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Screening for resistance against major lepidopteran and stem weevil pests of amaranth in Tanzania

S. T. O. Othim · R. Srinivasan · R. Kahuthia-Gathu · T. Dubois ·
F. F. Dinssa · S. Ekesi · K. K. M. Fiaboe

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Abstract Insect pests pose major challenges to optimum productivity of amaranth in Africa and Asia. The use of insecticides is the main control strategy, but is expensive and may pose health and environmental concerns, especially if proper care is not taken. Host plant resistance offers a cheap and sustainable pest management alternative. Open field experiments were conducted during two cropping seasons in 2016 and 2017 to screen 35 amaranth accessions and lines for resistance to leaf-webbers and stem weevils. The diversity (H) of lepidopteran defoliators and their parasitoids on each accession ranged from 0.00 to 1.57 and 0.00 to 1.65, respectively during the long rainy season and from 0.00 to 1.58 and 0.00 to 1.01 in the short rainy season. Accessions VI036227, RVI00027, VI054569, VI033487, VI044432, VI048076, VI049639, VI049530 and VI049698 had high levels of pest resistance with significantly lower infestations ($\leq 11.11 \pm 2.14\%$) and damage ($\leq 68.06 \pm 3.90\%$) by leaf-webbers and leaf-worms. Stem weevil infestations ranged from $68.70 \pm 2.0\%$ to $90.42 \pm 1.0\%$ during the long and short rainy seasons, respectively. Accessions VI047517-B, VI036227 and VI056563 had the least stem weevil infestations ($< 62.5\%$) but differences among accessions for damage incidences were non-significant. Parasitism was observed in all the accessions except seven of them. Amaranth accessions exhibiting pest resistance or at least non-preference traits are important for success of breeding programs. The importance of deploying such accessions to breed for improvement of susceptible lines (by introgression) or their release to farmers, if they have desirable horticultural traits that are required by vegetable producers and consumers, for effective management of amaranth pests is also discussed.

Keywords Host plant resistance · Leaf-webbers · Non-preference · Parasitoids · Incidence · Abundance

S. T. O. Othim · R. Kahuthia-Gathu
School of Agriculture and Enterprise Development, Kenyatta University, P.O. Box 43844-00100, Nairobi, Kenya

S. T. O. Othim · S. Ekesi · K. K. M. Fiaboe (✉)
Plant Health Unit, International Centre of Insect Physiology and Ecology (icipe),
P. O. Box 30772-00100, Nairobi, Kenya
e-mail: K.Fiaboe@cgiar.org

R. Srinivasan
World Vegetable Center, P.O. Box 42, Shanhua, Tainan, Taiwan

T. Dubois · F. F. Dinssa
World Vegetable Center - Eastern and Southern Africa, P.O. Box 10, Duluti, Arusha, Tanzania

K. K. M. Fiaboe
International Institute of Tropical Agriculture, BP. 2008 (Messa), Yaoundé, Cameroon

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Introduction

Amaranth have a versatile adaptation to extreme environmental conditions, exceptionally high nutritional quality and provide income for subsistence farmers as well as serving as vegetable for a vast majority of low-income households in Africa (Amicarelli and Camaggio 2012; Tadele and Assefa 2012; Moskova 2013). The major bottlenecks to the sustainable productivity of *Amaranthus* in Africa and across the world are abiotic and biotic factors such as drought and arthropod pests and diseases (NRC 2006; Aderolu et al. 2013; Kagali et al. 2013). More than 50 insect pest species are known to feed on amaranth, of which leaf-webbers (Hawaiian beet webworm—*Spoladea recurvalis* F., and *Psara basalis* Walker, *Herpetogramma bipunctalis* F. (Lepidoptera: Crambidae), leaf worms *Spodoptera exigua* Hübner and *Spodoptera littoralis* F. (Lepidoptera: Noctuidae) and amaranth stem weevils *Hypolixus truncatulus* F. (Coleoptera: Curculionidae) are major pests worldwide (Clarke-Harris et al. 2004; Sharma and Ramamurthy 2009; James et al. 2010; Aderolu et al. 2013). These pests feed voraciously on amaranth leaves and within stems causing complete yield losses, during outbreaks, to the farmers (James et al. 2010). Of major concern to amaranth farmers is the amaranth leaf-webber *S. recurvalis* and the amaranth stem weevils *Hypolixus* spp. which have been reported to cause havoc in amaranth farms in several parts of the world (Clarke-Harris et al. 2004; Sharma and Ramamurthy 2009; James et al. 2010; Aderolu et al. 2013).

For several decades, pest management in most vegetable production systems around the world has been through the use of synthetic pesticides (Chahal et al. 1997; Arivudainambi et al. 2010). This was largely occasioned by the stringent cosmetic and aesthetic requirements for most vegetables (Eigenbrode and Trumble 1994). However, there have been recent changes on this strategy including increased market and regulatory pressure to reduce pesticide use, problems with insect resistance to pesticides, resurgence of secondary pests, decimation of natural enemies and changes in consumer preferences (Eigenbrode and Trumble 1994; Chahal et al. 1997; Arivudainambi et al. 2010; Srinivasan 2012). In amaranth production, Clarke-Harris et al. (2004) observed failures of insecticides in the field in managing lepidopteran pests of amaranth in Jamaica due to pesticide resistance. These changes necessitate the need to explore alternative pest management strategies in amaranth production systems that would be effective and ecologically sound, economically feasible and socially acceptable (Sharma and Ortiz 2002).

Alternative pest management strategies have been demonstrated to be effective in the management of certain pests known to attack amaranth in laboratory and field conditions in several parts of the world. These include botanical pesticides (Mohan et al. 2007; Aderolu et al. 2013), microbial control agents (Delplanque and Gruner 1975; Kuruvilla and Jacob 1980; James et al. 2007), and plant volatiles (Landolt et al. 2011). Natural enemies, especially parasitoids of lepidoptera larvae, though still underutilized in the management of amaranth pests, are reported to cause considerable (up to 60%) field parasitism on webworms (Narayanan et al. 1957; James et al. 2010; Kedar and Kumaranag 2013; Grovida 2015).

Host plant resistance (HPR) to insect pests is, however, an extremely underutilized pest management strategy in amaranth production systems (Eigenbrode and Trumble 1994), despite its affordability (economical), ease of integration with other pest management tools, ecological soundness and sustainability for the resource poor subsistence farmers (Sharma and Ortiz 2002). Additionally, HPR requires no skills in its application and no additional cash investment, in pest management, by the resource-poor farmers (Sharma and Ortiz 2002). Pest resistance in crops has been widely studied in recent decades and resistant traits in some of the vegetables including tomatoes *Solanum lycopersicum* L. (Solanales: Solanaceae), carrots *Daucus carota* L. (Apiales: Apiaceae), lettuce *Lactuca sativa* L. (Asterales: Asteraceae), okra *Abelmoschus* spp. (Malvales: Malvaceae) and onion *Allium cepa* L. (Asparagales: Amaryllidaceae) are well documented (Eigenbrode and Trumble 1994; Srinivasan and Uthamasamy 2005; Abang et al. 2014, 2016; Rakha et al. 2017a, b, c; Njau et al. 2017). However, HPR in most African Indigenous Vegetables (AIVs) has not been given much attention. That notwithstanding, some reports and observations have been made regarding possible resistance by certain accessions/lines of amaranth against the leaf-webbers. For example, National Research Council (NRC) (1984) reported that *Amaranthus hypochondriacus* exhibited greater resistance to pest damage when compared to *Amaranthus cruentus*. However, this potent tool remains largely untapped in AIV production systems.

