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Resistance of cacao (*Theobroma cacao* L.) to *Sahlbergella singularis* (Hemiptera: Miridae): investigation of antixenosis, antibiosis and tolerance

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Abstract. Cacao genotypes of various origins were evaluated for resistance to the cocoa mirid (*Sahlbergella singularis* (Haglund)) based on field damage, antixenosis, antibiosis and tolerance. Field damage was assessed by scoring recent and cumulative damage by the mirid to the major genetic groups of cacao. Antixenosis assessment was based on the number of feeding lesions on twig segments using a choice test. Antibiosis was measured through survival of young mirid nymphs on shoots and pods, whereas tolerance was assessed through the reaction of the twigs to mirid feeding punctures. Among the genetic groups of cocoa, the Upper Amazon, the materials from Guiana and hybrid genotypes were the least damaged by the mirids, both for recent and cumulative damage. The Catongo group was, by far, the most susceptible group with more than 50% of the canopy showing both recent dieback and cumulative canker damage. With regard to antixenosis, antibiosis and tolerance, significant differences ($P < 0.05$) were found between the genotypes. The least preferred clones sustained between 2 and 3 lesions compared with the most preferred ones with 6–8 lesions per twig segment. Clones UPA402, T79/501 and IMC67 gave the lowest rate of mirid nymph survival, indicating that they exhibit antibiosis. The clones PA107, SCA6 and C151-61 sustained high numbers of mirid feeding lesions and relatively high levels of shoot death, but have a good ability for re-growth and can be considered as tolerant genotypes.

Key words: cocoa, mirid, *Sahlbergella singularis*, antixenosis, antibiosis, tolerance

Introduction

The cocoa mirids *Sahlbergella singularis* (Haglund) and *Distantiella theobromae* (Distant) are the most damaging insect pests of cocoa in Côte d'Ivoire. These insects are also serious pests in other cocoa-producing countries such as Ghana, Nigeria and Cameroon (Lavabre, 1970, 1977*a*; Entwistle, 1972).

The biology and behaviour of the mirids have been extensively studied (Williams, 1953; Taylor, 1954; Kay, 1961; Gibbs and Pickett, 1966; Braudeau, 1969; Kumar and Ansari, 1974). Mirids feed on every part of the plant except the leaves and the roots. Both adult and immature stages cause damage through punctures made on vegetative parts or fruiting structures. During feeding, saliva is injected into the wound and this has a marked histolytic effect, probably due to the action of esterases (Williams, 1953). On young shoots, the mechanical damage and the effect of the toxic saliva are sufficient to cause their death. On the other hand, on hardened twigs and stems, the mechanical

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effect is less important. However, subsequent invasion of the wounds by a pathogenic fungus, *Albonectria rigidiuscula* (Berk. and Br.) has been reported (Crowdy, 1947). These infections result in cankering or bark roughening, destruction of the flower cushions and a severe dieback of twigs and branches.

On fully grown pods, the feeding sites are marked by black spots of dead tissue, but maturation may continue. However, on young pods or cherelles, a high number of feeding punctures may cause distortion during growth or even death of the fruit. Yield losses attributed to mirids alone have been estimated to be 30–40% (Lavabre, 1977*a*).

In Côte d'Ivoire, cocoa mirids are controlled by combining agronomic practices and insecticide applications (Lavabre, 1960; Marchart, 1971; Nguyen-Ban, 1971; Decazy, 1979; Decazy and Essono, 1979; Coulibaly *et al.*, 1998). However, many problems are associated with chemical use. First of all, farmers have been reluctant to adopt chemical control because of high costs of chemicals and application equipment, and low availability of water for the preparation of the spray mixture. Other problems are related to environmental contamination, disruption of biodiversity, effect on non-target organisms and potential residues in cocoa beans. As a result, research has been oriented towards the development of alternative methods.

The development and use of mirid resistant cocoa varieties is one of the alternatives to chemical control. Mirid resistance studies in cocoa have been carried out by several workers, including Bruneau De Miré and Lotodé (1974), Decazy and Lotodé (1975), Decazy and Coulibaly (1981), Nguyen-Ban (1993) and Sounigo *et al.* (1993). However, these studies have mostly concentrated on assessment of field damage and progress has so far been limited. No work has elucidated the mechanisms of mirid resistance in cocoa. The current study was designed to evaluate selected cocoa genotypes for resistance to mirids, through antixenosis, antibiosis and tolerance.

