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Multi-trophic level interactions in a cassava–maize mixed cropping system in the humid tropics of West Africa

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Abstract

Multi-trophic level interactions in a mixed crop, involving cassava and maize, were studied in derived-savanna in Benin, West Africa. Two trials were planted, one during the short rainy season two months before onset of the dry season and one during the long rainy season in spring. Key pests under study on maize were the noctuid *Sesamia calamistis* Hampson and the pyralids *Eldana saccharina* Walker and *Mussidia nigrivenella* Ragonot, and on cassava, the exotic mealybug, *Phenacoccus manihoti* Matile-Ferrero and its encyrtid parasitoid *Apoanagyrus lopezi* De Santis. Both crops received insecticide treatments to assess the crop loss by a pest species. On maize, intercropping with cassava reduced egg and immature numbers of *S. calamistis* by 67 and 83%, respectively, as a result of reduced host finding by the ovipositing adult moth and of higher egg parasitism by *Telenomus* spp. Both trials showed similar effects on maize yields: on insecticide-treated maize, intercropping with cassava reduced maize yields by 9–16%, while on untreated maize the net effect of reduced pest density and increased plant competition resulted in zero yield differences; yield losses were lower in inter- compared to monocropped maize. For cassava, cropping system had no effect on parasitism by *A. lopezi*. Yield differences between mono- and intercropped cassava depended on time of harvest: they were large at the beginning and zero at final harvest. Land equivalent ratios were mostly > 1.5 indicating that a maize/cassava mixed crop, protected or unprotected, considerably increased the productivity per unit area of land.

Introduction

Maize and cassava are both of increasing importance in western Africa. Both crops are grown in all major agro-ecological zones, from the humid forest to the Sudan savannah, and from sea level to the highlands. Average yields are around 1.2 t ha^{-1} for maize (CIMMYT, 2001) and 9 t ha^{-1} for cassava (FAO, 2001), which is far below the 4.3 t and 14 t ha^{-1} world averages, respectively. In West Africa, the most cited biotic constraints to maize production are indigenous lepidopterous borers, namely the noctuid *Sesamia calamistis* Hampson and the pyralid *Eldana saccharina* Walker, which feed in both the stems and the ears (Schulthess *et al.*, 1997a). The most important pests of cassava are exotic species such as the cassava mealybug; *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) and the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae) (Yaninek & Schulthess, 1993). The major emphasis for solving pest problems in cassava has been through classical

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biological control (Herren & Neuenschwander, 1991; Yaninek & Hanna, 1999). For maize pests an integrated approach has been adopted, which includes host plant resistance (Bosque-Pérez *et al.*, 1997), biological control (Schulthess *et al.*, 1997a, 2001; Ndemah *et al.*, 2001a,b), and habitat management technologies based on management of soil nutrients (Sétamou *et al.*, 1993, 1995; Denké *et al.*, 2000), trap plants (Ndemah *et al.*, 2002) and mixed cropping (Schulthess & Ajala, 1999; Chabi-Olaye *et al.*, 2002; Ndemah *et al.*, 2003).

In Africa, small-scale farmers traditionally practice intercropping in order to achieve greater total land productivity and as an insurance against the failure or unsure market value of a single crop (Vandermeer, 1989; Mutsaers *et al.*, 1993). In addition, many studies in tropical as well as temperate zones have reported reduced pest densities in diversified systems (Altieri & Letourneau, 1982; Risch *et al.*, 1983; Andow, 1991; Thies & Tscharntke, 1999; Kruess & Tscharntke, 2000). In Africa, semi-perennial cassava *Manihot esculenta* Crantz (Euphorbiaceae) is commonly associated with an early maturing crop such as maize *Zea mays* L. (Poaceae). The early crop is harvested after 3–4 months and the cassava harvest may start as early as 9 months after planting. However, the bulk of cassava is harvested after 12–35 months (Mutsaers *et al.*, 1993). There are a number of studies in Africa that have shown a reduction in stemborer densities when maize was intercropped with other host plants such as sorghum or non-host such as cassava or legumes (see overview by Van den Berg *et al.*, 1998). Mechanisms involved were unsuitable hosts acting as trap plants, increased parasitism as a result of volatiles produced by the intercrop or increased mortality due to starvation and/or predation of migrating larvae on non-hosts in the crop mixture (Adesiyun, 1983; Omolo & Seshu Reddy, 1985; Omolo, 1986; Seshu Reddy & Masyanga, 1988; Dissemond & Hindorf, 1990; Oloo & Ogeda, 1990; Seshu Reddy *et al.*, 1990; Päts, 1992; Khan *et al.*, 1997a). By contrast, no information exists on the effects of early-maturing maize on pest infestation or natural enemy activity when grown with cassava.

The present work presents data on multi-trophic level interactions in a cassava–maize mixed cropping system in the derived savanna of the Republic of Benin, West Africa.

Materials and methods

Experimental site

Two field trials were carried out at the International Institute of Tropical Agriculture (IITA)-Benin Station in Abomey-Calavi, Republic of Benin (latitude 6°24′N, longitude 2°20′E, elevation 25 m) in 1987/1988 and 1988/1989 (herewith referred to as experiments I and II, respectively). The experimental site was situated in the derived savanna zone, characterized by a bimodal rainfall distribution with peaks in June and September, and an annual precipitation of about 1200 mm. A short dry spell of about four weeks may occur between July and September. The major dry season normally starts in November and lasts through to March. Monthly mean temperatures range from about 24°C to 29°C with minima in July and August and maxima during the dry season (fig. 1). Experiment I was planted during the second season of 1987 and experiment II during the early season of 1988. In maize, pest infestations peak during the second growing season (Schulthess *et al.*, 1997a) and in cassava during the dry season (Yaninek & Schulthess, 1993).