In order to implement HPR as a strategy for integrated pest management (IPM) in amaranths, various accessions/lines/species of this crop need to be screened to identify those with pest resistant traits followed by understanding the underlying mechanisms of resistance. Subsequently, screening for resistance against the amaranth leaf-webber *S. recurvalis* was conducted on 777 accessions at WorldVeg headquarters in Taiwan. Out of these, 31 accessions that exhibited the least damage were advanced for further screening against African populations of leaf-webbers and stem weevils under open field conditions at Arusha, Tanzania. Four improved lines from WorldVeg Eastern and Southern Africa (ESA) were also included for the resistance screening. In addition, this study sought to understand the parasitoid diversity relative to the pests attacking amaranth accessions/lines and how the combined effect of HPR and parasitism fits within IPM.

Materials and methods

Study location

The World Vegetable Center (WorldVeg) farm located at its Eastern and Southern Africa (ESA) hub at Arusha, Tanzania, 36.86°E, 3.374°S and 1309 m a.s.l. was used for the open field screening of the amaranth accessions and lines for resistance against leaf-webbers and amaranth stem weevils. This area experiences average temperatures of 19.5 °C and an average rainfall of 1098 mm per annum. The area receives bimodal rainfall with the long rains between late March and early May and the short rains between September and December. The site has a clay loamy soil with pH ranging between 6.0 and 6.7.

The first season of field screening was carried out during the long rainy season between March and June 2016 characterized by 22.50 ± 0.28 °C temperature, 544 mm total rainfall and 79.70 ± 0.79% average relative humidity. The second season was during the short rainy season (which started late) between December 2016 and March 2017 characterized by 23.45 ± 0.19 °C temperature, 233 mm total rainfall and 78.34 ± 0.99% average relative humidity.

Plant materials

Eighteen and 36 amaranth accessions and lines (hereafter both referred to as accessions) in the long and short rainy seasons, respectively were sown in trays in the screen house and transplanted into plots as described below, at 3 weeks old. During both seasons, a susceptible check for lepidopteran defoliators, selected from a preliminary screening in Taiwan, was included among the accessions. This was assumed to be the susceptible check for the stem weevils, since resistance screening against amaranth stem weevils has never been conducted. The plots were manually constructed, ploughed using a hand hoe, after which the 3-week-old seedlings were transplanted with an inter-row spacing of 50 cm and intra-row of 20 cm to obtain 12 plants per row. Fertilizers were applied during the second week after transplanting at rates of NPK (200 kg/ha) and Urea (120 kgN/ha). Weeding was done manually once a month and watering done regularly for the duration of each growing season. No insecticides or fungicides were applied to the crops.

Experimental design

The trial was laid out in a randomized complete block design (RCBD) with three replications for each accession. During the long rainy season, the field was laid out into three blocks consisting of 35.5×3.5 m^2, each with a spacing of 2 m between the blocks. Each block contained 18 plots, each measuring 3.0×1.2 m^2 (2 rows per plot and 12 plants per row) with a spacing of 0.5 m between the plots. Eighteen amaranth accessions were randomly assigned to each plot. During the short rainy season, the field was laid out into three blocks of 64.2×3.5 m^2 each with a spacing of 2 m between the blocks. Each block was then subdivided into 36 plots each measuring 3.0×1.2 m^2 with a spacing of 0.5 m between plots where 36 amaranth accessions (Table 1) were assigned.

Non-destructive sampling was done weekly, starting from the second week after transplanting. Eight plants were sampled randomly within each plot visually scored for damage by leaf-webbers using a modified (0–5 instead of 0-7) assessment scale described by Gilbert and Gregoire (2003) where 0 = 0%; 1 = 1–20%; 2 = 21–40%; 3 = 41–60%; 4 = 61–80% and 5 = 81–100% of damage.

Table 1 Amaranth accessions, and lines developed by single plant selection from germplasm collections studied in two seasons and some of their morphological characteristics, Arusha, Tanzania, 2016 and 2017

Gene bank code	Species	Type	Leaf colour	Leaf shape	Country of origin	Number of branches per plant (mean)	Plant height (mean) cm	Leaf width (mean) cm	Leaf length (mean) cm	Petiole length (mean) cm	Days to flowering (weeks)b
VI033482[a]	*A. tricolor*	Accession	Green	Reniform	Malaysia	9.0	100.9	10.6	19.3	5.0	6
RVI00002	*A. cruentus*	Line	Green	Ovate	Zambia	12.5	122.6	6.6	16.5	10.2	4
RVI00005	*A. dubious*	Line	Reddish	Ovate	Tanzania	12.2	140.3	6.0	12.5	7.6	5
RVI00027	*Amaranthus* sp.	Line	Green	Ovate	Malawi	7.3	96.3	6.2	11.1	7.8	2
RVI00053	*A. dubious*	Line	Green	Ovate	Uganda	11.0	167.0	8.7	15.6	8.0	7
VI033477	*Amaranthus* sp.	Accession	Reddish	Ovate	Malaysia	9.2	99.7	7.9	12.3	5.2	6
VI033479	*Amaranthus* sp.	Accession	Green	Ovate	Malaysia	11.3	100.8	4.9	7.6	4.2	2
VI033487	*A. cruentus*	Accession	Green	Reniform	Malaysia	13.5	128.7	5.6	7.7	6.6	4
VI036225	*A. graecizans*	Accession	Green	Ovate	Hungary	15.4	77.2	1.6	3.2	2.3	3
VI036227	*A. blitoides*	Accession	Green	Oblanceolate	Hungary	15.8	67.4	1.2	3.2	1.6	4
VI044367	*A. cruentus*	Accession	Green	Lanceolate	Tanzania	9.1	123.5	5.8	13.7	10.2	5
VI044369	*A. hypochondriacus*	Accession	Green	Lanceolate	Ghana	13.7	129.0	6.1	17.0	9.2	4
VI044388	*A. graecizans*	Accession	Green	Oblanceolate	India	14.6	89.8	2.3	4.3	2.5	3
VI044432	*A. viridis*	Accession	Green	Cordate	Indonesia	11.0	102.9	4.5	6.9	4.0	2
VI044437-A	*A. cruentus*	Accession	Green	Lanceolate	Malaysia	11.5	89.5	5.5	13.0	7.2	2
VI044473	*A. palmeri*	Accession	Green	Obovate	Senegal	9.0	80.1	2.2	4.4	2.4	3
VI046233-A	*Amaranthus* sp.	Accession	Reddish	Lanceolate	Vietnam	8.0	142.1	6.8	17.0	10.6	5
VI047517-B	*A. tricolor*	Accession	Green	Ovate	Bangladesh	12.9	119.8	8.1	15.9	7.7	6
VI047555-B	*A. tricolor*	Accession	Green	Lanceolate	Vietnam	10.9	135.6	4.5	13.4	4.8	5
VI048076	*A. tricolor*	Accession	Green	Cordate	Bangladesh	13.1	130.1	8.0	13.5	7.1	6
VI048864-A	*A. viridis*	Accession	Green	Cordate	Thailand	10.2	95.1	4.1	5.8	3.6	2
VI048919	*Amaranthus* sp.	Accession	Green	Ovate	Thailand	11.6	126.1	3.7	7.0	4.3	3
VI049242	*Amaranthus* sp.	Accession	Green	Ovate	Thailand	11.6	87.8	4.4	5.8	3.7	2
VI049502	*Amaranthus* sp.	Accession	Green	Cordate	Thailand	10.0	103.1	4.7	6.8	4.1	2
VI049504	*Amaranthus* sp.	Accession	Green	Lanceolate	Thailand	12.1	134.2	3.0	6.6	3.2	3

