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Towards More Efficient Breeding for Striga Resistance in Sorghum

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Abstract

The parasitic flowering weed *Striga hermonthica* (Del.) Benth. (*Scrophulariaceae*) seriously limits cereal production in sub-Saharan Africa. Our BMZ-financed project (i) developed more efficient methods of screening sorghum [*Sorghum bicolor* (L.) Moench] for resistance to *S. hermonthica*; (ii) studied the inheritance of striga resistance in sorghum using classical approaches; (iii) identified and mapped genes for qualitative and quantitative resistance by means of molecular markers; and (iv) developed new strategies, including marker-assisted approaches, for improving resistance. In this paper, we summarize major findings from 4½ years of collaborative research involving ICRISAT, the University of Hohenheim, African National Agricultural Research Systems (NARS), and the Private Sector.

Keywords: striga resistance, sorghum, genetics, molecular markers

Introduction

Sorghum (*Poaceae*) is an important cereal crop in the semi-arid tropics. It is diploid with 2n = 20 chromosomes, and 80 to 95% self-pollinating. Mean grain yield worldwide is 1.4 t ha^{-1}, ranging from 0.8 t ha^{-1} in Africa to 3.4 t ha^{-1} in North and South America (FAO, 1999). The parasitic flowering weed *Striga hermonthica* (*Scrophulariaceae*) seriously limits cereal production in sub-Saharan Africa where it attaches to the roots of the host, diverting water and nutrients. Where infestations are high, susceptible sorghum cultivars can be killed by the parasite.

Striga-resistant sorghums could be a major component of integrated striga control strategies but known resistance sources are frequently low-yielding with poor genetic background. Breeding progress has been slow due to limited knowledge on the genetics of resistance, and the difficulty of evaluating resistance in the field. Our collaborative project was designed to: (i) develop more efficient methods of screening sorghum for resistance to striga (*Striga hermonthica)*; (ii) study the inheritance of striga resistance in sorghum using classical approaches; (iii) identify and map genes for qualitative and quantitative resistance to striga in

sorghum lines by means of molecular markers; and (iv) develop new strategies (including marker-assisted techniques) for improving striga resistance in sorghum.

Materials and Methods

Genetic materials

Nine sorghum lines were crossed in a diallel fashion (i.e., in all possible combinations). Of the nine lines, four (Framida, 555, N 13, and IS 9830) are resistant to striga; one (Seredo) is striga-tolerant; and the remaining four lines (M 35-1, E 36-1, DJ 1195 and IS 1037) are susceptible. The F_1 hybrids of the half diallel (i.e., without reciprocal crosses) were selfed to obtain 36 F_2 populations.

For the mapping study, two recombinant inbred populations (RIPs), each consisting of 226 F_3-derived F_5 lines (also called F_3 families), were developed from the crosses (1) IS 9830 × E 36-1, and (2) N 13 × E 36-1. IS 9830 is a striga-resistant variety producing very low levels of the stimulants required by striga seeds to germinate. N 13 stimulates striga seed germination but presumably possesses mechanical barriers to the penetration of striga into its roots. Both lines appear to have additional resistance mechanisms. Line E 36-1 is a striga-susceptible but drought-resistant cultivar with high yield potential.

Resistance tests

The complete 9×9 F_1 diallel was evaluated in 1995 for stimulation of striga seed germination using an agar-gel assay (Hess et al., 1992), and in pot trials in Mali and Niger. The half F_2 diallel was planted in 1996 in striga-infested fields at Samanko and Cinzana (Mali) and at Alupe and Kibos (Kenya). Three selected F_2 populations derived from crosses between low-stimulant lines (555, Framida, IS 9830) and a high-stimulant line (E 36-1) were tested in the agar-gel assay using striga seeds from a Samanko, Mali, population.

To assess their reaction to striga, both mapping populations were divided into two sets. Set 1 consisted of 116 $F_{3:5}$ lines which were tested in 1997 together with their parental lines and three local checks. Set 2 consisted of 110 $F_{3:5}$ lines, and was screened in 1998 together with the parental lines and nine checks. RIP 1 was tested in the agar-gel assay using striga populations from Mali, Niger, and Kenya. Both RIPs were evaluated in striga-infested pots at Samanko, Sadoré (Niger), and Kibos, and in field trials at Samanko, Cinzana, Kibos and Alupe in the Long Rains, and at Alupe in the Short Rains. Results from the agar-gel assays and the field trials will be presented here.

