Biocontrol Science and Technology, 2006; 16(2): 205–214

Population dynamics of *Bemisia tabaci* (Homoptera: Aleyrodidae) parasitoids on cassava mosaic disease–resistant and susceptible varieties

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(Received 17 February 2004; returned 10 April 2004; accepted 8 July 2005)

Abstract
Three field trials were conducted at Namulonge Agricultural and Animal Production Research Institute to investigate the population dynamics of *Bemisia tabaci* Gennadius and its associated aphelinid parasitoids in Uganda. Results showed that more whitefly occurred on the cassava mosaic disease-resistant variety, (Nase 4) compared to the susceptible variety, (Ebwanatereka). Two species of aphelinid parasitoids, *Eretmocerus mundus* Mercet and *Encarsia sophia* Girault and Dodd, were identified during the study. Overall percent parasitism did not differ significantly ($P > 0.05$) between varieties in all the trials, but significant differences occurred at 13, 15 and 21 weeks after planting during late season (2000), 18 weeks after planting during early season (2001), and 8 weeks after planting during late season (2001). The trends in the build up in numbers of both parasitoids species and apparent parasitism were similar, differed significantly on certain dates. It was, however, noted that percent parasitism decreased with nymph number. The significance of this phenomenon on the potential use of these aphelinid parasitoids as biocontrol agents of the cassava whitefly is discussed.

Keywords: Bemisia tabaci, *biological control, cassava mosaic disease,* Encarsia sophia, Eretmocerus mundus, *population dynamics*

Introduction

The whitefly, *Bemisia tabaci* Gennadius is one of the most important insect pests in world agriculture because of its direct feeding, contamination from honeydew, and ability to transmit plant viruses (Perring 2001). On cassava, *B. tabaci* is the vector of cassava mosaic geminiviruses (CMGs) that cause cassava mosaic disease (CMD) (Thresh et al. 1994). Positive correlations have been observed between *B. tabaci* populations and CMD spread into initially healthy cassava plantings (Fishpool et al.

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ISSN 0958-3157 print/ISSN 1360-0478 online
DOI: 10.1080/09583150500335558

1987; Fargette et al. 1993; Legg et al. 1997). Recently, Legg et al. (2003) observed large populations of *B. tabaci* on disease-free resistant varieties introduced to control CMD. This population explosion poses danger in the use of CMD-resistant varieties in the management of CMD. In Africa, plans are underway to combine resistance to the viral disease with that of *B. tabaci.* Nevertheless, there is a need to combine host plant resistance with the use of natural enemies, especially parasitoids that have been used for long to control pests. Preliminary reports exist on the occurrence of *B. tabaci* parasitoids on cassava (Legg 1994), but there are no studies on the population dynamics of parasitoids of *B. tabaci* in Uganda.

To explore strategies for controlling *B. tabaci* on cassava, the population dynamics of the whitefly and its parasitoids were studied using a CMD-resistant variety, SS4, and a CMD-susceptible variety, Ebwanatereka. The resistant variety was chosen because it has been preferred for multiplication and dissemination to farmers in southern and central districts of Uganda as it is highly CMD-resistant and low in cyanide levels (Legg 1999), whilst the susceptible variety was chosen because it is highly susceptible, but liked by farmers because of its high tuberous root yield, early maturity and good taste (Otim-Nape et al. 1998, 2001). We report on the population dynamics of *B. tabaci* and its parasitoids on these two varieties of cassava and possible interactions between parasitism and CMD.

Materials and methods

Three field trials were conducted at Namulonge Agricultural and Animal Production Research Institute (NAARI) (0°31′N, 32°35′E and 1128 m a.s.1.). The soils of the area are mostly deep tropical red clay loamy types, well drained with pH 5.0–6.0 and have organic matter levels of 2–3%. The climate in the region is tropical, with average temperatures of about 22°C. The rainfall is bimodal, with an annual mean of 1270 mm. It consists of one long wet season (from March to July) and a shorter one (from late September to December) (Yost & Eswaran 1990). This area was chosen because of the high populations of *B. tabaci* and rapid CMD spread.

