

Inheritance of resistance to the panicle-feeding bug *Eurystylus oldi* and the sorghum midge *Stenodiplosis sorghicola* in sorghum

A. Ratnadass^{1,2,*}, J. Chantereau^{1,2}, M.F. Coulibaly¹ & C. Cilas³

¹ICRISAT-CIRAD, BP 320, Bamako, Mali; ²Current address: CIRAD-CA, TA 73/09, 34398 Montpellier cedex 5, France; 3 CIRAD-CP, TA 80/03, 34398 Montpellier Cedex 5, France; (* author for correspondence)

Received 12 May 2000; accepted 15 March 2001

Key words: diallel, head-bug, inheritance, Mali, sorghum midge

Summary

A study of the inheritance of sorghum resistance to head-bug *Eurystylus oldi* and midge *Stenodiplosis sorghicola* has been conducted from an F1-based complete diallel involving four parental lines (namely head-bug resistant Malisor 84-7 & 87W810, and susceptible S 34 & ICSV 197). The trial was conducted at Samanko, Mali, under both natural and artificial head-bug infestation, in one date of sowing (DOS) in 1995 and two DOS in 1996. Head-bug visual damage scores (under both types of infestation) were indicated and analyzed in all these trials. Head-bug numbers under artificial infestation on the two DOS of 1996, and midge damage score under natural infestation on the second DOS of 1996 were recorded. All four parents confirmed their expected level of resistance to head-bugs, while ICSV 197 confirmed its resistance to midge. Diallel analyses showed that general combining ability (GCA) and thus additive gene effects were very important in the inheritance of resistance to both pests. Specific combining ability and maternal effects were generally of minor importance. Mean performance of the parents and their GCA effects were linked, which suggests high heritability. Head-bug resistant parents, Malisor 84-7 & 87W810, with high *per se* resistance and negative GCA should therefore be used in breeding for resistance to this pest, while for a similar reason, ICSV 197 should be used in breeding for midge resistance. Results concerning independance between resistance to head-bugs and to midge, are also discussed.

Introduction

Sorghum [Sorghum bicolor (L.) Moench] is the most important food crop in the savanna areas of the West and Central Africa (WCA) region, notably in Nigeria, Burkina Faso, Mali and Niger, where average annual production during the 1992-1994 period where respectively 6.10, 1.25, 0.73 and 0.42 million kg (FAO & ICRISAT, 1996). The mirid panicle-feeding bugs, particularly Eurystylus oldi Poppius (Heteroptera: Miridae) have recently become key-pests of this cereal in all these countries (Ratnadass & Ajayi, 1995; MacFarlane, 1989; Steck et al., 1989; Doumbia & Bonzi, 1985). Feeding and oviposition of these head-bugs on maturing sorghum grains result in severe quantitative and qualitative losses, particularly on improved compact-headed types (Ratnadass et al., 1994a). These pests are therefore a major threat to the

increase of sorghum production through the extension of improved cultivars, which, although better yielding, are more susceptible to head-bug damage than local loose-panicled guinea landraces (Ratnadass et al., 1994b; Ratnadass et al., 1995).

Earlier efforts by ICRISAT, CIRAD and NARS in West Africa, have resulted in the development of reliable screening techniques, which made it possible to identify sources of resistance to *E. oldi*. High and stable resistance in compact-panicled sorghum cultivar Malisor 84-7 (Shetty et al., 1991) was confirmed and some of the factors associated with head-bug resistance in sorghum identified (Sharma et al., 1994a), while the status of S 34 as susceptible check was ascertained (Ratnadass et al., 1994b). Using pedigree breeding selection, it has been possible to transfer head-bug resistance from Malisor 84-7 to several advanced progenies such as 87W810, which combines reasonable head-bug tolerance and acceptable agronomic traits (Ratnadass et al., 1995).

Panicle laxity, glume length (> 5 mm), number of days to glume opening (> 20 days after anthesis), covering of the grain by the glumes (> 50%) and grain hardness were reported to contribute towards resistance to *E. oldi* (Sharma et al., 1994a). The major factor associated with this resistance in compact-panicled cultivar Malisor 84-7 appears to be a quicker endosperm hardening pattern, resulting in a shorter period during which head-bugs can feed and lay their eggs in the maturing grains (Fliedel et al., 1993).