In the agar-gel assay, preconditioned striga seeds are dispersed in agar in petri dishes, a pre-germinated sorghum seedling is placed in each dish, and the maximum distance between sorghum rootlet and germinated striga seed is measured after five days of incubation at 28°C in the dark. This "germination distance" is a measure of the amount of striga seed germination stimulant produced by the sorghum entry. Germination distances below 10 mm are characteristic of low-stimulant genotypes (Hess et al.,1992).

Our improved field testing methodology included: artificial infestation of on-station trials; use of six replications and incomplete block designs; a specific plot layout; and the use of improved resistance indices.

Each plot consisted of two rows of 3 m length, separated from the neighboring plot by one empty row each. This arrangement has several distinct advantages. For each entry, traits can be easily assessed in both rows, and no land is lost to border rows. Neighbor effects are reduced due to the empty row and more light reaches the ground, reducing shading which is deleterious to striga emergence and development.

Among the newly defined resistance indices is the striga “vigor score” (1-9 scale), based on striga height and extent of branching (Haussmann et al., 1999a). Assessment of striga vigor is important because it takes into account biomass and not only emerged striga number. The "striga severity" index results from multiplying the striga count with the average striga vigor. Successive striga counts were also used to calculate an "area under the striga number progress curve" (ASNPC), using the formula for “area under the disease progress curve“ (AUDPC; Shaner and Finney, 1977; see also Haussmann et al., 1999a). Similarly, an "area under the striga severity progress curve" (ASVPC) was computed, using striga severity indices instead of the striga counts. In addition to striga emergence and development, we also assessed grain yield and, when present, host plant damage expressed as chlorosis, stunting, reduced head exertion and/or sterility. This was found to be important as highly susceptible plants may support only a few emerged striga plants due to strongly reduced host vigor.

Marker analyses

Marker analyses of the two mapping populations were performed with bulked DNA from 20 plants per F_3 family. AFLP, RFLP, and SSR analyses were carried out by commercial laboratories and RAPD analyses by ICRISAT. RIP 1 was genotyped for 177 marker loci (131 codominantly and 20 dominantly scored AFLPs, 16 RFLPs, 4 SSRs, 6 RAPDs) and RIP 2 for 243 marker loci (122 codominantly and 75 dominantly scored AFLPs, 20 RFLPs, 9 SSRs, 17 RAPDs). The lower number of markers in RIP 1 was due to a lower genetic distance between IS 9830 and E 36-1 compared to N 13 and E 36-1. The AFLP markers were created using 10 *Eco*RI/*Mse* primer combinations. Seven of the ten primer combinations were common to both RIPs. These yielded 34 common markers. The RFLP markers (about two anchors per linkage group) were selected from the sorghum genetic maps recently published by Boivin et al. (1999), Dufour et al. (1997), and Pereira et al. (1994). The SSRs had been developed by Brown et al. (1996) and Taramino et al. (1997).

Statistical analyses

Phenotypic data were analyzed using the computer program PLABSTAT (Utz, 1998). The chi-square goodness-of fit test was performed as described by Gomez and Gomez (1984). Heritability was estimated as outlined by Fehr (1987). The computer software Joinmap 2.0 (Stam and Van Ooijen, 1995) was used for map construction. Mapping striga resistance (or other) genes, i.e., estimating their position on the chromosomes, is based on co-segregation of individual markers with striga resistance. Several methods have been proposed. In our study, the quantitative trait loci (QTL) for striga resistance (i.e., genomic regions which contribute to variation in resistance) were detected using the method of composite interval mapping (Jansen

and Stam, 1994; Utz and Melchinger, 1994; Zeng, 1994) and the program PLABQTL (Utz and Melchinger, 1995). The program was run with default settings; results are therefore preliminary.

Results and discussion

Agar-gel assays

In the agar-gel assay, genotypes Framida, 555, and IS 9830 were observed to be low-stimulant producers. Differences among parents and among F_1 hybrids were highly significant. On average, hybrids differed from the respective midparent values by +11.7% for the germination distance (i.e., they tended towards a stronger stimulation). The interaction between sorghum genotypes and striga populations was highly significant. The coefficient of correlation between the germination distances of the two striga populations (Mali and Niger) was r=0.86, suggesting that, across all entries, the genotype × striga population interaction was less important than the genotypic differentiation. Variation in hybrid performance was determined by general and specific combining ability effects. Reciprocal effects were significant but unstable across striga populations. A close correlation between midparent values and hybrid performance, and, correspondingly, between line performance *per se* and general combining ability (GCA), reflected the predominance of additive gene action. Differing GCA effects for the germination distance in the agar-gel assay indicated that the genes for low stimulant production differ between 555 and Framida or IS 9830. For lines and hybrids, estimates of broad-sense heritability were 0.97 and 0.91 for the *in vitro* germination distance. For additional results from the F_1 diallel studies see Haussmann et al. (1996, 1999b).

