

Impact of shade on the spatial distribution of *Sahlbergella singularis* in traditional cocoa agroforests

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- Abstract**
- 1 Shade management is commonly considered to be an effective pest management strategy for cocoa mirids, yet shade management recommendations are not based on extensive knowledge of the mirid ecology in traditional cocoa agroforests.
 - 2 The main objectives of the present study were an assessment of the impact of shade on the spatial distribution of mirid populations and thus the evaluation of shade management strategies.
 - 3 Mirid densities were measured and shade was characterized for three plots located in three different agroecological zones in the Centre region of Cameroon. Mirid densities generally followed a negative binomial law. Geostatistical procedures were used to characterize spatial distribution of mirid density. Light conditions were assessed using hemispherical photography.
 - 4 Populations of *Sahlbergella singularis* were highly aggregated in the plots. Semivariance analysis and kriging visualized the spatial dependence of mirid densities. Clearly distinguishable mirid pockets of 20–30 adjacent infested cocoa trees were identified in two of the three plots.
 - 5 The high diversity of shade tree species and the large variability in density and size of shade trees resulted in a considerable heterogeneity of plot light conditions. Percentage transmitted light varied in the range 9.4–80.1% in the most heterogeneous plot.
 - 6 For two of the three plots, mirid pockets were aggregated in those areas where light transmission was highest. In the third plot, relatively high mirid densities and the presence of an alternative host resulted in a more homogeneous distribution. The importance of these findings for improved mirid control is discussed.

Keywords Cocoa mirids, *Distantiella theobroma*, geostatistics, Hemiptera, hemispherical photography, Miridae, *Sahlbergella singularis* Hagl, shade, spatial distribution, *Theobroma cacao*.

Introduction

In Cameroon, cocoa (*Theobroma cacao* L.) is usually grown in multi-strata, dense and highly diversified agroforestry systems (Dounias & Hladick, 1996; Laird *et al.*, 2007; Sonwa *et al.*, 2007). In such systems, qualified as agroforests (Torquebiau, 2007), cocoa tree canopies are usually joined up and form a thick layer of foliage, which is shaded by the canopy of

associated trees. Until recently, these systems have received relatively little attention contrary to cocoa growing systems in which shade is more simplified (Boyer, 1970; Wessel, 1985; Wood, 1985). However, over the last few years, there has been a growing interest in agroforests worldwide because such cropping systems offer numerous advantages, such as food security and income source diversity for smallholders, biodiversity conservation and soil preservation (Philpott & Armbrrecht, 2006; Franzen & Borgerhoff Mulder, 2007; Laird *et al.*, 2007; Schroth & Harvey, 2007; Torquebiau, 2007). Cocoa production in these Cameroonian cocoa agroforests is,

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however, severely impacted as a result of the presence of pests and diseases.

The mirids *Sahlbergella singularis* Hagl. and *Distantiella theobroma* Distant (Hemiptera: Miridae) are the most harmful insects to cocoa trees in Africa (N'Guessan & Coulibaly, 2000; Padi *et al.*, 2000; Sounigo *et al.*, 2003; Babin *et al.*, 2008). These two insects have very similar life histories and regularly live together in cocoa agroforests. Mirids feed by sucking sap from pods and young shoots, causing varying degrees of damage to the cocoa tree (Williams, 1953; Entwistle, 1972; Collingwood, 1977). Feeding wounds eventually develop into cankers, subsequent to infection by parasitic fungi (Crowdy, 1947). A combination of mirid attacks and fungal infections leads to premature ageing of plantations and can kill the trees, thus resulting in significant production losses. In shaded plantations, mirid damage is usually confined to groups of up to 50 cocoa trees (Williams, 1953). Such groups of severely damaged and unproductive cocoa trees are known as mirid pockets. Mirid pockets often occur in sunny areas of plantations, where there are gaps in the shade tree canopy (Williams, 1953; Entwistle, 1972; Youdeowei, 1977), although few studies have focused on the actual effect of shade on the spatial distribution of mirid populations. Mirid populations in plantations are normally strongly aggregated (Williams, 1953; Youdeowei, 1965; Lotodé, 1969; Nwana & Youdeowei, 1978). To our knowledge, only Youdeowei (1971) has established a link between light intensity and the degree of cocoa tree infestation by *S. singularis*.

Environmental conditions in these multi-strata cocoa agroforests are highly diversified, particularly when shade conditions are highly heterogeneous. One of the mirid control recommendations, widely disseminated in African cocoa producing countries, is to maintain a uniform shade level in cocoa plantations (Idowu *et al.*, 2001; Mpé, 2001; Padi *et al.*, 2001). Unfortunately, to date, this recommendation has not been rigorously verified and, because it is primarily derived from damage observations and not based on in-depth knowledge of mirid ecology, lacks sufficient scientific support. Therefore, the overall objective of the present study was to contribute to the improvement of mirid control strategies, through a better

knowledge of the ecology of these pests in traditional agroforests. To that end, we studied three agroforestry plots with a view to: (i) describing the spatial distribution of mirid populations; (ii) characterizing the shade of the study plots; and (iii) determining the type of relationship between shade and the spatial distribution of mirid populations.

