variable parasite and has an extraordinary capacity to adapt to new hosts (Ejeta et al., 1992; Koyama, 2000a, 2000b), thereby complicating resistance breeding. Sorghum- and millet-specific races have been reported, whereas other populations attack both host species (Vasudeva Rao & Musselman, 1987; Ramaiah, 1984; Hess, 1994; Freitag et al., 1996). Resistance to *S. hermonthica* may not necessarily hold against *S. asiatica* and *vice versa* (Ramaiah, 1987). Koyama (2000a), using isozyme and random amplified polymorphic DNA (RAPD) marker techniques, found striga samples from West African sites to be more closely related to each other than West and East African populations. Haussmann et al. (2001a) reported a higher sensitivity to germination stimulants of a striga population from Kenya compared to striga from Mali and Niger when evaluating 226 $F_{3:5}$ lines derived from the cross IS 9830 × E 36-1 in the agar-gel assay developed by Hess et al. (1992). *In vitro* germination distance was more highly correlated between the two West African striga populations than between either of the West African and the Kenyan striga populations, suggesting greater similarity between the two West-African populations, and supporting Koyama's (2000a) molecular data.

In field trials planted under striga infestation across diverse geographic regions, the total genotype × environment (G × E) interaction variance contains interaction effects between (i) genotypes and specific climatic and edaphic factors differing at the test locations, (ii) between host genotypes and putative striga races or biotypes, and (iii) the threefold interaction genotypes × putative striga races or biotypes × edaphic/climatic factors. Theoretically, the three types of interaction could be separated by testing the genetic materials at each location against several striga populations of different geographic origin. However, in practice, this cannot be done in the field, as striga is quarantined and seed should not be transferred from one region to another. Size and pattern of G×E interactions have important implications for sorghum breeding. The objective of the present study was to examine the pattern of G×E interaction for striga resistance and grain yield in sorghum grown under striga infestation at two locations in both Mali and Kenya, and to come up with appropriate recommendations on selection procedures in breeding for striga resistance in sorghum.

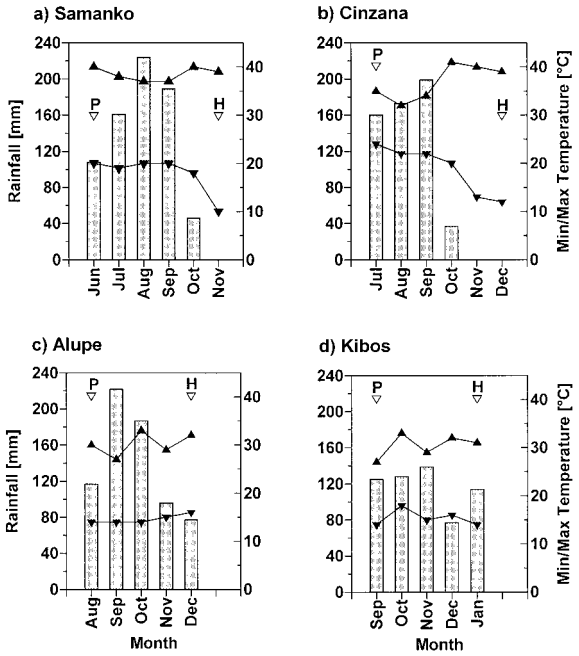

Figure 1. Monthly rainfall (vertical bars), mean minimum (▼) and maximum (▲) air temperatures, and dates of planting (P) and harvesting (H) at a) Samanko, b) Cinzana, c) Alupe, and d) Kibos.

Materials and methods

The genetic materials used in this study comprised nine parent lines, 36 F_2 populations derived from diallel crosses of the nine parent lines, and five local checks differing for country of origin and reported reaction to striga (Table 1). This material was evaluated in striga-infested fields at two locations in Mali in 1996 and at two locations in Kenya in the 1996/97 short rainy season. The sites were Samanko (12°31′N, 08°04′W, 358 m altitude) and Cinzana (13°15′N, 05°57′W, 285 m altitude) in Mali, and Alupe (00°29′N, 34°08′E, 1189 m altitude) and Kibos (00°04′S, 34°48′E, 1214 m altitude) in Kenya. The total rainfall amounted to 728 mm at Samanko, 569 mm at Cinzana, 699 mm at Alupe, and 583 mm at Kibos, distributed over four or five months (Figure 1). The mean minimum and maximum temperatures were

Table 1. Description of parent lines and local check cultivars, and codes used in the pattern analysis

Designation	Code	Origin	Reported reaction to striga[a]
Parent lines			
N 13	R1	India	Resistant: mechanical barriers, antibiosis
Framida	R2	Southern Africa	Resistant: low-stimulant, mechanical barriers
555	R3	India	Resistant: low-stimulant
IS 9830	R4	Sudan	Resistant: low-stimulant, cell wall thickening
Seredo	T5	Uganda	Tolerant
M 35-1	S6	India	Susceptible
E 36-1	S7	Ethiopia	Susceptible
DJ 1195	S8	India	Susceptible
IS 1037	S9	India	Susceptible
Local cultivars			
Wagita	L1EA	East Africa	Tolerant
Nakhadabo	L2EA	East Africa	Tolerant
CSM 228	L3WA	Mali	Susceptible
CSM 335	L4WA	Mali	Tolerant
Bengou Local	L5WA	Niger	Tolerant