Table 1 continued

Gene bank code	Species	Type	Leaf colour	Leaf shape	Country of origin	Number of branches per plant (mean)	Plant height (mean) cm	Leaf width (mean) cm	Leaf length (mean) cm	Petiole length (mean) cm	Days to flowering (weeks)b
VI049530	*Amaranthus* sp.	Accession	Green	Ovate	Thailand	10.4	89.2	4.3	6.4	3.9	2
VI049639	*A. viridis*	Accession	Green	Ovate	Thailand	11.3	91.7	4.2	6.1	3.5	2
VI049698	*A. viridis*	Accession	Green	Ovate	Thailand	12.4	100.5	3.9	5.5	3.4	2
VI050609-A	*A. tricolor*	Accession	Variegated	Cordate	Vietnam	9.8	129.1	9.2	11.7	6.8	5
VI050609-B	*A. tricolor*	Accession	Variegated	Ovate	Vietnam	8.5	140.9	9.6	15.0	6.1	5
VI054569	*A. gracilis*	Accession	Green	Ovate	Philippines	11.0	95.1	4.5	7.2	3.9	2
VI054798	*Amaranthus* sp.	Accession	Green	Ovate	Lao PDR	12.4	89.3	4.1	6.2	3.3	2
VI055127	*A. viridis*	Accession	Green	Ovate	Malaysia	11.4	108.1	5.6	10.3	6.6	3
VI055128	*A. viridis*	Accession	Green	Cordate	Malaysia	10.7	123.4	5.0	7.0	3.9	2
VI055135	*A. viridis*	Accession	Green	Cordate	Malaysia	10.8	92.0	5.0	7.2	4.1	2
VI056563	*Amaranthus* sp.	Accession	Reddish	Ovate	Bangladesh	9.7	136.9	9.0	17.1	8.3	6
Mean						11.2	110.7	5.5	10.0	5.5	
LSD (5%)						4.38	26.74	1.4	3.69	2.33	

[a]Susceptible check

[b]Days to flowering recorded from the date of transplanting

Developmental stages of lepidopteran pests of amaranth including eggs, larvae and pupae as well as pupae of associated parasitoids encountered were also collected and incubated in the laboratory in ventilated plastic containers. They were supplied with fresh amaranth leaves until adult pest/parasitoid emergence.

Destructive sampling was done once at the end of the season when the crop had reached maturity for stem weevil damage assessment. It involved cutting the stems of 8 randomly selected plants at the base, approximately 1 cm below the ground level, and transferred to the laboratory for dissection to check for the developmental stages of the stem weevils. Both the main stem and the branches also were dissected to assess levels of stem weevil infestations and their associated damage. The number of weevils and their associated parasitoids within each stem and number of mined tunnels created by the weevils was recorded for each plant. The number of tunnels was recorded as a measure of severity of damage. The adults of Lepidoptera and stem weevils were identified using the available taxonomic keys described by Dugdale (1988) and Dombroskie (2011), while the parasitoids were identified at the Natural History Museum, UK. The voucher specimens are held at the WorldVeg ESA's entomology laboratory at Arusha, Tanzania.

Data analysis

One-way analysis of variance (ANOVA) was used to compare the morphological characteristics of amaranth accessions including number of branches per plant, plant height, leaf length and width and petiole length in GENSTAT version 19.1. Abundance of lepidopteran defoliators, amaranth stem weevils and number of stem tunnels was analysed using the Generalised Linear Model (GLM) with the quasipoisson family and the log link function. The data on pest incidence and damage caused by lepidopteran defoliators and stem weevils was analysed using GLM with the binomial family and the logit link. Pest (infestation) and damage incidence was calculated as the proportion or percentage of plants infested with the pest according to Ibeawuchi et al. (2007).

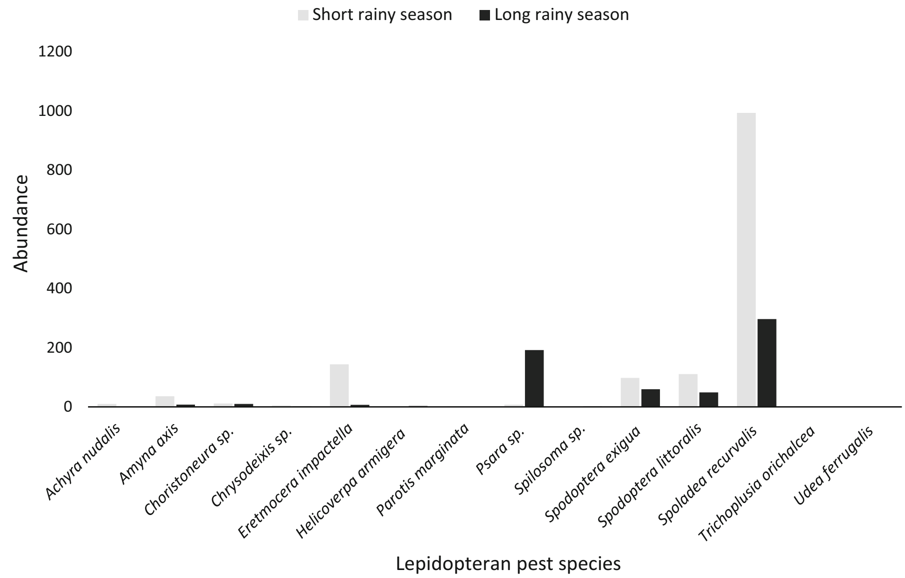
Severity of damage by lepidopteran defoliators was analysed using ordered logistic regression in GLM. Pearson's product-moment correlation test was used to determine the correlation between stem weevil abundance and tunnelling damage during the short rainy season. Percent parasitism on each accession was calculated using the number of parasitoids recovered divided by the total number of lepidopteran pests sampled. These analyses were conducted using R version 3.4.0 statistical software (R Development Core Team 2017). Species diversity of lepidopteran defoliators and their associated parasitoids on each accession during the two seasons was determined using Shannon diversity index and Evenness (Magurran 2004).

Results

Composition and abundance of lepidopteran defoliators and stem weevils attacking amaranth and their associated parasitoids

During the long rainy season of 2016, a total of 630 lepidopteran larvae belonging to five families (Crambidae, Erebidae, Noctuidae, Scythrididae and Tortricidae), seven sub-families (Arctiinae, Heliothinae, Noctuinae, Plusiinae, Spilomelinae, Scythridinae and Tortricinae) and nine species were recovered from 18 different accessions of amaranth (Fig. 1). Of these, 80.45% were leaf-webbers, while 19.55% were leaf-worms. Among the leaf-webbers, 58.70% were *S. recurvalis*, 37.94% *Psara basalis* Walker, 1.98% *Choristoneura* sp. (Lepidoptera: Tortricidae) and 1.38% *Eretmocera impactella* Walker (Lepidoptera: Scythrididae). The leaf-worms were composed of *S. exigua* (48.39%), *S. littoralis* (39.52%), *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) (2.42%), *Spilosoma* sp. (Lepidoptera: Erebidae) (1.61%), *Chrysodeixis* sp. (Lepidoptera: Noctuidae) (1.61%) and *Amyna axis* Guenee (Lepidoptera: Noctuidae) (6.45%) (Table 2). In the short rainy season of 2017, a total of 1424 lepidopteran larvae belonging to four families (Crambidae, Noctuidae, Scythrididae and Tortricidae), seven sub-families (Heliothinae, Noctuinae, Plusiinae, Pyraustinae, Spilomelinae, Scythridinae and Tortricinae) and 14 species were recovered from 36 different accessions of amaranth (Fig. 1). Leaf-webbers comprised 82.23% of the total number of lepidopterans while leaf-worms were 17.77%. The leaf-webbers were comprised of *S. recurvalis* (84.80%), *E. impactella* (12.30%), *Choristoneura* sp. (1.02%), *Achyra nudalis* Hübner (Lepidoptera: Crambidae) (0.85%), *P. basalis* (0.68%), *Udea ferrugalis*

Fig. 1 Species abundance of lepidopteran defoliators attacking amaranths during the long (2016) and short (2017) rainy seasons, Arusha, Tanzania



Hübner (Lepidoptera: Crambidae) (0.17%) and *Parotis marginata* Hampson (Lepidoptera: Crambidae) (0.17%). The leaf-worms included *S. littoralis* (43.87%), *S. exigua* (38.74%), *Chrysodeixis* sp. (Lepidoptera: Noctuidae) (1.98%), *Trichoplusia orichalcea* F. (Lepidoptera: Noctuidae) (0.79%), *H. armigera* (0.40%) and *A. axis* (14.23%) (Table 2).