In the RIP 1 agar-gel assays, the striga seeds from Kenya displayed a 57% higher germination distance than striga seeds from Mali or Niger. These results suggest a higher sensitivity of the Kenyan striga to germination stimulants exuded by sorghum roots. The low-stimulant character may therefore be a less effective resistance mechanism in Kenyan fields. The correlation between germination distances of striga populations from Mali *versus* Niger (r=0.92, pooled over the two sets) was slightly higher than the correlation between either West African and the Kenyan striga (r = 0.81, pooled over the West African striga populations and the two sets of F_3 families). The changing correlations point to some diversity among East- and West African striga populations, and to the presence of genotype × striga population interactions.

Frequency distributions of RIP 1 F_3 families and of individual plants from the three selected F_2 populations were bimodal for the germination distance in the agar-gel assay. Chi-square tests of the observed ratio of phenotypic classes indicate that low germination distance in the agar-gel assay was determined by a single major recessive gene. Additional minor genes modified germination distance in the F_3 families, as indicated by a significant genetic variation within the moderate-to-high stimulant groups. These findings confirm but also go beyond the results from earlier studies with *S. asiatica* where the phenotypic variation within the moderate-to-high stimulant groups was not further examined (Ramaiah et al., 1990; Vogler et al., 1996). The presence of at least three germination stimulants in sorghum root exudates (Ejeta et al., 1992; Siame et al., 1993) supports our finding of multiple genes controlling the stimulation of *S. hermonthica* seed germination.

Field evaluation of the F_2 population diallel

In the field evaluation of the F_2 population diallel in Kenya and Mali, environmental means ranged from 39 to 70 emerged striga plants m^{-2} at 85 days after planting (d.a.p.), and from 132 to 254 g m^{-2} for grain yield. Averaged across the four locations, the F_2 populations significantly out-yielded their parental lines by 18%. Individual heterosis values for the area under striga severity progress curve ranged from –21% (more resistant) to +228% (more susceptible), depending on the parental combination and the environment. The genetic variation among lines and among F_2 populations, and genotype × environment (G×E) interaction variances were highly significant. Broad-sense heritability estimates for the number of emerged striga at 85 d.a.p., area under striga severity progress curve, and grain yield were 0.87, 0.83, and 0.90 in lines, and 0.74, 0.81, and 0.89 in F_2s, respectively. Mean squares due to general and specific combining ability (GCA and SCA, respectively), and their interaction with locations were significant for all traits considered. Among the parent lines, Framida and IS 9830 were good general combiners for both striga resistance and grain yield. Lines 555 and N 13 also revealed GCA for low striga emergence, but were poorly adapted to the test locations.

Genetic maps of the two mapping populations

For RIP 1, the genetic map had a total length of 872 cM, and contained 147 markers distributed over 10 linkage groups at a LOD grouping threshold of 5.1. Thirty marker loci were unlinked or largely disturbed the map construction, thereby decreasing the goodness-of-fit of the map. These markers were removed from the data set. For RIP 2, the map extended to a total length of 939 cM, and contained 191 markers distributed over 11 linkage groups (at a LOD grouping threshold of 4.5). Fifty-two markers were unlinked or largely decreased the goodness-of fit value of the map. Markers which largely disturbed the mapping process (mostly RAPDs and dominantly scored AFLP markers) were removed from the data set.

The average and maximal distance between two individual markers were 5.9 and 28 cM in RIP 1, and 4.9 and 31 cM in RIP 2, respectively. A high goodness of fit (low mean χ^2 value in the map construction of all linkage groups) indicated high reliability of the linkage maps for both RIPs. However, the total lengths of the genetic maps are lower than those published previously for sorghum (Chittenden et al., 1994; Pereira et al., 1994; Xu et al., 1994; Dufour et al., 1997; Boivin et al. 1999). As considerable clustering of the AFLP markers was visible around centromeric regions, there may be too few markers in telomeric regions of the linkage groups. An increase in the total number of markers may help to better cover the whole genome and assign more of the unlinked markers to the maps.

Resistance data of the two mapping populations

Striga infestation in the field experiments was high at all five sites in both years. The area under striga number progress curve showed a continuous distribution. Transgressive segregation was, when observed, involved striga susceptibility. In both RIPs and in both years, estimated genetic and genotype × environment interaction variances were highly significant for the area under striga number progress curve. The genotype × environment interaction variance contains genotype × location, genotype × year, and genotype × striga

population interaction effects. These effects, however, cannot be separated with the current experimental design. Broad-sense heritability estimates were 0.66 and 0.74 in Sets 1 and 2 of RIP 1, and 0.81 and 0.82 in Sets 1 and 2 of RIP 2, respectively.

