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Plant–Insect Interactions

The Effects of Pest-Resistant Amaranth Accessions on the Performance of the Solitary Endoparasitoid *Apanteles hemara* (Hymenoptera: Braconidae) Against the Amaranth Leaf-Webber *Spoladea recurvalis* (Lepidoptera: Crambidae)

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Abstract

The leaf-webber *Spoladea recurvalis* F. is the most devastating pest of amaranths in East Africa. Recent collaborative research in Asia and East Africa revealed one highly resistant amaranth accession (VI036227) to the pest and seven moderately resistant ones (RVI00053, VI033479, VI044437-A, VI047555-B, VI048076, VI049698, and VI056563). The solitary koinobiontic endoparasitoid *Apanteles hemara* Nixon has also been reported as efficient against the pest. Plant resistance to herbivores may have bottom-up effects on their parasitoids. In this study, we assessed the effects of the seven moderately resistant amaranth accessions and one susceptible accession (VI033482) on the performance of *A. hemara*. Except VI056563 that recorded lower parasitism rates compared to the susceptible accession, *A. hemara* performed well on all the other moderately resistant accessions. The longevity of the parasitoid was significantly extended on the resistant accessions compared to the susceptible one. While the parasitoid's body size, developmental time, and survival differed significantly between resistant accessions, they were similar to results obtained on the susceptible accession. Furthermore, while the parasitoid's sex ratio was male-biased in the susceptible accession, balanced sex ratios were obtained from accessions RVI00053, VI033479, VI044437-A, VI047555-B, VI048076, and VI049698. Significant nonreproductive host larval mortality was induced by *A. hemara* on all the tested accessions. These results suggest that the moderately resistant accessions can be used in combination with the endoparasitoid *A. hemara* to manage *S. recurvalis* and other amaranth leaf-webbers in the context of integrated pest management.

Key words: allelochemical, fitness, IPM, mortality, parasitism

Spoladea recurvalis F. has been reported to be one of the most devastating pests of cultivated amaranth in Africa and Asia (Batra and Bhattacherjee 1960, Aderolu et al. 2013, Kedar and Kumaranag 2013, Mureithi et al. 2017, Jeyasankar and Gokilamani 2016). The use of synthetic pesticides to manage pests attacking short-cycle crops such as amaranth is not only uneconomical to the resource-poor farmers but also presents health and environmental risks (Arivudainambi et al. 2010, Aderolu et al. 2013). In order to manage these pests, studies have recently begun to explore and recommend host plant resistance (HPR) against arthropod pests of amaranth as

an affordable and sustainable alternative pest management strategy (Othim et al. 2018b, Smith et al. 2018).

Several accessions of amaranth obtained from different regions of the world and preserved at the World Vegetable Center (WorldVeg) have been screened both in the open field and in the laboratory for resistance against *S. recurvalis* and a few resistant accessions identified (Othim et al. 2018a,c). Selection and identification of resistant accessions was based on the levels of infestation and damage caused by *S. recurvalis* and the effects elicited by the accessions on the biology and reproduction of the pest (Othim et al. 2018a,c). Among

the screened amaranth accessions, VI036227 was found to be highly resistant against *S. recurvalis* reporting less than 1% infestation and damage and causing 100% pest larvae mortality. Several accessions including RVI00053, VI033479, VI044437-A, VI047555-B, VI048076, VI049698, and VI056563 among others were moderately resistant, having significantly low levels of pest infestation and damage compared to the susceptible check (Othim et al. 2018a,c). These accessions represented different species of amaranth although some among them belonged to the same species but exhibited different morphological characteristics. Whereas it is known that HPR is compatible with other pest management strategies such as chemical control, botanicals, and microbials (Rose et al. 1988, Hare 1992, Meade and Hare 1993, Smith 1999), different interactions including antagonistic, synergistic, and additive effects have been reported with biological control (Eigenbrode and Trumble 1994, Faria et al. 2007). Since several studies demonstrate that different host plants elicit various effects on the natural enemies including parasitoids and predators (Turlings and Benrey 1998; Ode et al. 2004; Sétamou et al. 2005; Harvey et al. 2007a,b; Gols and Harvey 2009; Harvey and Gols 2011a), there is a need to understand the interaction between the parasitoids and the resistant amaranth accessions.

Apanteles hemara Nixon, a koinobiontic endoparasitoid of *S. recurvalis* indigenous to Kenya and Tanzania, has often been found parasitizing the larvae of *S. recurvalis* in open field conditions (Othim et al. 2017, 2018b). The parasitoid has also been recorded from over 25 countries, including those in the continents of Europe, Africa, Asia, and Australia (Kedar and Kumaranag 2013, Madl and van Achterberg 2014, Yu et al. 2016, Fernandez-Triana et al. 2017, Othim et al. 2017). Parasitism rates by *A. hemara* of up to 94% have been reported in the laboratory (Othim et al. 2017) and 62% in open field conditions (Narayanan et al. 1957). The parasitoids have been recommended for biological control of *S. recurvalis* within an integrated pest management (IPM) program through conservation or augmentation (Narayanan et al. 1957, Bhattacherjee and Ramdas 1964, Arivudainambi et al. 2010, Kedar and Kumaranag 2013, Othim et al. 2017). Integrating these indigenous parasitoids with HPR to pests in the management of leaf-webber pests of amaranth, particularly *S. recurvalis*, may prove to be sustainable and economical for the resource-poor growers of amaranth in several parts of Africa and Asia. HPR to pests is exhibited through mechanisms such as antixenosis and antibiosis which are both influenced by the plant chemistry (War et al. 2012). Findings from several studies conducted on various *Brassica* spp. have shown that plant chemistry affects the performance of individuals up in the food chain up to the third and fourth trophic levels consisting of parasitoids, predators, and hyperparasitoids (Harvey and Strand 2003, Ode et al. 2004, Soler et al. 2005, Ode 2006, Harvey et al. 2007b, Karimzadeh and Wright 2008). Being a koinobiontic parasitoid, the parasitized larvae of *S. recurvalis* continue to feed during the development of immature *A. hemara* within the host hence the quality of the host plant might not only affect the leaf-webber larvae but also the parasitoid (Sétamou et al. 2005, Harvey and Gols 2011a, Othim et al. 2017). According to Harvey and Gols (2011a), host plant quality may be linked to the manner in which a parasitoid regulates the growth of its host relative to healthy hosts and this regulation is intimately correlated with the size of the adult parasitoid relative to the maximum potential size of its herbivore host.