The trials were planted on 17 October 2000 (late season), 19 April 2001 (early season), and 3 November 2001 (late season). The single treatment comprised two cassava varieties: the resistant variety (Nase 4) and the susceptible variety (Ebwanatereka). Disease-free materials of each cultivar were established in a randomized complete block design, with three replicates in late season 2000 and four in the early and late seasons 2001. The plots measured 9 × 9 m with plants spaced at 1 × 1 m, and 2 m alleys left between plots. After sprouting, an inspection was carried out and any plant with CMD symptoms was removed and replaced with disease-free plants of the same age from the nursery and thereafter no more replacements were made.

Sampling began at 11 weeks after planting in late season 2000, and 8 weeks after planting during the early and late seasons 2001 when five plants were randomly selected from one row out of 10 rows in a plot. From each of these plants, CMD severity scores were taken using a scale of 1–5, developed by (Hahn et al. 1980) where '1' represents CMD-free plants and '5' the most severely diseased plants. For nymph and parasitoid counts, leaves of each of the five plants sampled above were examined for the presence of late fourth instars (pupae) of *B. tabaci.* The first pupa-bearing leaf and a maximum of nine more leaves below it were numbered and harvested. Harvested leaves were then placed in paper bags, and the bags were placed in a cool box and taken to the laboratory where the leaves were kept in a refrigerator until immature whitefly and parasitised nymphs could be counted. Counts were made on the underside of each leaf to determine the number of unparasitised and parasitised third and fourth instar nymphs of *B. tabaci. B. tabaci* was identified based on the description by (Martin 1987). Nymphs parasitised by *Encarsia sophia* Girault and Dodd appeared as black pupal cases with meconia symmetrically located on both sides posteriorly or contained banana-shaped larvae, while those parasitised by *Eretmocerus mundus* Mercet appeared orange with a shiny pupal skin (with the pupae having red eyes). The undifferentiated parasitoids on the other hand had displaced mycetomes as opposed to the unparasitised nymphs that were either translucent or mildly opaque and yellowish with yellow symmetrically located mycetomes. After counting the parasitoids, leaf portions containing parasitised nymphs were put in petri dishes and sealed with parafilm. The petridishes were stored under room conditions and adult parasitoids that emerged were identified using a binocular microscope and identification guides (Polaszek et al. 1992; Schauff et al. 1996; Rose & Zolnerowich 1997). Samples were sent to the British Natural History Museum to confirm their identity, while others were kept in the laboratory at Namulonge Agricultural and Animal Production Research Institute as voucher specimens.

Data analysis

Apparent parasitism was calculated as the percentage of total parasitoids to the total nymphs (both parasitised and unparasitised *B. tabaci* nymphs combined). Total parasitoids included immature parasitoid that could not be identified–but the nymphs appeared visibly parasitised. Data on counts of *B. tabaci* nymphs and parasitoids were transformed using square root transformation, while percent parasitism values were transformed using arcsine square root transformation. These were then subjected to a one-way analysis of variance using Genstat 5 Release 3.2 (PC/Windows NT). The data were first analysed combining all the dates within a trial, and subsequently for each date within a trial using variety as treatment. *B. tabaci* and parasitoid species, and percent parasitism were plotted against time for each variety. A simple linear regression with groups (using varieties as groups) was conducted to test the relationship between percent parasitism and total nymphs, and between percent parasitism and cassava mosaic disease severity.

Results

Abundance of B. tabaci

The numbers of nymphs of *B. tabaci* did not differ significantly between varieties in late season 2000 (39.4 and 33.5 nymphs per leaf on the resistant and susceptible varieties, respectively ($F=1.58$; df$=1$; $P=0.211$). But there were significantly higher nymph numbers on the resistant variety in both early and late seasons 2001 when compared to the susceptible variety. Nymph numbers averaged 35.8 and 17.2 per leaf on the resistant and susceptible varieties, respectively in early season 2001 ($F=34.4$; df$=1$; $P<0.001$), and 59.1 and 31.2 nymphs per leaf on the resistant variety and susceptible variety, respectively in late season 2001 ($F=20.8$; df$=1$; $P<0.001$).