Materials and methods

Study sites and experimental design

In Cameroon, cocoa is grown in the humid forest zone in the South of the country, mainly in three regions: Mungo, Centre-South and East (Losch *et al.*, 1991). The present study was located on three plantations in the Centre region of Cameroon. The choice of plantations was guided by: (i) crop management in compliance with traditional agroforests; (ii) the geographical location of the plantations with a view to covering contrasting agroecological conditions; (iii) the existence of recent mirid damage; and (iv) the absence of any insecticide treatment for at least 3 years. Table 1 lists the main geographical and agroecological characteristics of the chosen plantations. The Ngomedzap site is characterized by higher rainfall and a less marked dry season than the other sites. The vegetation is mainly comprised of degraded forest and the cocoa trees are old and low-yielding. The selected plot (Ngo) was planted exclusively with cocoa trees of the West African Amelonado type. The Obala site is characterized by a greater human pressure because of the proximity of the city of Yaoundé. The vegetation at the site is highly influenced by human activity. The cocoa trees are younger and better maintained and consequently more productive compared with the Ngomedzap site. The chosen plantation (Oba) had a mixture of West African Amelonado type cocoa trees and selected Trinitario type hybrids, disseminated in the 1960 s and 1970 s. The Bokito site has a bush-savanna type vegetation. Cocoa is normally grown there inside gallery forests or in man-made forests usually planted at the same time as the cocoa trees to shade the plantations. The chosen plantation (Bok) was installed in an artificial forest and had a mixture of Amelonado type trees and Trinitario hybrids. The plantation was very low-yielding

Table 1 Main geographical and agroecological characteristics of the selected plots

	Plots		
	Ngo	Oba	Bok
Site (Fig. 1)	Ngomedzap	Obala	Bokito
Latitude	03° 16' 09" N	04° 06' 19" N	04° 34' 29" N
Longitude	11° 13' 21" E	11° 28' 40" E	11° 10' 45" E
Annual rainfall (mm) ^a	1700–1800	1400–1500	1300–1500
Vegetation ^a	Mixed degraded forests and patches of evergreen forest	Domesticated forest landscapes, shrub crops	Bush savannah and gallery forests
Age of cocoa trees	Over 60 years	30–60 years	30–60 years
Type of cocoa trees	Amelonado	Amelonado and Trinitario hybrids	Amelonado and Trinitario hybrids
Planting density (trees per hectare)	1800	1500	1200
Average yields 2003 and 2004 (kg/ha) ²	800	1250	350

^aAccording to Santoir & Bopda (1995).

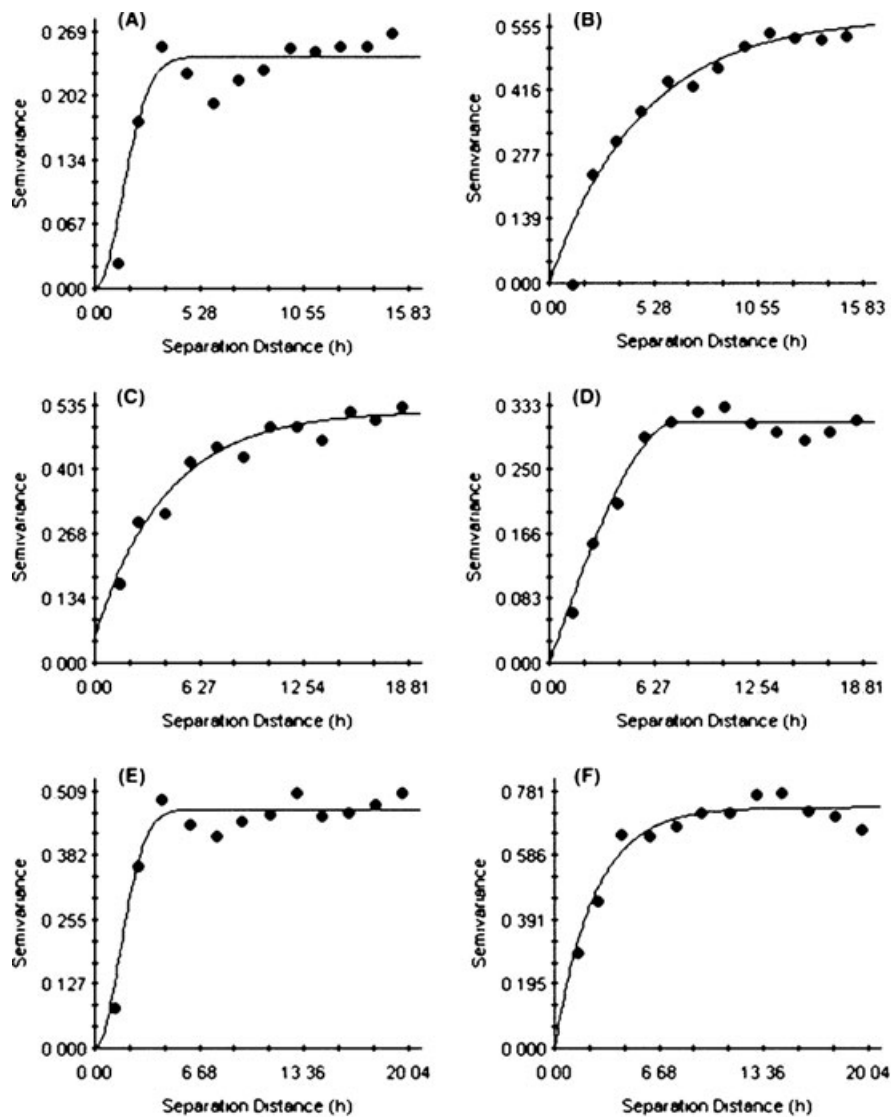


Figure 1 Observed semivariance (dots) and fitted models (curves) for the number of mirids per cocoa tree [after $\log_e(x + 1)$ transformation] for: (A) Ngo 2006, (B) Ngo 2007, (C) Oba 2006, (D) Oba 2007, (E) Bok 2006 and (F) Bok 2007. The separation distance (h) is expressed in metres.

for the zone, which generally displays yields that are three- to five-fold higher.

A total of 100 cocoa trees were selected in each plantation in an area with heterogeneous shade levels. Plots, measuring 2025 m² (45 × 45 m), were established centred around the selected cocoa trees and included all shade trees surrounding and influencing shade levels experienced by the observed cocoa trees. Plots were divided into smaller areas 3 × 3 m² and the position of the cocoa and shade trees was plotted on a map.