[a] Dixon & Parker, 1984; Maiti et al., 1984; Ramaiah, 1984; 1987; Sherif & Parker, 1990; Hess & Haussmann, unpublished data.

higher at the Malian than the Kenyan locations. Due to a longer daylength, the sorghum cropping season was longer in Mali (six months) than in Kenya (five months). (For more details of the environments, see Haussmann et al., 2001b).

The experimental design was a randomized complete block design with six replications at all four sites. Each plot consisted of two rows, 3 m long, separated from the neighboring entry by one empty row. The spacing between rows was 0.80 and 0.75 m, and the spacing between plants within rows 0.20 and 0.15 m in Mali and Kenya, respectively. The different inter- and intra-row spacings in Mali *versus* Kenya reflect different local recommendations or habits. All plots were sown by hand and thinned to one plant per hill. The previous crop was sorghum at all four sites. Multiple traits were assessed but only the following two characters are considered here:

1. Area under the striga severity progress curve [ASVPC]: striga severity values were computed by multiplying the striga count with the average striga vigor in each plot. Striga vigor was scored on a 0 – 9 scale, with 0 = no emerged striga, 1 = average striga height $\leq$ 5 cm and striga plants without branches; . . .; 5 = average striga height between 21 and 30 cm and average number of striga branches $>$ 5; . . .; 9 = average striga height $>$ 40 cm and average number of striga branches $>$ 10 (Haussmann et al., 2000); striga counts and vigor score were recorded four or five times (depending on the location) at two-week intervals, starting two weeks after the first emergence of striga in each trial. The series of striga severity values was combined using the equation for area under the disease progress curve (AUDPC; Shaner & Finney, 1977; Haussmann et al., 2000); ASVPC takes into account emerged striga number and development stage throughout the season; low ASVPC values indicate resistance, and high values susceptibility to striga.
2. Sorghum grain yield [gm^{-2}], measured from the whole two-row plot. After maturity, panicles of each plot were harvested, dried in the sun for 10 days, threshed, and the grain cleaned by hand.

Initial statistical analyses were performed with the computer program PLABSTAT (Utz, 1998). Frequency distributions of entry means at each individual site and across locations were plotted. Deviations from normality were tested by determining the coefficients of skewness and kurtosis and their significance as described by Snedecor & Cochran (1980). Estimates of heritability in a replicated trial were calculated using the formula:

$$\text{Heritability } [\%] = 100 \times \sigma^2_t / (\sigma^2_t + \sigma^2_e/R)$$

where σ^2_t and σ^2_e are the estimated treatment and error components of variance, respectively, and R

the number of replications (Allard, 1960). Variance components were estimated as described by Searle (1971). In the combined analysis of variance, the effects of genotypes and countries (Mali, Kenya) were assumed to be fixed, while the effect of the locations within countries were considered random. Coefficients of phenotypic correlation among locations were computed based on entry means at the individual sites, using standard procedures. Quantitative-genetic parameters estimated from the diallel analysis are published elsewhere (Haussmann et al., 2001b).

Pattern analysis, which consists of joint and complementary use of classification and ordination techniques, was applied to the environment-standardized matrix of the entry × environment means (Fox & Rosielle, 1982). The standardization was done according to the formula:

$$Y'_{ij} = (Y_{ij} - Y_{.j})/s_d,$$

where Y'_{ij} is the standardized mean of entry i in environment j, Y_{ij} the observed mean of entry i in environment j, $Y_{.j}$ the mean of all entries in environment j, and s_d the phenotypic standard deviation in environment j. The standardization of environments leads to a grouping of those environments that are most similar in the way they rank genotypes (Fox & Rosielle, 1982). The genotype groupings obtained with this standardization are such that genotypes revealing similar performance levels are placed in a group. An agglomerative hierarchical procedure with an incremental sum of squares grouping strategy known as Ward's method (Ward, 1963) was employed for the purpose of classification. The squared Euclidean distance was used as a dissimilarity measure required by Ward's method. A one-way classification of entries was chosen, maintaining all four test locations as separate. Each entry was therefore characterized by the four-dimensional vector of location yields and the Euclidian distance was based on this vector. Various entry groups were defined based on a minimum percentage (50%) of the sums of squares retained in the reduced entry × environment matrix. Performance plots of different entry groups were used to characterize adaptation patterns. The biplot derived from ordination (using environment-standardized data) assessed relations among entries, among environments, and between entries and environments (Kempton, 1984). Biplot scores were computed using singular value decomposition. In a biplot obtained from environment-standardized data, the origin (0,0) represents the average productivity for environments, and the biplot models the sum of genotypic and genotype × environment interaction (G + G×E) effects (DeLacy et al., 1996). Entries close to the origin are average in their performance across all environments. Entries that are close to each other tend to be similar. Small angles between two environment vectors indicate strong positive associations, i.e., high similarity between these two environments; 90° angles indicate no association and angles greater than 90° indicate negative associations. For grain yield, entries distributed in the increasing direction of an environment vector yield above-average in that environment, while those distributed in the opposite direction are lower yielding. To characterize entries, a line must be drawn perpendicularly from a particular entry to an environment vector. The point of intersection indicates the entry's relative performance in that environment, i.e., for the same environment vector, a better genotype would project an intersection point that is farther along in the positive direction of the environment vector. The reverse is true for ASVPC: entries distributed in the increasing direction of an environment vector are striga-susceptible in that environment, while those distributed in the opposite direction are striga-resistant. The software package GEBEI (Watson et al., 1996) was used to perform the pattern analysis.