Experimental procedures and layouts

Two cassava varieties, the profusely-branching variety TMS30572 from IITA and the local, late-branching cv. Odongbo, were used. It was hypothesized that the growth habit of the cassava variety should affect biomass

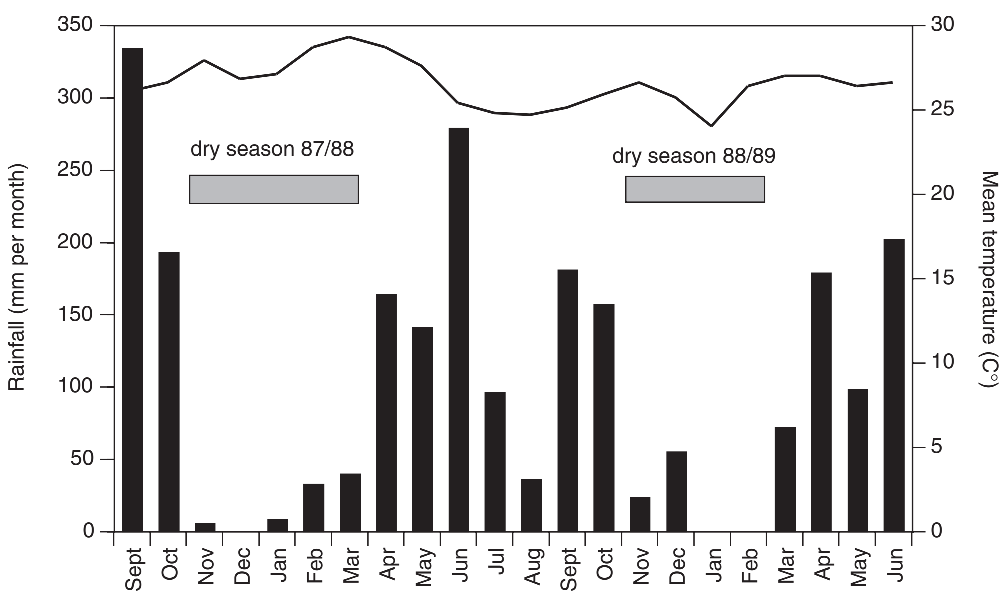

Fig. 1. Monthly rainfall (mm, columns) and mean temperature (°C, line) in southern Benin from September 1987 to June 1989.

production of and thereby pest infestation and yield loss in maize. Both varieties are resistant to the cassava mosaic virus but susceptible to *P. manihoti* and *M. tanajoa*. A 95-day streak virus resistant maize variety, Tropical Zea Early (TZE-SR) was used in both experiments. Maize was planted on 16 September 1987 in experiment I, and 5 May 1988 in experiment II, and cassava, in both experiments, two weeks later. Both crops were planted on 30 cm-high ridges that were 1 m apart. Maize was planted on top of the ridges at a density of 80,000 plants per ha (1 m × 0.25 m with two plants per hole) and cassava on the side of the ridge at 10,000 per ha (1 m × 1 m with one 25-cm cutting per hole). Forty days after planting maize, an NPK 15–15–15 composite fertilizer (N, P_2O_5 and K_2O) was applied at a rate of 60 kg ha^{-1} for each element. The fields were weeded as needed.

The experimental design for both trials was a split-plot design fitted into a randomized complete block in three replicates. Each block was divided into three sub-blocks (main-plots) consisting of two insecticides (the systemic insecticide 'Rogor' (dimethoate 400g l^{-1} EC) and 'Apollo II SC, an acaricide (15 g a.i. hl^{-1}) and a non-insecticide treatment. (Since *M. tanajoa* densities are usually low in southern Benin, no mite counts were done in the present experiments and their effects were only assessed via comparison between the acaricide treatment and the control.) The main-plots were separated by 2.5 m strip of non-cultivated land. The insecticide plots were sprayed monthly with either 260g a.i. ha^{-1} of dimethoate or 120 g a.i. ha^{-1} of acaricide, respectively; at sowing and 30 days later all maize in the protected plots received Furadan granules (i.e. carbofuran 5G, 50 g kg^{-2} a.i.) as a side-dressing and into the whorl, respectively, at the rate of 1500 g a.i. ha^{-1}. The sub-plot factor consisted of the cropping systems: cassava/maize mixed cropping and side-by-side cassava and maize pure stands. The sub-plot size was 41 m × 26 m (i.e. 26 ridges of 41 m length). However, for the pure cassava varieties and pure maize sub-plots the sub-plot size was halved (20.5 m × 26 m).

Sampling and measurements

Dry matter allocation in cassava and maize

For maize, twice a week, stem, leaf and tassel dry weight were assessed from five plants per plot, and for husk, cob and total grain weight from 20 plants per plot. In experiment I, samples were taken from 12 up to 90 days after planting while in experiment II, sampling lasted from 33 to 105 days after planting. After final harvest, maize stalks were cut to ground level and left in the field.

For cassava, random samples of five plants per plot were taken at 36, 57, 79, 102, 130, 160, 190, 217, 284, 333 and 441 days after planting in experiment I and at 79, 114, 150, 190, 227, 260, 290, 323, 387, 429, 512, 547 and 576 days after planting in experiment II. The plants were separated into leaves, stems and storage roots, sliced and dried at 105°C until final dry weight was reached.

Assessment of population of maize stem borers and natural enemies

Borer numbers and damage were assessed on the five randomly sampled plants per plot or 20 at harvest. After counting number of eggs, *S. calamistis* egg-masses were kept individually in plastic containers in the laboratory at 26 ± 1°C and 70 ± 5% RH until parasitoid or borer larva emergence. The egg parasitoids *Telenomus* spp. (Hymenoptera: Scelionidae) were not identified to species level since the *Telenomus isis* Polaszek had not been described at the time (Polaszek *et al.*, 1993). Mean per plot parasitism and percentage of egg batches with parasitoids were calculated for each sampling date. The latter was referred to as 'discovery efficiency' by Bin & Vinson (1991) and provides information about the searching ability of a parasitoid. The sex ratios of the parasitoids were calculated as the proportion of females in relation to the total number of parasitoids per egg batch. In experiment II, sampling started too late to allow assessment of *S. calamistis* egg infestation and parasitism.

Stem- and cobborer larvae were separated and reared on stem or cob pieces until adult moth or parasitoid emergence. Borer damage was assessed as the percentage of plants infested, number of internodes bored, length and percentage of stem tunnelled, and percentage cob damage.

Assessment of populations of the cassava mealybug and its natural enemies

Whole plant counts of *P. manihoti* were made on the five plants sampled per plot; in experiment II, they were made separately for leaves and growing tips. As shown by Schulthess *et al*. (1997b) *P. manihoti* densities and levels of parasitism tended to be higher on growing tips than leaves; this caused destruction of the growing tip and breakdown of apical dominance resulting in the formation of lateral shoots and concomitant losses in root biomass as a result of the remobilization of carbohydrates in roots and stem for growth and respiration (Schulthess *et al.*, 1991a; Schulthess & Saka, 1992). *Phenacoccus manihoti* stages 2 to 5, suitable for parasitoid development, were reared for 3–4 weeks on *Talinum triangulare* (Jacq.) Wild. (Portulacacae) in Petri dishes and checked daily for emergence of parasitoids or hyperparasitoids. In the present work, only the exotic parasitoid *Apoanagyrus (Epidinocarsis) lopezi* De Santis (Hymenoptera: Encyrtidae) was considered in the analyses, as other species, and among them hyperparasitoids, have little impact on the population dynamics of *P. manihoti* (Neuenschwander *et al.*, 1989; Herren & Neuenschwander, 1991; Schulthess *et al.*, 1997b). However, the numbers of hyperparasitoids were added to the numbers of *A. lopezi*.