Evaluation of mirid populations

In Cameroon, mirid populations are usually at their highest from July to September (Lavabre, 1960). To obtain adequate data for spatial analyses, population densities were evaluated during their peak time on two occasions, in September 2006 and

August 2007. The number of mirids per tree was recorded for each of the marked trees, using a knockdown method of sampling (Lavabre *et al.*, 1963). Plastic sheets measuring 4 × 4 m were spread at the foot of the cocoa trees. They were subsequently sprayed with an endosulfan-based insecticide using a motorized mistblower (Solo type 40123; Solo Kleinmotoren, Germany) at 100 mL/ha. Endosulfan was chosen because it has a broad action-spectrum and a sufficient 'shock' effect, which kills most of the insects within a few hours. Treatment was carried out at daybreak, when mirids are not very active (Youdeowei, 1977). The risk of winged adults escaping was thus limited. Seven hours after the treatment, insect bodies were collected from the plastic sheets and preserved in glass haemolysis tubes containing 70% alcohol. The insects were sorted in the laboratory and the number of *S. singularis* and/or *D. theobroma* individuals per tree and per development stage was determined. Because the knockdown method of sampling

could perturb the population dynamics, we sampled the mirid population once a year to prevent this risk.

Characterization of plot shade

Woody species present in each plot were identified to species. The basal area of each tree was assessed by measuring the circumference of the trees 1.30 m from the ground or 30 cm above the buttress on trees with a buttress. Horizontal crown area was estimated for each tree by measuring the ground-level crown projection (Bellow & Nair, 2003). Stand density (in trees per hectare), total basal area per hectare (in m²/ha) and crown cover per hectare (sum of the crown areas, in m²/ha) were calculated for each plot.

Plot shade was assessed by calculating the percentage transmitted light reaching the cocoa canopy through the foliage of associated trees (Isaac *et al.*, 2006). To that end, hemispherical photographs of the canopy overhanging the cocoa trees were taken with a digital camera (Nikon Coolpix 5400; Nikon, Japan) fitted with a fisheye lens (Nikon FC-E9-Fisheye 0.2 ×; Nikon). Thirty to 50 photographs were taken for each plot between 05.30 h and 07.30 h in the morning to avoid direct sunlight. Canopy openness and percentage transmitted light through the canopy were estimated by analysing the hemispherical photographs using the GAP LIGHT ANALYZER software, version 2.0 (Frazer *et al.*, 1999).

Statistical analysis

Mirid populations. Mirid densities (log_e-transformed) in the three selected plots were compared for 2 years with the appropriate generalized linear model (GLM) using SAS, version 9.1 (SAS Institute, Cary, North Carolina).

Mirid distribution. Insect populations are often aggregated in their environment, with their distribution generally obeying a negative binomial law (Anscombe, 1949; Elkinton, 1993).

To check the fit of the mirid density distribution to the negative binomial distribution, the expected values for the different count categories were calculated using the formulas described below, then compared with the observed values using a chi-square test in XLSTAT, version 2007.6 (Addinsoft SARL, France):

$$P(X = n) = \left(\frac{k + n - 1}{n} \right) \left(\frac{\mu}{\mu + k} \right) \times P(X = n - 1) \quad (1)$$

Where $P(X = n)$ is the probability of the sampled cocoa tree having n individuals, μ is the mean and the parameter k , an indicator of the degree of clumping in the data, given by the formula:

$$k = \frac{\mu^2}{\sigma^2 - \mu} \quad (2)$$

The parameter k is widely used as an index of dispersion for populations (Anscombe, 1949).

Spatial analysis. Each sampling point (marked cocoa tree) was assigned x and y coordinates by projecting the plot maps onto an orthonormal grid. Subsequently, the spatial relations between the sampling points were analysed by fitting semivariograms using GS⁺, version 9 (Robertson, 2008). Semivariance is given by the equation:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{N(h)} [z(s_i) - z(s_i + h)]^2 \quad (3)$$

where, in the present study, $z(s_i)$ was the log_e-transformed number of mirids plus one, per cocoa tree at point s_i , $z(s_i + h)$ was the log_e-transformed number of mirids plus one per cocoa tree at distance h from s_i and $N(h)$ was the total number of pairs of cocoa trees sampled for the distance interval h , expressed in metres. The software provides descriptive parameters for the semivariogram: (i) the range for which spatial dependence is apparent (marked A and expressed in metres in the present study); (ii) the nugget variance (i.e. the value γ at which the curve of the model cuts the y -axis) (indicated C_0); (iii) the sill of the model corresponding to the asymptote of the model [indicated $(C + C_0)$]. The quality of semivariogram fit to the common models was indicated by the residual sum of squares (RSS), the coefficient of determination R^2 and the ratio $C/(C_0 + C)$. The ratio of $C/(C_0 + C)$ is equal to 1 if the semivariogram does not display a nugget effect and is equal to 0 if the semivariogram is linear. A linear semivariogram reflects a 'pure nugget' effect and, consequently, an absence of spatial dependence for distribution (random distribution).

Kriging is an interpolation method that uses the structural properties of the semivariogram and the actual data of the studied parameter(s) (Robertson, 2008). Kriging maps were produced using GS⁺ by ordinary block kriging with a block size of 1 × 1 m across the plot and a 2 × 2 discretization grid within each block. Kriged log_e-transformed mirid counts were back-transformed to original units before mapping.

Effect of shade on the spatial distribution of mirids. The position, basal area and crown cover of shade trees were represented on maps produced with MAPINFO, version 7.0 (MapInfo Corporation, North Greenbush, New York). Using the data from the GAP LIGHT ANALYZER-analysed hemispherical photographs, transmitted light percentages were estimated for nonsampled points using Inverse Distance Weighting (IDW). The IDW technique estimates a value for unmeasured points based on the distance to neighbouring values. The weight accorded to those neighbouring values depends on the distance between neighbouring points (Robertson, 2008). The estimated values were calculated in a 1 × 1 m grid such that the grids for the transmitted light percentages and for the mirid densities corresponded. The IDW interpolation maps were produced with GS⁺.

Shade and mirid distribution maps were used to visualize the relationship between these variables. This relationship was then

validated statistically. Accordingly, the interpolation data for the percentage transmitted light were separated into two categories: the first category corresponded to the quartile containing the highest values for the variable and the second grouped the other three quartiles. The mirid density interpolation data of these two classes were compared with the appropriate GLM using SAS.