Results

Location means

Striga infestation was high at all four sites, with location means of 42, 70, 60 and 39 emerged striga plants m^{-2} at about 85 days after planting at Samanko, Cinzana, Alupe and Kibos, respectively. Average ASVPC values were highest at Alupe (Figure 2), due to a higher striga vigor at this location. Averaged across the 50 entries, the location means for grain yield ranged from 132 to 252 g m^{-2} with the highest value at Cinzana. The frequency distributions of the 50 entries were slightly skewed to the right for ASVPC at Samanko, Cinzana, and Alupe, and for grain yield at Samanko and Kibos. However, deviations from normal distribution were small and only weakly significant ($p = 0.1$ or 0.05). Therefore, no data transformation was undertaken before computing the analysis of variance.

Combined analysis of variance across locations

The combined analysis of variance indicated highly significant variation due to entries, locations-within-

Table 2. Analysis of variance in 50 sorghum entries (9 selected parent lines, 36 F_2 populations derived from crosses of the nine parent lines, and 5 local cultivars) evaluated for area under striga severity progress curve (ASVPC) and grain yield at two locations in both Mali and Kenya

Source of variance	df	ASVPC		Grain yield	
		Mean square	F-value	Mean square	F-value
Countries	1	2,121.1	0.07	135,387.3	0.73
Locations-within-countries	2	46,889.2	41.13**	185,083.0	70.71**
Entries	49	5,683.2	4.98**	18,454.9	7.05**
Entry × country interaction	49	2,604.5	2.28**	2,737.7	1.05
Entry × location-within-country interaction	98	1,140.1	2.68**	2,617.6	5.02**
Experimental error	952/959[a]	425.1		521.3	

** Significant at the 0.01 probability level.
[a] Different degrees of freedom for experimental error of ASVPC and grain yield due to different numbers of missing observations.

Table 3. Estimated heritabilities in a replicated trial (underlined italics on diagonal) at the four locations (two in Mali and Kenya each) and coefficients of phenotypic correlation among these sites for area under striga severity progress curve (ASVPC) and grain yield

Trait	Location	Mali		Kenya	
		Samanko	Cinzana	Alupe	Kibos
ASVPC	Samanko	*0.90*			
	Cinzana	0.71**	*0.91*		
	Alupe	0.25	0.34*	*0.78*	
	Kibos	0.22	0.46**	0.55**	*0.73*
Grain yield	Samanko	*0.95*			
	Cinzana	0.57**	*0.93*		
	Alupe	0.76**	0.47**	*0.89*	
	Kibos	0.68**	0.42**	0.71**	*0.89*

*,** Coefficient of correlation significant at the 0.05 and 0.01 probability levels, respectively.

countries, and interaction between entries and locations-within-countries for both ASVPC and grain yield (Table 2). Countries (Kenya *versus* Mali) had no significant effect on the two traits, while the entry × country interaction mean square was significant for ASVPC but not for grain yield. Similar F-values of entry × country and entry × location-within-country interaction indicated that the two types of interaction were equally important for ASVPC.

Correlations among locations

Coefficients of phenotypic correlation among locations for ASVPC were highest for the Malian location pair Samanko/Cinzana, followed by the Kenyan location pair Alupe/Kibos (Table 3). Correlations between Kenyan and Malian locations were lower or non-significant. The lower correlations were not due to a lack of differentiation among the entries, as estimates of heritability in a replicated trial were high at all four sites. For grain yield, the correlation was highest for the location pair Samanko/Alupe, followed by Kibos/Alupe and Samanko/Kibos. Overall, Cinzana displayed the lowest correlations with other locations.

Pattern analysis

The dendrograms of the four locations as revealed by the pattern analysis differed between ASVPC and grain yield (Figure 3). For ASVPC, the Malian and the Kenyan locations were clearly separated from each other. For grain yield, on the other hand, Cinzana was separated from the other three locations, and Samanko and Alupe grouped closest together. The grouping of the locations in the pattern analysis corresponds well to the coefficients of correlation presented in Table 3.