Although the sorghum midge [*Stenodiplosis* (*Contarinia*) sorghicola (Coquillett) (Diptera: Cecidomyidae)] is the most important and widely distributed of all sorghum insect pests (Harris, 1976), its incidence is usually reported as low in WCA. However, most farmers in the region do not recognize that the empty panicles of sorghum are caused by midge and are unaware of the midge itself. Some attribute the emptiness of the panicles to other causes such as pollen wash and poor soils (Ratnadass & Ajayi, 1995). Midge incidence is therefore probably more frequent than is usually reported.

Resistance to sorghum midge was reviewed by Sharma et al. (1994b). Considerable progress has been made in the identification and utilization of resistance to this pest. The size of glumes in relation to that of grain and the rate of grain development were considered to account for resistance by antibiosis by limiting the space for larval development between glumes and grain (Sharma et al., 1990a, 1990b). With such characters, a cultivar like ICSV 197 (Agrawal et al., 1987) is both highly resistant to sorghum midge and highly susceptible to head-bugs.

Resistance to sorghum midge was found to be controlled by recessive to partially dominant genes, the number of which is unknown. Both general and specific combining effects are significant (Agrawal et al., 1988), but resistance is controlled largely by additive gene action (Sharma et al., 1996b in Henzell et al., 1997).

On the other hand, apart from preliminary studies on the genetics of head-bug resistance which suggested that resistance was rather recessive and that there was no maternal effect (Ratnadass et al., 1995), the genetic basis of resistance to *E. oldi* in sorghum is largely unknown. The current research was undertaken to study the genetics of this resistance, based on a diallel analysis. The elucidation of the inheritance of this resistance must help to decide what could be the best breeding procedure to transfer this resistance into high-yielding background.

Materials and methods

Plant material and crosses

The lines used as parents were Malisor 84-7 (=83-F6-225), a head-bug resistant genotype derived from a random mating Malian population (Shetty et al., 1991) and 87W810, a head-bug resistant progeny from a cross between ICSV 1002 and Malisor 84-7 (Ratnadass et al., 1995) and S 34, a head-bug susceptible genotype (Dangi & Djonnewa, 1988; Ratnadass et al., 1995) and ICSV 197, a midge resistant progeny derived from a cross between IS 3443 and DJ 6514 (Agrawal et al., 1987), which is also susceptible to head-bugs (Ratnadass et al., 1995). These lines were crossed in all possible combinations, including reciprocals, during the 1994-1995 and 1995-1996 offseasons, to generate a complete diallel set of 12 F1 hybrids. Both emasculation by hand and plastic bag techniques were used (House, 1985).

Field experiment

These 12 F1 hybrids and their four parents, were planted in randomized complete block designs with three replications at ICRISAT-CIRAD Research Station at Samanko (Lat.8°25'N; Long.12°32'W), near Bamako, Mali, in one date of sowing during the 1995 cropping season (trial D1, sown on 22 Jul), and in two dates of sowing during the 1996 cropping season (trials D2 & D3, sown respectively on 7 Jul & 26 Jul).

The parents were planted in four row plots of 4 m length, while the F1 hybrids were planted in single-row plots, bordered with two rows of the female parent. Spacing between and within the rows was 75 cm and 20 cm, respectively. Plant were thinned to one plant per hill. True F1s were identified for onward studies 8 weeks after emergence, based on morphological markers or heterosis for agro-morphological traits, compared to the neighboring parent. No insecticide was applied at any stage of the crop.

At the heading stage, five plants randomly chosen from the two central rows for the parent plots, and from the unique row for the hybrid plots, were covered with a paper selfing-bag. At early anthesis, three of these bags, chosen at random, were removed and replaced by head-cages, and the panicles were confined with 40 *E. oldi* adults from late anthesis until 20 days

Table 1. Sorghum head-bug damage visual rating scale

Score	Symptoms
1	all grains fully developed, of which less than 10% showing a few head-bug feeding punctures
2	grains fully developed, of which 11 to 50% showing feeding punctures, no eggs, no browning/shriveling
3	51 to 75% grains with feeding punctures and some with eggs, no browing/shriveling
4	>75% grains showing feeding or egg-laying punctures, and a few (<5%) turning slightly brown
5	Some grains ($\leq 25\%$) brown or shriveled due to head-bug feeding or egg-laying punctures
6	26 to 50% grains showing browning or shriveling
7	51 to 75% grains brown or shriveled
8	>75% grains brown or shriveled
9	>75% grains remaining undeveloped and barely visible outside the glumes

later, following the technique described by Sharma et al. (1992a). Before removing head-cages, a cottonswab soaked with ethyl acetate was introduced and all dead bugs were shaken into a polyethylene bag and kept into a deep freeze until counting was performed. Uncovered panicles were then allowed to mature.