Materials and methods

The study was conducted during 2000–2003 at the research station of the National Agricultural Research Center (CNRA) in Divo, Côte d'Ivoire, within the framework of the CFC/ICCO/IPGRI project. The genotypes tested were from various origins. Some genotypes were clones used as parents in the reciprocal recurrent selection (RRS) programme in Côte d'Ivoire. Another group was made up of 'international clones', which were introduced from the quarantine facilities of the University of Reading (UK) and from CIRAD (France). Others were selected local clones either used as parents in the breeding programme or planted in the main germplasm collection in Divo. The genotypes were evaluated separately for field damage, antixenosis, antibiosis or tolerance *vis-à-vis* the mirids. The methods applied follow the recommended Working Procedures for the CFC/ICCO/IPGRI project (Eskes *et al.*, 2000), with some modifications.

Field observations on recent and cumulative damage

The study was conducted at the CNRA research station in Divo, Côte d'Ivoire and the materials tested were genotypes planted in a plot in the 1980s (few genotypes were added in the 1990s). A *Glyricidia* spp. (Fabaceae) planted in the plot and pruned when necessary provided light overhead shade. The materials are from various origins, some introduced from Latin American countries belonging to the major genetic groups of cacao such as Upper Amazon (UA; mainly Pound collections), Amelonado, 'Criollo' (Trinitario types near to Criollo), Trinitario and Catongo (near homozygous Amelonado selection from Brazil). Other genotypes studied here belonged to specific groups such as materials collected in the wild in French Guiana (identified as 'Guianan'; Lachenaud and Sallée, 1993), doubled haploids of UA origin, materials collected from Venezuela and local hybrid clones (mainly selected in crosses between UA and Amelonado clones). Four related *Theobroma* species (Sterculiaceae) were also included in the test (*Theobroma grandiflorum* (Willd. ex Spreng) K. Schum., *Theobroma bicolor* L., *Theobroma microcarpum* Mart. and *Theobroma speciosum* (Willd. ex Spreng)).

About 500 genotypes (clones) are represented in the plot. Each genotype was represented by five trees planted in a row. Before starting the observations, the *Glyricidia* spp. was pruned and the plot was left without insecticide treatment for a period of 1 year (2000) so that it was severely attacked by the mirids. The new damage caused by the mirids is classified here as 'recent damage'. The recent damage was characterized by death of leaves and twigs in the canopy of the trees. On the other hand, observations were made on mirid damage that had accumulated over several years on the trunk and branches; such damage is classified hereafter as 'cumulative damage'. Cumulative damage is made up of cankers of different sizes and intensity, visible on the trunks and branches. A score was given to each tree on the basis of the intensity (number and size) of these cankers on the trunks and the main branches.

Rating of cumulative damage has been used by several researchers to search for resistant cocoa genotypes (Decazy and Coulibaly, 1981; Sounigo *et al.*, 1993). The rating is given on a scale of 0–4, where 0 corresponds to no damage, 1 corresponds to 1/4 of surface of trunk and branches cankered, 2 corresponds to 1/2 of surface of trunk and branches cankered, 3 corresponds to 3/4 of surface of trunk and branches cankered and 4 corresponds to almost all the trunk and branches cankered. The rating of the recent damage was performed in a similar manner but the score was given according to the level of dieback of the leaves and twigs. Thus 0 corresponds to no dieback, 1 corresponds to 1/4 of the leaves and twigs showing dieback, 2 corresponds to 1/2 of the leaves and twigs showing dieback, 3 corresponds to 3/4 of the leaves and twigs showing dieback and 4 corresponds to almost all the leaves and twigs showing dieback. Four technicians carried out the ratings on all individual trees of each genotype.

Evaluation of antixenosis

This study was conducted with the objective of identifying cocoa genotypes showing no or low levels of preference by mirids. The material tested included RRS parents and the international clones.

