EFFECT OF SIX HOST PLANT SPECIES ON LIFE HISTORY AND POPULATION GROWTH

PARAMETERS OF *RASTROCOCCUS ICERYOIDES* (HEMIPTERA: PSEUDOCOCCIDAE)

CHRYSANTUS M. TANGA[1, 2], SUNDAY EKESI[1,*], P. GOVENDER[2] AND SAMIRA A. MOHAMED[1]

[1]International Centre of Insect Physiology and Ecology (ICIPE), P.O. Box 30772-00100, Nairobi, Kenya

[2]Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

*Corresponding author; Email: sekesi@icipe.org

Dr. Sunday Ekesi,
The International Centre of Insect
Physiology and Ecology (ICIPE),
P.O. Box 30772-00100, Nairobi, Kenya.
Tel: +254-20-8632000,
Fax +254-20-8632001,
E-mail: sekesi@icipe.org

ABSTRACT

The effect of 6 host plant species [*Mangifera indica* L., *Cajanus cajan* (L.) Millspaugh, *Coffea arabica* L., *Cucurbita moschata* Duchesne, *Parkinsonia aculeata* L., and *Ficus benjamina* Roxb.], on bionomics of the mango mealybug *Rastrococcus iceryoides* Green (Hemiptera: Pseudococcidae) was studied in the screenhouse. Biological and life table parameters of the mealybug differed significantly among the host plants. Developmental period (egg to adult) was shortest on *M. indica* (23.5days and 25.3days for females and males, respectively), whereas it was longest on *F. benjamina* (33.0 days and 37.3 days for females and males, respectively). The egg to adult female survivorship was highest on *C. moschata* (79.6%) and lowest on *C. arabica* (30.9%). Fecundity was highest on *C. moschata* (811.3 egg/female) followed by *M. indica* (716.8 egg/female). The sex ratio was female-biased on *C. moschata, M. indica, C. cajan* and *P. aculeata*. Adult mealybug longevity also varied with host plant for both mated and unmated females. Adult female body length and width were significantly higher on *C. moschata, M. indica, C. cajan* and *P.*

aculeata than on *F. benjamina* and *C. arabica*. The highest intrinsic rate of natural increase (r_m), finite rate of increase (λ) and the shortest mean generation time (GT) and doubling time (T_d) were recorded on *M. indica*. The highest and lowest net reproductive rate (R_o) occurred on *C. moschata* and *C. arabica,* respectively. The implication of these findings in relation to damage, population growth and management of *R. iceryoides* on the target crops is discussed.

Key Words: mango mealybug, invasive pest, insect-host plant interactions, development, survivorship, life table

RESUMEN

Palbras Clave:

_____

In Africa, *Rastrococcus invadens* Williams and *Rastrococcus iceryoides* Green are regarded as 2 important exotic mealybug species native to Southern Asia that commonly infest mango, *Mangifera indica* Linnaeus (Anacardiaceae). The former devastated mango production in West and Central Africa, but was brought under biological control through introduction of an exotic parasitoid *Gyranusoidea tebygi* Noyes from India (Noyes 1988; Bokonon-Ganta & Neuenschwander 1995). Based on its economic importance and the ease with which it colonized major parts of West and Central Africa, *R. invadens* has been the subject of many studies, both descriptive and experimental (Williams 1986; Agounké et al. 1988; Willink & Moore 1988; Bokonon-Ganta et al. 1995; Tobih et al. 2002). On the other hand, *Rastrococcus iceryoides* is restricted to East Africa (mainly Tanzania and coastal Kenya) and northern Malawi where it has remained a major pest of mango (Williams 1989; Luhanga & Gwinner, 1993; CABI, 2000).

In Southern Asia, *R. iceryoides* is believed to be highly polyphagous and has been reported from over 65 host plants from 35 families (Williams 1989; Ben-Dov 1994). In Kenya and Tanzania, recent observation showed that the insect attacks 29 host plants from 16 families with mango, *Mangifera indica* L. (Anacardiaceae), as the most preferred cultivated host plant and *Parkinsonia aculeata* L. (Fabaceae) as the most preferred wild host plant (Tanga 2012). As with other mealybug species, *R. iceryoides* sucks sap from leaves, young shoots, inflorescences and fruits and their damage can result in shedding of mango fruit-lets. They also excrete sugary honeydew on which sooty mold develops thus reducing fruit marketability. As a result of the development of sooty mould, export opportunities

are often impaired due to quarantine regulations (CPC 2002). Sooty mold that fouls the leaves reduces photosynthetic efficiency and can cause leaf drop. In village homesteads, heavy infestations usually render the trees unsuitable for shade. In Kenya, Tanzania and Malawi, fruit losses can range from 30% to complete crop failure in unmanaged orchards (CABI 2000; Tanga 2012). In Tanzania, the pest has become a main target for majority of insecticidal sprays on mango (in addition to pruning and burning of infested plant parts) (Willink & Moore 1988; Tanga 2012). In addition to health concerns attributed to chemical pesticides, resource-limited farmers cannot afford to use them. Chemical pesticides also do not provide adequate control owing to the waxy coating of mealybugs. As a result, some growers have resorted to cutting down mango trees, because of heavy *R. iceryoides* infestations, while others have abandoned mango cultivation altogether. It has been speculated that the increasing intensity of damage by mealybugs may be due to the expansion of mango production and the introduction of hybrid cultivars, which are highly susceptible to attack by the pest (Boussienguet & Mouloungou 1993).

Like all other herbivorous arthropod pests, host plant range is a key ecological characteristic of the mealybug species, as it defines their resource base, which in turn is an important factor influencing their population dynamics and interactions with other herbivorous species, predators and parasites (Williams 1989; Ben-Dov 1994; Neuenschwander 2003; Calatayud & Le Rü 2006). Understanding insect-host plant interactions and their impact on development and various fitness parameters of an insect pest is a central theme in ecology (Miller et al. 1986; Benrays & Chapman 1994). Also in mealybugs, different host plant species have been shown to affect the insect's life history parameters. For example, the mortality of the citrus mealybug *Planococcus citri* (Risso) (Hemiptera: Pseudococcidae) was reported to be higher on green than red or yellow variegated *Coleus blumei* Bellevue (Bentham) (Lamiaceae) plants, and development was faster and fecundity higher on red variegated plants (Yang & Sadof 1995). The developmental time of *Planococcus kraunhiae* (Kuwana) (Hemiptera: Pseudococcidae) was shorter when reared on germinated faba bean, *Vicia faba* L. (Fabaceae) seeds than on leaves of a *Citrus* sp. and on *Cucurbita maxima* Duchesne, and it survived better when reared on germinated faba bean seeds than on citrus leaves (Narai & Murai 2002). The pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green) (Hemiptera: Pseudococcidae), was able to develop equally well on *Cucurbita pepo* L. as on *C. maxima* (Serrano & Lapointe 2002).

The current *R. iceryoides* host plant data from Africa (Tanga 2012) are based on field observations of damage by the pest. Compared with *R. invadens*, there are no comparative data on the biology and demographic parameters of *R. iceryoides* on different host plants to determine the true value of each plant species as a host of *R. iceryoides*. Host plants that slow or accelerate the development of the insect are likely to be of considerable relevance to the development of management methods. Studies on the biology and life table parameters of *R. iceryoides* on different host plants should also provide information in understanding the population dynamics of this pest.

The main objective of this study was to investigate the development and reproduction of *R. iceryoides* on 6 host plant species, namely mango (*M. indica*), pigeon pea [*Cajanus cajan* (L.) Millspaugh, Fabaceae], arabica coffee (*Coffea arabica* L., Rubiaceae), butternut squash (*Cucurbita moschata* Duchesne, Cucurbitaceae), Jerusalem thorn (*P. aculeata*) and weeping fig (*Ficus benjamina* Roxb., Moraceae), in order to develop life table strictures for the insect and estimate parameters for population increase on the different host plants to guide pest management decisions. The host plants selected represent some of the most economically important plants in terms of horticulture, beverage, ornamental or shade uses in Kenya and Tanzania.