Results

Mirid populations

Of the 1257 mirids collected, 1250 individuals (99.4%) belonged to *S. singularis* and 7 (0.6%) to *D. theobroma*. Consequently, our analyses were limited to *S. singularis*. Mean mirid density for all plots was 2.10 mirids/cocoa tree. However, densities were highly variable, varying on the range 0.61–6.53 mirids/cocoa tree (Table 2). Densities of the Bok plot were significantly higher than densities of the two other plots in 2006 ($F_{2,294} = 23.06$, $P < 0.0001$) and in 2007 ($F_{2,294} = 94.10$, $P < 0.0001$). Moreover, for the Ngo and Bok plots, densities were significantly higher in the second year of sampling compared with the first year (Ngo plot, $F_{1,198} = 13.43$, $P < 0.0001$; Bok plot, $F_{1,194} = 45.56$, $P < 0.0001$). At the Oba plot, the reverse was true ($F_{1,196} = 6.83$, $P < 0.01$). Larvae were two- to ten-fold more numerous than adults, with a maximum of 0.57 adults/cocoa tree as opposed to 5.96 larvae/cocoa tree (Bok plot, 2007; Table 2). For each plot, the variance was higher than the mean. The results of tests to fit the distribution to a negative binomial law gave probability values over 5% for 14 out of 18 tests. Those results confirm that mirid populations were aggregated in the plots. The index of dispersion k was generally low, with a mean of 0.87 ± 0.52 for the set of tests. The k values varied substantially between plots and between years, with a minimum value of 0.25 and a maximum value of 1.71. In addition, the k values obtained for adults were generally higher than those obtained for larvae (Table 2).

Spatial distribution of mirids

Analysis of the semivariograms revealed a spatial dependence of mirid densities for all three plots and both sampling years. The semivariograms were either Gaussian (Ngo and Bok in 2006), exponential (Ngo in 2007, Oba in 2006 and Bok in 2007) or spherical (Oba in 2007) (Fig. 1). The theoretical models fitted well to the observed semivariograms ($RSS \rightarrow 0$ and $R^2 \rightarrow 1$) (Table 3). The 'nugget' effect was limited [$C/(C_0 + C) \rightarrow 1$]. The mean range of spatial dependence (A) was 8.26 ± 4.44 m, with a minimum value of 3.36 m (Ngo in 2006) and a maximum value of 14.04 m (Ngo in 2007). The type of semivariogram and the range of spatial dependence differed between 2006 and 2007 for each plot. Larvae displayed two models of semivariograms similar to those for the total populations (Table 3), although with different models for adults in half the cases. In 2006, the mean range of spatial dependence was slightly greater in adults (6.96 ± 5.64 m) as opposed to larvae (5.07 ± 3.20 m). On the other hand, in 2007, the

mean range of spatial dependence was clearly greater for larvae (9.13 ± 2.56 m) as opposed to adults (4.68 ± 0.92).

Kriging maps confirmed the aggregated spatial distribution of mirid populations. Indeed, each plot contained one or more groups of severely infested trees and zones that were totally free of mirids (Figs 2C,D, 3C,D, 4C,D). The groups of infested trees varied in number and size. In 2006, the Ngo plot had five to six groups of two to three severely infested cocoa trees scattered throughout the plot. On the other hand, in 2007, this plot had only two groups of infested cocoa trees, which were relatively close to each other and of which one contained approximately 30 cocoa trees. The Oba plot had a group of 20–30 infested cocoa trees in the central zone of the plot for both years. On the other hand, the Bok plot had several small groups of infested cocoa trees scattered throughout the plot. In 2007, the plot was almost totally infested.

Impact of shade on mirid distribution

The Ngo plot had a balanced mixture of forest trees and fruit trees (Fig. 2A). The density of the associated trees was relatively low, at 80 trees per hectare. Total basal area and crown cover were around 43 and 17 000 m²/ha, respectively, as a result of the existence of large trees such as *Terminalia superba* (Combretaceae), *Ficus mucoso* and *Ficus exasperata* (Moraceae). The percentage transmitted light varied in the range 16.1–62.8% (Fig. 2B). The Oba plot was mostly planted with fruit trees, notably *Persea americana* (Lauraceae) and *Citrus* spp. (Rutaceae) (Fig. 3A). The planting density of the associated trees was very high, with approximately 250 trees per hectare. The shade trees were not highly developed, with a total basal area of approximately 30 m²/ha and a crown cover of approximately 17 000 m²/ha. The distribution of the shade trees in the plot was very heterogeneous. The percentage transmitted light varied in the range 9.4–80.1% (Fig. 3B). The Bok plot had a mixture of fruit trees and forest trees, planted at a density of approximately 130 trees per hectare (Fig. 4A). The fruit trees mainly consisted of the species *Cola nitida* (Malvaceae), which generally had a low basal area and crown area. The forest trees were more numerous and more diversified than in the other plots. The total basal area and the crown cover in the plot displayed relatively high values of approximately 34 and 20 000 m²/ha, respectively. The percentage transmitted light varied in the range 11.4–61.4% (Fig. 4B). A large proportion of the associated trees belonged to the family Malvaceae (*Triplochiton scleroxylon*, *Eriobroma oblonga* and *C. nitida*).