Evaluation of reaction to head pests

Genotypic reaction to head-bugs was assessed using three parameters, namely a damage score under natural infestation (natural infestation score, NIS), a damage score under artificial infestation (artificial infestation score, AIS), and head-bug population buildup under artificial infestation (head-bug number, HBN). At grain maturity, all panicles, namely both the ones exposed to artificial infestation, and those exposed to natural infestation, were visually scored for head-bug damage, using a 1–9 rating scale (Table 1). Headbug numbers under artificial infestation were recorded only in 1996, on trials D2 & D3. However, a few plots of hybrids (F1s) in trials D1 & D2 were not evaluated for these variables, since the crosses had obviously failed, all plants showing the female parent type.

On the other hand, on the panicles exposed to natural infestation of trial D3, which was the only one of the three trials to sustain significant infestation by sorghum midge, due to late sowing, the damage of this pest was rated visually at maturity (sorghum midge score, SMS), on a 1 to 9 rating scale (1 = < 10%, 2 =11-20%, 3 = 21-30%, 4 = 31-40%, 5 = 41-50%, 6 =51-60%, 7 = 61-70%, 8 = 71-80%, and 9 = > 80%midge damaged spikelets) (Sharma et al., 1992b).

Data analysis

Although lines and F1 hybrids can be analyzed together, the diallel analysis was done only on F1 hybrids, including reciprocals but excluding parental lines values, to comply with the recommendations of Gallais (1990). Because the trial was repeated three times (with one date of sowing in 1995, and two in 1996), an additional factor, namely 'sowing date', was considered. To fulfill ANOVA conditions relating to normality of residuals and homoscedasticity, head-bug numbers were square root-transformed before analysis.

Because of unbalanced data, those relating with head-bug reaction were analyzed in two steps. In the first step, SAS software (SAS, 1989), allowed the analysis of the date, block (within date), F1 hybrid, and date*F1 hybrid interaction. In the second step, the OPEP software (Baradat & Labbé, 1995) was used to test the significance of general combining ability (GCA), specific combining ability (SCA), general reciprocal (GR) and specific reciprocal (SR) following the unbalanced fixed model (Griffing, 1956; Garretsen & Keuls, 1978).

Results

Head-bug resistance

Results presented in Table 2 confirmed head-bug resistance in Malisor 84-7, and head-bug susceptibility in S 34 and ICSV 197. 87W810, which had low damage scores despite high head-bug numbers under cage conditions, showed reasonable tolerance for head-bug damage. Hybrids derived from these parents did not exhibit any heterosis effect, since their values

Male parent (Parameter) Female parent (Experiment)	P1: M (NIS)	lalisor 8 (AIS)(I	84-7 HBN)	P2: 8 (NIS	37W81)(AIS)	0 (HBN)	P3: S (NIS	534)(AIS)	(HBN)	P4: I (NIS	CSV 1)(AIS)	97 (HBN)
P1: Malisor 84-7												
(D1)	2.8^{1}	4.8	-	3.1	3.7	_	3.5	5.2	_	3.9	3.9	-
(D2)	2.6	3.1	8.6	4.0	3.9	18.2	3.9	5.3	11.8	4.3	4.5	11.7
(D3)	3.1	3.7	9.5	3.7	4.2	19.4	4.6	4.8	17.8	4.4	4.9	20.6
P2: 87W810												
(D1)	-	-	-	3.9	3.8	-	4.6	4.6	-	5.3	4.6	-
(D2)	2.9	3.9	16.7	3.1	3.9	23.3	4.7	5.5	22.5	4.8	5.0	23.6
(D3)	3.5	3.3	14.8	4.7	4.3	22.2	5.1	4.7	21.3	5.3	4.9	24.6
P3: S 34												
(D1)	_	_	_	5.5	5.5	_	4.9	7.0	-	6.2	5.1	-
(D2)	4.7	6.1	11.9	4.5	4.5	22.2	6.3	7.0	24.3	5.7	5.3	25.6
(D3)	5.5	6.2	17.4	5.8	5.5	21.5	6.4	7.1	24.7	6.4	6.2	29.4
P4: ICSV 197												
(D1)	-	-	-	4.3	4.3	-	5.9	5.5	-	4.7	6.0	-
(D2)	3.6	4.7	16.9	4.2	4.8	24.5	4.8	5.2	23.1	4.7	5.8	21.1
(D3)	5.1	5.1	22.7	4.9	4.8	22.3	5.9	7.1	28.0	5.0	6.1	24.5

Table 2. Mean head-bug visual damage scores of lines under natural (NIS) and artificial infestation (AIS) recorded across experiments D1, D2 and D3, and mean square roots of head-bugs numbers under artificial infestation (HBN) recorded across experiments D2 and D3

¹ Bold indicates parent's performance.

for the parameters considered were always within the intervals defined by their parental lines. However, susceptibility to head-bugs appeared rather dominant as per results of F1 hybrids.