Data analysis

The mixed model procedure (SAS, 1997) with repeated measures was used to determine variation of biomass, pests and damage variables between insecticide treatments, cropping systems and variety (for cassava only). The random effects were date after planting, block, replication, plot and plant. Plants were nested within plots, plots within replicates and replicates within blocks. The log-likelihood procedure was used to test for differences in parasitism and discovery efficiency.

Cassava dry matter, pest and natural enemy data were analysed according to growing periods, i.e. for experiment I, a first growing season plus dry season (S_1: 36–190 days after planting) and second growing season (S_2: 191–444 days after planting), and for experiment II, a first growing season (S_1: 79–150 days after planting), a dry season (S_2: 151–290 days after planting) and second growing season (S_3: 291–576 days after planting). Pest numbers were log (x+1)-transformed while percentages were arcsine-transformed before analysis. Means were separated using Tukey's test. Back-transformed results are given in the tables.

Land equivalent ratio (LER)

According to Vandermeer (1989) the measurement most frequently used to evaluate the effectiveness of an intercrop is the land equivalent ratio (LER), which explains how much land one would need to produce as much in monoculture as is produced on one hectare of mixed cropping.

For the growth period S_2, and S_2 and S_3 in experiments I and II, respectively, the land equivalent ratio were calculated as:

$$LER = I_{maize}/M_{maize} + I_{cassava}/M_{cassava}$$

where I_x and M_x = yield per ha of a crop (i.e. for cassava, means across sampling dates in S_2, and S_2 and S_3 in experiment I and II, respectively) in inter- (I) and mono-cropping (M), respectively. If LER is greater than 1, the intercrop is more efficient and if it is less than one, the monoculture is more efficient.

Results

Maize

Pest infestations and egg parasitism on maize

In experiment I, egg batches per plant and percent plants with *S. calamistis* egg batches were 4–6 times higher in the monocropped than intercropping treatments while egg batch size did not vary significantly with treatment (table 1). Cassava variety had no significant effect. Egg infestations significantly changed with days after planting ($P < 0.0001$). It increased from 20 to 35 days after planting and then decreased gradually with few eggs found after 50 days after planting (fig. 2). Across sampling dates, *Telenomus* spp. egg parasitism and discovery efficiency were 2–3 times higher in intercropped than monocropped maize ($P < 0.05$) but the sex ratios were not different (table 1).

In both experiments, numbers of *S. calamistis* larvae and pupae were 2–3 times higher in the mono- than intercropping treatments and similar among the intercropped cassava varieties (table 1). Pest numbers significantly changed with days after planting ($P < 0.0001$). In experiment I, the first *S. calamistis* larvae were collected at 27 days after planting and the numbers increased until day 43 and then decreased (fig. 2); a second peak was observed around 79 days after planting. For *E. saccharina* and other Lepidoptera mainly *Mussidia nigrivenella* Ragonot (Pyralidae) and *Cryptophlebia leucotreta* (Meyrick) (Tortricidae), which only feed in the ear (Schulthess *et al.*, 1991b) no differences between treatments were found in either experiment (table 1). In experiment I, the first *E. saccharina* larvae were collected at 50 days after planting (fig. 2) and reached peaks between day 68 and 86, though the trends were not clear for all treatments. In experiment II, *S. calamistis* densities increased until day 77 and then decreased, while for *E. saccharina*, the first larvae were collected at 68 days after planting but again the temporal trends were not as clear as for *S. calamistis* (fig. 3). Larval and pupal parasitism was too low and erratic to draw any conclusions and so no data are presented here.

Table 1. Effect of cropping system on pest infestations, egg parasitism by *Telenomus* spp. and parasitoid sex ratio (± SE) in the 1987/88 (I) and 1988/89 (II) experiments.

	Sesamia calamistis		
	Eggs per batch	Egg batch per plant	% plant with eggs
Experiment I			
Maize mono-TMS30572	16.9 ± 0.73	0.16 ± 0.02a	14.7 ± 2.43a
Maize mono-Odongbo	17.0 ± 0.84	0.14 ± 0.02a	13.0 ± 2.15a
Maize-TMS30572 intercrop	17.6 ± 2.44	0.03 ± 0.01b	2.8 ± 0.93b
Maize-Odongbo intercrop	14.5 ± 1.71	0.02 ± 0.01b	2.1 ± 0.82b
	Egg parasitism	Discovery efficiency	Sex ratio of parasitoids
Maize mono-TMS30572	38.3 ± 6.9a	37.2 ± 7.4a	0.79 ± .12
Maize mono-Odongbo	31.9 ± 7.0a	41.7 ± 8.6a	0.80 ± .11
Maize-TMS30572 intercrop	80.8 ± 11.9b	87.5 ± 12.5b	0.80 ± .20
Maize-Odongbo intercrop	79.5 ± 16.1b	83.3 ± 16.7b	0.81 ± .16
	No of larvae + pupa per plant		
	S. calamistis	*E. saccharina*	Others
Maize mono-TMS30572	0.25 ± 0.1a	0.16 ± 0.01	0.19 ± 0.03
Maize mono-Odongbo	0.16 ± 0.01ab	0.11 ± 0.01	0.27 ± 0.06
Maize-TMS30572 intercrop	0.09 ± 0.01bc	0.14 ± 0.01	0.12 ± 0.02
Maize-Odongbo intercrop	0.05 ± 0.01c	0.13 ± 0.01	0.23 ± 0.05
Experiment II			
Maize mono-TMS30572	0.22 ± 0.01a	0.21 ± 0.01	0.30 ± 0.03
Maize mono-Odongbo	0.19 ± 0.01a	0.23 ± 0.01	0.21 ± 0.03
Maize-TMS30572 intercrop	0.06 ± 0.01b	0.16 ± 0.01	0.18 ± 0.03
Maize-Odongbo intercrop	0.06 ± 0.01b	0.14 ± 0.01	0.23 ± 0.03

Means within columns, followed by the same letter are not significantly different (Tukey test, $P = 0.05$).