Fifty RRS parental clones were evaluated in two separate groups of 25. One group was made up of the Lower Amazon (LA) and Trinitario parents and the second by UA parents. The experimental design was an incomplete block with 6 replicates and 30 blocks. Such a design allows the comparison of each genotype with the others within the same experimental set-up (Cochran and Cox, 1957). Twenty-four international clones, and one locally selected clone (C151-61), were evaluated in a similar manner, using clone T79/501 as a resistant control, as it was previously shown to be promising for mirid resistance on the basis of damage in the field (Sounigo *et al.*, 1993).

Healthy green twigs of young flushes obtained from the field were brought to the laboratory and cut into 6 cm sections. Five fragments of twigs with the same diameter and representing five different cocoa genotypes were placed end to end in 30 large Petri dishes (16 cm diameter × 2 cm height), according to the statistical design. One fourth instar mirid nymph that was starved for 24 h was placed in each Petri dish. Mirid nymphs were collected from the field 1 day before using in the experiment. The insects were allowed to feed for 24 h and the feeding lesions on the twig fragments were counted for each genotype to assess preference for the different genotypes.

Evaluation of antibiosis

This study was carried out with the objective of assessing the survival and the development of cocoa mirids on selected cocoa genotypes. The material evaluated included 16 selected local clones. These clones were tested on both twigs and pods.

A no-choice test was conducted to assess mirid survival and development. The design was a completely randomized design with five replications for the test on twigs and eight replications for the test on pods. Healthy green flush or chupon twigs were labelled in the field or in a budwood garden. The second instar mirid nymphs were obtained from a field collection. A nylon mesh sleeve cage (170 cm height × 30 cm diameter) was used to confine second instar mirid nymphs on a twig or on a chupon. Both ends of the cage were securely tied to prevent the insects from escaping. The shoots were kept in their natural position by tying the sleeve cage to a wooden stake. Glue was applied below the cage on the twigs or chupons and around the stake to prevent any ants from attacking the mirids in the cages. In addition, any other shoots in contact with the cages were cut off. On susceptible genotypes, the twigs sometimes dried up from feeding punctures before the insects completed full development into adults. In such a situation, the nymph was moved to a new twig on the same tree to continue observations on their development. For the test on pods, five second instar nymphs were confined on mature green pods. Usually more than five mirid nymphs can complete development on one pod. Here, again precautions were taken to prevent ants from attacking the mirids.

The nymphs were allowed to feed on the shoots or pods until they died or became adults. On the shoots, a replicate is a tree with three cages and on the pods a replicate is a tree with two cages. The mortality of the nymphs was recorded every 2 days, and at the end of the experiment, the rate of mirid larval survival was determined for each genotype.

Evaluation of tolerance

The study was conducted on 17 international clones with the objective of identifying cocoa genotypes capable of withstanding or recovering from mirid damage. The experiment was based on the assessment of level of death of twigs and recovery from damage in response to mirid feeding punctures. The experimental design was a complete randomization of four replicates. A sleeve cage (170 cm height × 30 cm diameter) made with mosquito screen nylon mesh was used to confine one fourth instar mirid nymph on a single semi-hardened healthy twig for 48 h. The insect was then removed and the initial number of feeding lesions counted. The twig was inspected for death and regrowth weekly for the first month and thereafter monthly for 3 months. For assessment of the degree of shoot death, a score of 0–4 was given to the shoot, with 0 corresponding to no dieback symptoms, 1 to 1/4 of the leaves showing dieback, 2 to 1/2 of the leaves showing dieback, 3 to 3/4 of the leaves showing dieback and 4 corresponding to shoots with all the leaves showing dieback. The number of feeding lesions was counted again at the end of the third month to determine the percentage of recovery for each genotype.

Data analysis

The data were submitted to an ANOVA using the General Linear Model (GLM) procedure of SAS (SAS Institute, 1996). Mean separation was performed by the Waller–Duncan *k*-ratio *t*-test. For the field observation data, the mean scores of each genotype were used to analyse variation between genetic groups. For the analyses of variation within each group, the mean score of each technician was considered as a replicate in the statistical analysis. The genotypes having at least one off-type in the row of five trees were excluded from the analysis. A Pearson correlation coefficient was estimated between the cumulative and recent damage, and between the antibiosis tests on pods and twigs.