A host plant may affect a parasitoid's host location by emitting volatiles that attract the parasitoids especially when the plant is damaged through feeding by a herbivore (herbivore-induced volatiles) (Benrey et al. 1997, Turlings and Benrey 1998, Eben et al. 2000, Hoballah et al. 2002, Gols and Harvey 2009, Gols et al. 2012). In

some cases, a plant's morphological and physical features such as leaf shelters formed by most leaf-webbing Lepidoptera and trichomes can directly interfere with a parasitoid's access to the herbivore host and make them less accessible to natural enemies (Turlings and Benrey 1998). Plant metabolites may also have profound effects on the development of immature parasitoids within the herbivorous host (Ode et al. 2004, Sétamou et al. 2005, Gols et al. 2008b, Harvey and Gols 2011b). The effects elicited by a host plant may be due to the presence or absence of specific nutrients in the host's diet, action of toxic allelochemicals that are detrimental to the parasitoid or an interaction between nutrients and allelochemicals (Fox et al. 1990, Turlings and Benrey 1998, Gols et al. 2008a, Gols and Harvey 2009, Harvey and Gols 2011a). These effects can be either direct (if plant chemicals present in the herbivorous host tissues have an effect on the developing parasitoid) or indirect (when the chemicals affect suitability of the herbivore as a host for the developing parasitoid) (Turlings and Benrey 1998, Gols and Harvey 2009, Harvey and Gols 2011a). On the parasitoid, these effects are expressed in a variety of its fitness parameters including parasitism rate, nonreproductive mortality, sex ratio, and adult body size among others (Ode et al. 2004; Gols et al. 2008a,b; Gols and Harvey 2009; Harvey and Gols 2011a). The parasitism rate and nonreproductive mortality form together the total mortality caused by parasitoid to their insect hosts. We hypothesize that the more suitable the host plant to the parasitoid, the higher the mortality in the pest. Similarly, more females in the progeny infers stability and efficiency of parasitoids through increased parasitism, and we hypothesize that the more female-biased sex ratio in the progeny, the more suitable the host plant to the parasitoid. Higher female body size also is known to correlate with higher fecundity. We hypothesize, therefore, that the more suitable hosts will enable bigger size adult parasitoids (Ode et al. 2004; Gols et al. 2008a,b; Gols and Harvey 2009; Harvey and Gols 2011a).

This study was designed to provide insights into the effects of selected pest-resistant amaranth accessions on the performance of the indigenous parasitoid *A. hemara* which has been recommended as a potential biocontrol agent for *S. recurvalis* (Othim et al. 2017). We investigated several parasitoid fitness parameters, including parasitism, nonreproductive mortality, pupal mortality, developmental time, sex ratio, adult body size and longevity on the selected accessions relative to a susceptible check.

Materials and Methods

Amaranth Accessions

Eight amaranth accessions/lines exhibiting pest resistance and one susceptible accession were selected from an open field screening conducted in 2016 and 2017 using 36 accessions and lines obtained from the WorldVeg's genebanks in Shanhua, Taiwan and Arusha, Tanzania (Table 1) (Othim et al. 2018a). However, the most resistant accession VI036227 could not be tested as it led to 100% mortality of *S. recurvalis* larvae at an early stage. Therefore, seven moderately resistant accessions RVI00053, VI033479, VI044437-A, VI047555-B, VI048076, VI049698, and VI056563 were tested against a susceptible accession VI033482. For the purpose of pest colony maintenance and parasitoid colony maintenance, *Amaranthus dubius* (Ex-zan) obtained from the WorldVeg genebank in Arusha was used. The selected accessions and lines (hereafter both called accessions) were raised in the screenhouse at WorldVeg (3.38°S, 36.8°E) in Arusha. The seeds were sown in plastic trays containing a substrate of soil and manure in the ratio 4:1. Two to three weeks after germination, the seedlings were transplanted into plastic pots of 10 cm diameter (1,000 cm^3) and maintained with regular watering for use in the experiments.

Table 1. Resistance status, description, and certain morphological characteristics of amaranth accessions and lines assessed