A comparison of the mirid population distribution maps and the percentage transmitted light maps showed that, for the Ngo (Fig. 2) and Oba (Fig. 3) plots, the groups of cocoa trees infested by mirids were located in zones where the percentage transmitted light was greatest. These results were confirmed by the analysis of variance. Mirid density was significantly higher in areas with high light transmission compared with medium to low light transmission for the Ngo plot in 2006 (0.60 ± 1.09 versus 0.41 ± 0.57 mirids/tree, respectively; $F_{1,990} = 5.29$, $P < 0.05$) and 2007 (2.06 ± 1.70 versus 0.68 ± 0.73 mirids/tree, respectively; $F_{1,990} = 260.82$, $P < 0.0001$). The same was true for the Oba plot in 2006

Table 2 Main statistical parameters of mirid densities per cocoa tree per site and development stage for 2006 and 2007 and results of fitting the density distribution to a negative binomial distribution

Plot:	Ngo						Oba						Bok					
	2006		2007		2006		2007		2006		2007		2006		2007			
	Larvae	Adults	Total	Larvae	Adults	Total	Larvae	Adults	Total	Larvae	Adults	Total	Larvae	Adults	Total	Larvae	Adults	Total
Minimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maximum	8	2	9	6	3	7	8	3	9	7	3	9	8	2	10	33	3	33
Mean	0.46	0.14	0.61	1.09	0.24	1.33	1.05	0.29	1.34	0.49	0.24	0.73	1.89	0.25	2.13	5.96	0.57	6.53
Variance	1.71	0.18	2.12	2.89	0.27	3.50	2.92	0.43	4.19	1.04	0.27	1.69	4.12	0.29	4.80	39.90	0.66	41.78
k	0.17	0.46	0.25	0.66	2.30	0.82	0.60	0.61	0.64	0.44	2.38	0.56	1.60	1.33	1.71	1.05	3.70	1.21
Observed χ^2	10.40	1.43	10.10	18.52	2.39	12.57	10.32	1.63	22.81	7.56	2.42	13.04	9.62	1.76	12.36	38.94	1.93	41.58
d.f.	7	1	8	5	2	6	7	2	8	6	2	8	7	1	9	32	2	32
Probability (%)	16.7	0.01 ^a	25.8	0.24 ^a	30.3	5.0	17.1	44.2	0.4 ^a	27.2	29.8	11.1	21.1	0.01 ^a	19.4	18.6	38.2	12.0

^aDoes not follow a negative binomial distribution at the 5% level. d.f., degrees of freedom.

Table 3 Descriptive parameters of the semivariograms and statistics for model fit obtained for the number of adult, larvae and total mirids per cocoa tree for the three plots and two study years

Plot/year	Stage	Model	Range (A) (m)	Sill ($C_0 + C$)	$C/(C_0 + C)$	RSS	R^2
Ngo (2006)	Adult	Gaussian	3.83	0.065	0.998	0.001	0.907
	Larvae	Gaussian	2.53	0.191	0.999	0.005	0.694
	Total	Gaussian	3.36	0.242	1.000	0.006	0.883
Ngo (2007)	Adult	Gaussian	3.62	0.096	0.999	0.001	0.874
	Larvae	Exponential	12.03	0.523	0.998	0.022	0.924
	Total	Exponential	14.04	0.574	0.998	0.018	0.948
Oba (2006)	Adult	Exponential	13.47	0.172	0.980	0.001	0.929
	Larvae	Exponential	8.67	0.439	0.815	0.009	0.856
	Total	Exponential	12.90	0.522	0.895	0.006	0.956
Oba (2007)	Adult	Gaussian	5.14	0.104	0.999	0.001	0.880
	Larvae	Spherical	7.17	0.221	0.962	0.004	0.870
	Total	Spherical	7.74	0.311	1.000	0.002	0.973
Bok (2006)	Adult	Gaussian	3.57	0.099	0.999	0.003	0.777
	Larvae	Gaussian	4.02	0.465	0.998	0.009	0.940
	Total	Gaussian	3.91	0.473	0.998	0.009	0.945
Bok (2007)	Adult	Gaussian	5.28	0.190	0.999	0.003	0.924
	Larvae	Exponential	8.19	0.796	0.999	0.017	0.942
	Total	Exponential	7.62	0.732	0.999	0.015	0.933

The density data underwent $\log_e(x + 1)$ transformation prior to analysis.

(2.03 ± 1.45 versus 0.86 ± 0.85 mirids/tree, respectively; $F_{1,978} = 250.55$, $P < 0.0001$) and 2007 (1.42 ± 1.12 versus 0.43 ± 0.56 mirids/tree, respectively; $F_{1,978} = 323.58$, $P < 0.0001$). However, for the Bok plot, mirid density was significantly higher for high light transmission compared with medium to low light transmission only in 2006 (2.17 ± 1.45 versus 1.92 ± 1.57 mirids/tree, respectively; $F_{1,1293} = 10.65$, $P < 0.01$). In 2007 the effect was reversed (3.85 ± 2.58 versus 4.91 ± 3.14 mirids/tree, respectively; $F_{1,1293} = 35.79$, $P < 0.0001$).

Discussion

With a mean of 2.1 mirids/tree, population densities observed in the present study were relatively high for *S. singularis*. As a result of extensive damage caused by cacao mirids, the economic threshold for phytosanitary intervention has been fixed at only 0.7 mirids/tree in Cameroon (Decazy & Essono, 1979) and 0.6 mirids/tree in Ghana (Padi & Owusu, 1998). The results obtained in the present study also show that the highest densities were reached in the Bok plot for both years. This result is consistent with previous work, which showed that cocoa plantations in the savannah area of Cameroon are generally more infested than plantations in the forest area (Lavabre, 1960, 1977). The presence of numerous trees of the Malvaceae family, which is known to contain alternative host plants of *S. singularis* such as *C. nitida*, could also explain the high mirid densities in the Bok plot. Two plots had higher mirid densities in 2007 compared with 2006. These results appear to indicate that the colonization conditions were more suitable in 2007 for these plots.

The results of the present study show that mirids were highly aggregated in the plots, which is consistent with previous research (Youdeowei, 1965; Lotodé, 1969; Nwana & Youdeowei, 1978). However, in previous studies, an index of aggregation was calculated according to Taylor's law (1961). This index can only be estimated by collecting data from different populations that differ in density. Therefore, this index cannot be used to assess differences in dispersion between populations (Elkinton, 1993). Conversely, the index of dispersion k enabled comparison of the different plots for mirid aggregation. Thus, the k value displayed considerable variability in the present study. A similar result was found for the coffee tree bug *Antestiopsis orbitalis* (Pentatomidae), with a k value varying in the range 1.16–5.36 (Cilas *et al.*, 1998). Elkinton (1993) suggested that the increase in the density of an insect is usually accompanied by changes in its pattern of spatial distribution and consequent degree of aggregation. This theory could be illustrated by the Bok plot, where densities were very high and aggregation not as marked as in the other two plots.