Results and Discussion

Field damage

Significant differences were found between the major groups of cacao for recent mirid damage ($P < 0.001$) and cumulative damage ($P < 0.001$; Table 1). The UA, Guianan and hybrid genotypes were the least damaged by the mirids (Tables 2 and 3). The average scores of these genetic groups varied between 0.1 and 0.3 for the recent damage and between 0.4 and 0.8 for the cumulative damage, indicating that very little of their canopies showed dieback of branches and less than 1/4 of the surfaces of the trunks and branches were covered with cankers. On the other hand, Catongo was by far the most susceptible group. This group had scores of 2.3 for recent damage and 2.0 for cumulative damage. This indicated that the Catongo group had more than 50% of the canopy showing dieback and more than 50% of the surfaces of the trunks and branches covered with cankers. The Trinitario, the Amelonado and the Criollo were also found to be susceptible, but to a lesser extent.

These results suggest that the UA, the Guianan and the hybrid groups contain several promising genotypes for mirid resistance. Our results corroborate those of Sounigo *et al.* (1993) who showed, from a study on the behaviour of a group of parents and their progenies *vis-à-vis* cocoa mirids, that UAs and their progenies were found to be more promising for mirid resistance than the other tested groups and their progenies. In our study, the good performance of the cloned hybrids could be explained by the fact that the initial breeding programme in Côte d'Ivoire was founded on crosses made between introduced UA and local Amelonado genotypes and that these cloned hybrids were already selected for their agronomic characteristics.

The average recent and cumulative damage for the genetic groups was significantly positively correlated ($r = 0.86$; $P < 0.001$), suggesting that groups that showed heavy cumulative damage also showed heavy recent damage. A similar result was found for the correlation between all individual genotypes evaluated ($r = 0.48$; $P < 0.001$). Moreover, correlation analysis between the recent and cumulative damage to genotypes within each group also resulted in varying levels of positive and often significant correlations (Table 4). These results indicate that genotypes that showed heavy cumulative damage are the same as those showing heavy recent damage.

Significant differences were also found between genotypes within the groups for both recent and cumulative damage (Table 1). Several UA and Guianan clones showed low levels of recent and cumulative mirid damage, corroborating earlier results of Sounigo *et al.* (1993) who found, in a similar study, that the least susceptible clones belong to the UA group. Indeed, UA clones PA120, PA150, NA32, P7, UPA402, UPA413, UPA401 and Amelonado clone IFC2 showed low mirid damage in both studies. On the other hand, clone ICS100 ('Criollo') was among the most susceptible genotypes in both studies.

The results obtained in this study indicate that susceptibility or resistance of cocoa genotypes to mirids varies from one genotype to another, and from one major cocoa group to another. The low level of damage to some of these clones has been attributed to either antixenosis (due to the lack of preference) or antibiosis (due to the larval mortality) (Coulibaly, 2005). Although the mechanism of resistance has not been clearly investigated, it has been suggested that the behaviour of the clones *vis-à-vis* mirid attacks is controlled by several mechanisms, including colour of the young leaves in the field (Lavabre, 1977*b*), water content of the twigs (Nguyen-Ban, 1993) and the presence of phenolic compounds such as flavonol-4 and flavonol-7 (Cros *et al.*, 1996).

Antixenosis

Significant differences were found between the Lower Amazon RRS parents ($P < 0.05$) and

Table 1. Result of the ANOVA of scores of recent and cumulative mirid damage for genotypes within major genetic groups in the cacao collection in Divo

	Recent damage				Cumulative damage			
Sources of variation	Treatment DF	Error DF	F	P	Treatment DF	Error DF	F	P
Variance between genetic groups of cacao	9	1738	77.9	$P < 0.001^{***}$	9	1700	52.2	$P < 0.001^{***}$
Variance within groups								
Catongo	15	45	16.8	$P < 0.001^{***}$	15	45	2.3	$P < 0.05^{*}$
Trinitario	69	207	6.6	$P < 0.001^{***}$	69	207	3.8	$P < 0.001^{***}$
Amelonado	75	224	12.4	$P < 0.001^{***}$	75	222	2.6	$P < 0.001^{**}$
UA doubled haploids	46	138	7.9	$P < 0.001^{***}$	46	113	1.3	$P > 0.05$ NS
'Criollo'	18	54	10.6	$P < 0.001^{***}$	18	54	2.5	$P < 0.01^{**}$
Venezuelan	7	21	3.2	$P < 0.05^{*}$	7	21	4.3	$P < 0.01^{**}$
Guianan	43	128	10.9	$P < 0.001^{***}$	43	119	3.9	$P < 0.001^{***}$
Hybrids	49	146	4.1	$P < 0.001^{***}$	49	147	3.2	$P < 0.001^{***}$
UA	103	307	2.5	$P < 0.001^{***}$	103	304	3.1	$P < 0.001^{***}$
Related *Theobroma* species	5	—	—	—	5	—	—	—