Amaranth accession code	Species	Type	Leaf color	Leaf shape	Country of origin	No. of branches per plant (mean)	Plant height (mean) cm	Leaf width (mean) cm	Leaf length (mean) cm	Petiole length (mean) cm	Resistance status
VI033482	*A. tricolor*	Accession	Green	Reniform	Malaysia	9.0	100.9	10.6	19.3	5.0	S
RVI00053	*A. dubious*	Line	Green	Ovate	Uganda	11.0	167.0	8.7	15.6	8.0	MR
VI033479	*Amaranthus* sp.	Accession	Green	Ovate	Malaysia	11.3	100.8	4.9	7.6	4.2	MR
VI036227	*A. blitoides*	Accession	Green	Oblanceolate	Hungary	15.8	67.4	1.2	3.2	1.6	HR[a]
VI044437-A	*A. cruentus*	Accession	Green	Lanceolate	Malaysia	11.5	89.5	5.5	13.0	7.2	MR
VI047555-B	*A. tricolor*	Accession	Green	Lanceolate	Vietnam	10.9	135.6	4.5	13.4	4.8	MR
VI048076	*A. tricolor*	Accession	Green	Cordate	Bangladesh	13.1	130.1	8.0	13.5	7.1	MR
VI049698	*A. viridis*	Accession	Green	Ovate	Thailand	12.4	100.5	3.9	5.5	3.4	MR
VI056563	*Amaranthus* sp.	Accession	Reddish	Ovate	Bangladesh	9.7	136.9	9.0	17.1	8.3	MR
Mean						11.6	114.3	6.3	12.0	5.5	
LSD (5%)						6.1	35.2	1.5	4.8	1.6	

MR, moderately resistant; HR, highly resistant; S, susceptible; LSD, least significant difference.

[a]The highly resistant accession could not support development of the host pest hence was not included in the assessment of the parasitoid's performance.

S. recurvalis Colony

A colony of *S. recurvalis* was established and maintained in the entomology laboratory at WorldVeg ESA, Arusha on *A. dubius* (Ex-Zan) for five generations prior to their experimental use. The adults and larvae of *S. recurvalis* were originally collected from amaranth fields at WorldVeg in Arusha in November and December 2015. In the laboratory, the larvae were maintained in ventilated plastic containers (15 × 7 × 5 cm) lined with paper towel to absorb excess moisture. Fresh amaranth leaves were supplied daily to the larvae until they completed their development. Adult moths were placed in transparent perspex cages (40 × 40 × 45 cm) with a sliding door and a netting material at the back and on the sides for ventilation. The moths were fed on 10% honey solution soaked in cotton wool and provided with potted amaranth plants for oviposition. The plants were replaced after every 24 h and placed in separate holding cages (50 × 50 × 60 cm) made from transparent perspex material with netting material at the back and on the sides for the eggs to hatch. Newly hatched larvae were left to feed on the live plants for 3–4 d and then transferred into plastic containers (15 × 7 × 5 cm) lined with paper towel and fine netting material on the lid for ventilation. Fresh amaranth leaves were supplied to the larvae daily for food until pupation. The pupae were incubated under similar conditions in the plastic containers until adult emergence. The laboratory condition was maintained at 25 ± 2°C, 50–70% relative humidity (RH) and photoperiod of 12:12 (L: D) h.

A. hemara Colony

A colony of *A. hemara* was established at the laboratory of WorldVeg, Arusha from pupal samples obtained from *S. recurvalis* larvae collected from amaranth fields at WorldVeg in Arusha. Colonies were replenished quarterly from new field collections performed. Adults were placed in a ventilated perspex cage (40 × 40 × 45 cm) with a sleeve on one side and fed honey from strips of paper. The rearing was maintained at 25 ± 2°C, 50–70% RH, and 12:12 (L:D) h photoperiod. Potted plants containing 3-d-old larvae of *S. recurvalis* were then introduced into the cage for the parasitoids to oviposit. The exposed larvae were removed on a daily basis and placed in ventilated plastic lunch boxes (15 × 7 × 5 cm) lined with paper towel. Fresh amaranth leaves were added into the lunch boxes as and when required until pupation. The parasitoid pupae were collected and transferred to clean Petri dishes (9-cm diameter), kept inside a perspex cage under similar conditions for adult emergence. These parasitoids were mass reared on *S. recurvalis* feeding on *A. dubius* (Ex-Zan) for several generations before their use for experiments with different accessions. Our preliminary experiments carried out to design adequate methodology showed that female parasitoids oviposited almost immediately after adult emergence, attacked first to third instar larvae but preferred the second instar host larvae (Our unpublished data).

Assessing the Performance of *A. hemara*

Potted amaranth plants of the seven selected resistant and one susceptible accession were exposed to adult *S. recurvalis* for 24 h to oviposit. The plants were then kept in separate perspex cages (40 × 40 × 45 cm; six plants per cage) with adequate ventilation until the eggs hatched. The hatched larvae were allowed to feed on the plants until their second instar before they were used in the experiment. A leaf/branch of each accession infested with 25 second instar larvae of the leaf-webber *S. recurvalis* was cut and placed in a ventilated cylindrical container 10 cm diameter and 5 cm height. A 2-d-old mated naïve (no prior contact with the pest) female parasitoid of *A. hemara* was then introduced into the container with *S. recurvalis* larvae and allowed to oviposit in the larvae of the leaf-webber for 24 h. The parasitoid was fed on honey smeared on a strip of paper during the 24 h period. After the 24 h of exposure to the parasitoid, the larvae of *S. recurvalis* were removed from the container and incubated in plastic lunch boxes where they were supplied with fresh amaranth leaves and monitored daily until parasitoid or host pupation. The pupae were collected, counted and then placed in a clean plastic petri dish under similar conditions and monitored daily until adult eclosion. The adults were then transferred into plastic vials (20 ml) covered with a netting material at the top where they were supplied with honey and monitored individually until they died. This procedure was followed with each accession and replicated six times on each accession. A control was also set up along each accession in which no parasitoid was introduced into the vial containing larvae.

The fitness parameters recorded to assess performance of the parasitoid on different accessions included: number of parasitoid pupae emerging from incubated larvae, the number of adult parasitoids that emerge, the development time of the parasitoid, adult longevity, F1 sex ratios, length of adult hind tibia and forewing (as indices of

body size) of 20 randomly chosen parasitoids of each sex, as well as larval and pupal mortalities.