When analysed by dates, there were significantly higher *B. tabaci* nymphs at 13 weeks after planting ($F=5.97$; df$=6$; $P=0.022$) and at 21 weeks after planting ($F=14.06$; df$=6$; $P<0.001$) on the resistant variety than on the susceptible variety in late season 2000. In early season 2001, the numbers of *B. tabaci* nymphs were significantly higher on the resistant variety at all the dates: 8 weeks after planting ($F=7.26$; df$=6$; $P=0.011$), 10 weeks after planting ($F=12.75$; df$=6$; $P=0.001$), 12 weeks after planting ($F=17.42$; df$=6$; $P\leq0.001$), 14 weeks after planting ($F=7.07$; df$=6$; $P=0.012$), 16 weeks after planting ($F=4.38$; df$=6$; $P=0.044$), 18 weeks after planting ($F=32.16$; df$=6$; $P<0.001$), and 20 weeks after planting ($F=6.99$; df$=6$; $P=0.012$). In late season 2001, number of *B. tabaci* were again significantly higher on the resistant variety 8 weeks after planting ($F=69.53$; df$=5$; $P<0.001$), 10 weeks after planting ($F=16.09$; df$=5$; $P\leq0.001$), 12 weeks after planting ($F=7.14$; df$=5$; $P=0.011$), 14 weeks after planting ($F=7.93$; df$=5$; $P=0.008$), 16 weeks after planting ($F=5.47$; df$=5$; $P=0.025$), and 18 weeks after planting ($F=8.8$; df$=5$; $P=0.005$) (Figure 1)

Incidence of parasitoids of B. tabaci *and apparent parasitism*

Two species of parasitoids, *Eretmocerus mundus* Mercet and *Encarsia sophia* Girault and Dodd were observed parasitising *B. tabaci* during the three trials (Table I). The numbers of *E. mundus* on the resistant variety ranged from 0 to 10.9 pupae per leaf in late season 2000, 0 to 50 in early season 2001 and 0 to 87.4 in late season 2001. On the susceptible variety, the numbers of *E. mundus* pupae ranged from 0 to 37.8 pupae per leaf in late season 2000, 0 to 25.7 in early season 2001 and 0 to 19 in late season 2001. The numbers of *E. mundus* did not differ significantly between varieties in late season 2000, but differed significantly in both early and late seasons 2001, when significantly higher numbers were recorded on the resistant variety (Table I). When analysed separately by dates, the numbers of *E. mundus* were significantly higher on the resistant variety at 13 weeks after planting ($F=6.59$; df$=6$; $P=0.016$) and on the susceptible variety at 15 weeks after planting ($F=4.99$; df$=6$; $P=0.034$) in late season 2000. In early and late seasons 2001, the numbers of *E. mundus* were higher on the resistant variety than on the susceptible variety on all dates that showed significant differences between varieties; in early season 2001, the numbers of *E. mundus* were higher on the resistant variety at 10 weeks after planting ($F=4.7$; df$=6$; $P=0.037$), 12 weeks after planting ($F=10.36$; df$=6$; $P=0.003$), 14 weeks after planting ($F=8.25$; df$=6$; $P=0.007$), 16 weeks after planting ($F=23.23$; df$=6$; $P\leq0.001$), 18

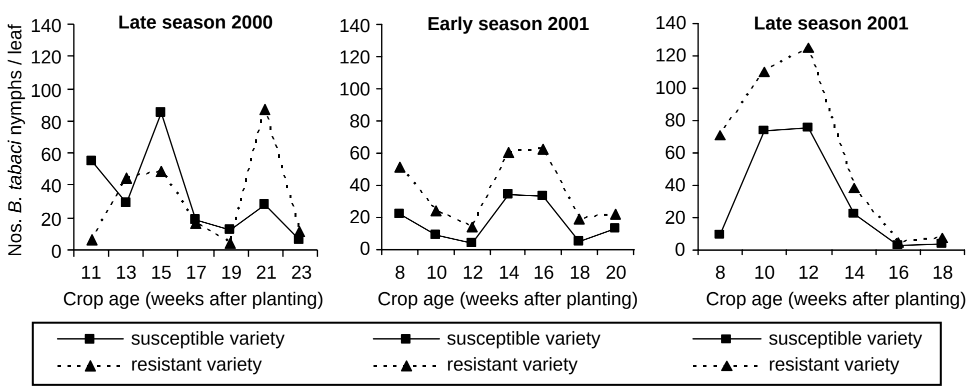

Figure 1. Variations in numbers of *B. tabaci* nymphs on cassava planted in late season 2000, and early and late seasons 2001 with crop age (weeks after planting).