NS, not significant; UA, Upper Amazon.
*Significant at $P < 0.05$.
**Significant at $P < 0.01$.
***Significant at $P < 0.001$.

between the Upper Amazon RRS parents ($P < 0.001$) with regard to the number of lesions. However, there was a relatively large overlapping of groups of significance according to the Waller–Duncan test. Clones T79/501, UPA134, ICS60, UPA409, PA150, IMC57 (UA parents) and IFC14, N38, R15, IFC6, IFC15, IFC5 (LA parents) appeared to be the least preferred (Table 5). These clones showed between 2 and 3.5 lesions compared with the most preferred ones that showed between 6 and 8 lesions.

The number of feeding lesions also varied significantly ($P < 0.001$) among the international clones. The clones PA150, LCT-EEN46, EET59, SCA6, PA107 and Playa Alta2 were the most promising with regard to antixenosis (Table 6). These clones had fewer lesions (2–3) than the five most preferred clones (4.5–6 lesions). Antixenosis denotes the presence of morphological or chemical plant factors that adversely alter the insect behaviour, resulting in the insect moving away and selecting a different host plant (Smith, 1989). In cocoa, this is usually expressed by the differences in the number of feeding lesions in the laboratory and the level of dieback in the canopy in the field (Coulibaly, 2005; N'Guessan *et al.*, 2006). Our results partly correspond with those obtained by Sounigo *et al.* (1993) who found T79/501 and PA150 also to be promising for mirid resistance based on cumulative field damage observed in clone trials. In addition, other studies indicated that UPA134 was comparatively less attacked by mirids in the field (Lavabre, 1977*b*).

Table 2. Score of recent mirid damage for selected cacao groups

Genetic groups of cacao	Score of recent damage	Mean separation
Catongo	2.32	A
Trinitario	1.15	B
Amelonado	1.08	B
UA doubled haploids	0.78	C
'Criollo'	0.75	C
Venezuelan	0.50	D
Guianan	0.32	DE
Hybrids	0.30	DE
UA	0.19	EF
Related *Theobroma* species	0.00	F

UA, Upper Amazon.
Means within the same column followed by different letters significantly different at $P < 0.05$ according to the Waller–Duncan *k*-ratio *t*-test (SAS Institute, 1996).

Table 3. Scores of cumulative mirid damage for selected cacao groups

Genetic groups of cacao	Score of cankers	Mean separation
Catongo	2.03	A
'Criollo'	1.59	B
Trinitario	1.34	C
Amelonado	0.98	D
UA doubled haploids	0.93	D
Venezuelan	0.84	DE
Hybrids	0.83	DE
UA	0.69	E
Guianan	0.39	F
Related *Theobroma* species	0.00	G

UA, Upper Amazon.
Means within the same column followed by different letters significantly different at $P < 0.05$ according to the Waller–Duncan k-ratio t-test (SAS Institute, 1996).

Antibiosis

Significant differences were found between clones with regard to mirid survival on twigs ($P < 0.05$) and on pods ($P < 0.001$). On pods, clones with the lowest rate of mirid survival were UPA402, T79/501 and IMC67, and two of these (T79/501 and UPA402) showed the lowest rate of survival on twigs (Table 7). The correlation between the antibiosis test on pods and on twigs was found to be positive and highly significant ($r = 0.90$; $P < 0.001$), indicating that the results from both tests were consistent. When considering ranking for both traits, the best three clones were UPA402, T79/

Table 4. Correlation between cumulative and recent mirid damage for genotypes within different genetic groups of cacao