MATERIALS AND METHODS

Host Plant

Twelve-month-old *M. indica* and *C. arabica* seedlings were obtained from the commercial nurseries of the Kenya Agricultural Research Institute (KARI) and Coffee Research Foundation (CRF) in Ruiru, Kenya, respectively. *Ficus benjamina* plants grown from cuttings and *P. aculeata* of same age as *M. indica* and *C. arabica* were obtained from Tropical Nursery, in Nairobi and Malindi, Kenya, respectively. The production polythene bag of each seedling was removed and then the seedling was transplanted into a white plastic container (35 cm height × 29 cm top diam × 20 cm bottom diam) in a soil mix containing sieved sterilized forest soil and sand (1:1 by volume). *Cajanus cajan* were propagated from seeds (va. ICEAP00040) (Høgh-Jensen et al. 2007) obtained from KARI Seed Unit (KSU), Nairobi, Kenya. All the seedlings of the test plant species were placed on benches in a screenhouse (2

m height by 2.9 m diameter) at the Duduville campus of the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. Conditions in the screenhouse were: 23 ± 5˚C, 40 - 80% RH and 12L: 12D photoperiod.

Plants were fertilized with equal volume of farmyard manure as described above, a common agronomic practice by the growers and watered on alternate days. Matured *C. moschata* fruits were purchased from a local grocery store in Kasarani, Nairobi, Kenya. Since *R. iceryoides* predominantly infested fruits of *C. moschata* in the field (C.M. Tanga, unpublished data), all experiments were conducted on fruits of this plant. Prior to commencement of the experiments, mealybugs were reared on mature *C. moschata* fruits that had been washed in a 0.5% bleach solution to reduce mold growth, triple rinsed with distilled water and air-dried for 24 h. Therefore, *C. moschata* served in this study as a check against other test plants on which experiments were carried out on seedlings. The fruits of *C. moschata* were kept in the laboratory maintained at room temperature (25-26°C), photoperiod of 12 h L: 12 h D, and 40-70% relative humidity (RH).

Insect Culture

Colony of *R. iceryoides* was initiated from a cohort of 300 adult mealybugs collected from heavily infested mango orchard in Mombasa, Coast Province, Kenya in February 2008. Insects were transported to the laboratory at *icipe*, Nairobi, Kenya and reared on mature *C. moschata* fruits (purchased from a local grocery store) in the laboratory maintained at room temperature described above. The colony was maintained on an open table surface (76 cm wide x 245 cm length) in the laboratory for over 20 generations before the start of the experiment. Plywood was fixed firmly on the sides of the table (10.5 cm height x 245 cm length) to prevent the crawling insects from falling off. The colonies were maintained by exposing uninfested *C. moschata* fruits to adult females with fully developed ovisacs. Eggs hatched within 6-8 days and newly emerged nymphs were allowed to colonize the uninfested *C. moschata*. This procedure was repeated on a weekly basis. After every 6 months, fresh wild *R. iceryoides* from mango were injected into the established colonies to ensure broader genetic diversity.

Maintenance of *R. iceryoides* on the Study Plant Materials

For the bioassay, insects were reared on the different host plants for at least 3 generations in the screenhouse to allow them adapt to the new host and to remove maternal effects (Lacey 1998) before commencement of the experiments. Approximately 40 adult female mealybugs with well-formed ovisacs were obtained from the stock colony to infest each of the different host plants under investigation. The ovisacs were carefully teased open with blunt probes under a stereomicroscope and the number of eggs present in each ovisac counted. The eggs were then refolded into the fine cottony ovisac before inoculation. After the first generation on these host plants, subsequent uninfested plants were similarly infested with ovisacs from their respective cultures. In the screenhouse, the plants were maintained in large cages (30 cm length × 30 cm width × 60 cm height) consisting of a glass top and screened mesh (30 cm length × 30 cm width × 60 cm height) on the sides. Experimental conditions in the screenhouse were as described above.

Assessment of *R. iceryoides* Development, Survivorship and Sex Ratio on the Different Host Plants

Thirty eggs (collected within 12 h) were obtained from a single female ovisac arising from the different host plant species and transferred to the seedlings of their respective host plants using a camel hair brush. The seedlings of *M. indica, C. arabica, P. aculeata* and *F. benjamina* were 12 months old at the commencement of the experiments while *C. cajan* was 3 months. In the case of *C. moschata*, the insects were maintained on matured fruits similar to the rearing conditions. After inoculation, each host plant seedling and fruit was housed individually in wooden cages (30 cm length × 30 cm width × 60 cm height).

Host plants were checked twice daily for egg hatch and exuviae to identify emergence of nymphal instars. The sex of each individual mealybug was determined during the latter part of the second instar when the males finally shed-off the white mealy-covering on their body and change their colour from orange to pale yellow with light ashy deposit on their body. Development of the males at this point continued with their body completely devoid of lateral processes and the duration of development of each sex could be recorded separately. The following data were collected for each host plant: (1) developmental duration for each stage, (2) the number of insects reaching

adult stage for the sexes, (3) sex ratio, measured as proportion of females out of the total number of *R. iceryoides* [♀/(♀ + ♂)], and (4) percentage survival of each of the immature stages. The experiment was replicated 5 times.

Morphometry

Fifty randomly selected adult females from the plant species under investigation were slide-mounted using the methodology of Watson and Kubiriba (2005). The body length (in millimeters) was measured along each insect's dorsal midline from the vertex of the head to the tip of the abdomen. The width (in millimeters) was measured at the widest point across the middle surface of the insect. Images from the slide-mounted specimens were captured using video microscopy – [Leica MZ 125 Microscope (Leica Microsystems Switzerland Limited)], fitted with Toshiba 3CCD camera using the Auto Montage software (Syncroscopy, Synoptics group, Cambridge, UK) at magnification of X25. Measurements were taken using Image-Pro® Plus version 4.1 for Windows^{TM} (Media Cybernetics, Bethesda, MD, USA) and the data were exported directly to an Excel data sheet. For all parts, measurements were taken in triplicate (to an accuracy of 0.001 mm).

Reproduction, Longevity and Assessment of Demographic Parameters

Forty randomly selected newly moulted virgin adult females (24 h old) derived from nymphs reared on each host plant species were used to determine the effect of host plant on *R. iceryoides* reproduction and longevity. Within each host plant treatment, half of the mealybugs (i.e. 20 females) were held alone to assess asexual reproduction (unmated females) and the other half (i.e. 20 females) were used to assess sexual reproduction (mated females). Each female used for sexual reproduction was transferred individually to plastic Petri dishes (5 cm in diameter and 1 cm height) with a wet cotton ball at the side together with 3 newly emerged males (24 h old) from the same plant species, and allowed to mate for 24 h. After mating, females were transferred to their respective host plants and observed daily until they died. The total number of eggs produced by each female was recorded daily. The eggs were kept separately in transparent polyvinyl chloride (PVC) cylinder (4 cm diameter x 10 cm height x 0.21 mm thick) lined with pieces of moistened black filter paper (3.5 by 1.5 cm) to prevent desiccation, and egg

hatch was determined every 12 h for a period of 7 days. Emerging nymphs from each daily cohort of eggs were removed using a camel hair brush (#000) with the help of a magnifier hand lens (size: 100 mm in diameter). Females for asexual reproduction were also observed daily until they died.

The following data were collected for each host plant: (1) pre-oviposition, oviposition, and post-oviposition periods, (2) daily egg production, and (3) adult longevity. Standard life table parameters including age-specific fertility (m_x; mean number of female progeny per female per day) and female survivorship (l_x; the fraction of females surviving to age x) were calculated from daily records of mortality and fecundity of cohorts on each host plant. For each of the 2 reproductive stages (sexual and asexual), each female was considered a replicate.

Statistical Analysis

Data for developmental times, pre-oviposition, oviposition, post-oviposition periods, adult female longevity, egg production and size of *R. iceryoides* were subjected to one-way analysis of variance (ANOVA) using PROC GLM (SAS Institute 2010). Sex ratio and percentage survival of *R. iceryoides* were arcsine transformed before analysis of variance (Sokal & Rohlf 1981). Means were separated by Student-Newman-Keuls (SNK) test. T-test ($\alpha = 0.05$) was used to compare the developmental time (egg–adult) and longevity of different sexes reared on the same host plant. Life table for each host plant species was constructed following the method described by Carey (1993) and the intrinsic rate of increase (r_m), net reproductive rate (R_o), mean generation time (GT), doubling time (T_d) and finite rate of increase (λ)) were estimated using the Jackknife program (Maia et al. 2000). Differences between life table parameters across the different host plant species based on estimates of variance for each parameter value were separated using SNK (Meyer et al. 1986).

RESULTS

Developmental Time, Percentage Female Progeny and Survival of Immature Stages

The overall developmental duration from egg to adult as well as that of the various developmental stages of both sexes of *R. iceryoides* varied significantly across the host plants (Table 1). Eggs took comparably longer period to hatch on all host plants, being relatively shorter on *M. indica* (7.8 d), and significantly different from those reared on *F. benjamina* (8.7 d).