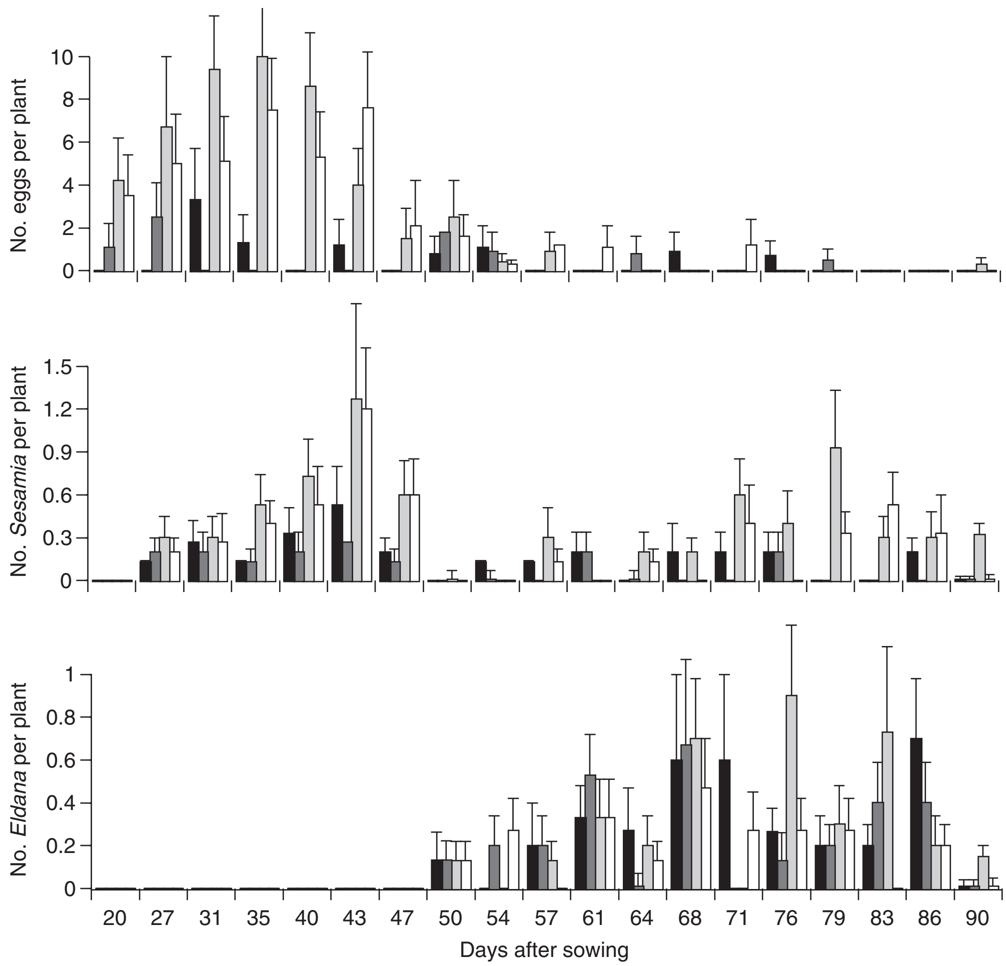

Fig. 2. Stemborer infestations on monocropped maize and maize intercropped with the cassava cultivars TMS30572 or Odongbo in a field trial in southern Benin 1987. The bars indicate SEs. ■, Maize/TMS30572; ■, maize/Odongbo; □, maize mono-TM30572; □, maize mono-Odongbo.

Plant damage and yield

In experiment I, the percentage of infested plants (P(I)) in the mixed crop was reduced by 26–29% and stem damage by 27–35% compared to monocropped maize, while ear damage was not significantly different between treatments (table 2). Similarly, in experiment II, P(I) was 33–35% lower in intercropped maize while both stem and ear damage were not significant.

In experiment I, when comparing between the insecticide-free control and the Furadan treatments, all crop mixtures yielded significant differences in ear and grain yields but the differences were 16–20% in monocropped maize vs. 4.7–7.0% in intercropped maize (table 3). By contrast, when comparing between mono- and intercropped maize, no differences were found in the insecticide-free control while in the Furadan-treated treatments yields were 10.0–16.6% higher in mono- than intercropped maize.

In experiment II, the trends were the same but the yield differences were generally smaller (table 3). In both experiments, cassava variety had no effect.

Cassava

Pest infestation and parasitism

In experiment I during the first season, which included a short rainy season and the dry season, densities of the mealybug *P. manihoti* were 3–4 times higher on mono- than intercropped cassava but variety had no effect (table 4). Similarly, during the second season, which included the second post-dry season period through to final harvest at 444 days after planting, *P. manihoti* densities were 3–6 times higher in the two monocrops than in the TMS30572 cassava–maize intercrop. Parasitism was not affected by cropping system or cassava variety and was mostly around 20%. In experiment II during the first season (S_1), which included the first long rainy period, *P. manihoti* densities on growing tips and total numbers per plant were highest in monocropped TMS30572 and intercropped Odongbo, and 2–3 times lower in the remaining treatments (table 5). Pest densities were lower on leaves than tips but on leaves they did not vary with cropping system. During the second season (S_2), which included the dry season, mealybug

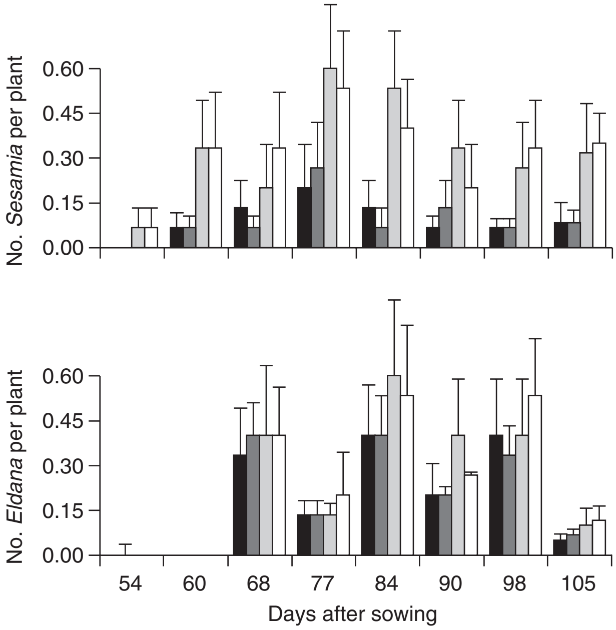

Fig. 3. Stemborer infestations on monocropped maize and maize intercropped with the cassava cultivars TMS30572 or Odongbo in a field trial in southern Benin 1988. The bars indicate SEs. ■, Maize/TMS30572; ■, maize/Odongbo; □, maize mono-TM30572; □, maize mono-Odongbo.

densities on both tips and leaves tended to be considerably higher than during the rainy season. On tips, they were highest on mono- and intercropped cv. Odongbo and about a third on cv. TMS30572, while on leaves, they tended to be highest on monocropped TMS30572 and intercropped cv. Odongbo, and similar in the remaining treatments. Per plant densities followed mealybug numbers on growing tips. During the second rainy period, *P. manihoti* infestations declined but similar trends were observed during the dry season, thus, on both tips and leaves, pest densities were highest on mono- and intercropped cv. Odongbo and less than a third of that on cv. TMS30572 treatments. During seasons 2 and 3, pest infestations and the proportion of pest load on the growing tips were considerably higher for Odongbo than for TMS30572 (table 5). Parasitism by *A. lopezi* tended to be higher on growing tips than on leaves but it did not vary with cropping system, except for leaves during season I when it was higher on monocropped TMS30572 and intercropped Odongbo.