The dendrograms of the 50 entries show six entry groups for each trait, based on similar reaction patterns and performance levels in the four locations (A1–A6 for ASVPC, and Y1–Y6 for grain yield, see Figure 4). The percentages of the entry × environment interaction sums of squares retained in the reduced matrix were 73.2% for ASVPC and 51.9% for grain yield. The respective percentages retained from the entries' sums of squares were 80.8 and 86.5%. For ASVPC, grouping patterns are visible corresponding to the entries' reported reaction to striga: group A1 contains mainly resistant parent lines and F_2s derived from crosses between resistant parents or between a resistant and a tolerant parent. Groups A2 and A3 are mainly composed of F_2s derived from crosses of resistant or tolerant with susceptible parents. Groups A4 and A5 are mainly comprised of susceptible lines, F_2

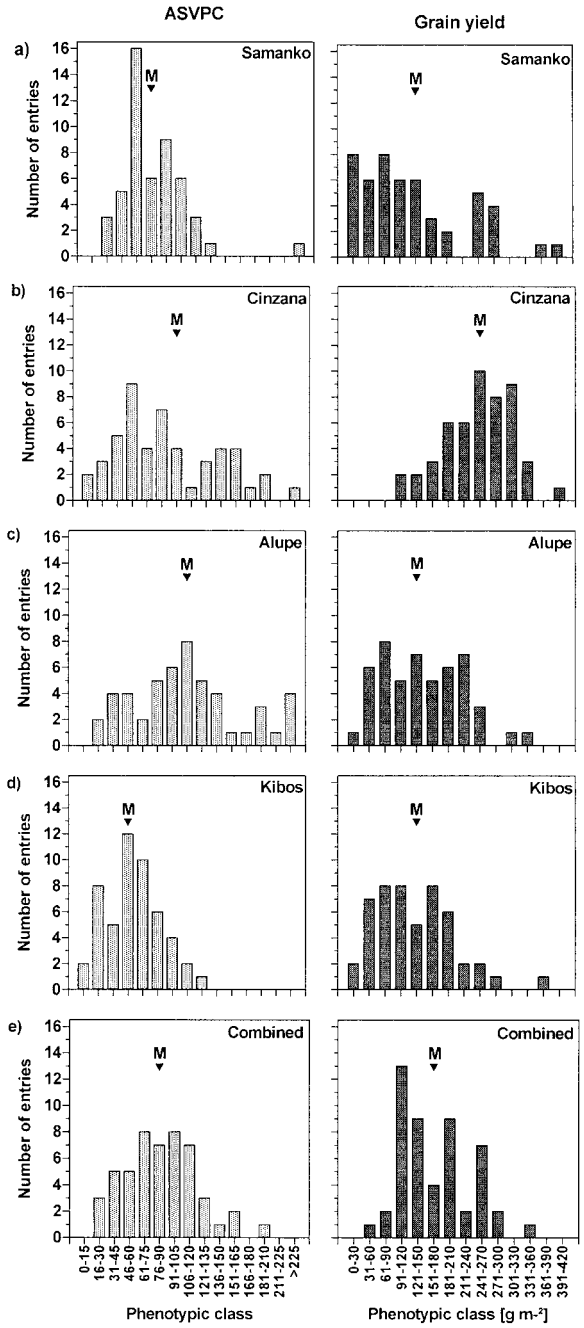

Figure 2. Frequency distribution of the fifty entries for area under striga severity progress curve (ASVPC, left) and grain yield (right) at a) Samanko, b) Cinzana, c) Alupe, d) Kibos, and e) for entry means across the four locations; m indicates the location means.

crosses among susceptible parents, and local checks. Group A6 consists of only one entry, namely the highly striga-susceptible, local cultivar CSM 228. For grain yield, grouping patterns revealed genetic and adaptation similarities. For example, the striga-tolerant cultivar Seredo (T5) and its progenies occurred only in groups Y1 to Y3. The genotype grouping did not correspond to the entries' reported reaction to striga, e.g., resistant lines and F_2 crosses involving them appeared in all groups except Y2.

Performance plots of the individual entry groups show various patterns of adaptation to the test environments (Figure 5). For ASVPC, group A1 shows superior resistance (below-average ASVPC values) in all environments, with a slightly higher resistance level at the Kenyan locations. Group A2 displayed above-average resistance in the Malian environments but only an average susceptibility in Kenya. Group A3 was inconsistent in its reaction across sites while A4 was highly susceptible at the Kenyan locations and medium in Mali. Group A5 tended to be striga-susceptible in all environments. The local cultivar CSM 228 (group A6) is remarkable in that it had much higher ASVPC values in Mali than in Kenya. For grain yield, groups Y1 and Y2 showed above-average performance in all environments. While Y1 was slightly better adapted to Mali, Y2 tended to yield relatively higher in Kenya. Group Y3 was also relatively better adapted to the Kenyan environments, but overall had a lower yield level than Y2. Group Y5, which contained two West African local cultivars, showed specific adaptation to Cinzana but poor yield at the remaining three locations. Groups Y4 and Y6 yielded below average at all four locations. The two groups differed in that Y6 revealed its best and Y4 its worst performance at the same location, Cinzana.