Table I. Average numbers of *E. mundus* and *E. sophia* pupae, and apparent parasitism of *B. tabaci* on the different cassava varieties during the three trials.

	Numbers of *E. mundus* pupae per leaf			Numbers of *E. sophia* pupae per leaf			Apparent parasitism (%)		
	Late seaon 2000	Early season 2001	Late season 2001	Late seaon 2000	Early season 2001	Late season 2001	Late seaon 2000	Early season 2001	Late season 2001
Resistant variety	1.2 (1.2)	7.6 (2.5)	9.3 (2.6)	1.5 (1.3)	1.8 (1.3)	1.4 (1.2)	36.8 (46.6)	56.2 (60.4)	22.6 (36.4)
Susceptible variety	1.9 (1.3)	3.2 (1.7)	3.2 (1.6)	1.3 (1.2)	0.6 (1.0)	0.9 (1.1)	40.4 (49.8)	58.0 (62.4)	20.0 (33.5)
Mean	1.5 (1.3)	5.4 (2.1)	6.3 (2.1)	1.4 (1.2)	1.2 (1.2)	1.1 (1.2)	38.6 (48.2)	57.1 (61.4)	21.3 (35)
Standard error of means	0.06	0.08	0.08	0.04	0.04	0.04	1.6	2.2	1.3
P value	0.193	<0.001	<0.001	<0.056	<0.001	0.006	0.173	0.377	0.106

Figures in parentheses are square root transformed values for numbers, and arcsine square root transformed values for percent parasitism.

weeks after planting ($F = 20.23$; df $= 6$; $P \leq 0.001$) and 20 weeks after planting ($F = 6.09$; df $= 6$; $P = 0.019$). In late season 2001, the numbers of *E. mundus* were significantly higher at 8 weeks after planting ($F = 91.23$; df $= 5$; $P < 0.001$), 12 weeks after planting ($F = 5.44$; df $= 5$; $P = 0.026$), 14 weeks after planting ($F = 6.29$; df $= 5$; $P = 0.017$), 16 weeks after planting ($F = 15.19$; df $= 5$; $P \leq 0.001$) and at 18 weeks after planting ($F = 12.13$; df $= 5$; $P = 0.001$) (Figure 2).

The numbers of *E. sophia* on the resistant variety ranged from 0 to 9.4 pupae per leaf in late season 2000, 0 to 11.1 in early season 2001 and 0 to 10.8 in late season 2001, while on the susceptible variety, the numbers of *E. sophia* ranged from 0 to 17.3 per leaf in late season 2000, 0 to 11.4 in early season 2001 and 0 to 7.8 in late season 2001. The numbers of *E. sophia* did not differ significantly between varieties in late season 2000, but differed significantly between varieties in both early and seasons 2001 when significantly higher numbers were recorded on the resistant variety (Table I). Similarly, the numbers of *E. sophia* were generally higher on the resistant variety on most of the dates that showed significant differences between varieties, except at 15