Genetic groups of cacao	Pearson correlation coefficient (R)	P
Catongo	0.66	$P < 0.001^{***}$
'Criollo'	0.34	$P < 0.01^{**}$
Trinitario	0.51	$P < 0.001^{***}$
Amelonado	0.42	$P < 0.001^{***}$
UA doubled haploids	0.01	$P < 0.85$ NS
Venezuelan	0.18	$P < 0.31$ NS
Hybrids	0.15	$P < 0.05^{*}$
UA	0.20	$P < 0.001^{***}$
Guianan	0.55	$P < 0.001^{***}$
Related *Theobroma* species	—	—

NS, not significant; UA, Upper Amazon.
*Significant at $P < 0.05$.
**Significant at $P < 0.01$.
***Significant at $P < 0.001$.

Table 5. Feeding preference for UA and LA clones by the cocoa mirid (*Sahlbergella singularis*)

Clones	Lesions	Means grouping
UA parents		
P19A	7.6	a
POR	7.3	ab
MO98	6.8	abc
NA32	6.8	abc
P7	6.7	abc
UPA413	6.7	abc
T85/799	6.1	abcd
MO81	6.0	abcd
PA4	5.7	abcde
UPA401	5.4	abcdef
NA58	5.0	bcdefg
T60/887	4.6	cdefgh
DLOC61	4.5	cdefgh
SCA6	4.4	cdefgh
IMC6	4.0	defgh
UPA402	4.0	defgh
ICS39	4.0	defgh
IMC67	3.9	defgh
G8	3.9	defgh
IMC57	3.4	efgh
PA150	3.1	fgh
UPA409	3.1	fgh
ICS60	2.7	gh
UPA134	2.6	h
T79/501	2.5	h
LA parents		
UF667	8.0	a
IFC371	7.7	ab
SNK12	7.6	ab
ACU85	7.4	abc
MAT1-9	6.0	abcd
ICS84	5.7	abcd
W41	5.5	abcd
WA40	5.5	abcd
ICS6	5.1	abcd
UF676	5.0	abcd
ICS89	4.5	abcd
IFC11	4.4	abcd
GS29	4.3	abcd
MAT1-6	4.1	abcd
ICS95	4.0	abcd
ICS46	4.0	abcd
CC10	3.9	bcd
IFC29	3.5	bcd
IFC8	3.5	bcd
IFC5	3.3	bcd
IFC15	3.2	bcd
IFC6	3.1	cd
R15	3.0	cd
N38	2.9	cd
IFC14	2.0	d

UA, Upper Amazon; LA, Lower Amazon.
Means followed by the same letters within the same group type of cocoa are non-significantly different ($P > 0.5$, Waller–Duncan k-ratio t-test).

Table 6. Feeding preference for the international cacao clones by the cocoa mirid (*Sahlbergella singularis*)

Clones	Lesions	Means grouping
AMAZ5-2	5.9	a
AMAZ15-15	4.9	ab
SPEC54-1	4.7	abc
C151-61	4.5	abcd
GU255v	4.5	abcd
Catie1000	4.4	abcd
MAN15-2	4.2	bcde
T85/799	4.1	bcde
Mocorongo	4.1	bcdef
PA120	3.9	bcdefg
T79/501	3.8	bcdefg
BE10	3.7	bcdefg
P7	3.6	bcdefgh
ICS1	3.3	bcdefgh
MXC67	3.1	cdefgh
IMC47	3.1	cdefgh
VENC4-4	3.0	defgh
IFC5	3.1	defgh
EQX3360-3	2.9	defgh
PA150	2.7	efgh
EET59	2.6	efgh
LCT-EEN46	2.6	efgh
PA107	2.4	fgh
SCA6	2.2	gh
Playa Alta2	2.0	h

Means followed by the same letters are non-significantly different ($P > 0.5$, Waller–Duncan k-ratio t-test).

501 and IMC67, and the worst three clones SNK12, P7 and NA32.