Dry matter allocation and yield

In experiment I, more than 50% of the intercropped cassava of the TMS30572 variety died due to the early onset of the dry season. Thus, dry matter data for the second growing period (S_2) of this treatment were not included in the analysis. During both seasons, insecticide treatment and variety had no effect on leaf, stem and root production (table 6). During the first growing season (S_1), leaf, stem and storage root dry matter in the intercropping treatments were reduced by > 60%, *c.* 50 and > 90%, respectively, compared to monocropped cassava. During the second growing season, differences in leaf and root biomass did not vary significantly with cropping system, while stem dry matter in the Rogor treatment was highest in monocropped TMS30572 and lowest in intercropped Odongbo.

In experiment II, during all three growing seasons, insecticide treatment and variety again had no effect on leaf, stem and root production (table 7). During season 1, leaf biomass was 45–63% higher in mono- than intercropped cassava. During season 2, it was highest on monocropped TMS30572 and lowest on intercropped Odongbo, while during season 3, within variety, no differences were found between cropping system but TMS30572 had a considerably higher leaf biomass than cv. Odongbo. For stem dry matter the trends were less distinct; during season 1, they followed those of leaves while during season 2, stem biomass tended to be lowest in intercropped Odongbo but similar in the other treatments; in season 3, monocropped TMS30572 in the control had greater stem dry matter than intercropped TMS30572 while in the acaricide and Rogor treatments monocropped cv. Odongbo had greater stem dry matter than intercropped Odongbo (table 7). During seasons 1 and 2, root dry matter of intercropped cassava was reduced by around 70% and *c.* 30%, respectively. During season 3, root biomass did not vary among treatments in the untreated controls; it was highest for monocropped Odongbo following acaricide treatment and lowest for intercropped Odongbo following Rogor treatment.

Land equivalent ratios varied between 1.4 and 1.98 (table 8). They were higher during the later than the early growth periods. Maximum land equivalent ratios, i.e. using maximum yields reached during the second and third growing periods in experiments I and II, respectively, were approximately 2.2.

Table 2. Effect of the cropping system on the percentage of infested maize plants, stem tunnelling and cob damage in the 1987/88 (I) and 1988/89 (II) experiments.

	P(I)	% tunnelling	% cob damage
Experiment I			
Maize mono-TMS30572	38.2 ± 2.8a	4.0 ± 0.3a	10.3 ± 2.3
Maize mono-Odongbo	36.2 ± 3.0a	3.5 ± 0.3ab	8.3 ± 3.4
Maize-TMS30572 intercrop	27.1 ± 2.9b	2.6 ± 0.2b	11.0 ± 3.3
Maize-Odongbo intercrop	26.8 ± 3.0b	2.8 ± 0.3b	11.3 ± 3.2
Experiment II			
Maize mono-TMS30572	25.9 ± 2.9a	6.1 ± 0.5	9.9 ± 3.3
Maize mono-Odongbo	23.9 ± 2.3a	5.9 ± 0.9	8.3 ± 3.5
Maize-TMS30572 intercrop	16.9 ± 2.4b	4.3 ± 0.5	7.9 ± 2.5
Maize-Odongbo intercrop	16.2 ± 2.3b	4.5 ± 0.5	13.1 ± 4.6

Means within columns, followed by the same letter are not significantly different (Tukey test, $P = 0.05$).

Table 3. Effect of cropping system and insecticide treatment on maize yields, and yield loss as a percentage of monocropping in the 1987/88 (I) and 1988/89 (II) experiments.

	Ear yield (g per plant)			Grain yield (g per plant)		
Experiment I	Control	Furadan	% loss	Control	Furadan	% loss
Maize mono-TMS30572	61.2 ± 1.8A	73.0 ± 0.9aB	16.2	47.6 ± 1.4A	59.7 ± 1.7B	20.3
Maize mono-Odongbo	61.0 ± 0.5A	72.4 ± 1.4aB	15.5	48.0 ± 0.9A	58.7 ± 1.4aB	18.2
Maize-TMS30572 intercrop	60.5 ± 1.2A	65.0 ± 1.6bB	7.0	46.5 ± 2.1A	49.8 ± 1.6bB	6.6
Maize-Odongbo intercrop	60.9 ± 1.3A	65.1 ± 1.9bB	6.5	47.6 ± 0.9A	52.3 ± 2.0bB	4.7
Mono-inter (%) TMS 30572	ns	10.9		ns	16.6	
Mono-inter (%) Odongbo	ns	10.1		ns	10.9	
Experiment II						
Maize mono-TMS30572	81.2 ± 1.8A	92.6 ± 2.4aB	12.3	67.6 ± 1.4A	79.7 ± 1.8aB	15.3
Maize mono-Odongbo	81.0 ± 0.5A	92.4 ± 1.4aB	12.3	68.0 ± 0.9A	78.7 ± 1.4aB	13.6
Maize-TMS30572 intercrop	79.5 ± 2.2A	86.0 ± 2.5bB	7.6	66.5 ± 2.1	69.8 ± 1.6b	ns
Maize-Odongbo intercrop	80.2 ± 1.7A	85.1 ± 1.9bB	5.8	67.6 ± 0.9A	72.3 ± 2.0bB	6.5
Mono-inter (%) TMS 30572	ns	7.1		ns	12.4	
Mono-inter (%) Odongbo	ns	7.9		ns	8.9	

Means within row, followed by the same capital letters and means within column followed by the same lower case letters are not significantly different (Tukey test, $P = 0.05$).

Table 4. Comparison of *Phenacoccus manihoti* densities and parasitism by *Apoanagyrus lopezi* on two cassava cultivars (C1 = TMS 30572, C2 = Odongbo), as a monocrop or intercrop with maize (M), and left untreated (0) during the seasons (S) of 1987/88.

	P. manihoti density		Parasitism	
	S_1	S_2	S_1	S_2
0C1	14.9 ± 6.2a	13.9 ± 4.6a	18.2 ± 7.6	18.9 ± 5.8
0C2	11.8 ± 5.9a	17.4 ± 7.2a	18.6 ± 13.7	19.6 ± 9.8
0C1M	3.3 ± 2.4b	2.9 ± 2.9b	23.5 ± 0.4	24.1 ± 3.1
0C2M	3.6 ± 3.3b	8.5 ± 4.3ab	21.6 ± 9.5	7.3 ± 2.6

Comparisons were done across all insecticide and crop mixture treatments, between leaves and tips and varieties.
S_1, short rainy + dry season; S_2, main growing season.