The predominant pests during the long rainy season were *S. recurvalis* (47.14%) and *P. basalis* (30.48%). Within the first 4 weeks of the season, the predominant pest was *P. basalis*. The typical symptom of this pest is folded leaves in characteristic leaf shelters at the apical region thereby hindering apical development of the plant. *Spoladea recurvalis* populations began to build up progressively from the second week, becoming the dominant pest from the fifth week, until the end of the season. Unlike *P. basalis* which exhibited a constant reduction in its proportion compared to *S. recurvalis, S. recurvalis* was on a constant rise throughout the season (Fig. 2). During the short rainy season, *P. basalis* was replaced by *E. impactella* (10.11%) as the second most dominant leaf-webber after *S. recurvalis* (69.73%). *Spoladea recurvalis* dominated from the sixth week until the end of the season while *E. impactella* declined from the sixth week (Fig. 2). In both seasons, *S. recurvalis* was the most frequent pest with an overall abundance of 63.24%, followed by *P. basalis* at 9.80%.

A total of 518 hymenopteran parasitoid adults comprising 14 different species were recovered from the lepidopteran larvae feeding on amaranth during the two seasons. These were from two families (Braconidae and Ichneumonidae) and 10 sub-families (Braconidae: Agathidinae, Braconinae, Cardiochilinae and Microgastrinae; Ichneumonidae: Banchinae, Campopleginae, Cremastinae, Cryptinae, Mesochorinae and Metopiinae) (Table 2). Total parasitism of 26.35 and 24.72% was observed during the long and short rainy seasons, respectively. During the long rainy season, the most prevalent parasitoid was a solitary endoparasitoid *Apanteles* sp. (Hymenoptera: Braconidae) with 48.80% abundance and parasitism rate of 16.56% on *S. recurvalis* and *P. basalis*. During the short rainy season, *Apanteles* sp. remained as the most abundant parasitoid (86.93%) with a total parasitism rate of 30.60% on *S. recurvalis* and *P. basalis*. The second most abundant parasitoid during both seasons was *Atropha tricolor* Szepligeti (Hymenoptera: Ichneumonidae) with parasitism rates of 4.70 and 2.0% in the long and short rainy seasons, respectively. *Spodoptera exigua* and *S. littoralis* were mainly parasitized by *Cotesia icipe* Fernandez-Triana and Fiaboe (Hymenoptera: Braconidae) during both seasons with parasitism rates of 18.33 and 5.10% on *S. exigua* and 2.04 and 1.80% on *S. littoralis* in the long and short rainy seasons, respectively.

The Shannon diversity indices (H) for the lepidopteran defoliators during the long and short rainy seasons were H = 1.372 and H = 1.116, respectively with the long rainy season recording significantly

Table 2 Composition (%) of lepidopteran defoliators and their associated parasitoids during the long (2016) and short (2017) rainy seasons, Arusha, Tanzania

Lepidopteran defoliators					Parasitoids					
Family	Sub-family	Species	Short rainy season	Long rainy season	Family	Sub-family	Species	Host pest	Long rainy season	Short rainy season
Erebidae	Arctiinae	*Spilosoma* sp.	0.00	0.32	Ichneumonidae	Campopleginae	*Diadegma* sp.	*S. recurvalis*	1.20	0.57
Crambidae	Spilomelinae	*Spoladea recurvalis*	69.74	47.14	Ichneumonidae	Cremastinae	*Pristomerus* sp.	*S. recurvalis*	0.60	0.00
Crambidae	Spilomelinae	*Udea ferrugalis*	0.14	0.00	Ichneumonidae	Metopiinae	*Triclistus bicolor*	*S. recurvalis*	5.42	0.00
Crambidae	Spilomelinae	*Psara basalis*	0.56	30.47	Ichneumonidae	Cryptinae	*Phygadeuontini* (tribe)	*S. recurvalis*	0.60	0.00
Crambidae	Pyraustinae	*Achyra nudalis*	0.70	0.00	Ichneumonidae	Mesochorinae	*Mesochorus* sp.	*S. recurvalis*	0.60	0.00
Crambidae	Spilomelinae	*Parotis marginata*	0.14	0.00	Ichneumonidae	Banchinae	*Atropha tricolor*	*S. recurvalis*	13.86	5.68
Scythrididae	Scythridinae	*Eretmocera impactella*	10.11	1.11	Ichneumonidae	Cremastinae	*Temelucha* sp.	*S. recurvalis*	1.81	0.00
Tortricidae	Tortricinae	*Choristoneura* sp.	0.84	1.59	Braconidae	Microgastrinae	*Apanteles* sp.	*S. recurvalis/ P. basalis*	48.80	86.93
Noctuidae	Noctuinae	*Spodoptera exigua*	6.88	9.52	Braconidae	Microgastrinae	*Cotesia icipe*	*S. littoralis/S exigua*	11.45	1.99
Noctuidae	Noctuinae	*Spodoptera littoralis*	7.80	7.78	Braconidae	Microgastrinae	*Cotesia* sp.	*Choristoneura sp.*	1.81	0.85
Noctuidae	Plusiinae	*Chrysodeixis* sp.	0.35	0.32	Braconidae	Agathidinae	*Coccygidium luteum*	*S. littoralis/S. exigua*	2.41	2.56
Noctuidae	Plusiinae	*Trichoplusia orichalcea*	0.14	0.00	Braconidae	Agathidinae	*Braunsia occidentalis*	*S. recurvalis*	6.02	0.00
Noctuidae	Heliothinae	*Helicoverpa armigera*	0.07	0.48	Braconidae	Braconinae	*Bracon* sp.	*S. recurvalis*	3.01	0.57
Noctuidae	Acontiinae	*Amyna axis*	2.53	1.27	Braconidae	Cardiochilinae	*Schoenlandella testacea*	*S. recurvalis*	2.41	0.85

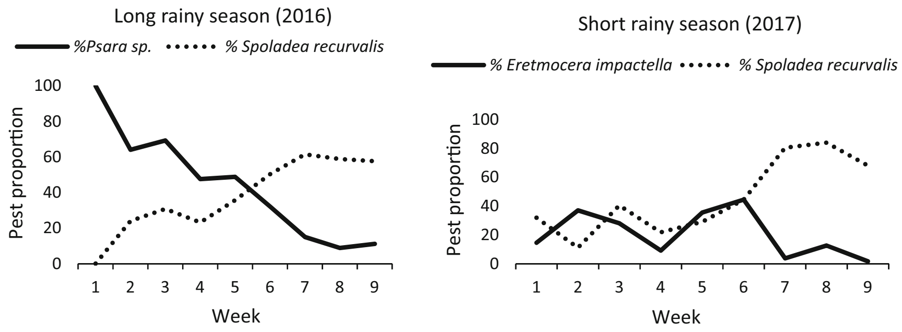


Fig. 2 Weekly proportion (%) of the two most abundant lepidopteran pests during the long (2016) and short (2017) rainy seasons in Arusha, Tanzania

higher diversity of lepidopteran pests than the short rainy season ($t = 5.056$; $P = 0.006$). The H diversity index of lepidopteran defoliators varied from 0.00 to 1.57 and from 0.00 to 1.58 during the long and short rainy seasons, respectively. Except VI036227, all other accessions had higher H diversity index compared to the susceptible check during the long rainy season (Table 3). Only VI033479, VI036227, VI044473, VI049698 and VI056563 had lower H diversity index for the pests compared to the susceptible check during the short rainy season (Table 4). VI044367 and VI036227 had the highest and lowest species richness, respectively, during the long rainy season whereas VI050609-B and four accessions (VI033479, VI036227, VI044473 and VI049698) had the highest and lowest species richness, respectively, during the short rainy season (Tables 3 and 4).