The low rate of survival of mirid nymphs shown by clones UPA402, T79/501 and IMC67 suggests that these clones show some level of antibiosis. Two of these clones (UPA402 and T79/501) also showed low cumulative mirid damage in field observations (Sounigo *et al.*, 1993). In addition, clone T79/501 also showed low to intermediate preference (Tables 5 and 6). These results also partly corroborate those of Decazy and Coulibaly (1981) who found that UPA402 is associated with low number of mirids in the field. Although the causes of antibiosis have not been investigated in this study, previous work on other crops has attributed antibiosis to either the presence of toxins or growth inhibitors in the plant (Smith, 1989).

Tolerance

Our results showed high variability among the clones tested with regard to the number of mirid feeding lesions ($P < 0.001$), the level of the resulting dieback ($P < 0.05$), the percentage of recovery from lesions ($P < 0.05$) and the level of regrowth ($P < 0.001$; Figs 1–4). Clones SCA6, PA107 and C151-61 can be considered as promising for

Table 7. Survival of mirid nymphs on twigs and pods of selected cacao genotypes

Clone	Survival rate	Means grouping
Survival rate on twigs		
P7	100.00	a
PA150	91.67	ab
SNK12	91.67	ab
SCA6	88.89	abc
GS36	88.89	abc
IFC5	83.34	abc
NA32	77.78	abc
IFC371	75.00	abc
UF667	73.34	abc
ICS39	66.67	abcd
T85/799	66.67	abcd
ICS95	66.67	abcd
IMC67	66.67	abcd
T60/887	58.34	bcd
T79/501	55.56	cd
UPA402	33.33	d
Survival rate on pods		
SNK12	92.50	a
NA32	92.00	a
T60/887	90.00	a
UF667	87.50	ab
IFC371	86.67	ab
ICS95	83.33	ab
P7	82.86	ab
ICS39	82.50	ab
PA150	80.00	abc
SCA6	80.00	abc
IFC5	80.00	abc
T85/799	70.00	bcd
GS36	62.86	cd
UPA402	62.86	cd
T79/501	62.86	cd
IMC67	60.00	d

Means followed by the same letter are non-significantly different ($P > 0.5$, Waller–Duncan k-ratio t-test).

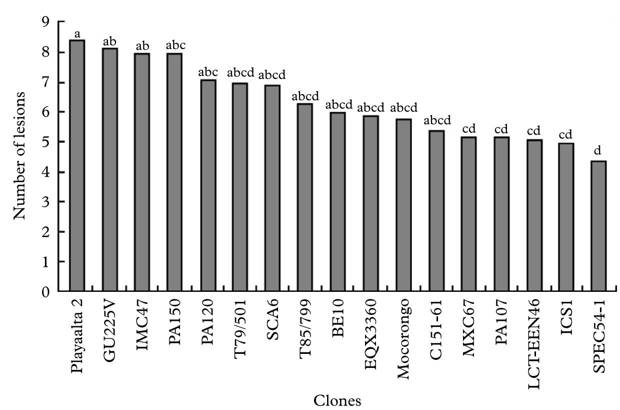

Fig. 1. Numbers of mirid feeding lesions recorded from forced feeding on twigs of selected international cocoa clones.

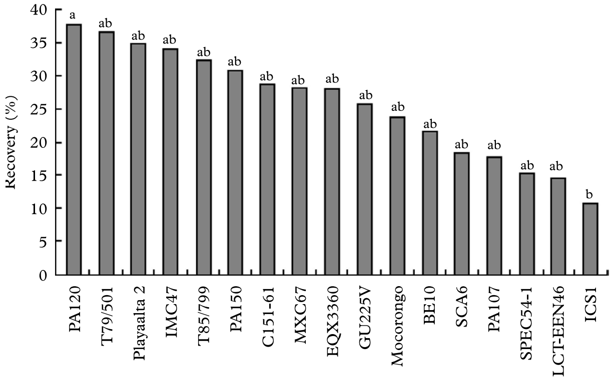

Fig. 2. Recovery from mirid feeding lesions of selected international cocoa clones.