Results of global analysis of variance are given in Table 3. For all three parameters relating to headbug resistance, date, F1 hybrid and date*F1 hybrid interaction effects are highly significant. The diallel analysis is given in Table 4. Results are consistent: for all three parameters relating to head-bug resistance, GCA effects are larger than SCA effects, low and non significant, except for head-bug numbers. Maternal effects are generally not significant. However, a general maternal effect is highly significant for head-bug score under natural infestation. This result is due to S 34 which statistically shows, in its progenies, a different effect on the expression of the NIS variable depending on the direction of the cross.

Discrimination between resistant and susceptible varieties translates also when considering GCA values (Table 5). Sums of GCA values are not centered on 0 in the cases of trials D1 and D2, due to unbalanced data. Ranking of parental GCA values considered trial by trial shows a good stability of results. For NIS, only one change is observed in the group consisting of sus-

Table 3. Analysis of variance for reaction to head-bugs

Source of variation	Degrees of freedom	Mean square	F-test	
Date	NIS ¹	2	133.70	15.10**
	AIS ²	2	103.03	18.75**
	HBN ³	1	80.57	12.36**
Block/Date	NIS	6	6.36	0.72
	AIS	6	8.34	1.52
	HBN	4	7.32	1.12
F1 hybrid	NIS	11	29.39	3.32**
	AIS	11	23.06	4.20**
	HBN	11	111.49	17.11**
Date*F1 hybrid	NIS	22	21.79	2.46**
	AIS	22	22.40	4.08**
	HBN	11	20.36	3.12**
Error	NIS	66	8.85	
	AIS	66	5.49	
	HBN	39	6.52	

¹ NIS: Head-bug visual damage score under natural infestation.
² AIS: Head-bug visual damage score under artificial infestation.

³ HBN: Square roots of head-bug numbers under artificial infestation.

** F highly significant at p = 0.01.

Table 4. Diallel analysis of reaction to head-bugs

Source of variation	Degrees of freedom	Mean square	F-test				
General Combining Ability (GCA)							
NIS ¹	3	16.91	38.81**				
AIS ²	3	11.77	30.06**				
HBN ³	3	337.53	36.00**				
Specific Combining Ability (SCA)							
NIS	2	0.01	0.03				
AIS	2	0.47	1.21				
HBN	2	41.88	4.47*				
General Reciprocal (GR)							
NIS	3	1.93	4.43**				
AIS	3	0.29	0.75				
HBN	3	2.90	0.31				
Specific Reciprocal (SR)							
NIS	3	0.89	2.06				
AIS	3	1.02	2.61				
HBN	3	26.62	2.84*				
Error							
NIS	69	0.44					
AIS	69	0.39					
HBN	51	9.38					

^{1,2,3} cf. Table 3.

* F significant at p = 0.05.

** F highly significant at p = 0.01.

Table 5. General Combining Ability estimates for visual score under natural head-bug infestation (NIS), for visual score under artificial head-bug infestation (AIS), and for head-bug numbers under artificial head-bug infestation (HBN)

Experiment Parameter Parent	D1	D2	D3	Combined
Turumeter Turent				
NIS				
P1: Malisor 84-7	–1.55 a ¹	–0.72 a	–0.85 a	–0.99 a
P2: 87W810	–0.24 b	–0.10 b	–0.44 a	–0.29 b
P3: S 34	0.51 c	0.56 c	0.82 b	0.69 c
P4: ICSV 197	0.72 c	0.37 bc	0.46 b	0.51 c
AIS				
P1: Malisor 84-7	–0.58 a	–0.33 a	–0.59 a	–0.51 a
P2: 87W810	–0.34 a	–0.37 a	–0.85 a	–0.57 a
P3: S 34	0.78 b	0.61 b	0.90 b	0.79 c
P4: ICSV 197	–0.15 a	0.16 ab	0.54 b	0.23 b
HBN				
P1: Malisor 84-7	-	–7.00 a	-4.31 a	–5.45 a
P2: 87W810	-	4.06 c	-1.50 b	0.95 b
P3: S 34	-	0.95 b	1.39 c	1.11 b
P4: ICSV 197	-	3.00 bc	4.42 d	3.64 c