Table 5. Comparison of densities of *Phenacoccus manihoti* and parasitism by *Apanagyrus lopezi* on leaves and tips of two cassava cultivars (C1 = TMS 30572, C2 = Odongbo) as a monocrop or intercrop with maize (M) and left untreated (0) during the seasons (S) of 1988/89.

	S_1			S_2			S_3		
	Tips	Leaves	Total	Tips	Leaves	Total	Tips	Leaves	Total
CM density									
0C1	6.2 ± 2.5a	2.6 ± 0.9	8.7 ± 3.1a	7.0 ± 1.5b	7.2 ± 1.8ab	14.2 ± 2.5b	1.7 ± 0.2b	0.4 ± 0.1b	2.1 ± 0.3b
0C2	2.3 ± 1.2b	0.7 ± 0.4	3.1 ± 1.2b	20.0 ± 3.3a	4.2 ± 1.7bc	24.2 ± 4.0a	5.6 ± 0.8a	1.1 ± 0.5a	6.7 ± 1.1a
0C1M	2.3 ± 1.3b	0.4 ± 0.3	2.7 ± 1.3b	7.9 ± 1.7b	3.2 ± 1.0c	11.1 ± 2.2b	1.6 ± 0.3b	0.2 ± 0.1b	1.8 ± 0.3b
0C2M	5.8 ± 2.8b	4.0 ± 1.9	9.8 ± 3.8a	19.3 ± 5.2a	8.8 ± 2.6a	28.1 ± 6.3a	5.3 ± 1.0a	0.6 ± 0.2a	5.9 ± 0.8a
Parasitism									
0C1	10.7 ± 4.8	7.0 ± 3.4a	9.5 ± 4.4	17.5 ± 4.8	14.2 ± 3.8	15.5 ± 2.7	33.7 ± 8.1	7.8 ± 3.2	28.0 ± 5.4
0C2	10.6 ± 1.1	0.0 ± 0.0b	10.6 ± 1.0	12.4 ± 3.2	18.9 ± 15.7	8.5 ± 1.3	23.1 ± 4.4	14.8 ± 4.9	18.2 ± 2.7
0C1M	10.8 ± 9.0	0.0 ± 0.0b	9.7 ± 8.0	13.9 ± 3.7	7.6 ± 3.4	13.6 ± 3.1	21.4 ± 8.0	15.1 ± 7.8	19.4 ± 5.8
0C2M	13.0 ± 5.1	7.3 ± 5.9a	11.0 ± 3.7	11.1 ± 2.6	7.7 ± 2.2	9.9 ± 1.8	18.1 ± 3.4	11.5 ± 3.8	17.5 ± 2.7

Comparisons were done across all crop mixture treatments, between leaves and tips and varieties.
S_1, first growing season; S_2, dry season; S_3, second growing season.

Discussion

Intercropping considerably reduced *S. calamistis* infestations. Vandermeer (1989) listed three possible mechanisms responsible for reducing pest infestation in mixed cropping systems: (i) the disruptive-crop hypothesis in which a second non-host plant species disrupts the ability of the pest to attack its proper host plant species; (ii) the trap crop hypothesis in which a second non-suitable host plant species attracts the pest away from its primary host; and (iii) the natural enemy hypothesis in which the intercropping setup attracts more predators and parasitoids than the monocrop thereby reducing pests on the primary host plant. For African cereal stemborer species, all three mechanisms

Table 6. Comparison of leaf, stem and root dry matter (g) of two cassava cultivars (C1 = TMS 30572, C2 = Odongbo) as a monocrop or intercrop with maize (M) treated with Apollo II SC (A) (15 g a.i. hl^{-1}), Rogor (R) (dimethoate 40% EC) or left untreated (0) during different growth periods (S) of 1987/88.

Treatment	Leaves		Stems		Roots	
	S_1	S_2	S_1	S_2	S_1	S_2
0C1	40.9 ± 6.5a	69.9 ± 12.2	76.6 ± 12.3ab	242.6 ± 29.8	119.2 ± 18.2a	525.7 ± 120.9
0C2	43.7 ± 5.7a	62.4 ± 11.8	94.4 ± 11.6a	289.6 ± 45.7	90.2 ± 14.1a	508.9 ± 96.8
0C1M	16.2 ± 5.8b	–	39.4 ± 4.6c	–	10.2 ± 4.8b	–
0C2M	16.6 ± 4.2b	68.0 ± 9.7	57.4 ± 4.1b	224.9 ± 41.5	7.2 ± 1.5b	500.2 ± 116.6
AC1	41.8 ± 6.2a	73.1 ± 10.6	75.1 ± 10.6ab	339.3 ± 60.6	111.9 ± 15.6a	655.9 ± 133.5
AC2	42.0 ± 5.5a	68.1 ± 11.6	94.9 ± 11.6a	328.3 ± 46.1	79.4 ± 13.5a	471.6 ± 84.97
AC1M	13.6 ± 4.8b	–	41.0 ± 3.9c	–	5.7 ± 1.3b	–
AC2M	13.9 ± 4.1b	61.7 ± 7.2	51.5 ± 3.7bc	273.1 ± 58.1	15.4 ± 8.9b	619.3 ± 160.8
RC1	42.3 ± 7.3a	94.7 ± 13.1	74.3 ± 12.9ab	414.0 ± 55.5a	119.1 ± 21.2a	614.6 ± 88.7
RC2	45.7 ± 6.8a	85.8 ± 15.8	94.6 ± 13.5a	373.6 ± 50.1ab	78.5 ± 18.6a	578.6 ± 92.2
RC1M	13.8 ± 6.2b	–	32.6 ± 3.6c	–	11.0 ± 4.4b	–
RC2M	16.3 ± 5.6b	79.8 ± 10.2	48.8 ± 4.4b	264.7 ± 56.0b	9.5 ± 4.8b	676.3 ± 171.4

Comparisons were done across all insecticide, crop mixture treatments and varieties.
S_1, short rainy + dry season (36–190 days after planting); S_2, main growing season (191–444 days after planting).

Table 7. Comparison of leaf, stem and root dry matter (g) of two cassava cultivars (C1 = TMS 30572, C2 = Odongbo) as a monocrop or intercrop with maize (M) treated with an acaricide (A), Rogor (R) or left untreated (0) during different growth periods (S) of 1988/89/90.