The development of the first instar nymphs ranged from 5.5 d (on *M. indica*) to 9.6 d (on *F. benjamina*). Male second instar development was shortest on *M. indica*, *C. moschata*, *C. cajan* and *P. aculeata* (4.8-5.0 d) and longest on *F. benjamina* (11.4 d) (Table 1). The longest developmental duration for female second instars on *F. benjamina* was 8.1 days. The developmental time of the third instar male ranged from 3.4 d on *C. moschata* to 9.5 d
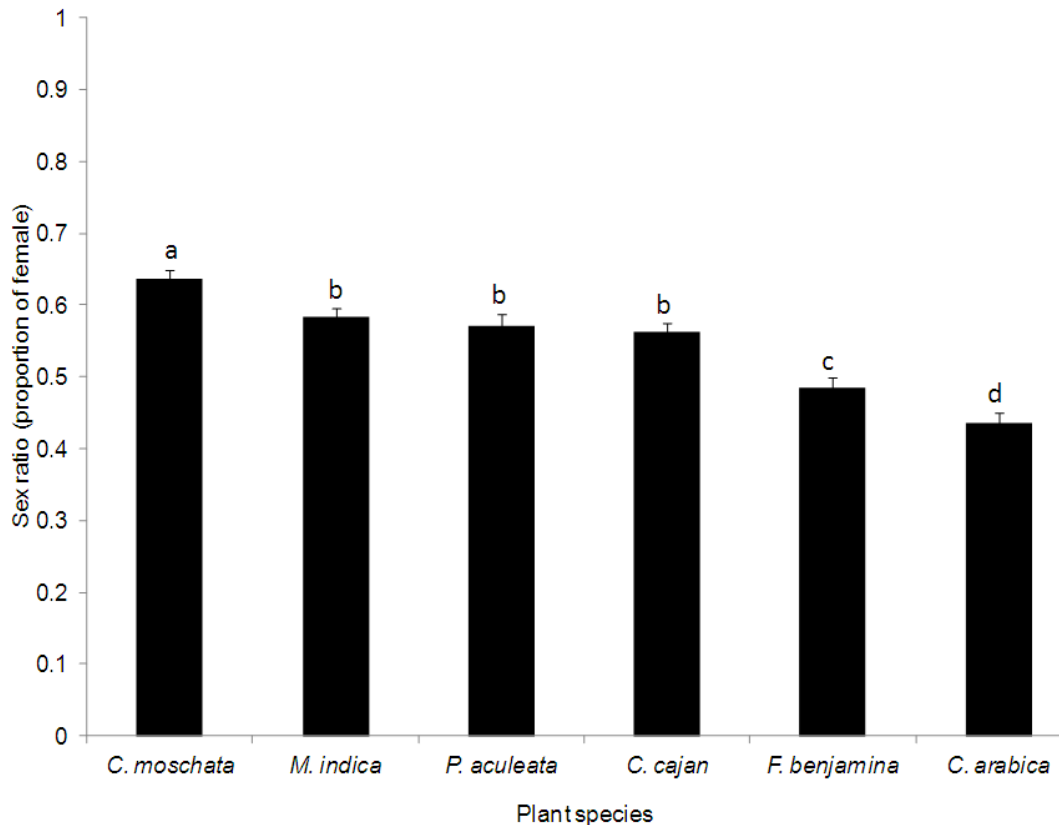

Fig. 1. Sex ratio (proportion of females ± SE) of *Rastrococcus iceryoides* reared on 6 host plant species. Bars sharing the same letter do not differ significantly from each other by Student–Newman–Keuls (SNK) test (*P* = 0.05).

TABLE 1. MEAN NUMBER OF DAYS (± SE) FOR EACH DEVELOPMENTAL STAGE OF *RASTROCOCCUS ICERYOIDES* REARED ON SIX HOST PLANT SPECIES (*CUCURBITA MOSCHATA, MANGIFERA INDICA, PARKINSONIA ACULEATA, CAJANUS CAJAN, FICUS BENJAMINA*, AND *COFFEA ARABICA*).

| Plant species | Egg | First | Second | | Third | | Fourth | Egg-adult | | Statistics (♂ and ♀ egg-adult) | | |
			Male	Female	Male	Female	Male	Male	Female	t	df	P
C. moschata	8.4 ± 0.2ab	6.1 ± 0.2c	4.8 ± 0.2c	5.7 ± 0.6c	3.4 ± 0.1d	5.8 ± 0.2b	5.8 ± 0.2d	26.2 ± 0.7deA	25.9 ± 0.4cA	-0.87	38	0.3907
M. indica	7.8 ± 0.2b	5.5 ± 0.2c	4.9 ± 0.1c	5.1 ± 0.2cd	4.2 ± 0.1c	5.1 ± 0.6cd	4.7 ± 0.2e	25.3 ± 0.9eA	23.5 ± 0.3dB	-4.66	38	< 0.0001
P. aculeata	8.4 ± 0.2ab	5.8 ± 0.1c	5.0 ± 0.2c	4.8 ± 0.2d	4.6 ± 0.2c	5.5 ± 0.1bc	6.4 ± 0.1c	28.4 ± 0.4cA	24.4 ± 0.2dB	-8.55	38	< 0.0001
C. cajan	8.4 ± 0.2ab	5.8 ± 0.2c	4.9 ± 0.1c	5.4 ± 0.2cd	4.6 ± 0.5c	4.8 ± 0.2d	5.6 ± 0.2d	27.4 ± 0.3cdA	24.4 ± 0.4dB	-5.82	38	< 0.0001
F. benjamina	8.7 ± 0.2a	9.6 ± 0.3a	11.4 ± 0.4a	8.1 ± 0.3a	8.5 ± 0.8b	6.7 ± 0.3a	8.7 ± 0.3a	37.3 ± 0.7aA	33.0 ± 0.6aB	-4.72	38	< 0.0001
C. arabica	8.3 ± 0.2ab	6.7 ± 0.2b	9.6 ± 0.3b	6.6 ± 0.1b	9.5 ± 0.2a	6.7 ± 0.2a	7.4 ± 0.3b	34.4 ± 0.6bA	28.3 ± 0.4bB	-8.82	38	< 0.0001
F	46.38	145.66	96.16	63.81	113.23	38.63	84.47	230.22	77.58			
df	5, 894	5, 894	5, 294	5, 294	5, 294	5, 294	5, 294	5, 294	5, 294			
P	0.0431	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001			

Means within a column followed by the same lower case letter do not differ significantly by Student–Newman–Keuls test (α = 0.05); and within a row followed by the same upper case letter by *t*-test (α = 0.05).

on *C. arabica*, while that of the female ranged from 4.8 d on *C. cajan* to 6.7 d on both *F. benjamina* and *C. arabica* (Table 1). The developmental time of fourth instar males was significantly shortest on *M. indica* (4.7 d) and longest on *F. benjamina* (8.7 d). On the same host plant, males took significantly longer time to complete development to adult than females on all host plant except on *C. moschata* where the development of both sexes was similar .

Sex ratio was female biased (0.56-0.64) on *M. indica*, *P. aculeata*, *C. cajan* and *C. moschata*; and ranged from 0.44-0.49 on *F. benjamina* and *C. arabica* ($F = 12.13$; df = 5,24; $P = 0.0017$) (Fig. 1).

The rearing host plant had a strong influence on both overall survival as well as the various developmental stages of *R. iceryoides* survival (Table 2). Egg survival was highest on *M. indica*, *C. moschata* and *F. benjamina* (85-90%) compared with the other host plants while more of the first instar survived on *C. moschata*, *P. aculeata* and *C. cajan* (80-84%) (Table 2). Survival of second male instar was highest on *C. cajan* (90%), while it was highest for females on *C. moschata*, *P. aculeata* and *C. cajan* (86, 86 and 87%, respectively) (Table 2). Third instar males survived better on *C. moschata*, *P. aculeata* and *C. cajan* (91, 90, and 91%, respectively) while third female and fourth instar male survival was highest on *C. moschata* (90 and 94%, respectively) (Table 2).

Morphometry

The body size of female *R. iceryoides* was significantly influenced by host plant species (Length: $F = 328.5$; df = 5,54; $P = 0.0001$; width: $F = 218.4$; df = 5,54; $P = 0.0001$) (Fig. 2). Adult female *R. iceryoides* reared on *C. moschata* and *M. indica* were significantly larger (3.93 mm and 3.87 mm, respectively) in body length than females reared on the other host plants while those reared on *C. arabica* had body length of only 2.24 mm. Adult female body width was significantly higher among *R. iceryoides* reared on *M. indica*, *P. aculeata*, *C. cajan* and *C. moschata* (2.63-2.68 mm) compared with those reared on *F. benjamina* and *C. arabica* (2.52-1.80 mm) (Fig. 2).