Data Analysis

The data on parasitism rates, developmental time (larval, pupal, and total), female F1 proportions, adult longevity and length of forewings and hind tibia of *A. hemara* across the accessions were analyzed using one-way analysis of variance (ANOVA). The count numbers were $\log_{10}(x+1)$-transformed while the percentages were square-root transformed before analysis to obtain normally distributed datasets with similar variance among treatments. Longevity and length of forewing and hind tibia between males and female *A. hemara* was compared using independent samples *t*-test. The significance of nonreproductive mortality was assessed by comparing natural mortalities in the control with mortalities in the presence of parasitoid using paired *t*-test. The actual nonreproductive host mortality was identified using Abbott's formula (Abbott 1925). Paired *t*-test was used to determine the sex ratios of F1 progenies on each accession. Where significant differences occurred, the means were separated using Tukey's test at the level of significance of $P < 0.05$. All data were analyzed in R version 3.4.0 statistical software (R Development Core Team, Vienna, Austria).

Results

The average parasitism rate caused by *A. hemara* on *S. recurvalis* raised on the different amaranth accessions was $81.4 \pm 3.1\%$ and ranged between 34.3 ± 11.5 and $91.7 \pm 6.5\%$ across the accessions. There were significant differences ($F = 5.4$; df = 7, 44; $P < 0.001$) in the levels of parasitism across the accessions with VI056563 recording lower parasitism rates compared to RVI00053, VI044437-A, VI047555-B, VI048076, VI033479, VI049698, and the susceptible check VI033482 (Table 2). Parasitism rates did not differ significantly between the susceptible check and all the other moderately resistant accessions.

Egg and larval developmental time (from the time the parasitoid lays an egg into the host larva until it pupates) of *A. hemara* within the larvae of *S. recurvalis* differed significantly ($F = 3.2$; df = 7, 52; $P = 0.007$) with accession RVI00053 having shorter developmental time compared to VI044437-A. The parasitoid's egg and larval development time did not differ significantly between the resistant accessions compared to the susceptible check (Table 2). Similarly, the pupal development time differed significantly ($F = 2.0$; df = 7,

46; $P = 0.042$) with accession RVI00053 recording shorter pupal development time compared to VI033479. The pupal development time did not differ significantly between the resistant accessions and the susceptible check. The parasitoid's total developmental time was significantly shorter ($F = 3.8$; df = 7, 44; $P = 0.002$) on RVI00053 compared to VI033479, VI044437-A, VI048076, and VI049698. The total development time also did not differ significantly between the resistant accessions and the susceptible check.

There were significant differences ($F = 2.5$; df = 6, 71; $P = 0.031$) in the proportion of females among the F1 parasitoids obtained from the various amaranth accessions tested. RVI00053 and VI048076 had significantly higher proportions of female parasitoids compared to the susceptible check VI033482, whereas VI033479, VI044437-A, VI047555-B, and VI049698 did not show significant differences in the proportion of F1 females compared to the susceptible check (Fig. 1). There were no significant differences in the female to male sex ratios among the F1 parasitoids obtained from accessions RVI00053 ($t = 0.6$; df = 10; $P = 0.576$), VI033479 ($t = 1.2$; df = 8; $P = 0.252$), VI044437-A ($t = 1.9$; df = 13; $P = 0.086$), VI047555-B ($t = 0.7$; df = 4; $P = 0.553$), VI048076 ($t = 0.4$; df = 20; $P = 0.676$), and VI049698 ($t = 0.3$; df = 9; $P = 0.777$) whereas the susceptible check VI033482 led to male biased sex ratios among the F1 parasitoids ($t = 6.2$; df = 5; $P = 0.002$).

The parasitoid's pupal mortality did not differ significantly ($F = 0.4$; df = 7, 44; $P = 0.870$) among the amaranth accessions and ranged between 40.0 ± 18.8 and $66.0 \pm 18.9\%$ (Table 3). The parasitoid induced an average nonreproductive mortality of $32.1 \pm 2.8\%$ on *S. recurvalis* larvae across all the accessions. Significant nonreproductive host larval mortality due to the activity of the parasitoid was recorded in the accessions RVI00053 ($t = 3.9$; df = 5; $P = 0.011$), VI033479 ($t = 5.2$; df = 6; $P = 0.002$), VI044437-A ($t = 6.8$; df = 8; $P < 0.001$), VI047555-B ($t = 4.9$; df = 5; $P = 0.004$), VI048076 ($t = 9.8$; df = 9; $P < 0.001$), VI049698 ($t = 3.9$; df = 5; $P = 0.011$), VI056563 ($t = 4.8$; df = 6; $P = 0.003$), and the susceptible check VI033482 ($t = 9.2$; df = 7; $P < 0.001$) (Table 3). There were also significant differences in the nonreproductive larval mortalities ($F = 2.4$; df = 7, 51; $P = 0.031$) induced by the parasitoid among the resistant accessions. The accession VI047555-B recorded significantly lower nonreproductive mortalities compared to VI033479. There was, however, no significant difference in the nonreproductive mortality between the susceptible check and all the resistant accessions. Significant nonreproductive host pupal mortality was recorded on accessions VI033479 ($t = 4.1$; df = 4; $P = 0.015$), VI044437-A

Table 2. Parasitism rates and developmental times (mean ± SE) of *Apanteles hemara* on selected moderately resistant amaranth accessions