Treatment	Leaves			Stems			Roots		
	S_1	S_2	S_3	S_1	S_2	S_3	S_1	S_2	S_3
0C1	57.7 ± 11.8a	55.5 ± 7.7a	63.6 ± 4.4a	97.5 ± 19.1a	265.2 ± 15.7a	624.9 ± 54.6a	158.9 ± 54.1a	590.7 ± 39.9a	1187.8 ± 85.4
0C2	36.8 ± 5.2a	35.1 ± 3.0ab	41.5 ± 3.5b	59.3 ± 8.3b	192.2 ± 20.8b	526.2 ± 52.2ab	125.5 ± 35.5a	605.4 ± 62.7a	1181.2 ± 65.8
0C1M	21.5 ± 3.9b	37.6 ± 4.6ab	63.9 ± 5.0a	50.7 ± 4.4b	184.2 ± 22.4b	447.2 ± 50.3b	37.3 ± 11.2b	383.6 ± 55.2b	1044.4 ± 116.3
0C2M	20.1 ± 4.5b	32.8 ± 3.3b	46.7 ± 3.2b	46.9 ± 5.8b	142.9 ± 14.2b	548.4 ± 61.4ab	67.8 ± 15.9b	398.1 ± 52.2b	1049.3 ± 79.7
AC1	63.5 ± 13.7a	60.0 ± 10.3a	61.9 ± 6.2a	103.2 ± 23.4a	284.0 ± 17.5a	601.5 ± 51.3ab	167.9 ± 61.1a	564.8 ± 26.7a	1200.4 ± 98.6b
AC2	49.0 ± 6.0a	43.5 ± 4.3ab	51.4 ± 4.9ab	73.7 ± 10.6a	256.9 ± 25.9a	698.1 ± 65.7a	115.0 ± 29.4a	738.8 ± 78.6a	1554.2 ± 82.0a
AC1M	23.3 ± 5.3b	49.6 ± 7.8ab	71.1 ± 6.6a	60.1 ± 5.5ab	247.9 ± 26.5a	641.5 ± 69.9ab	39.7 ± 13.2b	445.0 ± 54.9b	1245.1 ± 129.6b
AC2M	19.6 ± 4.0b	31.4 ± 2.6b	40.3 ± 3.2b	41.2 ± 4.2b	178.8 ± 23.0b	496.2 ± 50.7b	33.9 ± 11.3b	405.8 ± 59.8b	1005.9 ± 68.0b
RC1	63.8 ± 13.3a	62.8 ± 10.2a	70.7 ± 6.2a	99.0 ± 25.1a	377.1 ± 31.8a	743.3 ± 73.0a	129.8 ± 47.6a	640.6 ± 55.3ab	1356.2 ± 111.0a
RC2	52.3 ± 8.1a	51.6 ± 5.9ab	47.4 ± 3.7b	130.6 ± 36.8a	365.7 ± 32.2ab	715.7 ± 64.4a	208.8 ± 70.7a	859.1 ± 54.2a	1417.8 ± 66.4a
RC1M	23.3 ± 4.3b	49.3 ± 8.5ab	70.5 ± 7.5a	51.5 ± 6.3b	293.5 ± 37.4bc	644.2 ± 49.4ab	24.6 ± 8.3b	501.1 ± 64.2c	1194.4 ± 99.2ab
RC2M	25.5 ± 4.5b	36.6 ± 3.4b	36.3 ± 2.8b	49.1 ± 7.5b	245.7 ± 33.0c	532.5 ± 49.2b	58.5 ± 21.9b	591.6 ± 79.7bc	1007.9 ± 64.5b

Comparisons were done across all insecticide, crop mixture treatments and varieties.
S_1, first growing season (79–150 days after planting); S_2, dry season (151–290 days after planting); S_3, second growing season (291–576 days after planting).

Table 8. Land equivalent ratios of cassava–maize intercrops using Furadan-protected or unprotected maize as standard over different growth periods.

	With unprotected maize			With Furadan-protected maize			Maximum	
	Exp I S_2	Exp II S_2	Exp II S_3	Exp I S_2	Exp II S_2	Exp II S_3	Exp I S_2	Exp II S_3
0C1M	–	1.45	1.77	–	1.40	1.88	–	2.07
0C2M	1.89	1.58	1.81	1.98	1.54	1.89	2.16	2.16

Values were calculated using mean across season cassava yields and maximum values (i.e. highest cassava yield) reached during the later growing seasons (S_2 and S_3) in experiment I and II.
See table 5 for explanation of OC1M and OC2M.

have been shown to be involved. In the present study in experiment I, the highest reduction in pest densities (i.e. 67%) occurred during oviposition. *Sesamia calamistis* lays eggs cryptically between the leaf sheath and stem (Kaufmann, 1983) of plant species belonging to the families Poaceae and Cyperaceae (Khan *et al*., 1997b; Schulthess *et al*., 1997a). No eggs have ever been found on dicotyledonous plants such as cassava or on exposed plant surfaces, e.g. leaves or stems. On maize, most eggs are laid on pre-tasselling plants (Kaufmann, 1983; Sétamou & Schulthess, 1995). It is therefore suggested that the non-host cassava disrupts the host-finding capacity of the ovipositing

S. calamistis, leading to lower egg loads on intercropped maize. This corroborates the findings of Chabi-Olaye *et al*. (2002) in Cameroon, who showed a considerable reduction in egg densities of *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) in maize–cassava, maize–cowpea and maize–soybean intercrops. Ampong-Nyarko *et al*. (1995), working with *Chilo partellus* Swinhoe (Lepidoptera: Crambidae), reported that in a maize–cowpea intercrop, *C. partellus* laid eggs on leaves of the unsuitable non-host cowpea which, thereby, acted as a reproductive sink (i.e. trap plant). However, in contrast to noctuid stemborers, *C. partellus* oviposits its eggs on the surface of leaves (Durbey & Sarup, 1982) and since the canopy of the different crop species overlap, female moths might lay their eggs on the wrong host plant. Skovgard & Päts (1996) working in Kenya could not show an effect of a maize–cowpea intercrop on oviposition by *C. partellus* and *C. orichalcociliellus* Strand (Lepidoptera: Crambidae) and no mention was made if oviposition on cowpea took place.