TABLE 2. MEAN (± SE) PERCENTAGE SURVIVAL OF THE DIFFERENT DEVELOPMENTAL STAGES OF *RASTROCOCCUS ICERYOIDES* REARED ON SIX HOST PLANT SPECIES (*CUCURBITA MOSCHATA, MANGIFERA INDICA, PARKINSONIA ACULEATA, CAJANUS CAJAN, FICUS BENJAMINA,* AND *COFFEA ARABICA*).

Host plant	Egg	First	Second		Third		Fourth	Egg to adult	
			Male	Female	Male	Female	Male	Female	Male
C. moschata	89.7 ± 1.4a	84.4 ± 2.3a	80.1 ± 1.8b	86.2 ± 1.0a	91.2 ± 0.6a	90.1 ± 1.0a	94.0 ± 1.1a	79.6 ± 1.4a	87.9 ± 0.6a
M. indica	88.4 ± 1.4a	66.1 ± 3.0b	74.0 ± 2.3b	70.3 ± 1.7b	83.6 ± 2.2b	80.5 ± 3.2b	87.3 ± 1.8b	64.4 ± 1.6b	79.9 ± 1.0c
P. aculeata	78.4 ± 1.0b	80.1 ± 0.5a	83.6 ± 2.3ab	85.9 ± 0.9a	90.3 ± 1.0a	88.1 ± 0.8ab	88.8 ± 0.7ab	74.9 ± 2.2a	84.2 ± 0.7b
C. cajan	83.7 ± 1.5ab	84.3 ± 1.4a	90.1 ± 1.9a	86.6 ± 1.1a	91.4 ± 1.4a	89.0 ± 0.8ab	90.0 ± 0.7ab	78.2 ± 2.4a	87.8 ± 0.9a
F. benjamina	84.8 ± 1.7a	37.3 ± 3.0d	76.0 ± 3.3b	37.4 ± 3.3d	71.1 ± 2.1c	32.9 ± 5.1d	73.2 ± 1.9c	32.2 ± 1.9c	68.5 ± 0.8e
C. arabica	83.6 ± 2.6ab	48.2 ± 1.8c	73.7 ± 3.0b	51.2 ± 2.7c	88.4 ± 0.6a	54.6 ± 3.3c	89.3 ± 0.7ab	30.9 ± 1.1c	76.6 ± 0.6d
F	6.07	75.51	6.60	112.06	26.00	69.50	20.95	121.21	94.18
df	5, 24	5, 24	5, 24	5, 24	5, 24	5, 24	5, 24	5, 24	5, 24
P	0.0002	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Means within a column followed by the same letter do not differ significantly by Student–Newman–Keuls test ($\alpha = 0.05$).
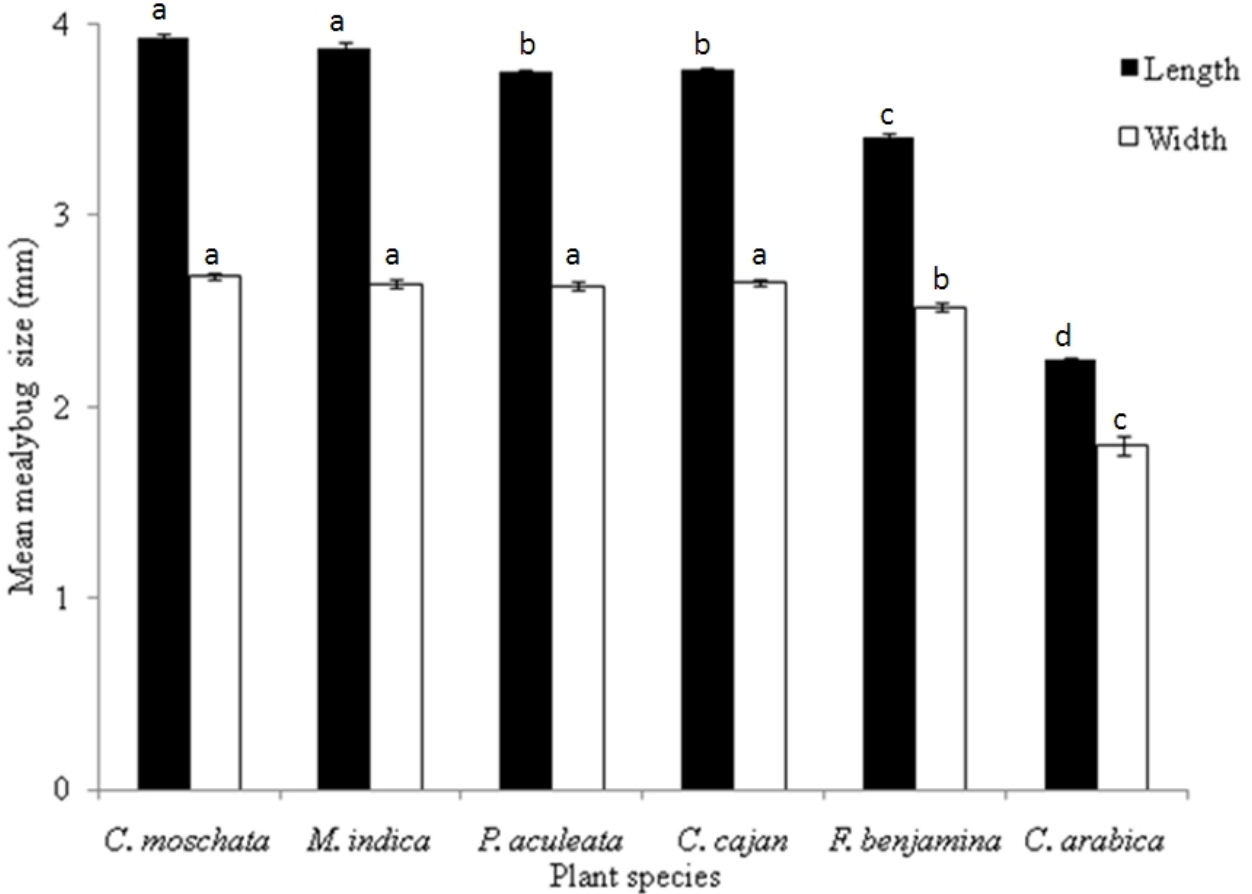
Fig. 2. Length and width (millimetres ± SE) of adult female *Rastrococcus iceryoides* reared on 6 host plant species. For each parameter, bars sharing the letter do not differ significantly by Student–Newman–Keuls (SNK) test ($P = 0.05$).

Reproduction and Longevity

The mean pre-oviposition, oviposition and post-oviposition periods of *R. iceryoides* were significantly affected by host plant species (Table 3). The pre-oviposition period was significantly shortest on *M. indica* (20.4 days) and longest on *F. benjamina* (29.4 days). Oviposition period was significantly longest on *C. moschata* (36.8 days) and shortest on *C. arabica* (15 days) (Table 3). Post-oviposition period of *R. iceryoides* was longest on *C. arabica* (15.7 days) and shortest on *C. moschata* and *P. aculeata* (6.4 and 7.2 days, respectively) (Table 3).

TABLE 3. MEAN DURATION (DAYS ± SE) OF PRE-OVIPOSITION, OVIPOSITION AND POST-OVIPOSITION PERIODS, REPRODUCTIVE RATE AND LONGEVITY OF *RASTROCOCCUS ICERYOIDES* REARED ON SIX HOST PLANT SPECIES (*CUCURBITA MOSCHATA, MANGIFERA INDICA, PARKINSONIA ACULEATA, CAJANUS CAJAN, FICUS BENJAMINA*, AND *COFFEA ARABICA*).