The diversity of the parasitoids differed significantly between the two seasons ($t = 10.45$; $P = 0.039$)

Table 3 Diversity indices of amaranth lepidopteran defoliators and their associated parasitoids and parasitism rates (%) per accession during the long rainy season (2016), Arusha, Tanzania

Accession code	Lepidopteran defoliators			Parasitoids			
	H	Richness (individuals)	Evenness	H	Richness (individuals)	Evenness	Parasitism (%)
VI033482[a]	0.67	7 (96)	0.34	1.12	6 (25)	0.63	26.04
RVI00002	1.12	5 (63)	0.70	0.41	2 (14)	0.59	22.22
RVI00005	1.21	4 (50)	0.88	1.65	6 (16)	0.92	32.00
RVI00027	1.04	3 (11)	0.94	0.50	2 (5)	0.72	45.45
RVI00053	1.33	5 (16)	0.83	1.33	5 (16)	0.83	29.63
VI033487	1.57	6 (19)	0.88	0.69	2 (2)	1.00	10.53
VI036225	1.07	4 (26)	0.77	1.07	4 (8)	0.77	30.77
VI036227	0.00	0 (0)	0.00	0.00	0 (0)	0.00	0.00
VI044367	1.48	8 (60)	0.71	1.17	4 (14)	0.84	23.33
VI044369	1.16	5 (52)	0.72	1.38	5 (14)	0.85	26.92
VI044388	1.07	4 (30)	0.77	1.42	5 (12)	0.88	40.00
VI044432	1.54	6 (20)	0.86	1.04	3 (4)	0.95	20.00
VI044437-A	1.26	7 (45)	0.65	0.90	4 (14)	0.65	31.11
VI044473	1.12	4 (33)	0.80	1.61	6 (10)	0.90	30.30
VI048076	1.56	6 (22)	0.87	0.69	2 (2)	1.00	9.09
VI049639	1.54	6 (22)	0.86	1.10	3 (3)	1.00	13.64
VI049698	0.80	3 (10)	0.73	0.64	2 (3)	0.92	30.00
VI054569	1.25	4 (17)	0.90	1.04	3 (4)	0.95	23.53

[a]Susceptible check

Table 4 Diversity indices of amaranth lepidopteran defoliators and their associated parasitoids and parasitism rates (%) per accession during the short rainy season (2017), Arusha, Tanzania

Accession code	Lepidopteran defoliators			Parasitoids			
	H	Richness (individuals)	Evenness	H	Richness (individuals)	Evenness	Parasitism (%)
VI033482[a]	0.52	7 (542)	0.27	0.35	4 (122)	0.25	22.51
RVI00002	0.79	3 (18)	0.72	0.74	3 (10)	0.67	55.56
RVI00005	0.80	3 (7)	0.72	0.00	1 (3)	Na	42.86
RVI00027	0.72	3 (12)	0.66	0.56	2 (7)	0.81	58.33
RVI00053	1.04	5 (16)	0.64	1.01	3 (6)	0.92	37.50
VI033477	0.72	4 (104)	0.52	0.41	3 (44)	0.37	42.31
VI033479	0.00	1 (3)	Na	0.69	2 (2)	1.00	66.67
VI033487	0.64	4 (28)	0.46	0.00	1 (14)	Na	50.00
VI036225	1.58	5 (9)	0.98	0.00	1 (3)	0.00	33.33
VI036227	0.00	1 (2)	Na	0.00	0 (0)	1.00	0.00
VI044367	0.56	2 (4)	0.81	0.00	1 (2)	0.00	50.00
VI044369	1.07	5 (27)	0.67	0.50	2 (3)	0.32	11.11
VI044388	0.64	2 (3)	0.92	0.00	1 (1)	0.00	33.33
VI044432	1.07	4 (8)	0.77	0.00	1 (2)	0.00	25.00
VI044437-A	0.96	3 (7)	0.87	0.64	2 (3)	0.44	42.86
VI044473	0.00	1 (5)	Na	0.00	1 (1)	0.00	20.00
VI046233-A	0.75	3 (17)	0.69	0.00	1 (8)	0.00	47.06
VI047517-B	0.78	6 (40)	0.43	0.00	1 (8)	0.00	20.00
VI047555-B	0.81	5 (30)	0.50	0.30	2 (11)	0.17	36.67
VI048076	1.27	7 (34)	0.65	0.45	2 (6)	0.28	17.65
VI048864-A	1.17	4 (10)	0.84	0.00	0 (0)	1.00	0.00
VI048919	0.91	4 (53)	0.65	0.00	1 (3)	0.00	5.66
VI049242	0.85	3 (9)	0.77	0.69	2 (2)	0.50	22.22
VI049502	1.08	5 (18)	0.67	0.00	1 (2)	0.00	11.11
VI049504	0.90	3 (14)	0.82	0.00	0 (0)	1.00	0.00
VI049530	0.69	2 (2)	1.00	0.00	1 (1)	0.00	50.00
VI049639	1.21	4 (8)	0.88	0.00	0 (0)	1.00	0.00
VI049698	0.00	1 (2)	Na	0.00	0 (0)	1.00	0.00
VI050609-A	0.78	5 (120)	0.48	0.47	3 (24)	0.23	20.00
VI050609-B	1.58	9 (49)	0.72	0.41	2 (15)	0.24	30.61
VI054569	1.21	5 (20)	0.75	0.64	3 (10)	0.34	50.00
VI054798	0.83	3 (14)	0.76	0.00	0 (0)	1.00	0.00
VI055127	1.13	5 (14)	0.70	0.00	1 (1)	Na	7.14
VI055128	0.69	2 (2)	1.00	0.00	0 (0)	0.00	0.00
VI055135	1.39	4 (4)	1.00	0.00	0 (0)	0.00	0.00
VI056563	0.34	5 (169)	0.21	0.57	4 (38)	0.41	22.49

[a]Susceptible check

with the long rainy season having higher parasitoid diversity (H = 1.775) than the short rainy season (H = 0.596). Parasitoid diversity was highest (H = 1.61) on VI044473 and RVI00005, RVI00053, VI044367, VI044369 and VI044388 also recorded H index above the susceptible check during the long rainy season (Table 3). Parasitism was recorded in all the accessions except VI036227 (0.00%) with the highest on RVI00027 (45.45%) during the season. Parasitoid species richness in the same season was highest on VI033482, RVI00005 and VI044473 and lowest on VI036227. During the short rainy season, parasitoid diversity was highest on RVI00053 (H = 1.01) while 21 accessions had diversity H = 0.00 (Table 4). The susceptible check and VI056563 had the highest parasitoid richness whereas VI036227, VI048864-A, VI49504, VI049639, VI049698, VI054798, VI055128 and VI055135 did not record any parasitoids and consequently no cases of parasitism. Nonetheless, parasitism was recorded in 28 accessions with VI033479 recording the highest (66.67%) compared to the susceptible check (22.51%) (Table 4).