¹ GCA estimates followed by same letter within column are nonsignificantly different at p = 0.05. ceptible parents, namely in trial D1 where ICSV 197 appears to influence more than S 34 its progenies for head-bug resistance, whereas in the other two trials S 34 shows the strongest influence. However, as in all three trials ICSV 197 and S 34 belong to the same significance group, this change should not be regarded as significant. The date*F1 hybrid interaction was not due to a modification of parental hierarchy for reaction to head-bug attack, but to a mere modification of the gaps between them. It is therefore justified to carry out a combined analysis of all three trials, which constantly validate the resistant status of Malisor 84-7 and 87W810, as compared to the susceptible reaction of S 34 and ICSV 197.

All the same for AIS, where only one change was noted among resistant parents. In trial D1, Malisor 84-7 appears to have a stronger influence on its progenies than 87W810, while the reverse is observed in the other two trials. However, as Malisor 84-7 and 87W810 belong to the same significance group in all three trials, this inversion is not significant.

On the other hand, as far as HBN is concerned, parental GCA rankings are different in the two trials of 1996 (D2 & D3). This is due to 87W810, which in D2 appears to influence the more its progenies towards higher head-bug population build-up, while in D3, it influences them towards lower population build-up. Therefore, the global analysis is not justified. However, like for the other two parameters, Malisor 84-7 consistently appears to be head-bug resistant.

As for head-bug visual scores (NIS & AIS). The higher the field value for head-bug susceptibility of a parental line, the higher its GCA value, and vice-versa. Correlation coefficients were high, namely 0.969 and 0.994 respectively (2 degrees of freedom: d.f.). It suggests that these parents transmit to their progeny their own reaction to the pest. On the other hand, the correlation coefficient relating to HBN was lower, namely r = 0.927 (2 d.f.).

Midge resistance

Means of midge scores and GCA estimates are given in Table 6. Midge resistance in ICSV 197 is confirmed. Global analysis of variance showed non-significant block effect. Only F1 hybrid effect was significant (p = 0.05). As for the diallel analysis, only GCA effect was significant (p = 0.01). Statistically, SCA and maternal effects do not influence the expression of the score measuring midge resistance in hybrids. Results show that the transmission of midge resistance

Table 6. Mean visual scores and General Combining Ability (GCA) estimates for reaction to sorghum midge as assessed by midge visual scores (SMS) recorded on all genotypes on

trial D3 under natural infestation

· · · · · · ·				
P1: Malisor 84-7	2.7 $(0.40 a)^1$	4.0	2.7	2.2
P2: 87W810	4.0	6.7 (0.85 a)	4.0	1.3
P3: S 34	2.3	4.0	1.7 (0.27 a)	1.7
P4: ICSV 197	1.3	1.0	1.3	1.0 (-1.52 b)
1				

¹ Bold indicates parent's performance. GCA estimates are given in parentheses. GCA estimates followed by same letter along main diagonal are non-significantly different at p = 0.05.

by ICSV 197 in its crosses is confirmed by a negative GCA value.

The relationship between parental field values and GCA values, was lower than in the case of head-bug scores, with a correlation coefficient r = 0.717 (2 d.f.). On the other hand, GCAs for scores under natural infestation, relating to head-bugs on the one hand, and midge on the other, seem to be independent for the genitors used, with a correlation coefficient r = 0.508(2 d.f.). However, more experimental points would be needed to test the relationship between these two characters.

Discussion and conclusion

Whatever the variable considered to assess resistance to head-bugs and midge, there was a non-significant block effect. In the conditions of this study, pest pressure was uniform on the experimental layout, which in turn did not influence incidence distribution. On the other hand, F1 hybrid effect was always significant: genotypes reacted differently to pest incidence.

When, in the case of the study of head-bug resistance, the experiment was repeated, the sowing date effect was highly significant. The level of head-bug incidence, as assessed through the three variables, was influenced by the sowing date. Furthermore, the date*F1 hybrid interaction was also significant. Depending on the sowing date, genotype ranking for the three variables varied, although there were no dramatic changes. As illustrated in Table 2, the most resistant genotypes remained the same irrespective of the planting date (Malisor 84-7*87W810 or 87W810*Malisor 84-7): similar results were observed for the most susceptible genotypes (S 34*ICSV 197 or ICSV 197*S 34).