Plant species	Pre-oviposition period	Oviposition period	Post-oviposition period	Reproductive rate		Longevity		Statistics (mated and unmated ♀)		
				Fecundity (eggs/female life)	Oviposition rate (eggs/female/day)	Mated female	Unmated female	*t*	df	*P*
C. moschata	24.2 ± 0.4c	36.8 ± 0.4a	6.4 ± 0.3d	811.3 ± 7.3a	37.7 ± 3.5ab	67.4 ± 0.7aA	90.5 ± 0.8aB	-22.92	38	< 0.0001
M. indica	20.4 ± 0.4e	32.5 ± 0.3b	8.6 ± 0.3c	716.8 ± 12.7b	46.6 ± 4.3a	61.4 ± 0.5bA	87.3 ± 1.0abB	-22.65	38	< 0.0001
P. aculeata	21.7 ± 0.3d	30.5 ± 0.5c	7.2 ± 0.3d	655.3 ± 20.8c	39.3 ± 3.3ab	59.3 ± 0.7cA	84.6 ± 1.6bB	-14.79	38	< 0.0001
C. cajan	22.1 ± 0.3d	27.7 ± 0.2d	8.1 ± 0.2c	618.6 ± 17.3c	37.7 ± 3.5ab	57.8 ± 0.5cA	81.0 ± 1.4cB	-15.51	38	< 0.0001
F. benjamina	29.4 ± 0.3a	16.8 ± 0.3e	12.7 ± 0.3b	364.4 ± 15.2d	28.0 ± 3.6b	58.9 ± 0.5cA	78.6 ± 1.2cB	-14.98	38	< 0.0001
C. arabica	25.4 ± 0.3b	15.0 ± 0.4f	15.7 ± 0.3a	267.9 ± 15.5e	25.4 ± 3.0b	56.0 ± 0.5dA	70.8 ± 0.7dB	-16.30	38	< 0.0001
F	92.91	597.16	147.27	184.32	3.94	48.24	36.36			
df	5, 114	5, 114	5, 114	5, 114	5, 114	5, 114	5, 114			
P M	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0016	< 0.0001	< 0.0001			

Means within a column followed by the same lower case letter do not differ significantly by Student–Newman–Keuls test (α = 0.05); and within a row followed by the same upper case letter by *t*-test (α = 0.05).

The females reared on *C. moschata* laid the highest number of eggs (811.3) compared to females reared on other host plants (Table 3). There was no significant difference in the number of eggs laid by *R. iceryoides* when reared on *P. aculeata* and *C. cajan*. Daily egg production was highest on *M. indica* (46.6 eggs) although this did not differ significantly from egg production on *P. aculeata*, *C. cajan* and *C. moschata* (37.7-39.3 eggs/female/day) (Table 3). Unmated adult female mealybugs did not lay eggs on any of the 6 host plant species tested.

Longevity of mated as well as unmated *R. iceryoides* females varied significantly with the host plant (Table 3). Longevity of mated female mealybugs ranged from 56.0 days on *C. arabica* to 67.4 days on *C. moschata*. No difference in mated adult female longevities were observed when *R. iceryoides* was reared on *P. aculeata* (59.3 days), *C. cajan* (57.8 days) and *F. benjamina* (58.9 days) (Table 3). Longevity of unmated adult females ranged from 70.8 days on *C. arabica* to 90.5 days on *C. moschata* (Table 3). On the same host plant unmated females lived significantly longer than their corresponding mated ones on all host plants tested (Table 3).

Age-Specific Fecundity and Survivorship

The curves of age-specific fecundity (m_x) peaked soon after the onset of reproduction and varied considerably among the different host plant species (Fig. 3). The age-specific fecundity for *R. iceryoides* reared on *M. indica* peaked on day 24, *P. aculeata* on day 25, *F. benjamina* on day 33 and *C. arabica* on day 29 (Fig. 3). Age-specific fecundity observed for *R. iceryoides* reared on *C. moschata* and *C. cajan* were remarkably different, each having 2 peaks (Fig. 3). Major peaks for *R. iceryoides* reared on *C. moschata* were on day 30 and 33 while on *C. cajan*, a major peak was recorded on day 27 and a minor peak on day 31. The age-specific survivorship (l_x) curves decreased gradually and asymptotically as *R. iceryoides* aged (Fig. 3). On *M. indica*, 50% of mortality occurred on day 43, and the entire mealybug cohort died on day 62. On *C. moschata*, 50% of mortality occurred on day 48, and all mealybugs died on day 68.
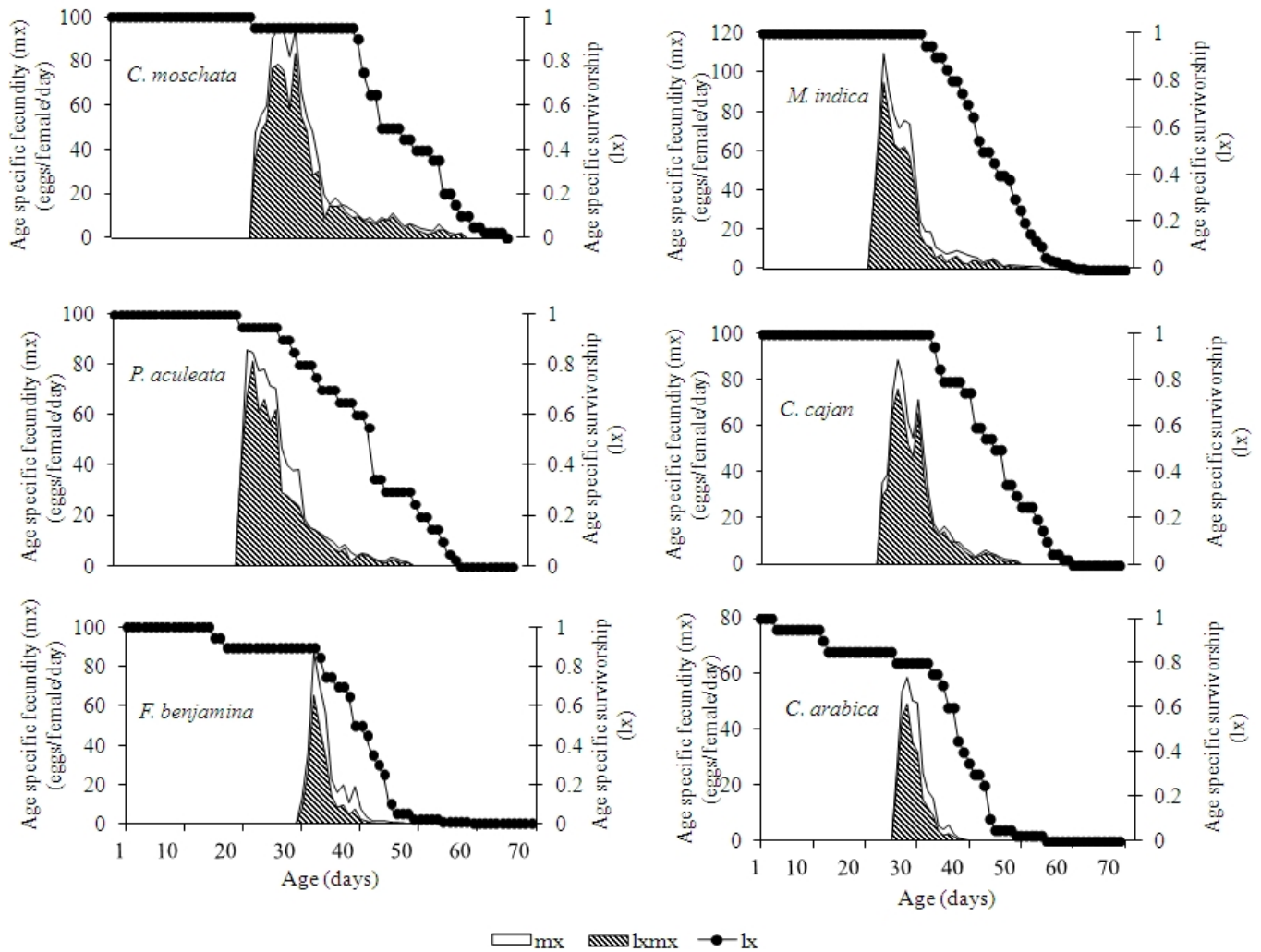
Fig. 3. Age-specific fecundity (m_x), age-stage specific maternity (l_xm_x), and age-specific survivorship (l_x) of *Rastrococcus iceryoides* reared on 6 host plant species.

Population Growth Statistics

Host plant had a profound effect on all growth parameters [net reproductive rate (R_o), intrinsic rate of increase (r_m), population doubling time (T_d), generation time (GT) and infinite rate of increase (λ)] evaluated (Table 4). The net reproductive rate (R_o) on *C. moschata* was 1.6, 1.4, 1.6, 6.5 and 10.5 times higher than on *M. indica, P. aculeata, C. cajan, F. benjamina* and *C. arabica*, respectively. The intrinsic rate of increase was higher on *M. indica*

TABLE 4. EFFECTS OF VARIOUS HOST PLANT SPECIES (*CUCURBITA MOSCHATA, MANGIFERA INDICA, PARKINSONIA ACULEATA, CAJANUS CAJAN, FICUS BENJAMINA*, AND *COFFEA ARABICA*) ON LIFE TABLE PARAMETERS OF *RASTROCOCCUS ICERYOIDES*.