Larval and pupal (i.e. immature) densities were reduced on average by 83% on intercropped maize, thus, the additional reduction not attributable to reduced oviposition was only 17%. In contrast to Chabi-Olaye *et al*. (2002), who worked on *B. fusca* in the forest zone of Cameroon, considerable differences were found in levels of parasitism and discovery efficiency of *Telenomus* spp., the most important egg parasitoids of noctuid stemborers in West and Central Africa (Chabi-Olaye, 1992; Sétamou & Schulthess, 1995; Schulthess *et al*., 2001; Ndemah *et al*., 2003). Host finding of *Telenomus* spp. is affected by the pheromone of the calling virgin female moth (Fiaboé *et al*., 2003), kairomones deposited by the female at oviposition and volatiles from host plants (Chabi-Olaye *et al*., 2001). It is doubtful that the non-host cassava would improve host-finding of the parasitoid and it is suggested that the differences in parasitism were a result of negative density-dependence. Similarly, Skovgard & Päts (1996) reported significantly higher egg parasitism on inter- compared to monocropped maize, while larval and pupal parasitism, and numbers of the main predators, ants (Formicidae) and wandering spiders (Araneae) did not vary. In the present experiment, predator numbers were not assessed and larval and pupal parasitism was too low to draw any conclusions. Thus, it cannot be determined if the remaining differences in immature numbers were due to differences in egg parasitism only, or due to differences in predation, or to starvation of migrating larvae, as a result of reduced host-finding when maize was intercropped with the non-host cassava.

For *E. saccharina* and the ear-boring pests *M. nigrivenella* and *C. leucotreta* intercropping with cassava had no effect. All three species attack maize late. *Eldana saccharina* infests plants at the tasselling stage or later (Kaufmann, 1983) whereas both ear-borer species oviposit on the silk or husks of young ears from where they penetrate into the ear (Sétamou *et al*., 2000a). Moreover, the main ear pest *M. nigrivenella* is highly polyphagous and was found on about 20 plant species from 11 different plant families of which maize is the only gramineous host (Sétamou *et al*., 2000b). In the present experiment, maize was planted earlier and therefore had a head start over cassava. Thus the ability of cassava to disrupt host-finding of borers decreased as maize increasingly outgrew cassava.

In contrast to insecticide-treated plots, no differences in yield between mono- and intercropped maize were observed for untreated maize suggesting that the benefit of reduced pest densities in mixed cropping equalled the negative effect of interspecific plant competition. Differences in yield reductions due to the effect of interspecific competition (calculated as the percentage yield difference between inter- and monocropped maize in the insecticide treatments), when intercropped with the profusely, early-branching cassava variety TMS30572 or the late-branching Odongbo, were small with means across both trials of 14.4 vs. 9.9%, respectively (table 3). However, at the early growth stage of cassava, differences in leaf, stem and root biomass between the two growth types were small and mostly not significant. Taking into consideration the negative effect of interspecific competition on plant growth, the yield increase due to reduced borer infestation when cassava was present (means across both varieties calculated as differences in yield loss between mono- and intercropped maize; table 3) was 13.6 and 14.8% in experiments I and II, respectively.

The reduction in mealybug densities on intercropped compared to monocropped cassava in experiment I was very likely due to a 70% reduction in leaf biomass (table 6) and not due to differences in parasitism by *A. lopezi*, which was similar in all treatments. In experiment II, during the dry season and the ensuing second rainy period, when leaf biomasses were similar in all treatments and for both varieties, *P. manihoti* densities, especially on growing tips, were considerably higher on cv. Odongbo than cv. TMS30572, which could not be attributed to varietal differences in parasitism. Schulthess *et al*. (1997b) in a mulch experiment showed large differences in nitrogen content between tips and leaves as well as between early- and late-branching varieties with higher values for tips and for late-branching varieties. They found a close negative correlation between nitrogen content and *P. manihoti* densities, which seemed counter-intuitive. It was found, however, that a higher nutritional status of the plant led to larger mealybugs, and large hosts also tended to yield female offspring of *A. lopezi* (van Dijken *et al*., 1989; Schulthess *et al*., 1997b), which resulted in a higher female biased sex ratio and higher parasitism. Thus, improving the nutritional status of the plant indirectly enhanced the efficiency of *A. lopezi* resulting in a decrease in pest densities. The present findings corroborate these results only in part: *P. manihoti* densities and parasitism were higher on growing tips than leaves, but the late-branching cv. Odongbo had higher leaf and tip infestations than the early-branching TMS30572. However, of all the varieties tested at IITA, cv. Odongbo was consistently the most susceptible variety and had the highest proportion of *P. manihoti* living on growing tips. In life table studies more than half of the crawlers escaped from leaf clips (Schulthess, unpublished data) indicating that the leaves of cv. Odongbo probably had a xenobiotic effect which may have affected overall parasitism in spite of superior nitrogen contents (S. Bocks, IITA-Benin, unpublished data).

In the late planting experiment (I), 50% of the profusely-branching TMS30572 planted as an intercrop died because of a combination of drought and interspecific plant competition. Oka *et al*. (1990) found that the volume density (g cm^{-3}) of cuttings was the major factor determining survival of plants in the dry and wet seasons, with cuttings from non-branching cultivars surviving better than early-branching cassava. During the transition from the dry to the wet season, TMS30572 invests large amounts of carbohydrates from its stems into growth of shoots and respiration, and stem weight (Schulthess *et al*., 1991a; Schulthess & Saka, 1992) and thus the quality of cuttings decreases drastically. This may explain the high levels of plant mortality often observed during stress conditions. Thus, when planting cassava in a mixed crop during the late season, a late-branching variety is superior to an early-branching variety.

In contrast to the findings of Okeke (1996), the cassava growth type did not affect the yields of maize. However, top growth during the period when maize was present did not vary significantly between the varieties used in the present experiments. Moreover, when planted shortly before the dry season, the cassava variety TMS30572 branches late, i.e. at a higher number of internodes (Schulthess *et al*., 1991a), and as a result leaf and stem growth did not vary significantly for the entire duration of the experiment.

Schulthess *et al*. (1991a) suggested that for cassava, the physiological costs incurred in storage roots during the dry season were proportional to the weight of the plant obtained at the beginning of the dry season. Consequently, the larger the plant the higher remobilization-related losses. Thus, in the present experiment, interspecific plant competition reduced biomass (leaf, stem and roots) during the initial growth period as also shown by Olasantan *et al*. (1995), but during the second wet season yields reached similar levels in both cropping systems. Hence, yield effects due to intercropping depend on the time of harvest of cassava.

As stated by Vandermeer (1989), a land equivalent ratio of 1 is critical since above this intercrop is favoured. In the present study, intercropping considerably increased the productivity per unit area of land since the land equivalent ratios were mostly > 1.5, and thus in the range of those reported by Kang & Wilson (1981) and Oyedokun *et al*. (1989). As also reported in a review paper by Mutsaers *et al*. (1993) land equivalent ratios can increase according to the timing of the cassava harvest indicating that the plant is able to recover from any stress incurred by an intercrop during the early stages of plant growth. The present findings show that under low-input, small-scale farming conditions, intercropping maize with cassava does not reduce yields of maize, and of cassava if it is harvested after 12 months. This underlines the suitability of using long-duration crops with a non-determinate growth habit such as cassava for intercropping with a short-duration crop such as maize.

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