The first two principal components from ordination analysis explained 82% of the total sums of squares of the entry × environment interaction for ASVPC and 86% for grain yield. The corresponding biplots (Figure 6) show that there was little correspondence between the discrimination abilities of the Malian *versus* the Kenyan locations for ASVPC (53°–73° angle between the respective environmental vectors). However, reportedly striga-resistant entries (black symbols) clustered together as did striga-susceptible lines and F_2 populations (white symbols). The biplot clearly illustrates the outstandingly high ASVPC values of the Malian local cultivar CSM 228 at the Malian locations. A different picture emerged for grain yield, where Cinzana was a unique environment and the

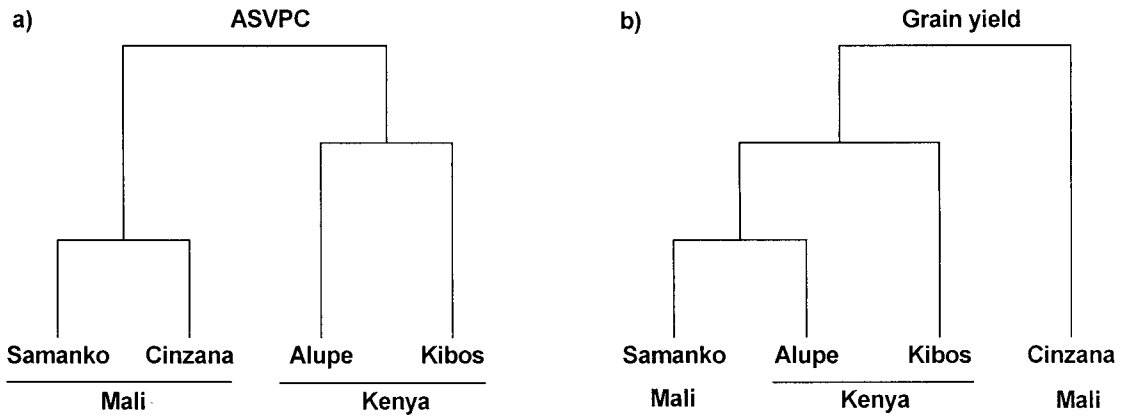

Figure 3. Dendrogram of the four locations for a) area under striga severity progress curve (ASVPC) and b) grain yield.

test entries ranked in a similar manner at the other three locations. Entries did not cluster according to their reported reaction to striga except that the tolerant cultivar Seredo and the F_2s derived from crosses of Seredo with resistant lines were relatively well adapted to all four test sites. Bengou Local was exceptional compared to all other entries in revealing specific adaptation to Cinzana.

Superior entries for ASVPC and grain yield

The F_2 derived from the cross of the striga-resistant line Framida with the striga-tolerant cultivar Seredo was the sole entry which appeared in both group A1 (lowest ASVPC at all four locations) and Y2 (high grain yield at all locations). In addition, the parent line Framida, and the F_2 crosses Framida × 555, Framida × IS 9830, and IS 9830 × Seredo belonged to group A1 as well as Y1, and therefore possessed superior striga resistance and grain yield across sites. Lines N 13 and 555 and the F_2 population from the cross N 13 × IS 9830 supported low emerged striga numbers (entry group A1) but were low-yielding at all four experimental sites (entry groups Y4 or Y6). Seredo, the local check Wagita, and the F_2 population derived from Seredo × E 36-1 can be considered as striga-tolerant, as they maintained high grain yields (entry group Y2) despite the presence of average or above-average emerged striga populations (entry groups A2, A4, and A5, respectively).

Discussion

In single environment experiments, G×E interactions result in an upward bias in the estimation of genetic variances which leads to discrepancies between expected and realized responses to selection. Effectiveness of selection in a single environment is therefore limited in the presence of significant G×E, forcing the breeder to evaluate breeding materials over a diverse range of environments. Strong interactions could even favor breeding for specific adaptation to individual locations within a country (e.g., Pham & Edmeades, 1987; Moreno-Gonzáles & Cubero, 1993). The study of G×E interaction patterns can help the breeder to identify distinct regions of adaptation, to select sites representative for each homogeneous sub-area, and thereby to develop more efficient testing procedures (Brown et al., 1983; Lin & Butler, 1988).