Amaranth accession code	Parasitism rate (%)	Parasitoid larval development time (days)	Parasitoid pupal development time (days)	Parasitoid total development time (days)
VI033482[a]	76.0 ± 9.8b	7.2 ± 0.3ab	3.9 ± 0.3ab	11.1 ± 0.5ab
RVI00053	83.2 ± 7.7b	6.0 ± 0.5a	3.4 ± 0.4a	9.4 ± 0.7a
VI033479	87.5 ± 4.9b	7.2 ± 0.4ab	4.7 ± 0.2b	11.9 ± 0.2b
VI044437-A	81.9 ± 6.8b	7.9 ± 0.2b	4.2 ± 0.2ab	11.9 ± 0.3b
VI047555-B	91.7 ± 6.5b	7.4 ± 0.3ab	4.0 ± 0.3ab	11.3 ± 0.2ab
VI048076	91.4 ± 4.0b	6.7 ± 0.3ab	4.3 ± 0.2ab	11.4 ± 0.3b
VI049698	85.5 ± 6.0b	7.0 ± 0.4ab	4.3 ± 0.3ab	11.3 ± 0.4b
VI056563	34.3 ± 11.5a	6.5 ± 0.4ab	4.7 ± 0.3ab	10.8 ± 0.2ab
P-value	<0.001	0.007	0.042	0.002
F	5.4	3.2	2.0	3.8
df	7,44	7,52	7,46	7,44

Means followed by the same letter(s) within a column are not significantly different at $P < 0.05$ (Tukey's test).
[a]Susceptible accession.
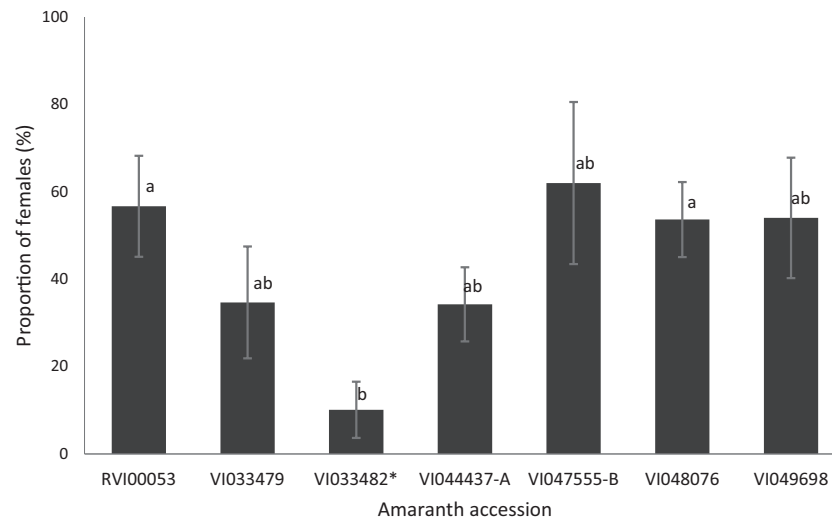
Fig. 1. Proportions (%) of female F1 parasitoids of *Apanteles hemara* across the selected moderately resistant amaranth accessions (means with the same letter are not significantly different at *P* < 0.05 [Tukey's test; *Susceptible accession])

Table 3. Nonreproductive host larval and pupal mortality (%) (mean ± SE) on selected moderately resistant amaranth accessions

Amaranth accession code	Nonreproductive host larval mortality	Nonreproductive host pupal mortality
VI033482[a]	25.8 ± 2.6ab	18.1 ± 4.9a
RVI00053	39.8 ± 14.2ab	20.6 ± 2.4a
VI033479	55.3 ± 11.2b	35.3 ± 8.4a
VI044437-A	28.6 ± 5.1ab	28.7 ± 11.1a
VI047555-B	15.0 ± 3.4a	16.6 ± 0.0a
VI048076	37.5 ± 5.8ab	27.7 ± 5.9a
VI049698	23.9 ± 6.7ab	16.7 ± 6.4a
VI056563	28.0 ± 6.9ab	21.2 ± 4.7a
P-value	0.031	0.513
F	2.4	0.9
df	7,51	7,26

Means followed by the same letter(s) within a column are not significantly different at *P* < 0.05 (Tukey's test).

[a]Susceptible accession.

(*t* =2.9; df = 4; *P* = 0.043), VI048076 (*t* = 4.6; df =3; *P* = 0.019), VI048076 (*t* = 4.0; df = 5; *P* = 0.010) and the susceptible check VI033482 (*t* = 3.5; df = 4; *P* = 0.025). Nonreproductive pupal mortality was not significant in VI049698 (*t* = 2.4; df = 3; *P* = 0.092), VI047555-B (*t* = 1; df = 3; *P* = 0.5) and RVI00053 (*t* = 2.3; df = 3; *P* = 0.101). Nonreproductive host pupal mortality did not differ significantly among the tested accessions (*F* = 0.9; df = 7,26; *P* = 0.513) (Table 3).

The female F1 parasitoids obtained from RVI00053 had significantly shorter (*F* = 5.6; df = 7, 74; *P* < 0.001) forewing length compared to those of females obtained from VI033479, VI044437-A, VI047555-B, VI048076, and VI056563 (Table 4). The forewing length of F1 female parasitoids obtained from the susceptible check was not significantly different from those obtained from the resistant amaranth accessions. The forewings of F1 parasitoid females from accession VI033479 (*t* = 3.6; df = 20; *P* = 0.002) were significantly longer compared to forewings of their male counterparts.

The forewing length of F1 male parasitoids obtained from the different accessions did not show significant difference (*F* = 1.2; df = 7, 56; *P* = 0.314). The hind tibial length of the F1 female parasitoids also showed significant difference (*F* = 4.4; df = 7, 82; *P* < 0.001) with accession RVI00053 producing shorter hind tibia compared to VI033479, VI044437-A, and VI047555-B. F1 female hind tibia from accessions VI033479, VI044437-A, VI047555-B, VI048076, VI049698, and VI056563 were significantly longer than hind tibia of their F1 male counterparts (Table 5). The hind tibial length of males differed significantly (*F* = 2.6; df =7, 61; *P* = 0.023) across the tested accessions with VI056563 producing males with the shortest hind tibia (Table 5).