An analysis of the semivariograms and kriging maps also clearly revealed that *S. singularis* was not randomly distributed in the study plots. Gaussian type semivariograms were characteristic of plots containing small infested zones involving fewer than ten cocoa trees. On the other hand, exponential type variograms were characteristic of plots with adjacent groups of 20–30 infested cocoa trees. These groups had fuzzier contours, revealing infestation gradients reaching more than 10 m, in keeping with the high ranges of spatial dependence. Williams (1953) defined a mirid pocket as 'a small area of severely damaged trees which stands out in sharp contrast to the surrounding healthy cocoa'. Youdeowei (1971) used the term mirid pockets for groups of around twenty infested adjacent cocoa trees. On

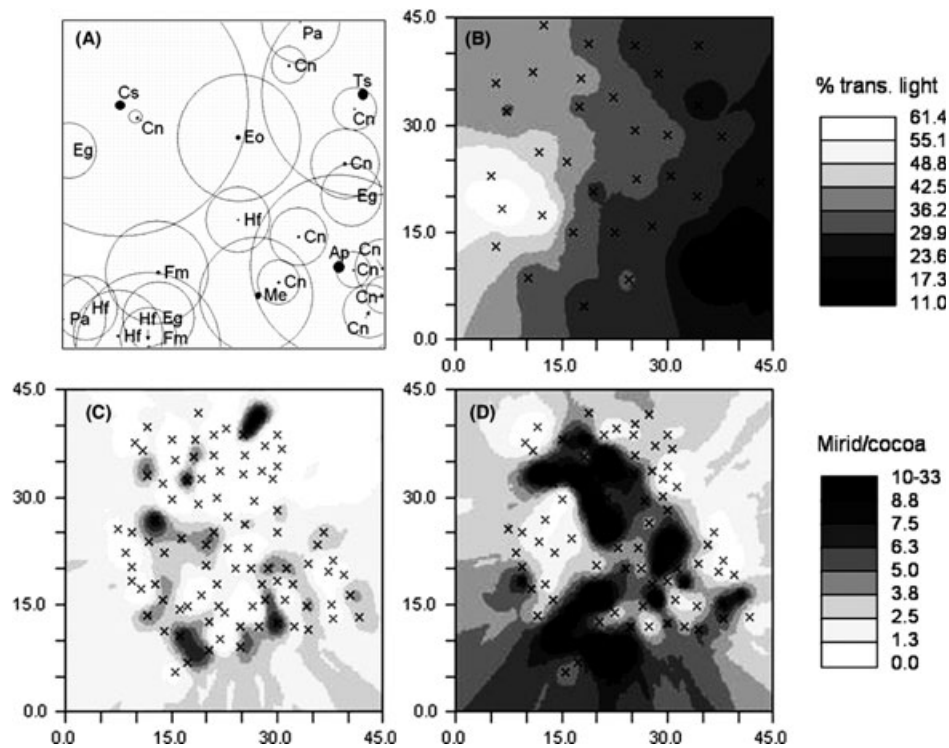


Figure 4 Maps of the Bok plot showing: (A) the position, basal area and crown cover of the shade trees; (B) % light transmitted to the cocoa trees through the canopy; and kriging maps for spatial distribution of mirid populations for (C) 2006 and (D) 2007. Crosses indicate the sampling points; hemispherical photos for (B) and marked cocoa trees for (C, D). Ap, *Amphimas pterocarpoides*; Cs, *Canarium schweinfurthii*; Cn, *Cola nitida*; Eg, *Elaeis guineensis*; Eo, *Eriobroma oblonga*; Fm, *Ficus mucoso*; Hf, *Holarrhena floribunda*; Me, *Milicia excelsa*; Pa, *Persea americana*; Ts, *Triplochiton scleroxylon*.

the kriging maps of the Ngo and Oba plots, such mirid pockets were clearly delimited. Because the Bok plot was almost totally infested, mirid pockets were not so easy defined.

The results we obtained show that mirid pockets generally appeared in zones where the percentage transmitted light reaching the cocoa trees was at its highest. However, cocoa trees deprived of shade display light and microclimatic conditions unsuitable for nymphal development. Indeed, cocoa mirids display negative phototropism during nymphal development (Madge, 1968; Youdeowei, 1971). Furthermore, direct sunlight and wind lead to considerable variations in temperature and relative humidity, which can kill larvae through desiccation (Gibbs *et al.*, 1968; Nwana & Youdeowei, 1976). However, flush intensity is greater on cocoa trees exposed to sunlight than on trees in a shaded zone (Boyer, 1970) and it is hypothesized that the distribution of *S. singularis* may also be linked to food availability. Research is currently underway to assess the impact of cocoa tree phenology and cocoa canopy microclimatic conditions on nymphal development, survival and fecundity of *S. singularis*.

Characterization of plot shade shows that cocoa was grown in combination with a large number of fruit and forest tree species. The planting densities and cover of the associated trees were highly variable. This resulted in very heterogeneous shade conditions for cocoa trees, which were conducive to the formation of mirid pockets. The results obtained in the present study suggest that shade is more homogenous in areas with

large forest trees than in areas with fruit trees. The presence of large forest trees is therefore desirable provided they do not compete with cocoa trees for water and nutrients, and that they are not host plants for cocoa pests and diseases (Wood, 1985). The very high mirid densities obtained in the Bok plot and the related mirid spatial distribution are probably the result of the presence of numerous trees belonging to the family of the Malvaceae, which is known to contain host plants of mirids (Entwistle, 1972). For example, kola trees (*Cola* sp.) are often grown in traditional agroforests because they provide farmers with an additional income (Sonwa *et al.*, 2007). However, they are host plants for mirids and could comprise infestation foci. Yet, little is known about the biology of mirids on kola trees. If present in cocoa plantations, they probably require regular insecticide treatments.