In the present study, the significant entry × country interaction mean square as well as the lower correlations between Kenyan and Malian locations for ASVPC indicated that entries identified as striga-resistant in Kenya may not necessarily be resistant in Mali and *vice versa*. In any event, it is unlikely that a breeder would seek to select a single striga-resistant cultivar for both Mali and Kenya due to major differences in adaptation for other traits. However, the observed interaction does have implications for the identification of sources of resistance for use in a breeding program. Potential sources of resistance must be carefully evaluated in the target area before an extensive crossing program is initiated. Ramaiah (1987) also stressed the importance of selection for stable resistance by

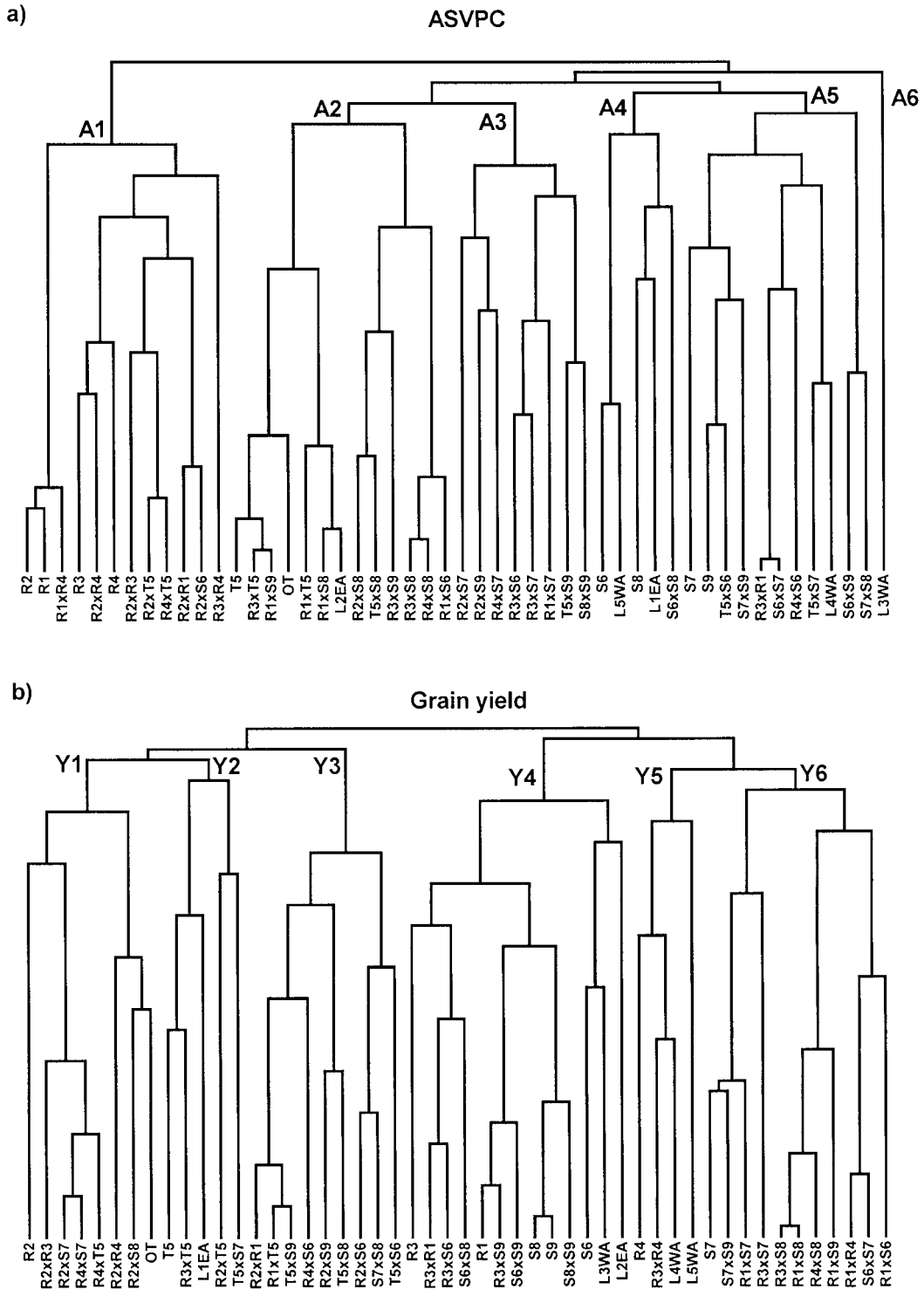

Figure 4. Dendrograms showing hierarchical classification of the 50 entries for a) area under striga severity progress curve (ASVPC) and b) grain yield; for genotype codes see Table 1; OT = off-type.