In contrast, such an interaction occurred with the parental GCA, though the ranking remained the same irrespective of the sowing date (Table 5). Except in one situation out of eight, GCA analysis trial-wise indicates that irrespective of the criteria studied, the crossing value has the same partition as for the per se value between resistant parents Malisor 84-7 and 87W810, and susceptible parents S 34 and ICSV 197. Otherwise, GCA values show that discrimination between resistant parents is better under natural infestation (namely under multiple-choice conditions) as compared to artificial infestation (namely under no-choice conditions). This translates a probable nonpreference component in Malisor 84-7 as compared to 87W810.

Although it seems to be suggestive, the visual rating scale described appears to provide more reliable results than head-bug counts. This is understandable under natural infestation because when sampling head-bug populations the peak of abundance can be 'missed', while cumulative damage assessed at grain maturity cannot. In contrast, the head-bug rating scale integrates several symptoms, which could account for the discrepancy observed between head-bug numbers and damage score, under artificial infestation. For example, extensive adult feeding damage results in dramatic shriveling of grains, making them unsuitable for egg-laying, which will somehow paradoxically translate into low population build-up despite high damage score. This bias could be overcome by evaluating separately damage by adult feeding (using only male adults), and damage by female oviposition (confining only mated females with sorghum panicles, for a limited time). A high population build-up resulting in low damage can also translate 'tolerance', as it was observed in 87W810.

For all the traits, GCA was the most important effect. It was by far predominant over all other effects (SCA or maternal), which were seldom significant. This result highlights the importance of additivity as the most important type of gene action for determining resistance to head-bugs in sorghum. In this study (which is that of a fixed diallel), levels of reaction to attacks by head pests appear to be heritable and amenable to fixation. In terms of breeding strategies, line creation through pedigree selection should be considered. Parental resistance or susceptibility per se and GCA being positively related, it is therefore justified to use resistant genotypes as sources of resistance in a program aiming at creating such lines. Parents with good level of resistance and desirable (negative) GCA effects were Malisor 84-7 and 87W810 for head-bugs, and ICSV 197 for sorghum midge.

A significant general maternal effect was found only in the case of head-bug score under natural infestation. It was due to S 34, whose effect on its progenies differed depending whether it was male or female in the crosses.

Genotypic non-preference observed under field conditions was highly influenced by the time of flowering and pest density at the time of flowering for different genotypes. Rather than affecting bug resistance per se, this maternal effect could actually affect number of days to flowering, so that under natural infestation, grain maturation in some genotypes could coincide with peak of head-bugs, while that in the reciprocals could 'escape' infestation. The average numbers of days to 50% flowering of the four parents (Malisor 84-7, 87W810, S 34 & ICSV 197) were not measured in this trial; however the means observed in eight screening trials from 1991 to 1995, were respectively 78.6 ± 6.2 , 81.4 ± 6.2 , 77.3 ± 6.3 and 75.5 ± 4.3 days (Ratnadass, unpublished data). This result could be linked to better germination owing to bigger seeds in some genotypes, which may promote a rapid early plant growth, thereby shortening the growth cycle.

The results suggested an independent genetic system for head-bug resistance and midge resistance. Parents resistant to one of the two pests are susceptible to the other, and vice-versa. Similarly, hybrids resistant to head-bugs are rather susceptible to midge and vice-versa (Tables 2 and 6). As a result, parents improving their progeny for a character had progeny with poor performance for the other character. Malisor 84-7 and 87W810-derived offspring showed an opposite response to these insect pests than those offspring derived from S 34 and ICSV 197. In the case of ICSV 197, those factors contributing to midge resistance also make this line susceptible to head-bugs. Short glumes and rapid ovary development, while exposing midge larvae to adverse biotic and abiotic factors (mainly predators and climate), also expose the maturing grain to head-bug damage during a long period. Whereas it is rapid ovary development (3–7 days after anthesis) that contributes towards midge resistance (Sharma et al., 1990a; 1990b), it is quicker endosperm hardening (1–3 weeks after anthesis) that contributes towards head-bug resistance (Fliedel et al., 1993). Although exposed outside the glumes, the grains in Malisor 84-7 and 87W810 harden quickly, thereby making them resistant to head-bugs.