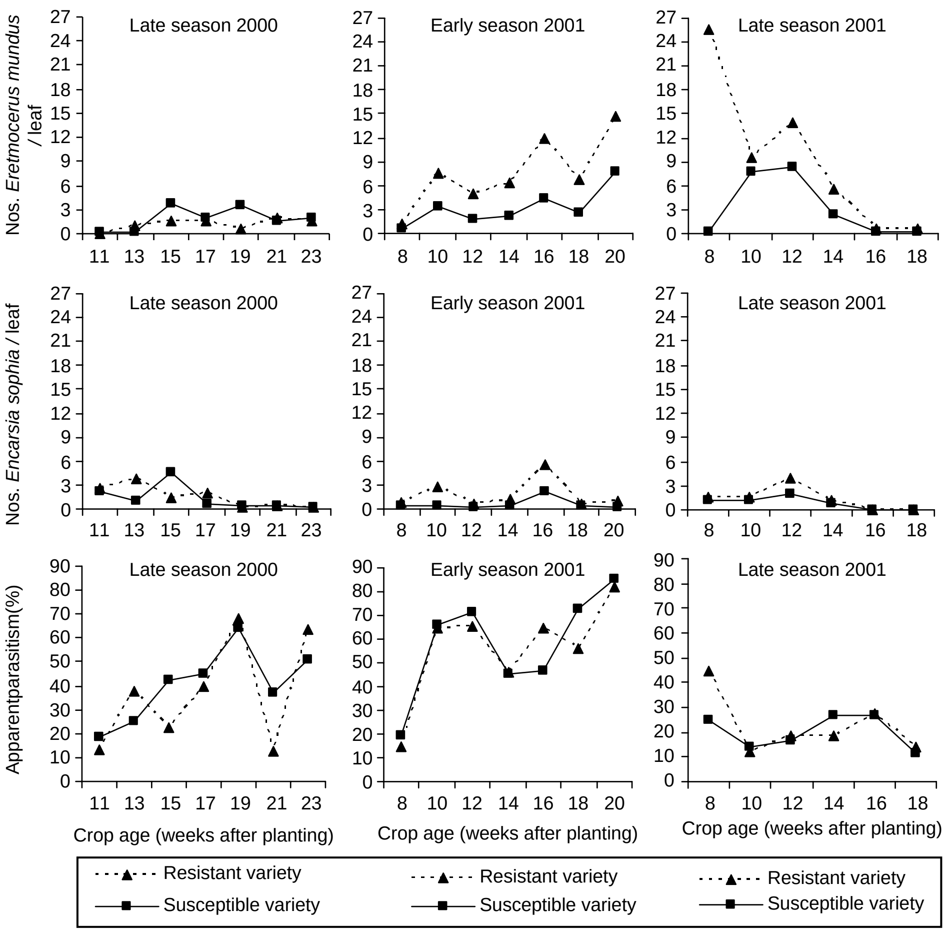

Figure 2. Variations in numbers of *E. mundus* (top panel) and *E. sophia* (middle panel) and apparent parasitism (bottom panel) in cassava planted in late season 2000 (left column), early season 2001 (middle column) and late season 2001 (right column) with crop age (weeks after planting).

weeks after planting ($F = 8.5$; df $= 6$; $P = 0.007$) in late season 2000 when significantly higher *E. sophia* numbers were recorded on the susceptible variety. In late season 2000, higher *E. sophia* numbers occurred on the resistant variety at 13 weeks after planting ($F = 19.49$; df $= 6$; $P \leq 0.001$) and 17 weeks after planting ($F = 18.26$; df $= 6$; $P \leq 0.001$). In early season 2001, there were higher numbers of *E. sophia* on the resistant variety at 10 weeks after planting ($F = 15.96$; df $= 6$; $P \leq 0.001$), 12 weeks after planting ($F = 6.41$; df $= 6$; $P = 0.016$), 14 weeks after planting ($F = 7.87$; df $= 6$; $P = 0.008$), 16 weeks after planting ($F = 21.43$; df $= 6$; $P \leq 0.001$) and at 20 weeks after planting ($F = 6.38$; df $= 6$; $P = 0.016$). Whilst in late season 2001, the numbers of *E. sophia* were only significantly higher on the resistant variety at 12 weeks after planting ($F = 5.45$; df $= 5$; $P = 0.025$) (Figure 2).

Apparent parasitism had the lowest values of 3.2% and 0 in late season 2000 on the resistant and susceptible varieties, respectively, 0 and 1% on both varieties in early and late seasons 2001, respectively. Maximum parasitism of 100% was recorded on both varieties in all the three trials. Apparent parasitism did not differ significantly between varieties in the three trials, and was similar between varieties at most dates in all the trials. The only exceptions where significant differences were observed between varieties were 13 weeks after planting ($F = 5.47$; df $= 6$; $P = 0.027$), 15 weeks after planting ($F = 9.02$; df $= 6$; $P = 0.006$) and 21 weeks after planting ($F = 25.17$; df $= 6$; $P \leq 0.001$) in late season 2000, 18 weeks after planting ($F = 6.36$; df $= 6$; $P = 0.016$) in early season 2001 and, 8 weeks after planting ($F = 24.55$; df $= 5$; $P \leq 0.001$) in late season 2001 (Figure 2).

Relationship between parasitism and B. tabaci *numbers, and cassava mosaic disease severity*

The regression results showed a significant ($P < 0.001$) negative relationship between percent parasitism and *B. tabaci* nymph numbers in late season 2000 and early season 2001 only, whilst there was no relationship between parasitism and cassava mosaic disease severity although the regression was significant during late season 2000 and late season 2001 (Table II).