Fruit trees such as *Mangifera indica* (Anacardiaceae), *Dacryodes edulis* (Burseraceae), *P. americana* and *Citrus* sp. provide dense although less extensive shade compared with remnant forest trees. Such trees could be planted uniformly in the plantation but at a low density to avoid excessive shading. Excessive shade can increase the severity of diseases, such as black pod rot, caused by *Phytophthora megakarya*, which is responsible for considerable production losses in Cameroon (Nyassé *et al.*, 1999; Ndoumbè-Nkeng & Sache, 2003). Pruning of the lower branches of trees is therefore advisable to ensure good ventilation in the plantation, which reduces the impact of black pod (Lass, 1985). Thus, to be effective, shade management

strategies have to find a balance between shade conditions unfavourable for both mirids and black pod. Determining this balance requires a better understanding of the effect of shade on mirids and disease epidemiology.

To our knowledge, this is the first time that a quantifiable link between light intensity at cocoa canopy level and mirid presence has been established. It is not the absolute light intensity but the relative light intensity that determines the spatial distribution of populations. Thus, the recommendation for homogenous shade to reduce the impact of mirid damage has been validated by the present study. However, when population pressures are high, other factors come into play that interact with the spatial distribution of mirids. Moreover, because shade also affects production as well as cocoa diseases, further studies should focus on the interactions between shade, diseases, pests and cocoa trees to ensure sustainable cocoa production in the highly diverse agroforests of Cameroon.

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References

- Anscombe, F.J. (1949) The statistical analysis of insect counts based on the negative binomial distribution. *Biometrics*, **5**, 165–173.
- Babin, R., Bisseleua, B.H.D., Dibog, L. & Lumaret, J.P. (2008) Rearing method and life table data for the cocoa mirid bug *Sahlbergella singularis* Haglund (Hemiptera: Miridae). *Journal of Applied Entomology*, **132**, 366–374.
- Bellow, J.G. & Nair, P.K.R. (2003) Comparing common methods for assessing understory light availability in shaded-perennial agroforestry systems. *Agricultural and Forest Meteorology*, **114**, 197–211.
- Boyer, J. (1970) Influence des régimes hydrique, radiatif et thermique du climat sur l'activité végétative et la floraison de cacaoyers au Cameroun. *Café Cacao Thé*, **14**, 189–199.
- Cilas, C., Bouyjou, B. & Decazy, B. (1998) Frequency and distribution of *Antestiopsis orbitalis* Westwood (Hem., Pentatomidae) in coffee plantations in Burundi: implications for sampling techniques. *Journal of Applied Entomology*, **122**, 601–606.
- Collingwood, C.A. (1977) African mirids. *Les Mirides du Cacaoyer* (ed. by E. M. Lavabre), pp. 71–83. G-P. Maisonneuve et Larose, France.
- Crowdy, S.H. (1947) Observations on the pathogenicity of *Calonectria rigidiuscula* (Berk. & Br.) Sacc. on *Theobroma cacao* L. *The Annals of Applied Biology*, **34**, 45–59.
- Decazy, B. & Essono, B. (1979) Tests de contrôle d'infestation et traitements anti-mirides. *Café Cacao Thé*, **23**, 35–41.
- Dounias, E. & Hladik, C.M. (1996) Les agroforêts Mvae et Yassa du Cameroun littoral: fonctions socioculturelles, structure, composition floristique. *L'alimentation en forêt tropicale: Interactions Bioculturelles et Perspectives de Développement* (ed. by C. M. Hladik, A. Hladik, H. Pagezy, O. F. Linares, G. J. A. Koppert and A. Froment), pp. 1103–1126. UNESCO, France.
- Elkinton, J.S. (1993) *Insect Population Ecology, An African Perspective*. ICIPE Science Press, Kenya.
- Entwistle, P.F. (1972) *Pests of Cocoa*. Longman Group Ltd, U.K.
- Franzen, M. & Borgerhoff Mulder, M. (2007) Ecological, economic and social perspectives on cocoa production worldwide. *Biodiversity Conservation*, **16**, 3835–3849.
- Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999) *Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation*. Simon Fraser University, Burnaby, British Columbia, and The Institute of Ecosystem Studies, Millbrook, New York, New York.
- Gibbs, D.G., Pickett, A.D. & Leston, L. (1968) Seasonal population changes in cocoa capsids (Hemiptera: Miridae) in Ghana. *Bulletin of Entomological Research*, **58**, 279–293.
- Idowu, O.L., Olejade, K.T.M. & Adebola, P.O. (2001) Cocoa IPM research and implementation in Nigeria. *Proceedings of the West Africa Regional Cocoa IPM Workshop* (ed. by J. Vos and P. Neuenschwander), pp. 67–70. CPL Press, Benin.
- Isaac, M.E., Timmer, V.R. & Quashie-Sam, S.J. (2006) Shade tree effects in an 8-year-old cocoa agroforestry system: biomass and nutrient diagnosis of *Theobroma cacao* by vector analysis. *Nutrient Cycling in Agroecosystems*, **78**, 155–165.
- Laird, S.A., Leke Awung, G. & Lysinge, R.J. (2007) Cocoa farms in the Mount Cameroon region: biological and cultural diversity in local livelihoods. *Biodiversity Conservation*, **16**, 2401–2427.
- Lass, R.A. (1985) Diseases. *Cocoa* (ed. by G. A. R. Wood and R. A. Lass), pp. 265–365. Longman Scientific and Technical, U.K.
- Lavabre, E.M. (1960) Recherches sur une méthode économique de contrôle des mirides du cacaoyer. *Café Cacao Thé*, **4**, 16–25.
- Lavabre, E.M. (1977) Variations saisonnières des populations. *Les Mirides du Cacaoyer* (ed. by E. M. Lavabre), pp. 155–170. G-P. Maisonneuve et Larose, France.
- Lavabre, E.M., Decelle, J. & Debord, P. (1963) Etude de l'évolution régionale et saisonnière des populations de Mirides (Capsides) en Côte d'Ivoire. *Café Cacao Thé*, **7**, 267–287.
- Losch, B., Fusillier, J.L. & Dupraz, P. (1991) *Stratégies des producteurs en zone caféière et cacaoyère du Cameroun. Quelles adaptations à la crise?* Collection DSA n° 12. DSA-CIRAD, France.
- Lotodé, R. (1969) Etude statistique de l'évolution d'une population de Mirides. *Café Cacao Thé*, **13**, 216–220.
- Madge, D.S. (1968) The behaviour of the cocoa mirid (*Sahlbergella singularis* Hagl.) to some environmental factors. *Bulletin of the Entomological Society of Nigeria*, **1**, 63–70.
- Mpé, J.M. (2001) Integrated management of cocoa mirids in Cameroon. *Proceedings of the West Africa Regional Cocoa IPM Workshop* (ed. by J. Vos and P. Neuenschwander), pp. 39. CPL Press, Benin.
- Ndoumbé-Nkeng, M. & Sache, I. (2003) Lutte contre la pourriture brune des cabosses du cacaoyer au Cameroun. *Phytoma, La défense des végétaux*, **562**, 26–32.
- N'Guessan, F.K. & Coulibaly, N. (2000) Dynamique des populations de mirides et de quelques autres déprédateurs du cacaoyer dans la région ouest de la Côte d'Ivoire. *Proceedings of the 13th International Cocoa Research Conference*, pp. 425–435. Cocoa Producer's Alliance, Malaysia.