Host plants	R_o	r_m	T_d	GT	λ
C. moschata	379.0 ± 11.9a	0.169 ± 0.002b	4.10 ± 0.05c	35.13 ± 0.60b	1.181 ± 0.003b
M. indica	241.0 ± 4.5c	0.178 ± 0.003a	3.90 ± 0.06d	30.81 ± 0.50e	1.204 ± 0.004a
P. aculeata	274.3 ± 3.6b	0.172 ± 0.001b	4.03 ± 0.01c	32.64 ± 0.06c	1.187 ± 0.001b
C. cajan	240.5 ± 3.3c	0.175 ± 0.001a	3.96 ± 0.01d	31.33 ± 0.08d	1.201 ± 0.001a
F. benjamina	58.3 ± 1.9d	0.108 ± 0.001c	6.42 ± 0.05b	37.64 ± 0.10a	1.113 ± 0.001c
C. arabica	36.1 ± 1.1e	0.102 ± 0.001d	6.79 ± 0.06a	35.17 ± 0.12b	1.111 ± 0.001c

Means ± SE within a column followed by the same letter do not differ significantly by Student–Newman–Keuls test ($P \leq 0.05$). r_m = intrinsic rate of increase (female eggs/female/day), R_o = net reproductive rate (female offspring/female/generation), GT = mean generation time (days), T_d = doubling time (days) and λ = infinite rate of increase for population (female offspring/female/day).

(0.178) and the population was expected to double in 3.9 days. The lowest r_m was recorded on *C. arabica* (0.102) with a doubling time of 6.8 days. *Mangifera indica* recorded the lowest generation time of 31 days and the highest duration occurred on *F. benjamina*. The finite rate of increase was 1.11 on *F. benjamina* and *C. arabica* and 1.20 on *M. indica* and *C. cajan* (Table 4).

DISCUSSION

Results of this study showed that the 6 host plant species tested support the development of *R. iceryoides* but the biological parameters measured varied significantly across the host plants tested. Previous field studies have suggested that *M. indica*, *P. aculeata* and *C. cajan* were the most heavily infested host plants by *R. iceryoides* (Williams 1989; Luhanga & Gwinner 1993; Gado & Neuenschwander 1993; CABI 2000; Tanga 2012). Our results concur with these findings as well as providing evidence that fruit of *C. moschata* is an equally suitable host for development and survival of *R. iceryoides*. The duration of development is potentially an important component of fitness in the field, as it will determine how long different developmental stages of the mealybug will be exposed to predators and parasites. For example, the effectiveness of several natural enemies depends on host growth rates: parasitism increases when host growth is slowed (Benrey & Denno 1997; Devine et al. 2000). The prolongation of nymphal stages of *R. iceryoides* on sub-optimal hosts may provide an important selective advantage under pressure from natural enemies, as demonstrated by several authors (Häggström & Larsson 1995; Parry et al. 1998; Awmack & Leather 2002). The 2 most efficient and widely distributed nymphal parasitoids of *R. iceryoides* (*Anagyrus pseudococci* (Girault) and *Praleurocerus viridis* (Agarwal) attack the second and third instars (Noyes & Hayat 1994; Tanga et al. 2012) and host plant-induced delays in development may increase parasitism rate on mealybugs although this could also be counterproductive in terms of parasitoid fitness if they are unable to make a choice for egg laying based on host quality (Tanga et al. 2012). On the other hand, a reduction in developmental duration on an optimal host could represent an advantage to the mealybug by reducing its vulnerability to parasitism and predation.

Although development and survival were poor on *F. benjamina* and *C. arabica*, these host plants supported establishment of *R. iceryoides*. It is probable that some constituent compounds or physiological barriers inherent in this host plant species significantly reduced feeding, and, consequently, led to a reduction in development and

survival of *R. iceryoides*. Despite these observations, *C. arabica* especially warrants careful monitoring given the previous history of invasion and impact of *Planococcus kenyae* Le Pelley on coffee in East Africa and its subsequent classical biological control by *Anagyrus kivuensis* Compere (Greathead 1971; 2003).

Our results illustrate that host plant affects adult reproductive output and longevity. We observed that in addition to increasing the speed of growth of *R. iceryoides*, rearing the mealybug on the most suitable host plant (*M. indica*, *P. aculeata*, *C. cajan* and *C. moschata*) resulted in higher progeny production and adult longevity. Van Lenteren & Noldus (1990) stated that shorter pre-reproductive period and increased reproductive capacity of an insect on a host reflect the suitability of the plant. This is confirmed by the current study and although we did not measure the nutritional content of the tested plant species, it is probable that it might have played a role in enhancing the reproductive success of the mealybug on the suitable host plants. Our findings also strongly corroborate the observations of Boavida & Neuenschwander (1995) who reported shorter pre-reproductive period and higher progeny production for *Rastrococcus invadens* Williams when reared on its most suitable host plant, *M. indica*. Matokot et al. (1992) showed that the development of *R. invadens* Williams (Homoptera: Pseudococcidae) varies considerably when reared on *M. indica*, *Ficus* sp., *Plumeria* sp. and *Citrus* spp. Marohasy (1997) reported no difference in development, survival and fecundity of cohorts of *Phenacoccus parvus* Morrison, when reared on *Lantana camara* L., *Lycopersicon esculentum* Miller and *Solanum melongena* L, but *Gossypium hirsutum* L., *Ageratum houstonianum* Miller and *Clerodendrum cunninghamii* Benth., were identified as less suitable host plants.

Although *R. iceryoides* was observed to lay eggs on *F. benjamina* and *C. arabica*, egg production was generally low when compared with reproduction on the other host plants. Leather (1995) noted that when an insect pest encounters a poor-quality host plant, it may modify its oviposition behavior, either by reducing the number of eggs laid on each plant or, in some cases, adjusting the size or nutritional content of the eggs. In extreme cases, where the quality of the host plant is too low to support adult survival, female insects may resorb eggs or embryos and use the nutrients gained to increase their longevity and thus their potential to find better-quality host plants for their offspring (Awmack & Leather 2002). Although we did not dissect the insects to observe the ovaries or measure the size and nutritional content of the eggs laid by *R. iceryoides*, Nelson-Rees (1960) noted egg resorption in the citrus mealybug, *Planococcus citri* (Rossi) and it is possible that such reproductive strategy occurs in the mango mealybug but this warrants further investigation.

Rastrococcus iceryoides sex ratio was significantly affected by host plant on which the insects were reared. Its progeny were female biased on *M. indica*, *P. aculeata*, *C. cajan* and *C. moschata* and male biased in the less suitable host plants (*F. benjamina* and *C. arabica*). This suggests that maternally influenced sex ratio distortion or mortality of either sex during egg and nymphal development are dependent on the host plant species used. Contrary to our study, developmental studies on *R. invadens* revealed a significantly male-biased sex ratio with male and female ratio ranging from 2.1:1 to 3.3:1 on its most preferred host plant, *M. indica* (Sahoo & Ghosh 2000). The reason for the discrepancy in results is unclear but in other insect herbivores, sex ratio on better quality host plants has been reported to be female-biased (Mopper & Whitham 1992; Craig et al. 1992; Barker & Maczka 1996).

The morphometric studies revealed that the body size of *R. iceryoides* was greatly influenced by the host plant type on which the mealybug was reared. As with the developmental studies, mealybugs reared on *M. indica*, *P. aculeata*, *C. cajan* and *C. moschata* had significantly larger body size than those reared on *F. benjamina* and *C. arabica*, which indicates that no fitness penalty is paid for rapid development and increased body size. Body size is influenced, among other factors, by differential nutritional quality of the host plant species, chemical constituents as well as physical differences in the plant structures that may affect development, reproduction, survival, behaviour and distribution of the phytophagous insect (Slansky & Rodriguez 1987; Bethke et al. 1998). Larger individual mealybugs have the potential to cause more plant damage, as food intake is positively correlated with body weight (Tanga 2012). Positive correlation between body size and fecundity are common in other insects (Haukioja & Neuvonen 1985; Sopow & Quiring 1998; Ekesi et al. 2007) and evidence suggests that similar relationships exist in female *R. iceryoides* (Tanga 2012). In other mealybug species, it has been reported that mealybugs feeding on host plant species with high nitrogen concentrations have increased egg loads, larger matured females, and shorter developmental time (Klingauf 1987; Bethke et al. 1998; Hogendorp et al. 2006). Conversely, it is likely that adult mealybugs emerging from suboptimal host plants tested may have less potential to inflict damage on the plant if their numbers, size and fecundity are lower.