Discussion

The present study confirmed the occurrence of higher populations of *B. tabaci* on the cassava mosaic disease resistant variety when compared to the susceptible one. This is consistent with the observations made by Legg et al. (2003), and is attributed to the whitefly preference for the resistant variety.

This study also showed that more parasitoids occurred on the resistant cassava variety compared to the susceptible one, yet there were similarities in percent parasitism between varieties suggesting that variety did not influence parasitism. Similarly, cassava mosaic disease did not influence parasitism. However, further assessments will be required comparing parasitism on healthy versus cassava mosaic diseased plants of the same variety to provide a more controlled evaluation of the interaction between cassava mosaic disease and parasitoid activity. If indeed cassava mosaic disease has no effect on parasitism, then any attempt to reduce disease incidence, including whitefly management, will have a neutral effect on parasitoid activity.

Table II. Parameters for the regression of arcsine square root transformed values of percent parasitism on square root transformed values of *B. tabaci* nymph numbers, and CMD severity.

Trial	Intercept	Slope	*F* value	R^2	*P* value
Parasitism on B. tabaci nymphs Intercept					
Late season 2000					
Resistant variety	76.3	−5.28	33.9	32.2	<0.001
Susceptible variety	61.5	−2.34			
Early season 2001					
Resistant variety	85.9	−4.68	41.3	30.3	<0.001
Susceptible variety	82.7	−5.71			
Late season 2001					
Resistant variety	39.9	−0.51	2.6	2	<0.001
Susceptible variety	37.5	−0.83			
Parasitism on cassava mosaic disease severity					
Late season 2000					
Resistant variety	38.7	3.7	3	2.7	0.033
Susceptible variety	41.6	3.5			
Early season 2001					
Resistant variety	51.3	4.2	1.9	1.2	0.125
Susceptible variety	48.3	3.5			
Late season 2001					
Resistant variety	27.8	6.6	2.6	2	0.05
Susceptible variety	37.7	−1.1			

The lack of a proportionate increase in parasitoid numbers with increase in nymph numbers indicates differences in the reproductive capacities of the parasitoids and their host. Noldus and van Lenteren (1995) indicated that direct density dependence is uncommon among parasitoids under field conditions and that direct density dependence is not required for stable host parasitoid interactions. In addition, Hassell (1971) and Hassell and Waage (1984) indicated that the lack of a density-dependent relationship between parasitoids and whitefly nymphs at high host densities might be attributable to constraints imposed by handling time and egg depletion.

There was evidence of a delayed parasitoid response to whitefly populations since parasitism peaked after the peaks of nymph populations. This is in agreement with the observations by Gerling (1984) on cotton in Israel, indicating that parasitoids are unable to have a substantial impact early in the season to prevent whitefly outbreaks resulting from migration from crop to crop. For *B. tabaci* on cassava, the major management considerations are its high reproductive rate and the rapid early colonisation of cassava plants when they are most susceptible to cassava mosaic geminiviruses (Fishpool et al. 1987) that allow it initially to achieve a high survival rate and to have a severe effect on cassava production through its role in cassava mosaic geminivirus transmission. Studies in California, have shown that *Eretmocerus* spp. readily move from collard and sunflower grown as a refuge into cotton and melon crops (Pickett et al. 2004). A thorough investigation of possible *B. tabaci* host plants should therefore allow identification of potential refuges that maintain a high parasitoid to whitefly ratio from which parasitoids migrate into cassava crop early in the season.

Although the present findings demonstrate that parasitoids are responsible for up to 100% parasitism under certain circumstances, this level of parasitism is not typical or sustained. It is therefore necessary to explore options for enhancing the activity of the most adaptable parasitoids. Information will be required on the biology and behaviour of the principal parasitoids under different whitefly populations and the other natural enemies including predators and fungi that attack *B. tabaci* and their impact. Such studies should provide valuable information that will enable scientists to develop and optimise the combined use of natural enemies in controlling *B. tabaci* and through this reduce the incidence of cassava mosaic disease.

Acknowledgement

We are grateful to the Rockefeller Forum for Agricultural Resource Husbandry (Grant No. FS 99006#183) for sponsoring this study. The technical and material support from the staff of International Institute of Tropical Agriculture is acknowledged. Sincere thanks go Dr James Ogwang and Thomas Odong Lapaka for the valuable advice.

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