In RIP 1, the relationship between *in vitro* germination distance and area under striga number progress curve in the field was location dependent. The correlation was generally moderate to high at the Malian sites, but low in the Kenyan test environments (for details see Omanya et al., this volume: poster No. 246).

QTL for area under striga number progress curve (preliminary results)

In RIP 1, five and six QTL were detected explaining 68% and 61% of the genotypic variance for ASNPC in Sets 1 and 2, respectively (pooled across the five test environments; Table 1). One QTL on linkage group E was common to both sets of F_3 families. In RIP 2, eleven and six QTL explaining 94% and 68% of the genotypic variance for ASNPC were detected in Sets 1 and 2, respectively (pooled across the test locations, Table 2). Two QTL on linkage groups C and J were common to both sets. For ASNPC in the individual environments, the number of QTL ranged from zero to six in RIP 1 and from three to eight in RIP 2. Overall, the QTL pattern was complex across test environments and sets of F_3 families, in both mapping populations. Several explanations are available for the rather low repeatability of the QTL: low power of QTL detection due to small population size and because our genetic maps do not cover the whole genome; and/or involvement of different genes for striga resistance at different locations or in different years (QTL × environment interaction). Our QTL analyses will be refined to determine precise positions and effects of the individual QTL.

Table 1. Linkage group positions and LOD scores of individual QTL, total number of QTL, and percentage of genetic variation explained by these QTL (%V_g expl.) in Sets 1 and 2 of RIP 1 (IS 9830 × E 36-1) for area under striga number progress curve in the individual field experiments, and in the combined analysis across environments.

Set / Year	Location [1)]	**LOD score of the QTL in linkage group position[2)]**									Total QTL	%V_g expl.
		A	B	C	D	E	F	G	I	J		
1	Sko						3				1	10
	Cza	7	3	5				9			4	49
1997	Kib.LR			3		3				4	3	47
	Alu.LR			4		3				6	3	68
	Alu.SR		5 | 3			3					3	85
	Pooled	**4**				**4**		**5 | 4**		**5**	**5**	**68**
2	Sko		3		3		7	6	5		5	64
	Cza		7		3			9	5		4	52
1998	Kib.LR										0	0
	Alu.LR						3				1	12
	Alu.SR	4	3			3	4	8		3	6	61
	Pooled		**5 | 3**			**4**	**4**	**7**	**5**		**6**	**61**

[1)] Sko = Samanko; Cza = Cinzana; Kib.LR = Kibos Long Rains; Alu.LR = Alupe Long Rains; Alu.SR = Alupe Short Rains.

[2] Divided cells indicate that two QTL mapped to the respective linkage group.

Table 2. Linkage group positions and LOD scores of individual QTL, total number of QTL, and percentage of genetic variation explained by these QTL (%V_g expl.) in Sets 1 and 2 of RIP 2 (N 13 × E 36-1) for area under striga number progress curve in the individual field experiments, and in the combined analysis across environments.

Set / Year	Location [1]	**LOD score of the QTL in linkage group position[2]**										Total QTL	%V_g expl.
		A	B	C	D	E	F	G	H	I	J		
1 1997	Sko		3 | 7			3		3			3 | 5	6	49
	Cza	7	8	3						4	4 | 7	6	76
	Kib.LR		8	3		3			3 | 5	3	3 | 3	8	60
	Alu.LR			9		4	5	3			10	5	63
	Alu.SR		5	6 | 5			3		3		3 | 7	7	70
	Pooled			**12**	**3**	**5**	**3 | 3**	**3**	**3 | 4**		**4 | 8 | 3**	**11**	**94**
2 1998	Sko	6	6	3		7 | 3	3				4	7	68
	Cza	5	3					3		5	7 | 7	6	66
	Kib.LR	3		4							4	3	42
	Alu.LR	3		8 | 3 | 3				3			3	6	74
	Alu.SR			4						3	6	3	41
	Pooled	**4**	**3 | 5**	**6 | 3**							**3**	**6**	**68**

[1] Sko = Samanko; Cza = Cinzana; Kib.LR = Kibos Long Rains; Alu.LR = Alupe Long Rains; Alu.SR = Alupe Short Rains.

[2] Divided cells indicate that two (or three) QTL mapped to the respective linkage group.

Conclusions

The accuracy of screening sorghum for striga resistance can be substantially improved by employing: six replications; striga seeds of different geographic origin in the laboratory assays; diverse test locations; a specific plot layout in the field trials; and appropriate resistance indices (e.g., striga severity or ASNPC).