The life table parameters provide, for the first time, comprehensive information on the survival, development and reproductive capacity of *R. iceryoides* on the different host plants tested. The intrinsic rate of natural increase (r_m) is the most important parameter for describing the growth potential of a population under given climatic and food conditions, as it reflects the overall effect of development, reproduction and survival (Southwood

& Handerson 2000). The results from this study indicate that *M. indica* and *C. cajan* are the most suitable among the plants tested for *R. iceryoides* with r_m of 0.178 and 0.175, respectively. For *R. invadens*, Boavida & Neuenschwander (1995) reported r_m values of 0.070-0.078 on *M. indica*. Considering the fact that the intrinsic rate of natural increase of *R. iceryoides* on mango is at least 2.2-fold that of *R. invadens* on the same host plant, the former pest could have a higher potential of threatening mango production in Africa compared to *R. invadens*. In addition to helping predict the population growth potential, and effectively time control strategies within an integrated pest management framework for the pest, life table statistics on the different host plants have practical implications for more efficient and effective production of mealybugs for parasitoid mass rearing and releases. Reproductive values (m_x) would be helpful in determining the best host plants for rearing. To judge from the R_o and r_m values, mass rearing would be suitable on the 4 most optimal host plants.

Overall, the results of this investigation provide strong indication that host plant species of *R. iceryoides* will have a significant impact on development and reproduction of the pest, thereby affecting the population growth parameters, and the timing and extent of mealybug damage to the plant species. *Rastrococcus iceryoides* development on highly suitable plants such as *M. indica* and *C. cajan*, as well as on the fruits of *C. moschata* may result in rapid development and greater numbers of mealybugs surviving to adulthood, and hence more damage on these host plants; and this observation has significant implications for management of the pest on the suitable host plants. Demographic parameters on the most suitable host also showed that these plant species as well as *C. moschata* fruits should be excellent targets for mass rearing of *R. iceryoides* parasitoids for field releases. The life table parameters also provide important new information on the biotic potential of the pest on its host plants that should be useful in developing simulation models that include other factors for field use and management of *R. iceryoides* (Gutierrez 1996; Sporleder et al. 2012). From the standpoint of conservation biological control, *P. aculeata* is an important ornamental shade plant used by growers in the vicinity of *M. indica* and *C. cajan* crops. An important management strategy would be to conserve the indigenous parasitoids of *R. iceryoides*: *Anagyrus pseudococci* Girault (Hymenoptera: Encyrtidae), *Leptomastrix dactylopii* Howard (Hymenoptera: Encyrtidae), *Leptomastidea tecta* Prinsloo (Hymenoptera: Encyrtidae), *Agarwalencyrtus citri* Agarwal (Hymenoptera: Encyrtidae), *Aenasius longiscapus* Compere (Hymenoptera: Encyrtidae) and *Anagyrus aegyptiacus* Moursi (Hymenoptera: Encyrtidae) (Tanga 2012) on these plants, and or augmentative releases of appropriate parasitoids on

P. aculeata for parasitoid population build-up and subsequent suppression of *R. iceryoides* population before their spread into the cultivated crop. The information provided in this investigation should be essential in understanding the dynamics of *R. iceryoides* and should contribute to an integrated management action plan that allows for targeted suppression of the pest in East Africa.

ACKNOWLEDGEMENTS

REFERENCES CITED

AGOUNKÉ, D., AGRICOLA, U., AND BOKONON-GANTA, A. 1988. *Rastrococcus invadens* Williams (Hemiptera, Pseudococcidae), a serious exotic pest of fruit trees and other plants in West Africa. Bull. Entomol. Res. 78: 695-702.

AWMACK, C. S., AND LEATHER, R. S. 2002. Host plant quality and fecundity in herbivorous insects. Annu. Rev. Entomol. 47: 817-844.

BARKER, A. M., AND MACZKA, C. J. M. 1996. The relationships between host selection and subsequent larval performance in three free-living graminivorous sawflies. Ecol. Entomol. 21: 317-327.

BEN-DOV, Y. 1994. A systematic catalogue of the mealybugs of the world (Insecta: Homoptera: Coccoidea: Pseudococcidae and Putoidae) with data on geographical distribution, host plants, biology and economic importance. Intercept Limited, Andover, UK.

BENRAYS, E. A., AND CHAPMAN, R. F. 1994. Host plant selection by phytophagous insects. Chapman & Hall, New York, USA.

BENREY, B., AND DENNO, R. F. 1997. The slow growth-high mortality hypothesis: a test using the cabbage butterfly. Ecology 78: 987-999.

BETHKE, J. A., REDAK, R. A., AND SCHUCH, U. K. 1998. Melon aphid performance on chrysanthemum as mediated by cultivar, and deferential levels of fertilization and irrigation. Entomol. Exp. Appl. 88: 41-47.

BOAVIDA, C., AND NEUENSCHWANDER, P. 1995. Influence of host plant on the mango mealybug, *Rastrococcus invadens*. Entomol. Exp. Appl. 76: 179-188.

BOKONON-GANTA, A.H., AND NEUENSCHWANDER, P. 1995. Impact of the biological control agent *Gyranusoidea tebygi* Noyes (Hymenoptera: Encyrtidae) on the mango mealybug, *Rastrococcus invadens* Williams (Homoptera: Pseudococcidae), in Benin. Biocontrol Sci. Technol. 5: 95-107.

BOKONON-GANTA, A.H., NEUENSCHWANDER, P., VAN ALPHEN, J. J. M., AND VOST, M. 1995. Host stage selection and sex allocation by *Anagyrus mangicola* Noyes (Hymenoptera: Encyrtidae) a parasitoid of the mango mealybug, *Rastrococcus invadens* Williams (Hemiptera: Pseudococcidae). Biol. Control 5: 479-486.

BOUSSIENGUET, J., AND MOULOUNGOU, J. 1993. Demographic pressure and host plant choice of *Rastrococcus invadens*, a pest of mango recently introduced into Africa. Bull. Soc. Entomol. France. 98: 139-148.

CABI. 2000. Crop protection compendium. Global module, 2nd edition. CABI Publishing, Wallingford, UK.

CALATAYUD, P. A., AND LE RÜ, B. 2006. Cassava-mealybug interactions. IRD éditions, Paris.

CAREY, J. R. 1993. Applied demography for biologists with special emphasis on insects. Oxford University Press, New York.

CPC [Crop Protection Compendium]. 2002. Crop protection compendium database. CAB International, Wallingford, UK.

CRAIG, T. P., PRICE, P. W., AND ITAMI, J. K. 1992. Facultative sex ratio shifts by a herbivorous insect in response to variation in host plant quality. Oecologia 92: 153-161.

DEVINE, G. J., WRIGHT, D. J., AND DENHOLM, I. 2000. A parasitic wasp (*Eretmocerus mundus* Mercet) can exploit chemically induced delays in the development rates of its whitefly host (*Bemisia tabaci* Genn.). Biol. Control 19: 64-75.

EKESI, S., NDERITU, P. W., AND CHANG, C. L. 2007. Adaptation to and small-scale rearing of invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) on artificial diet. Ann. Entomol. Soc. Am. 100: 562-567.

GADO, A., AND NEUENSCHWANDER, P. 1993. Survey for the mango mealybug *Rastrococcus iceryoides* and its natural enemies in Tanzania. International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria.

GREATHEAD, D. J. 1971. A review of biological control in the Ethiopian region. Technical Bulletin of the Commonwealth Institute of Biological Control, No. 5. Commonwealth Agricultural Bureaux, Farnham Royal, Slough.

GREATHEAD, D. J. 2003. Historical overview of biological control in Africa, pp. 1-26 *In* P. Neuenschwander, C. Borgemeister and J. Langewald [eds.] Biological Control in IPM Systems in Africa. CABI Publishing, Wallingford, UK.

GUTIERREZ, A. P. 1996. Applied population ecology: a supply-demand approach. Wiley and Son, New York, USA.

HÄGGSTRÖM, H., AND LARSSON, S. 1995. Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. Oecologia 104: 308-315.

HAUKIOJA, E., AND NEUVONEN, S. 1985. The relationship between size and reproductive potential in male and female *Epirita autumnata* (Lep., Geometridae). Ecol. Entomol. 10: 267-270.