Adult amaranth stem weevils and their grubs (larvae) were found feeding on leaves and within stems, respectively, with a total of 165 and 110 adult weevils recovered during the long and short rainy seasons, respectively. The stem weevil grubs found within the stems amounted to 962 and 3726 during the long and short rainy seasons, respectively. Overall four species of amaranth stem weevils were encountered during the two seasons namely *Cosmobaris* sp. (Curculionidae: Baridinae), *H. truncatulus* (Curculionidae: Lixinae), *Lixus* sp. (Curculionidae: Lixinae) and *Neocleonus* sp. (Curculionidae: Lixinae). The most abundant species was *H. truncatulus.* A parasitism of 0.50% was reported on amaranth stem weevils caused by the parasitoid *Entedon* sp. (Hymenoptera: Eulophidae).

Susceptibility of amaranth accessions to lepidopteran defoliators and stem weevils under field conditions during the long rainy season of 2016

The incidence of lepidopteran defoliators across the accessions varied between 0.00 ± 0.00% and 20.74 ± 2.50% with a mean incidence of 8.68 ± 0.40% and significantly lower than the susceptible check, except in accessions RVI00002, RVI00053 and VI044367 (χ^2 = 172.76; df = 17, 4842; $P < 0.001$) (Table 5). The abundance of lepidopteran defoliators during the long rainy season was significantly lower (F = 10.14; df = 17, 4842; $P < 0.001$) than the susceptible check except for RVI00002 (Table 5). Notably, no leaf-webbers were found on VI036227 during the season and the accession had the least relative risk (RR) of 0.01 compared to the susceptible check. RVI00002, RVI00005, RVI00053, VI044367 and VI044369 had significantly high ($P < 0.001$) abundance of lepidopteran defoliators (RR above 0.5) compared to VI036227, VI049698, RVI00027, VI054569, VI033487, VI044432, VI048076 and VI049639 (RR below 0.25) (Table 5). The mean abundance of lepidopteran defoliators ranged between 0.00 ± 0.00 and 0.36 ± 0.05.

The incidence of damage by lepidopteran defoliators varied from 5.56 ± 1.40% to 54.81 ± 3.03% with an overall mean of 35.82 ± 0.69%. There were significant differences (χ^2 = 457.89; df = 17, 4842; $P < 0.001$) in the incidences of damage among the accessions with VI036227, VI044473, VI054569, VI044388, VI036225, VI044432, VI049698, VI049639, RVI00027, VI048076 and VI044437-A having lower incidences of damage compared to the susceptible check (Table 5). VI033487, RVI00005, VI044369, RVI00053, VI044367 and RVI00002 did not differ significantly ($P < 0.001$) in their incidence of damage compared to the susceptible check (Table 5).

Severity of damage caused by leaf-webbers differed significantly (χ^2 = 544.65; df = 17, 4842; $P < 0.001$) among the accessions with all but five (VI044367, VI044369, RVI00002 and RVI00053) having significantly lower severity compared to the susceptible check. VI036227 had significantly less severe damage compared to all the other accessions with an odds ratio (OR) of 0.04.

The overall average incidence of amaranth stem weevils was 68.7 ± 2.0% during the long rainy season. The incidence of amaranth stem weevils was significantly different across the accessions with VI036227, VI036225, VI044473, VI044388, VI049698, VI049639 and RVI00027 having significantly lower pest incidence (RR 0–0.06) compared to the control (χ^2 = 141.11; df = 17, 522; $P < 0.001$). The incidence of stem weevils ranged from 0.0 ± 0.0% to 96.67 ± 3.33% with 11 accessions having incidence levels above 70% (Table 6). The abundance of stem weevils varied between 0.00 ± 0.00 and 3.60 ± 0.63 with an overall average of 1.80 ± 0.09 throughout the season. VI036227, VI036225, VI049698, VI049639, RVI00027,

Table 5 Comparative leaf-webbers' incidence, abundance, and damage incidence on various amaranth accessions and lines under field conditions during the long rainy season of 2016, Arusha, Tanzania

Gene bank code	Leaf-webber incidence	Relative risk	Leaf-webber abundance	Relative risk	Damage incidence by leaf-webbers	Relative risk
VI033482*	20.74 ± 2.47^{g}		0.36 ± 0.05^{j}		50.00 ± 3.05^{fg}	
RVI00002	16.67 ± 2.27^{fg}	0.77	0.23 ± 0.04^{ij}	0.66	54.81 ± 3.03^{g}	1.21
RVI00005	10.74 ± 1.89^{def}	0.47	0.19 ± 0.04$^{f–i}$	0.53	47.41 ± 3.04^{efg}	0.90
RVI00027	3.33 ± 1.09^{abc}	0.14	0.04 ± 0.02^{abc}	0.12	37.41 ± 2.95^{d}	0.60
RVI00053	13.70 ± 2.10^{fg}	0.61	0.20 ± 0.04^{ghi}	0.57	51.11 ± 3.05^{fg}	1.05
VI033487	6.30 ± 1.48^{bcd}	0.27	0.07 ± 0.02^{bcd}	0.21	46.30 ± 3.04$^{d–g}$	0.86
VI036225	5.19 ± 1.35^{bc}	0.22	0.10 ± 0.03$^{b–f}$	0.28	24.07 ± 2.61^{bc}	0.32
VI036227	0.00 ± 0.00^{a}	0.01	0.00 ± 0.00^{a}	0.01	5.56 ± 1.40^{a}	0.06
VI044367	15.19 ± 2.19^{fg}	0.69	0.22 ± 0.04^{hi}	0.63	52.59 ± 3.04^{g}	1.11
VI044369	12.59 ± 2.02^{ef}	0.56	0.19 ± 0.04^{ghi}	0.55	50.37 ± 3.05^{fg}	1.01
VI044388	7.41 ± 1.60^{cde}	0.32	0.11 ± 0.03$^{c–g}$	0.32	22.96 ± 2.56^{bc}	0.30
VI044432	6.67 ± 1.52^{bcd}	0.28	0.07 ± 0.02^{bcd}	0.22	24.81 ± 2.63^{bc}	0.33
VI044437-A	11.11 ± 1.92^{def}	0.48	0.17 ± 0.03$^{e–i}$	0.47	42.59 ± 3.01^{def}	0.74
VI044473	5.93 ± 1.44^{bcd}	0.25	0.12 ± 0.03$^{d–h}$	0.35	19.63 ± 2.42^{b}	0.24
VI048076	6.30 ± 1.48^{bcd}	0.27	0.08 ± 0.02$^{b–e}$	0.24	40.74 ± 3.00^{de}	0.69
VI049639	7.04 ± 1.56^{cde}	0.30	0.08 ± 0.02$^{b–e}$	0.24	28.52 ± 2.75^{c}	0.40
VI049698	2.59 ± 0.97^{ab}	0.11	0.04 ± 0.01^{ab}	0.11	24.81 ± 2.63^{bc}	0.33
VI054569	4.81 ± 1.31^{bc}	0.20	0.06 ± 0.02$^{a–d}$	0.19	21.11 ± 2.49^{bc}	0.27

*Susceptible check

Mean ± SE followed by the same lower-case letter within a column are not significantly different at $P < 0.05$ (Tukey's test)

VI044473, RVI00002, VI044432, VI054569, VI044437-A and VI044388 had significantly fewer (F = 10.16; df = 17, 517; $P < 0.001$) stem weevils (RR 0–0.55) compared to the susceptible check (Table 6). There was high incidence of damage caused by the amaranth stem weevils averaging to 97.55 ± 0.88%. There was no significant difference (χ^2 = 7.39; df = 17, 517; P = 0.978) in the incidence of stem weevil damage across all accessions including the susceptible check. The incidence of damage by stem weevils ranged between 85.0 ± 8.19% and 100.0 ± 0.00% (Table 6).