The average adult longevity of F1 parasitoids obtained from all the amaranth accessions was 13.3 ± 0.6 d. Significant differences (*F* = 9.2; df = 7, 218; *P* < 0.001) were recorded in adult longevity of the F1 parasitoids obtained from the different accessions with RVI00053 producing adults with more prolonged adult longevity compared to VI044437-A, VI048076, VI049698, VI056563, VI047555-B, and the susceptible check VI033482 (Table 6). The accessions VI048076 and VI033479 also produced parasitoids with significantly longer adult longevity compared to the susceptible check. There were significant differences (*F* = 7.2; df = 7, 92; *P* < 0.001) in the longevity of female parasitoids obtained from the different amaranth accessions with RVI00053 producing females with prolonged longevity compared to VI044437-A, VI048076, VI049698, VI056563, VI047555-B, and the susceptible check VI033482. The average female longevity of F1 parasitoids obtained from all the amaranth accessions was 16.0 ± 0.9 d. The male longevity also differed significantly (*F* = 3.3; df = 6,117; *P* = 0.005) across the amaranth accessions with RVI00053 producing males with prolonged longevity than VI044437-A, VI047555-B, and the susceptible check VI033482. The average male longevity of F1 parasitoids obtained from all the amaranth accessions was 11.1 ± 0.6 d. The overall female longevity of F1 parasitoids obtained from all the accessions was significantly longer (*t* = 4.7; df = 224; *P* < 0.001) than the male longevity. Females produced from accessions VI044437-A (*t* = 2.2; df = 36; *P* = 0.034), VI049698 (*t* = 2.2; df = 21; *P* = 0.038), RVI00053 (*t* = 2.5; df = 36; *P* = 0.019), and VI033479 (*t* = 3.1;

Table 4. Forewing length (mean ± SE) of F1 progeny of *Apanteles hemara* obtained from hosts reared on selected moderately resistant amaranth accessions

Amaranth accession code	Female (mm)	Male (mm)	t	df	P-value
VI033482[a]	2.62 ± 0.16abcA	2.71 ± 0.08aA	0.6	3	0.587
RVI00053	2.43 ± 0.07aA	2.58 ± 0.06aA	1.5	16	0.153
VI033479	2.77 ± 0.04cA	2.56 ± 0.03aB	3.6	20	0.002
VI044437-A	2.70 ± 0.04bcA	2.57 ± 0.06aA	1.9	23	0.065
VI047555-B	2.64 ± 0.05bcA	2.54 ± 0.02aA	1.8	19	0.090
VI048076	2.65 ± 0.04bcA	2.61 ± 0.03aA	0.8	24	0.422
VI049698	2.51 ± 0.04abA	2.49 ± 0.03aA	0.4	16	0.733
VI056563	2.72 ± 0.05bcA	2.49 ± 0.10aA	2.3	9	0.045
P-value	<0.001	0.314			
F	5.579	1.208			
df	7,74	7,56			

Means followed by the same lower-case letter(s) within a column and same uppercase letter(s) within a row are not significantly different at $P < 0.05$ (Tukey's test, t-test).

[a]Susceptible accession.

Table 5. Hind tibia length (mean ± SE) of F1 progeny of *Apanteles hemara* obtained from hosts reared on selected moderately resistant amaranth accessions

Amaranth accession code	Female (mm)	Male (mm)	t	df	P-value
VI033482[a]	0.75 ± 0.01abA	0.72 ± 0.04abA	0.6	4	0.554
RVI00053	0.72 ± 0.01aA	0.73 ± 0.03aA	0.4	16	0.705
VI033479	0.80 ± 0.02bA	0.72 ± 0.02abB	3.0	19	0.008
VI044437-A	0.83 ± 0.01bA	0.72 ± 0.02aB	4.9	25	<0.001
VI047555-B	0.79 ± 0.01bA	0.67 ± 0.02bcB	5.5	18	<0.001
VI048076	0.77 ± 0.02abA	0.73 ± 0.01aB	2.2	28	0.041
VI049698	0.78 ± 0.01abA	0.67 ± 0.02abcB	5.1	23	<0.001
VI056563	0.76 ± 0.01abA	0.63 ± 0.03cB	4.9	10	0.001
P-value	<0.001	0.023			
F	4.388	2.554			
df	7,82	7,61			

Means followed by the same lower-case letter(s) within a column and same uppercase letter(s) within a row are not significantly different at $P < 0.05$ (Tukey's test, t-test).

[a]Susceptible accession.

df = 28; $P = 0.004$) had significantly longer adult longevity compared to their male counterparts.

Discussion

Parasitism rates by *A. hemara* varied among the amaranth accessions on which *S. recurvalis* was tested. Differences in parasitism rates have been reported in various Braconidae. For instance, *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) caused significantly higher parasitism on larvae of *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) that were fed on *Sorghum bicolor* L. (40.3%) than those fed on *Sorghum arundinaceum* (Desv.) Stapf (13.6%) (Sétamou et al. 2005). Idris and Grafius (1996) also showed that *Diadegma insulare* Cresson (Hymenoptera: Ichneumonidae) achieved significantly higher parasitism rate of 91.5% on *Plutella xylostella* L. (Lepidoptera: Plutellidae) fed on *Brassica kaber* D. C. Wheeler compared to *B. oleracea* var. *capitata* L., where the level of parasitism was 76.5%. Benrey et al. (1997) reported a positive correlation between a host plant's attractiveness through release of certain volatile cues and parasitism of *Cotesia glomerata* L. (Hymenoptera: Braconidae). We hypothesize that this variance in parasitism among amaranth accessions could be due to the differences in attractiveness of the plants through the release of volatile blends or due to

structural and morphological features of the plants such as the red leaf coloration of accession VI056563 on which the least parasitism rates were recorded. Further studies are recommended to identify potential specific volatiles and/or morphological features of accessions that aid/deter parasitism. In addition, the immune response of a host larva feeding on an unsuitable host plant may be reduced and in turn increase parasitism success (Karimzadeh and Wright 2008, Gols and Harvey 2009). This might have been the case in all the moderately resistant accessions in which parasitism rates were high except accession VI056563.