Factors in ICSV 197 conferring resistance to sorghum midge, and those in Malisor 84-7 conferring resistance to head-bugs, can therefore be brought together through development of lines that combine short glumes, rapid ovary development and quick endosperm hardening. This was actually achieved by crossing the two cultivars. Several fixed progenies exhibiting multiple resistance were thus obtained (Ratnadass, unpublished data). Further screening aiming at detecting such factors within the existing genetic resource base is desirable. Likewise, one of the mechanisms of resistance to sorghum midge consists in asynchrony between time of sorghum spikelet flowering and presence of sorghum midge (Diarisso et al., 1998). Such a mechanism should also be used to develop such multiple-resistant varieties.

The results of this study could be completed by mapping resistance genes, using molecular markers. Research aiming at identifying markers linked with resistance is underway both for midge in Australia (Tao et al., 1996; Henzell et al., 1997) and headbugs in Mali and France (Deu et al., 1999), to use marker-assisted selection.

Acknowledgements

We thank Messrs B. Cissé, D. Diarra, C.A.T. Thiéro and Ms S. Togola for their help in conducting these experiments, Mr J.L. Marchand for his suggestions, and Drs R. Ortiz and P. Bramel-Cox for their useful comments on the manuscript. 138

- Agrawal, B.L., C.V. Abraham & L.R. House, 1988. Inheritance of resistance to midge, *Contarinia sorghicola* Coq., in sorghum, *Sorghum bicolor* (L.) Moench. Insect Sci Appl 9: 43–45.
- Agrawal, B.L., H.C. Sharma & K. Leuschner, 1987. Registration of 'ICSV 197' midge resistant sorghum cultivar. Crop Sci 27: 1312–1313.
- Baradat, P. & T. Labbé, 1995. OPEP. Un logiciel intégré pour l'Amélioration des plantes pérennes. In: CIRAD-CP (Ed.), Traitements Statistiques des Essais de Sélection. Stratégies de Sélection des Plantes Pérennes, pp. 303–330. Montpellier.
- Dangi, O.P. & A. Djonnewa, 1988. Present status of rainy season sorghum breeding in Cameroon. In: Traoré, M.D., C.C. Nwasiké, A. Tenkouano & O. Ajayi (Eds.), Proc 3rd regional sorghum workshop, WCASRN OAU/SAFGRAD, 20–23 Sep 1988, Maroua, Cameroon. pp. 36–47, Ouagadougou, Burkina Faso.
- Deu, M., L. Grivet, G. Trouche, C. Barro, A. Ratnadass, M. Diabaté, M. Ag Hamada, G. Fliedel, J.F. Rami, C. Grenier, P. Hamon, J.C. Glaszmann & J. Chantereau, 1999. Use of moleculars markers in the sorghum breeding program at CIRAD. In: Application of molecular markers in plant breeding: draft training manual, ICRISAT/IITA/University of Hohenheim/Eberhard-Karls University of Tübingen/Rockefeller Foundation Seminar, 16–17 Aug 1999, Ibadan, Nigeria, pp. 64–85.
- Diarisso, N.Y., B.R. Pendleton, G.L. Teetes, G.C Peterson & R.M. Anderson, 1998. Spikelet flowering time: cause of sorghum resistance to sorghum midge (Diptera: Cecidomyidae). J Econ Ent 91(6): 1464–1470.
- Doumbia, Y.O. & S.M. Bonzi, 1985. Note sur les problèmes des insectes des panicules du sorgho au Mali. In: SAFGRAD (Ed.), Proc of the West African Regional Sorghum Network Workshop, 21–24 Oct 1985, Bamako, Mali, pp. 173–182, Ouagadougou, Burkina Faso.
- Food and Agriculture Organization of the United Nations (FAO) & International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) 1996. The world sorghum and millet economies: facts, trends and outlook. 68 pp.
- Fliedel, G., A. Ratnadass & M. Yajid, 1993. Study of some physicochemical characteristics of developing sorghum grains in relation with head bug resistance. In: ICC (Ed.), Proc Int Symp on Cereals Sci and Technology: Impact on a Changing Africa, 9–13 May 1993, Pretoria, South Africa, pp. 46–63.
- Gallais, A., 1990. Théorie de la sélection en amélioration des plantes. Masson (Collection Sciences agronomiques), Paris, 588 pp.
- Garretzen, F. & M. Keuls, 1978. A general method for the analysis of genetic variation in complete and incomplete diallel and North Carolina II (NC II) designs. Part II: proceedure and general formulas for the fixed model. Euphytica 27: 49–68.
- Griffing, B., 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci 9: 463–493.
- Harris, K.M., 1976. The sorghum midge. Ann Appl Biol 64: 114–118.