Susceptibility of amaranth accessions to lepidopteran defoliators and stem weevils under field conditions during the short rainy season of 2017

The incidence of lepidopteran defoliators varied from 0.93 ± 0.05% to 46.30 ± 3.40% with an overall mean incidence of 7.09 ± 0.29%. The incidence was significantly lower (χ^2 = 531.38; df = 35, 7668; $P < 0.001$) than the susceptible check. VI033477, VI050609-B and VI056563 with RR above 0.22 had significantly higher incidence of lepidopteran defoliators than the accessions with RR below 0.11 (Table 7). VI036227, VI049530 and VI049698 had the least incidence of leaf-webbers with RR of 0.01 (Table 7). The overall mean abundance of lepidopteran defoliators across all accessions was 0.18 ± 0.02 larvae and ranged from 0.01 ± 0.01 to 2.51 ± 0.40 larvae. All the accessions had significantly lower (F = 22.08; df = 35, 7668; $P < 0.001$) pest abundance compared to the susceptible check. VI033477, VI050609-A and VI056563 with RR above 0.19 also had significantly high pest abundance compared to all other accessions with RR below 0.10 (Table 7). VI036227, VI049530 and VI049698 also had the least pest abundance with RR of 0.00 (Table 7).

The damage by lepidopteran defoliators on all the accessions varied from 1.39 ± 0.98% to 88.89 ± 2.63% with an overall mean of

Table 6 Comparative stem weevils' incidence, abundance, and damage incidence on various amaranth accessions and lines under field conditions during the long rainy season of 2016, Arusha, Tanzania

Gene bank code	Stem weevil incidence	Relative risk	Stem weevil abundance	Relative risk	Stem weevil damage incidence	Relative risk
VI033482*	96.67 ± 3.33^{f}		3.23 ± 0.44^{hi}		100.00 ± 0.00^{a}	
RVI00002	70.00 ± 8.51^{cde}	0.08	1.40 ± 0.25^{cdef}	0.43	100.00 ± 0.00^{a}	1.00
RVI00005	80.00 ± 7.43^{def}	0.14	2.03 ± 0.38^{efgh}	0.63	100.00 ± 0.00^{a}	1.00
RVI00027	63.33 ± 8.95^{bcde}	0.06	1.00 ± 0.19^{bcd}	0.31	93.33 ± 4.63^{a}	0.00
RVI00053	93.33 ± 4.63^{f}	0.48	3.37 ± 0.53^{i}	1.04	100.00 ± 0.00^{a}	1.00
VI033487	80.00 ± 7.43^{def}	0.14	2.23 ± 0.35^{efghi}	0.69	100.00 ± 0.00^{a}	1.00
VI036225	36.67 ± 8.95^{b}	0.02	0.53 ± 0.15^{ab}	0.16	100.00 ± 0.00^{a}	1.00
VI036227	0.00 ± 0.00^{a}	0.00	0.00 ± 0.00^{a}	0.01	85.00 ± 8.19^{a}	0.00
VI044367	73.33 ± 8.21^{cdef}	0.09	2.45 ± 0.50^{fghi}	0.76	100.00 ± 0.00^{a}	1.00
VI044369	93.33 ± 4.63^{f}	0.48	3.60 ± 0.63^{i}	1.11	100.00 ± 0.00^{a}	1.00
VI044388	56.67 ± 9.20^{bcd}	0.05	1.79 ± 0.52^{defg}	0.55	100.00 ± 0.00^{a}	1.00
VI044432	83.33 ± 6.92^{def}	0.17	1.60 ± 0.21^{cdef}	0.49	100.00 ± 0.00^{a}	1.00
VI044437-A	83.33 ± 6.92^{def}	0.17	1.69 ± 0.26^{defg}	0.52	93.10 ± 4.79^{a}	0.00
VI044473	43.33 ± 9.20^{bc}	0.03	1.30 ± 0.40^{bcde}	0.40	90.00 ± 5.57^{a}	0.00
VI048076	80.00 ± 7.43^{def}	0.14	2.87 ± 0.47^{ghi}	0.89	100.00 ± 0.00^{a}	1.00
VI049639	60.00 ± 9.10^{bcde}	0.05	0.90 ± 0.18^{bcd}	0.28	96.67 ± 3.33^{a}	0.00
VI049698	56.67 ± 9.20^{bcd}	0.05	0.72 ± 0.15^{abc}	0.22	96.55 ± 3.45^{a}	0.00
VI054569	86.67 ± 6.31^{ef}	0.22	1.63 ± 0.23^{def}	0.51	96.67 ± 3.33^{a}	0.00

*Susceptible check

Mean ± SE followed by the same lower-case letter within a column are not significantly different at $P < 0.05$ (Tukey's test)

67.72 ± 0.65%. Accessions RVI00005, VI049504, VI048076, VI046233-A, VI050609-B, VI054798, VI056563, RVI00053, VI033477 and VI050609-A had damage incidence that was not significantly different from the susceptible check with RR ranging from 0.49 to 1.37 while all the other accessions (RR below 0.49) had significantly lower incidence of damage compared to the susceptible check ($\chi^2 = 513.98$; df = 35, 5098; $P < 0.001$) (Table 7). VI036227 had the least incidence of damage by leaf-webbers with a RR of 0.00 which was significantly lower than all other accessions (Table 7).

The mean incidence of amaranth stem weevils was 90.42 ± 1.0% on all the accessions during the short rainy season. It ranged from 54.17 ± 10.39% to 100 ± 0.00% with 77.78% of the tested accessions having pest incidence levels above 80%. There were significant differences ($\chi^2 = 172.91$; df = 35, 828; $P < 0.001$) in the incidence of amaranth stem weevils across the accessions with VI047517-B, VI036227, VI048076, VI056563, and VI055128 having the least incidence and subsequently lower RRs compared to the susceptible check (Table 8). All other accessions had higher RRs compared to the susceptible check with 21 having significantly higher incidence of amaranth stem weevils compared to the susceptible check (Table 8). The abundance of stem weevils on the different amaranth accessions ranged from 0.75 ± 0.18 to 9.42 ± 1.89 with an overall mean of 4.35 ± 0.14. VI047517-B, VI056563 and VI036227 had the least stem weevil abundance but were not significantly different from the susceptible check (Table 8). The majority, 55.55% (20), of accessions had significantly higher ($F = 8.93$; df = 35, 820; $P < 0.001$) abundance of stem weevils compared to the susceptible check (Table 8).