Highly significant variation was found in the tested genetic materials for various striga resistance traits. Due to significant genotype × environment interactions and high parasite variability, multi-locational testing of breeding materials is essential.

The average F_2 heterosis of 18% for grain yield under striga infestation points to the potential merit of heterozygous cultivars for the target areas in Mali and Kenya. Both additive and dominant gene action are involved in striga resistance and grain yield under conditions of striga infestation. Due to the significant contribution of dominance effects, evaluation of testcrosses under striga infestation are essential in later stages of a hybrid breeding program. Available resistance should be transferred into farmer-selected varities, through combined use of laboratory and improved field screening methodologies. Breeders should try to incorporate different resistance mechanisms and tolerance to striga in hybrid-, synthetic-, or population varieties. In this context, further laboratory assays which allow a non-destructive, quick and

economical screening for resistance mechanisms other than the low stimulant character will increase the efficiency of breeding programs for striga resistance.

Although the pattern of QTL appearance in our study was rather complex, a few QTL were stable in the pooled analyses across environments in both sets of F_3 families in either RIP. These QTL could be first candidates for transfer into farmer-selected cultivars through marker-assisted selection. Given a tight linkage between marker loci and QTL, the application of marker-assisted selection in sorghum breeding for striga resistance would be particularly advantageous because: (1) resistance tests are difficult, complex, and often unreliable; (2) the parasite is quarantined; (3) breeding materials are advanced in off-season nurseries where striga does not occur; (4) striga occurrence is frequently erratic (e.g., the "non-striga year" phenomenon); and (5) some striga resistance genes are recessive, restricting the effectiveness of backcross schemes.

A major weakness in our QTL analyses may lie in the shortness of our genetic maps. With improved genetic maps, we expect the QTL results to be more consistent. Nonetheless, our preliminary results have shown that it is possible to detect QTL for striga resistance in sorghum under field conditions. It is also apparent that QTL found in single environments must be validated across diverse test locations and independent mapping population samples before applying marker-assisted selection.

Knowledge Partnerships within the Project

Only through close collaboration and knowledge partnerships among diverse, complementary organizations was it possible to generate such significant information within the short span of 4½ years. Principal collaborators were ICRISAT and the University of Hohenheim. ICRISAT's substantial expertise in *Striga* research and sorghum breeding was complemented by the expertise of the University in the areas of using molecular markers to analyze quantitative traits and breeding research. Because the majority of marker analyses was contracted out to commercial laboratories (Keygene and Perkin Elmer AgGen), the project profited maximally from recent marker technique developments in the Private Sector. Through collaborative conduct of field experiments with the Kenya Agricultural Research Institute (KARI, Kenya) and the Institut d'Economie Rurale (IER, Mali), the project both took advantage from NARS experience and made experimental results immediately available to them, thereby enhancing their ability to screen sorghum germplasm for striga resistance. Involvement in the project of a Kenyan Ph.D. (G.O. Omanya) student and students from the University of Mali (G. Mounkoro, N. Keïta) significantly contributed to the education of future NARS scientists.

To summarize the "state of the art" of cereal breeding for striga resistance, a workshop was held at the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria, from 18 to 20 August 1999. The meeting was jointly organized by ICRISAT, IITA, the University of Hohenheim, Eberhard-Karls University of Tübingen, and the Rockefeller Foundation. Funding was provided by the Bundesministerium für wirtschaftliche Zusammenarbeit (BMZ), Germany (within the framework of our project), The Rockefeller Foundation, and the International Fund for Agricultural Development (IFAD). The 56 participants included 26 cereal breeders or weed specialists from NARS of 17 African countries, and 30 scientists or representatives from the International Maize and Wheat Improvement Center (CIMMYT),

Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), ICRISAT, IITA, John Innes Center, Natural Resources Institute (NRI), Pan African Striga Control Network (PASCON), ProAgro Seed Company, the Rockefeller Foundation, Cornell University, University of Hohenheim, Purdue University, University of Sheffield, University of Tübingen, West Africa Rice Development Association (WARDA), and the Weizmann Institute of Science. Since many presentations dealt with molecular markers, the workshop was preceded by a two-day training course on the application of molecular markers in plant breeding (16-17 August). Participants had occasion to visit the IITA striga screenhouses at Ibadan, and several field trials (on-station and on-farm) at Mokwa. On the final day, working groups discussed future strategies in striga research and developed a number of recommendations to be published in electronic newsletters towards the end of 1999. Proceedings of the workshop are in preparation at ICRISAT and the University of Hohenheim.

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