Amaranth accessions on which *S. recurvalis* hosts were fed significantly affected developmental time of *A. hemara*. The fastest development from egg to adult occurred on the accession RVI00053 and the slowest on VI033479 and VI044437-A. Several reports exist where the development time of koinobiontic parasitoids is shown to vary depending on the host plant species/variety/cultivar and consequently reflect host plant quality for the herbivore involved (Sétamou et al. 2005; Gols et al. 2008a,b; Kahuthia-Gathu et al. 2008; Sarfraz et al. 2012). For example, *C. flavipes* parasitizing *C. partellus* took 18.4 and 20.6 d to complete its development on *S. bicolor* and *S. arundinaceum*, respectively (Sétamou et al. 2005). Similarly, *Cotesia vestalis* Haliday (Hymenoptera: Braconidae) (Rincon et al. 2006, Rousse and Gupta 2013, Fiaboe et al. 2017) and *D. semiclausum* parasitizing *P. xylostella* took significantly

Table 6. Longevity (mean ± SE) of F1 progenies of *Apanteles hemara* obtained from hosts reared on selected moderately resistant amaranth accessions

Amaranth accession code	Longevity of both males and females (days)	Female longevity (days)	Male longevity (days)	t	df	P
VI033482[a]	8.3 ± 1.2d	7.4 ± 1.9cA	8.6 ± 1.5bA	0.5	28	0.654
RVI00053	20.3 ± 1.6a	23.6 ± 2.2aA	16.2 ± 2.0aB	2.5	36	0.019
VI033479	15.1 ± 1.9ab	22.6 ± 3.1abA	11.4 ± 2.0abB	3.1	28	0.004
VI044437-A	9.6 ± 0.4cd	10.9 ± 0.8cA	9.0 ± 0.5bB	2.2	36	0.034
VI047555-B	10.0 ± 1.3bcd	12.3 ± 1.6cA	7.8 ± 1.3bA	2.2	6	0.073
VI048076	14.0 ± 1.0bc	15.0 ± 1.5bcA	12.7 ± 1.4abA	1.1	53	0.265
VI049698	11.2 ± 0.7bcd	12.4 ± 0.9cA	9.7 ± 0.8abB	2.2	21	0.038
VI056563	13.8 ± 1.9bcd	16.0 ± 0.0abc	-			
P-value	<0.001	<0.001	0.005			
F	9.2	7.2	3.3			
df	7,218	7,92	6,117			

Means followed by the same lower-case letter(s) within a column and same uppercase letter(s) within a row are not significantly different at *P* < 0.05 (Tukey's test, *t*-test).

[a]Susceptible accession.

longer to complete their development on *B. oleracea* var. *acephala* (14.2 d *C. vestalis*; 15.9 d *D. semiclausum*) than on *Brassica juncea* Czern (12.2 d *C. vestalis*; 14.0 d *D. semiclausum*) (Kahuthia-Gathu et al. 2008). Extended development time in koinobiontic parasitoids is often assumed to be a result of the host-herbivore's suboptimal nutrition (Godfray 1994, Harvey and Strand 2003, Othim et al. 2017), which is directly influenced by the host plant nutritional quality. It has also been reported in several studies that allelochemicals, such as glucosinolates which is common in Brassicaceae, found in the host diet can negatively affect growth and development of their parasitoids (Harvey and Strand 2003; Harvey et al. 2007a,b). Since such allelochemicals have not yet been identified in amaranths, further studies are recommended to identify the allelochemicals present among pest-resistant amaranth accessions and establish their mechanisms of action. According to the 'slow growth-high mortality hypothesis' by Benrey and Denno (1997) and reports by Sarfraz et al (2009) and Harvey and Gols (2011a), prolonged development time of a parasitoid in its host may open an extended window of its vulnerability to a wide range of natural enemies such as hyperparasitoids and other abiotic stresses. It can, therefore, be hypothesized that the prolonged developmental time of *A. hemara* on accessions VI033479 and VI044437-A could be disadvantageous to the parasitoid; however, little is known about existence or lack of hyperparasitoids against *A. hemara* in the vegetable production systems in Africa. Furthers studies are required to document potential hyperparasitoids of *A. hemara* and test this 'slow growth-high mortality hypothesis' for *A. hemara*.