- Nwana, I.E. & Youdeowei, A. (1976) The effect of relative humidity on the development and survival of the pre-imaginal stages of *Bathycocelia thalassina* (H-S) (Pentatomidae) and *Sahlbergella singularis* Hagl. (Miridae) in Nigeria. *Journal of Natural History*, **11**, 445–449.
- Nwana, I.E. & Youdeowei, A. (1978) The spatial distribution of three species of Heteroptera on a cocoa farm in Ibadan, Nigeria. *Nigerian Journal of Entomology*, **3**, 27–33.
- Nyassé, S., Grivet, L., Risterucci, A.M., Blaha, G., Berry, D., Lanaud, C. & Despréaux, D. (1999) Diversity of *Phytophthora megakarya* in Central and west Africa revealed by isozyme and RAPD markers. *Mycological Research*, **103**, 1225–1234.
- Padi, B. & Owusu, G.K. (1998) Towards an integrated pest management for sustainable cocoa production in Ghana. *Proceedings of the First Sustainable Cocoa Workshop*, pp 7–15. Smithsonian Institution, Washington, D.C.
- Padi, B., Downham, M., Farman, D. & Sarfo, J.E. (2000) Evidence of sex attractants in the cocoa mirids *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl. (Heteroptera: Miridae) in field-trapping experiments. *Proceedings of the 13th International Cocoa Research Conference*, pp. 395–400. Cocoa Producer's Alliance, Malaysia.
- Padi, B., Ackonor, J.B. & Opoku, I.Y. (2001) Cocoa IPM research and implementation in Ghana. *Proceedings of the West Africa Regional Cocoa IPM Workshop* (ed. by J. Vos and P. Neuenschwander), pp. 54–62. CPL Press, Benin.
- Philpott, S.M. & Armbrrecht, I. (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, **31**, 369–377.
- Robertson, G.P. (2008) *GS+ : Geostatistics for the Environmental Sciences*. Gamma Design Software, Plainwell, Michigan.
- Santoir, C. & Bopda, A. (1995) *Atlas régional Sud-Cameroun*. Orstom, France.
- Schroth, G. & Harvey, C.A. (2007) Biodiversity conservation in cocoa production landscapes: an overview. *Biodiversity Conservation*, **16**, 2237–2244.
- Sonwa, D.J., Nkongmeneck, B.A., Weise, S.F., Tchatat, M., Adesina, A.A. & Janssens, M.J.J. (2007) Diversity of plants in cocoa agroforests in the humid forest zone of Southern Cameroon. *Biodiversity Conservation*, **16**, 2385–2400.
- Sounigo, O., Coulibaly, N., Brun, L., N'Goran, J., Cilas, C. & Eskes, A.B. (2003) Evaluation of resistance of *Theobroma cacao* L. to mirids in Côte d'Ivoire: results of comparative progeny trials. *Crop Protection*, **22**, 615–621.
- Taylor, L.R. (1961) Aggregation variance and the mean. *Nature*, **189**, 732–735.
- Torquebiau, E. (2007) *L'agroforesterie. Des arbres et des champs*. L'Harmattan, France.
- Wessel, M. (1985) Shade and nutrition. *Cocoa* (ed. by G. A. R. Wood and R. A. Lass), pp. 166–194. Longman, U.K.
- Williams, G. (1953) Field Observations on the Cacao Mirids, *Sahlbergella singularis* Hagl. and *Distantiella theobroma* (Dist.), in the Gold Coast, I. Mirid Damage. *Bulletin of Entomological Research*, **44**, 101–119.
- Wood, G.A.R. (1985) Establishment. *Cocoa* (ed. by G. A. R. Wood and R. A. Lass), pp. 119–165. Longman, U.K.
- Youdeowei, A. (1965) A note on the spatial distribution of the cocoa mirid *Sahlbergella singularis* Hagl. in a cocoa farm in Western Nigeria. *Nigerian Agricultural Journal*, **2**, 66–67.
- Youdeowei, A. (1971) Studies on the pattern of distribution of the cacao capsid, *Sahlbergella singularis* Hagl., in relation to light intensity in an isolated plot of cacao, *Theobroma cacao* L. *Journal of the West African Science Association*, **16**, 5–12.
- Youdeowei, A. (1977) Behaviour and Activity. *Les Mirides du Cacaoyer* (ed. by E. M. Lavabre), pp. 223–236. G-P. Maisonneuve et Larose, France.

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