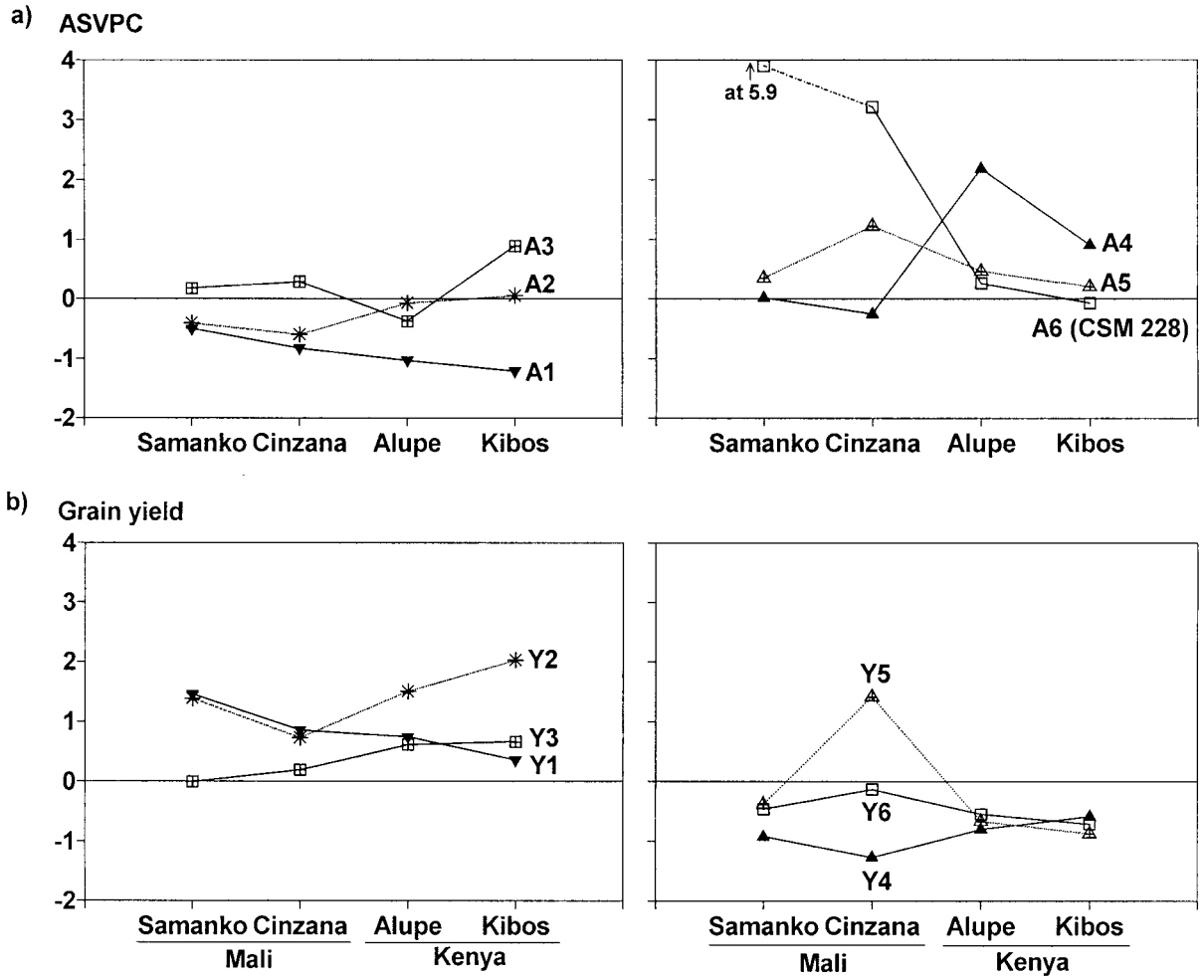

Figure 5. Performance plots of entry groups a) A1, . . ., A6 for area under striga severity progress curve (ASVPC) and b) Y1, . . ., Y6 for grain yield at the four test sites; for group compositions see Figure 4.

evaluating breeding materials at diverse locations and against different host-specific striga populations.

The performance plots for ASVPC clearly show that the genotype groups A4 and A6 contributed most to the entry × country interaction. Group A6 contained the striga-susceptible Malian local cultivar CSM 228 which supported much higher ASVPCs at the Malian locations compared to the Kenyan sites. This may be interpreted as specific adaptation of Malian striga to a local Malian cultivar. Kenyan striga, on the other hand, seemed to be specifically adapted to the East African cultivar Wagita, the two striga-susceptible lines (M 35-1 and DJS 1195) from India, and their derived F_2 population (members of entry group A4). The cultivar Bengou Local from Niger, also in group A4, might possess some effective defense mechanism against West African (Malian) striga which is ineffective against striga from Kenya. When the analysis of variance was computed excluding the local cultivars, the entry × country interaction was only weakly significant for the parent lines ($p = 0.1$) and non-significant for the F_2 populations (Haussmann, unpublished data), pointing to the importance of the local cultivars in causing the entry × country interaction in this data set. In conclusion, the observed entry × country interactions for ASVPC support the hypothesis of differentially adapted subpopulations of striga to local sorghum hosts in Mali *versus* Kenya. Similarly, Obilana (1984) and Ramaiah (1987) suggested that 'strains' of *Striga hermonthica* have developed in restricted ecological zones of Africa. It has also been suggested that 'strains' adapted to specific