Female parasitoids are the ones responsible for attacking the pests and also responsible for building up populations hence are desired in biological control programs (Chow and Heinz 2005, Ode and Hardy 2008, Othim et al. 2017). Higher proportions of female parasitoids were obtained from *S. recurvalis* larvae reared on accessions RVI00053 and VI048076 compared to the susceptible check VI033482. Furthermore, the ratio of male to female parasitoids obtained from all the resistant accessions was balanced except on VI033482 where the sex ratio was male biased. Female- and male-biased sex ratios have been reported in *A. hemara* on *S. recurvalis* and *Udea ferrugalis* Hübner (Lepidoptera: Crambidae), respectively when reared on a similar host plant (Othim et al. 2017). Eben et al. (2000) reported that the citrus fruit species on which the fruit fly *Anastepha ludens* Loew (Diptera: Tephritidae) was fed affected the sex ratio and proportion of female progeny of the parasitoid *Diachasmimorpha longicaudata* Ashmead (Hymenoptera:

Braconidae) with *Citrus paradisi* Macfaden producing higher female proportions than *Citrus aurantium* L. However, Ode et al. (2004), assessing *Heracleum sphondylium* L. and *H. mantegazzianum* Sommier and Levier, and Sétamou et al. (2005), assessing *S. bicolor* and *S. arundinaceum*, found that the different host plant varieties did not affect the sex ratios of *Copidosoma sosares* (Walker) (Hymenoptera: Encyrtidae) and *C. flavipes*, respectively. Parasitoids have a flexibility in their sex allocation which is normally reflected in sex-ratio shifts in response to various environmental conditions including herbivore host size and quality among others (Godfray 1994, King 2002, Ode and Heinz 2002, Ode et al. 2004, Colinet et al. 2005, Shuker et al. 2005, Lebreton et al. 2009, Bügler et al. 2014). Many studies have reported that the quality of a parasitoid's herbivore host is directly influenced by the host plant on which it feeds (Sétamou et al. 2005; Gols et al. 2008a,b; Harvey and Gols 2011b; Sarfraz et al. 2012). The nutritional characteristics of a herbivore's food plant can also affect the sex ratio of parasitoids, either by influencing decisions concerning sex allocation or by differentially affecting the survival of the sexes (Fox et al. 1990, 1996; Turlings and Benrey 1998). Our results suggest that the moderately resistant amaranth accessions improved the allocation and/or survival of the female sex compared to the susceptible accession.

In addition to parasitism, the parasitoid *A. hemara* caused significant nonreproductive larval mortalities of its host *S. recurvalis* fed on the different amaranth accessions. Nonreproductive mortalities are usually caused by host-feeding or stinging (ovipositor probing followed by host rejection) behavior of a parasitoid (Bellows and Fisher 1999, Foba et al. 2015, Othim et al. 2017). Othim et al. (2017) reported significant nonreproductive larval mortalities caused by *A. hemara* on the amaranth leaf-webbers *S. recurvalis* and *Udea ferrugalis*. Dannon et al. (2012) also reported host feeding by the koinobiontic endoparasitoid *Apanteles taragamae* Viereck (Hymenoptera: Braconidae) on *Maruca vitrata* F. (Lepidoptera: Crambidae). Host feeding has been shown to be of reproductive importance to synovigenic parasitoids as it aids egg maturation but does not have reproductive importance in proovigenic parasitoids (Bellows and Fisher 1999, Byeon et al. 2009, Dannon et al. 2012). Being a koinobiontic parasitoid, *A. hemara* is likely to cause nonreproductive host killing through host stinging than host feeding (Godfray 1994, Bellows and Fisher 1999).

The size of an emerging parasitoid is an important correlate of fitness because it often affects an individual's reproductive success through variations in fecundity, longevity, dispersal, searching

efficiency and host handling strategies (Visser 1994, Kazmer and Luck 1995, Turlings and Benrey 1998, Eben et al. 2000). Amaranth accessions had a significant effect on the sizes (forewing and hind tibia lengths) of *A. hemara* F1 progenies obtained from *S. recurvalis* larvae reared on them. Previous studies have shown that parasitoids emerging from hosts reared on different host plants differed significantly in their body sizes and longevities. When *P. xylostella* was fed on *B. oleracea* var. *acephala* and *B. oleracea* var. *capitata*, it produced *C. vestalis* parasitoids that had significantly longer hind tibia and forewings compared to those from *P. xylostella* that was fed on *B. juncea* (Kahuthia-Gathu et al. 2008). Similarly, the parasitoid *D. longicaudata* that developed from *Anastrepha ludens* Loew (Diptera: Tephritidae) fed on *C. aurantium* had significantly longer hind tibia than those from hosts reared on *C. paradisi* (Eben et al. 2000). In the present study, the smaller size of *A. hemara* obtained from accession RVI00053 may result in lower fecundity thus a lower rate of population increase. In addition, reduced wing area can adversely affect the dispersal and foraging efficiency of these parasitoids (Sarfraz et al. 2009).

Adult longevity of both male and female F1 progenies of *A. hemara* varied among the tested amaranth accessions. Accessions RVI00053, VI033479, and VI048076 had significantly extended adult longevity compared to the susceptible accession. In addition to size, a parasitoid's longevity is an important fitness correlate that affects reproductive success. A variation in adult longevity was observed on the parasitoid *Patrocloides montanus* Cresson (Hymenoptera: Ichneumonidae) that developed from *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae) with those fed on *B. oleracea var. capitata* living longer than those fed on *Brassica nigra* L. Koch (Fox et al. 1996). Extended female longevity not only enables the parasitoids to regenerate more fertilized eggs but also seek more hosts to parasitize. Thus, higher parasitism success can be obtained with females having prolonged longevity than those with short lifespan.

In conclusion, the performance of *A. hemara* was not adversely affected by most of the moderately resistant amaranth accessions compared to the susceptible accession. Except for VI056563 which had significantly lower parasitism rates and smaller male parasitoid's size than on susceptible accession, all other moderately resistant accessions tested did not affect parasitism rates of *A. hemara*. The moderately resistant accession RVI00053 produced F1 parasitoids that possess desirable fitness parameters including shortened developmental time, higher female proportions and prolonged male and female longevity but had smaller sized parasitoids. These moderately resistant accessions, apart from VI056563, can thus be used in combination with the endoparasitoid *A. hemara* to manage the leaf-webber *S. recurvalis* in amaranth in the context of IPM.

Acknowledgments

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