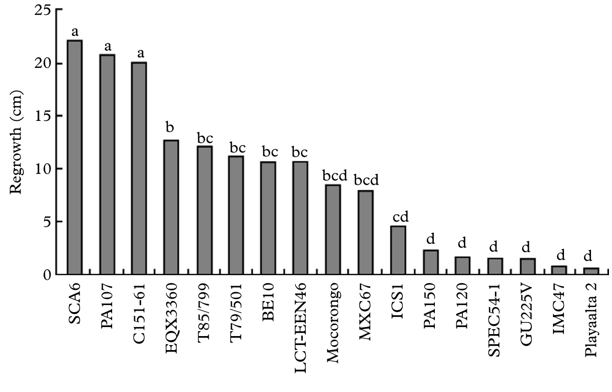

Fig. 4. Regrowth of cocoa shoots damaged by mirid feeding lesions on selected international cocoa clones.

tolerance because they have a good ability for regrowth after damage (Fig. 4).

Plant tolerance to insects is characterized by the ability of the host plant to grow or yield normally, while supporting an insect pest population that usually causes severe damage to a susceptible host (Painter, 1951). Thus tolerance is often determined by comparing the production of biomass (yield) in insect-infested and non-infested plants of the same cultivar (Smith, 1989). In the present study, determination of cocoa tolerance to the cocoa mirids was based on assessment of plant reaction to attacks. Clones SCA6, PA107 and C151-61 sustained a high number of lesions and relatively high levels of shoot death, but showed a good ability for regrowth. Such clones, with a good ability to regrow after dieback will be able to recover faster from damage than clones with low tolerance. As a result, they would be able to restore their canopy, maintain more flower cushions and yield better than clones with low tolerance.

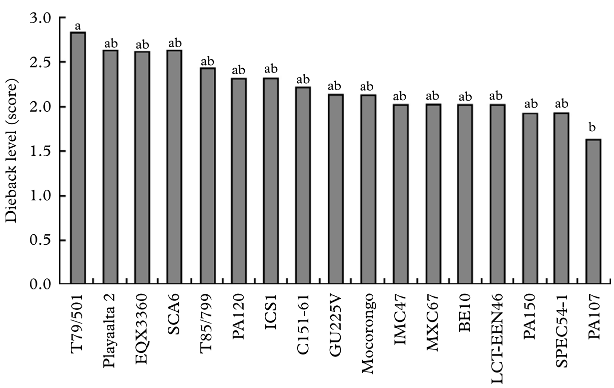

Fig. 3. Shoot senescence from mirid feeding lesions on selected international cocoa clones.

Conclusion

The results from this study on mirid damage in the field gave a general indication on the level of resistance and/or susceptibility of the major genetic groups of cacao in Côte d'Ivoire. These results provide useful information for the cocoa breeders. If the inheritance of the resistance characteristics is confirmed through the ongoing studies in Côte d'Ivoire, then the best parents for developing resistant cocoa materials would be mostly the UA and the Guianan genotypes. The early cocoa-breeding programme in Côte d'Ivoire considered mainly earliness, yield, fat content and low acidity. As a result, most of the cacao grown by the farmers is made up of Amelonado and mirid-susceptible hybrids. The current breeding programme is based on RRS and has been taking into account cocoa resistance to mirids and black pod disease. The choices of the genotypes making up initial populations are based on the available germplasm in the Divo collection of CNRA, and the main traits considered are ability for yield, and resistance to diseases and pests. The results obtained here have provided a good characterization of the different genotypes, planted in the germplasm collection in Divo, for field resistance to mirids.

With regard to antixenosis, antibiosis and tolerance, the significant differences found between the genotypes tested suggest that some genotypes have at least low to moderate levels of mirid resistance/tolerance. These results can be considered as a baseline for future studies regarding cocoa resistance to mirids.

The results also suggest that assessment of recent damage is a rapid method for screening for mirid resistance in the field; however, field observations may only give partial information. For instance, the results from the antixenosis, antibiosis and tolerance tests suggested that mirids resistance in cocoa is a complex phenomenon. The characteristic of a particular cacao genotype *vis-à-vis* the cocoa mirids may be a combination of two or three mechanisms. For example, although the mirids showed low preference for clones PA150 and T79/501 in the choice tests, these clones had among the highest number of lesions in the no-choice test. Similarly, although regrowth in the field was poor on PA150, it was significantly better on T79/501, probably because mirid survival was poorer on T79/501 than on PA150. Therefore, it is important to consider the different mechanisms of resistance, while searching for resistant cocoa genotypes, rather than relying on field resistance alone.

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