- Henzell, R.G., G.C. Peterson, G.L. Teetes, B.A. Franzmann, H.C. Sharma, O. Youm, A. Ratnadass, A. Toure, J. Raab & O. Ajayi, 1997. Breeding for resistance to panicle pests of sorghum and pearl millet. In: INTSORMIL & ICRISAT (Eds.), Proc Int Conf on Genetic Improvement of Sorghum and Pearl Millet, 22–27 Sep 1996, Lubbock, Texas, pp. 255–280, Lincoln, Nebraska.
- House, L.R., 1985. A guide to sorghum breeding. 2nd edn. ICRISAT, Patancheru, India, 206 pp.
- MacFarlane, J., 1989. The hemipterous insects and spiders of sorghum in Northern Nigeria. Insect Sci Appl 10: 277–284.
- Ratnadass, A., B. Cissé & K. Mallé, 1994a. Notes on the biology and immature stages of West African sorghum head bugs *Eurystylus immaculatus* and *Creontiades pallidus* (Heteroptera: Miridae). Bull Ent Res 84: 383–388.
- Ratnadass, A., K.V. Ramaiah, H.C. Sharma & B. Cissé, 1994b. Réaction de variétés de sorgho aux attaques de la punaise des panicules *Eurystylus immaculatus* Odhiambo (Heteroptera, Miridae) en Afrique de l'Ouest. In: J.M. Menyonga, T. Bezuneh, J.Y. Yayock & I. Soumana (Eds.), Progress in Food Grain Research and Production in Semi-Arid Africa: Proceedings of the SAFGRAD Inter-Network Conference, 7–14 Mar 1991, Palais des Congrès, Niamey, Niger, pp. 333–343, Ouagadougou, Burkina Faso.
- Ratnadass, A. & O. Ajayi, 1995. Panicle insect pests of sorghum in West Africa. In: K.F. Nwanze & O. Youm (Eds.), Panicle Insect Pests of Sorghum and Pearl Millet, Proc Int Consultative Workshop, 4–7 Oct 1993, ICRISAT Sahelian Center, Niamey, Niger, pp. 29–38, Patancheru, India.
- Ratnadass, A., O. Ajayi, G. Fliedel & K.V. Ramaiah, 1995. Host plant resistance in sorghum to *Eurystylus immaculatus* in West Africa. In: K.F. Nwanze & O. Youm (Eds.), Panicle Insect Pests of Sorghum and Pearl Millet, Proc Int Consultative Workshop, 4–7 Oct 1993, ICRISAT Sahelian Center, Niamey, Niger, pp. 191–199, Patancheru, India.
- SAS Institute Inc., 1989. SAS/STAT User's Guide, Version 6 [4th Edition]. SAS Institute Inc., Cary NC, USA.
- Sharma, H.C., Y.O. Doumbia & N.Y. Diorisso, 1992a. A head-cage technique to screen sorghum for resistance to mirid head bug *Eurystylus immaculatus* Odh. in West Africa. Insect Sci Appl 13: 417–427.
- Sharma, H.C., S.L. Taneja, K. Leuschner & K.F. Nwanze, 1992b. Techniques to screen sorghums for resistance to insect pests. Information Bulletin No. 32, ICRISAT, Patancheru, India, 48 pp.
- Sharma, H.C., Y.O. Doumbia, M. Haidara, J.F. Scheuring, K.V. Ramaiah & N.F. Beninati, 1994a. Sources and mechanisms of resistance to head bug, *Eurystylus immaculatus* Odh. in West Africa. Insect Sci Appl 15: 39–48.
- Sharma, H.C., B.V.S. Reddy, J.W. Stenhouse & K.F. Nwanze, 1994b. Host plant resistance to sorghum midge. Int Sorghum Millets Newsl 35: 30–41.
- Sharma, H.C., P. Vidyasagar & K. Leuschner, 1990a. Components of resistance to the sorghum midge, *Contarinia sorghicola*. Ann Appl Biol 116: 327–333.
- Sharma, H.C., P. Vidyasagar & K. Leuschner, 1990b. Componential analysis of the factors influencing resistance to sorghum midge, *Contarinia sorghicola* Coq. Insect Sci Appl 11: 889–898.
- Shetty, S.V.R., N.F. Beninati & S.R. Beckerman, 1991. Strengthening sorghum and pearl millet research in Mali. 85 pp.
- Steck, G.J., G.L. Teetes & S.D. Maïga, 1989. Species composition and injury to sorghum by panicle feeding bugs in Niger. Insect Sci Appl 10: 199–217.