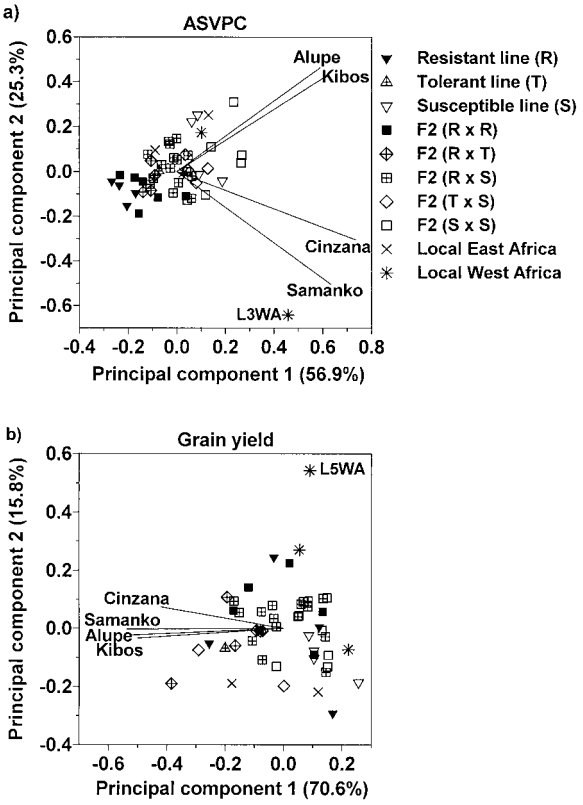

Figure 6. Biplots for principal components 1 and 2 obtained from the ordination of environment-standardized data for a) area under striga severity progress curve (ASVPC) and b) grain yield. Environments are characterized by vectors drawn from the origin. Entry L3WA = CSM 228; L5WA = Bengou Local.

host cultivars exist (Bebawi, 1981; Ramaiah & Parker, 1982).

Variability among striga subpopulations could be attributable to different requirements for preconditioning, stimulation of striga seed germination (Ramaiah, 1987), haustorium-inducing factors and nutritional requirements (Ejeta & Butler, 1993). In fact, Kenyan striga was more sensitive to germination stimulation in the agar-gel assay than striga from Mali or Niger (Haussmann et al., 2001a).

Ejeta & Butler (1993) emphasized that, while observations on intraspecific variability of *S. hermonthica* are significant, they need to be verified through inbreeding of the parasite followed by inoculation of host differentials. These studies have not yet been conducted. Of course the entry × country interaction observed in the present study cannot be attributed solely to entry × (putative) striga strain interactions but may also have resulted from differential reaction of sorghum and striga to the different climatic and edaphic factors in Mali and Kenya. That the different inter- and intra-row spacings used in Mali and Kenya had a significant effect on the entry × country interaction for ASVPC is unlikely: the empty row between plots reduced neighbor effects and competition among plants, and promoted striga emergence due to reduced shading at all sites (including the Kenyan sites with slightly higher plant density).

Differential patterns of G×E interaction for grain yield and ASVPC point to the necessity to select simultaneously for both traits using appropriate indices. The different patterns are partially caused by the lack of adaptation to the target areas and / or the low yield potential of some of the striga-resistant lines, i.e., N 13 and 555.

For grain yield, the entry × location-within-country interaction was most important, and Cinzana was separated from all other environments. Also for ASVPC, the entry × location-within-country interaction mean square was highly significant. Overall, Cinzana is a drier location than Samanko, and generally requires the cultivation of more drought-tolerant cultivars. Samanko, on the other hand, requires cultivars which are more resistant to grain anthracnose [*Colletotrichum graminicola* (Cesati) Wilson] and grain molds (*Curvularia* and *Fusarium* species), due to rains during the grain-filling stage. A breeder may therefore need to select for adaptation to specific regions within a country, like areas with similar rainfall. On the other hand, high annual fluctuations in rainfall amount and distribution are very common in the semi-arid tropics. Therefore, the performance of a cultivar must be stable across a range of diverse environmental conditions. Multilocational testing at test locations which represent the range of possible climatic conditions at a specific site can at least partially substitute for evaluation of yield stability over several years at a single location (Romagosa & Fox, 1993).

The F_2 population derived from the cross of the striga-resistant line Framida with the striga-tolerant cultivar Seredo clustered in both the most striga-resistant and the highest yielding entry group. The superiority of this F_2 population points to the importance of combining resistance with tolerance to striga when breeding improved cultivars. This strategy has also been recommended for striga resistance breeding in maize (DeVries, 2000). Under high striga infestation levels (as in the present study), even resistant cultivars will support some emerged striga, and toler-

ance will help to minimize yield reduction experienced by farmers.

Conclusions

The observed pattern of G×E interaction for striga resistance in sorghum supports the hypothesis of the presence of differentially adapted *Striga hermonthica* subpopulations in Kenya *versus* Mali. However, a more extensive striga variability study would be required to clearly separate genotype × location from genotype × striga population interactions, and to prove the genetic variability of striga for virulence characters. Multilocational testing, a combination of striga resistance with tolerance in individual cultivars, and simultaneous selection for both low striga emergence/vigor and high grain yield could be a useful approach for breeding sorghum for striga-infested zones of Kenya and Mali. Further, careful definition of target environments and farmer-participatory breeding are essential to ensure that the cultivars developed are adapted to farm conditions and will satisfy end-user preferences (Rattunde et al., 2000).

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