HOGENDORP, B. K., CLOYD, R. A., AND SWIADER, J. M. 2006. Effect of nitrogen fertility on reproduction and development of citrus mealybug, *Planococcus citri* Risso (Homoptera: Pseudococcidae), feeding on two colors of coleus, *Solenostemon scutellarioides* L. Codd. Environ. Entomol. 35: 201-211.

HØGH-JENSEN, H., MYAKA, F. A., SAKALA, W. D., KAMALONGO, D., NGWIRA, A., VESTERAGER, J. M., ODGAARD, R., AND ADU-GYAMFI, J. J. 2007. Yields and qualities of pigeon pea varieties grown under smallholder farmers' conditions in Eastern and Southern Africa. African J. Agr. Res. 2: 269-278.

KLINGAUF, F. A. 1987. Feeding, adaptation and excretion, pp. 225-253 In A. K. Minks and P. Harrewijn [eds.], Aphids-Their Biology, Natural Enemies and Control, Vol. A. Elsevier, Amsterdam, The Netherlands.

LACEY, E. P. 1998. What is an adaptive environmentally induced parental effect? pp. 54-66 *In* T. A. Mousseau and C. W. Fox [eds.], Maternal effects as adaptations. Oxford University Press, New York, USA.

LEATHER, S. R. 1995. The effect of temperature on oviposition, fecundity and egg hatch in the pine beauty moth, *Panolis flammea* (Lepidoptera: Noctuidae). Bull. Entomol. Res. 84: 515-520.

LUHANGA, W. W., AND GWINNER, J. 1993. Mango mealybug (*Rastrococcus iceryoides*) on *Mangifera indica* in Malawi. FAO Plant Prot. Bull. 41(2): 125-126.

MAIA, A. H. N., LUIZ, A. J. B., AND CAMPANHOLA, C. 2000. Statistical inference on associated fertility life table parameters using Jacknife technique: computational aspects. J. Econ. Entomol. 93: 511-518.

MAROHASY, J. 1997. Acceptability and suitability of seven plant species for the mealybug *Phenacoccus parvus*. Entomol. Exp. Appl. 84: 239-246.

MATOKOT, L., REYD, G., MALONGA, P., AND LE RU, B. 1992. Population dynamics of *Rastrococcus invadens* (Homoptera: Pseudococcidae) in the Congo; influence of accidental introduction of the Asiatic parasitoid *Gyranusoidea tebygi* (Hymenoptera: Encyrtidae). Entomophaga 37: 123-140.

MEYER, J. S., INGERSOLL, C. G., MCDONALD, L. L., AND BOYCE, M. S. 1986. Estimating uncertainty in population growth rates: Jackknife vs. bootstrap techniques. Ecology 67: 1156-1166.

MILLER, J. R., MILLER, T. A., AND BERENBAUM, M. 1986. Insect-plant interactions. Springer-Verlag, Dordrecht, The Netherlands.

MOPPER, S., AND WHITHAM, T. G. 1992. The plant stress paradox—effects on pinyon sawfly sex ratios and fecundity. Ecology 73: 515-25.

NARAI, Y., AND MURAI, T. 2002. Individual rearing of the Japanese mealybug, *Planococcus kraunhiae* (Kuwana) (Homoptera: Pseudococcidae) on germinated broad bean seeds. Appl. Entomol. Zool. 37: 295-298.

NELSON-REES, W. A. 1960. A study of sex predetermination in the mealybug, *Planococcus citri* (Rossi). J. Exp. Zool. 144: 111-137.

NEUENSCHWANDER, P. 2003. Biological control of cassava and mango mealybugs, pp. 45-59 *In* P Neuenschwander, C Borgemeister and J. Langewald [eds.], Biological Control in IPM Systems in Africa CABI Publishing, Wallingford, UK.

NOYES, J. S. 1988. *Gyranusoidea tebygi* sp. n. (Hymenoptera: Encyrtidae), a parasitoid of *Rastrococcus* (Hemiptera: Pseudococcidae) on mango in India. Bull. Entomol. Res. 78: 313-316.

NOYES, J. S., AND HAYAT, M. 1994. Oriental mealybug parasitoids of the Anagyrini (Hymenoptera: Encyrtidae). CAB International, University Press, Cambridge.

PARRY, D., SPENCE, J. R., AND VOLNEY, W. J. A. 1998. Budbreak phenology and natural enemies mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae). Environ. Entomol. 27: 1368-1374.

SAHOO, S. K., AND GHOSH, A. B. 2000. Biology of the mealybug *Rastrococcus invadens* Williams (Pseudococcidae: Hemiptera). J. Environ. Ecol. 18: 752-756.

SAS Institute. 2010. SAS/STAT Users Guide: Statistics, version 9.1.3, SAS Institute, Cary, NC.

SERRANO, M. S., AND LAPOINTE, S. L. 2002. Evaluation of host plants and a meridic diet for rearing *Maconellicoccus hirsutus* (Hemiptera: Pseudococcidae) and its parasitoid *Anagyrus kamali* (Hymenoptera: Encyrtidae). Florida Entomol. 85: 417-425.

SLANSKY, J. E., AND RODRIGUEZ, J. G. 1987. Nutritional ecology of insects, mites, spiders, and related invertebrates: an overview, pp 1-69 *In* E Slansky Jr and J. G. Rodriguez [eds.], Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York, USA.

SOKAL, R. R., AND ROHLF, F. J. 1981. Biometry: The principles and practices of statistics in biological research, 2nd ed. Freeman, New York, USA.

SOPOW, S. L., AND QUIRING, D. T. 1998. Body size of spruce-galling adelgids is positively related to realized fecundity in nature. Ecol. Entomol. 23: 467-479.

SOUTHWOOD, T. R. E., AND HANDERSON, P. A. 2000. Ecological methods, with particular reference to the study of insect populations, 3rd edn. Blackwell Science, Oxford, UK.

SPORLEDER, M., TONNANG, H. E. Z., CARHUAPOMA, P., GONZALES, J. C., JUAREZ, H., AND KROSCHEL, J. 2012. Insect Life Cycle Modeling (ILCYM) software−a new tool for regional and global insect pest risk assessments under current and future climate change scenarios. International Potato Centre (CIP), Lima, Peru.

TANGA, M. C. 2012. Bio-ecology of the mango mealybug, *Rastrococcus iceryoides* Green (Hemiptera: Pseudococcidae) and its associated natural enemies in Kenya and Tanzania. PhD Thesis, University of Pretoria, Pretoria 0002, South Africa.

TANGA, M. C., SAMIRA, A. M., GOVENDER, P., AND EKESI, S. 2012. Effect of host plant species on bionomic and life history parameters of *Anagyrus pseudococci* Girault (Hymenoptera: Encyrtidae), a parasitoid of the mango mealybug *Rastrococcus iceryoides* Green (Homoptera: Pseudococcidae). Biol. Control 65: 43-52.

TOBIH, F. O., OMOLOYE, A. A., IVBIJARO, M. F., AND ENOBAKHARE, D. A. 2002. Effects of field infestation by *Rastrococcus invadens* Williams (Hemiptera: Pseudococcidae) on the morphology and nutritional status of mango fruits, *Mangifera indica* L. Crop Prot. 21: 757-761.

VAN LENTEREN, J. C., AND NOLDUS, L. P. J. J. 1990. Whitefly–plant relationships: behavioural and ecological aspects, pp. 47-90 *In* D. Gerling [ed.], Whiteflies: Their Bionomics, Pest Status and Management. Intercept Ltd, Andover, Hants, UK.

WATSON, G. W., AND KUBIRIBA, J. 2005. Identification of mealybugs (Hemiptera: Pseudococcidae) on banana and plantain in Africa. African Entomol. 13: 35-47.

WILLIAMS, D. J. 1989. The mealybug genus *Rastrococcus* Ferris (Hemiptera: Pseudococcidae). Syst. Entomol. 14: 433-486.

WILLIAMS, D. J. 1986. *Rastrococcus invadens* sp. n. (Hemiptera : Pseudococcidae) introduced from the Oriental Region to West Africa and causing damage to mango, citrus and other trees. Bull. Entomol. Res. 76: 695-699.

WILLINK, E., AND MOORE, D. 1988. Aspects of the biology of *Rastrococcus invadens* Williams (Hemiptera: Pseudococcidae), a pest of fruit crops in West Africa, and one of its primary parasitoids, *Gyranusoidea tebygi* Noyes (Hymenoptera: Encyrtidae). Bull. Entomol. Res. 78: 709-715.

YANG, J., AND SADOF, C. S. 1995. Variegation in *Coleus blumei* and the life history of citrus mealybug (Homoptera: Pseudococcidae). Environ. Entomol. 24: 1650 -1655.