There was high incidence of damage caused by the amaranth stem weevils across all the accessions averaging to 97.20 ± 0.56% during the season. There was however no significant difference ($\chi^2 = 31.47$; df = 35, 820; $P = 0.64$) in the incidence of amaranth stem weevil damage which ranged from 79.17 ± 8.47

Table 7 Comparative leaf-webbers' incidence, abundance, and damage incidence on various amaranth accessions and lines under field conditions during the short rainy season of 2017, Arusha, Tanzania

Gene bank code	Leaf-webber incidence	Relative risk	Leaf-webber abundance	Relative risk	Damage incidence by leaf-webbers	Relative risk
VI033482*	46.30 ± 3.40^{m}		2.51 ± 0.40^{e}		85.42 ± 2.95^{kl}	
RVI00002	6.02 ± 1.62^{b-i}	0.07	0.08 ± 0.02^{a}	0.03	69.44 ± 3.85^{c-i}	0.39
RVI00005	3.24 ± 1.21^{a-d}	0.04	0.03 ± 0.01^{a}	0.01	74.31 ± 3.65^{e-k}	0.49
RVI00027	3.70 ± 1.29^{a-e}	0.04	0.06 ± 0.02^{a}	0.02	68.06 ± 3.9^{c-h}	0.36
RVI00053	6.48 ± 1.68^{b-i}	0.08	0.07 ± 0.02^{a}	0.03	82.64 ± 3.17^{jkl}	0.81
VI033477	16.67 ± 2.54^{kl}	0.23	0.48 ± 0.12^{bcd}	0.19	84.62 ± 3.03^{kl}	0.94
VI033479	1.39 ± 0.80^{a}	0.02	0.01 ± 0.01^{a}	0.01	65.97 ± 3.96^{c-g}	0.33
VI033487	9.72 ± 2.02^{f-k}	0.12	0.13 ± 0.03^{a}	0.05	71.53 ± 3.77^{d-j}	0.43
VI036225	4.17 ± 1.36^{a-f}	0.05	0.04 ± 0.01^{a}	0.02	48.61 ± 4.18^{b}	0.16
VI036227	0.93 ± 0.65^{a}	0.01	0.01 ± 0.01^{a}	0.00	1.39 ± 0.98^{a}	0.00
VI044367	1.85 ± 0.92^{ab}	0.02	0.02 ± 0.01^{a}	0.01	58.33 ± 4.12^{bc}	0.24
VI044369	8.33 ± 1.88^{d-i}	0.11	0.13 ± 0.03^{a}	0.05	65.28 ± 3.98^{c-f}	0.32
VI044388	1.39 ± 0.80^{a}	0.02	0.01 ± 0.01^{a}	0.01	61.11 ± 4.08^{bcd}	0.27
VI044432	3.24 ± 1.21^{a-d}	0.04	0.04 ± 0.01^{a}	0.01	60.42 ± 4.09^{bcd}	0.26
VI044437-A	2.78 ± 1.12^{abc}	0.03	0.03 ± 0.01^{a}	0.01	72.22 ± 3.75^{d-j}	0.44
VI044473	1.85 ± 0.92^{ab}	0.02	0.02 ± 0.01^{a}	0.01	62.50 ± 4.05^{cde}	0.28
VI046233-A	6.02 ± 1.62^{b-i}	0.07	0.08 ± 0.02^{a}	0.03	77.78 ± 3.48^{g-k}	0.60
VI047517-B	10.19 ± 2.06^{g-l}	0.13	0.19 ± 0.04^{ab}	0.07	69.44 ± 3.85^{c-i}	0.39
VI047555-B	8.80 ± 1.93^{e-j}	0.11	0.14 ± 0.03^{a}	0.06	69.44 ± 3.85^{c-i}	0.39
VI048076	11.11 ± 2.14^{h-l}	0.15	0.16 ± 0.03^{a}	0.06	77.08 ± 3.51^{f-k}	0.57
VI048864-A	3.24 ± 1.21^{a-d}	0.04	0.05 ± 0.02^{a}	0.02	63.89 ± 4.02^{cde}	0.30
VI048919	11.57 ± 2.18^{i-l}	0.15	0.25 ± 0.06^{abc}	0.10	67.36 ± 3.92^{c-h}	0.35
VI049242	3.24 ± 1.21^{a-d}	0.04	0.04 ± 0.02^{a}	0.02	65.28 ± 3.98^{c-f}	0.32
VI049502	6.48 ± 1.68^{b-i}	0.08	0.08 ± 0.02^{a}	0.03	65.97 ± 3.96^{c-g}	0.33
VI049504	3.24 ± 1.21^{a-d}	0.04	0.06 ± 0.03^{a}	0.03	75.00 ± 3.62^{e-k}	0.51
VI049530	0.93 ± 0.65^{a}	0.01	0.01 ± 0.01^{a}	0.00	62.50 ± 4.05^{cde}	0.28
VI049639	3.70 ± 1.29^{a-e}	0.04	0.04 ± 0.01^{a}	0.01	58.33 ± 4.12^{bc}	0.24
VI049698	0.93 ± 0.65^{a}	0.01	0.01 ± 0.01^{a}	0.00	65.97 ± 3.96^{c-g}	0.33
VI050609-A	11.57 ± 2.18^{i-l}	0.15	0.56 ± 0.37^{cd}	0.22	88.89 ± 2.63^{l}	1.37
VI050609-B	17.59 ± 2.60^{l}	0.25	0.23 ± 0.04^{ab}	0.09	78.47 ± 3.44^{h-k}	0.62
VI054569	7.41 ± 1.79^{c-i}	0.09	0.09 ± 0.02^{a}	0.04	70.14 ± 3.83^{c-i}	0.40
VI054798	4.63 ± 1.43^{a-g}	0.06	0.06 ± 0.02^{a}	0.03	81.25 ± 3.26^{i-l}	0.74
VI055127	5.09 ± 1.50^{a-g}	0.06	0.06 ± 0.02^{a}	0.03	57.64 ± 4.13^{bc}	0.23
VI055128	1.39 ± 0.98^{a}	0.02	0.01 ± 0.01^{a}	0.01	68.75 ± 4.76^{c-i}	0.38
VI055135	1.85 ± 0.92^{ab}	0.02	0.02 ± 0.01^{a}	0.01	61.11 ± 4.08^{bcd}	0.27
VI056563	16.20 ± 2.51^{jkl}	0.22	0.78 ± 0.32^{d}	0.31	82.52 ± 3.19^{jkl}	0.81

*Susceptible check

Mean ± SE followed by the same lower-case letter within a column are not significantly different at $P < 0.05$ (Tukey's test)

to 100 ± 0.00 (Table 8). The weevils created tunnels within amaranth stems with an overall mean of 9.20 ± 0.23 tunnels and ranged from 1.46 ± 0.29 to 17.54 ± 2.94 tunnels (Table 8). There were significant differences (F = 10.12; df = 35, 820; $P < 0.001$) in the number of tunnels (severity of weevil damage)

Table 8 Comparative stem weevils' incidence, abundance, and damage incidence on various amaranth accessions and lines to stem weevils under field conditions during the short rainy season of 2017, Arusha, Tanzania

Gene bank code	Stem weevil incidence	Relative risk	Tunneling mines	Relative risk	Stem weevil abundance	Relative risk	Stem weevil damage incidence	Relative risk
VI033482*	$70.83 \pm 9.48^{a–d}$		4.79 ± 0.62^{bcd}		1.42 ± 0.28^{abc}		87.5 ± 6.90^{a}	
RVI00002	100.00 ± 0.00^{e}	11.50	$10.00 \pm 1.27^{g–l}$	2.09	$5.75 \pm 0.85^{j–n}$	4.06	100.00 ± 0.00^{a}	4.60
RVI00005	95.83 ± 4.17^{e}	5.50	$8.63 \pm 0.68^{e–k}$	1.80	$4.08 \pm 0.58^{e–j}$	2.88	100.00 ± 0.00^{a}	4.60
RVI00027	100.00 ± 0.00^{e}	11.50	$10.17 \pm 1.26^{h–l}$	2.12	$5.88 \pm 0.88^{j–n}$	4.15	100.00 ± 0.00^{a}	4.60
RVI00053	95.83 ± 4.17^{e}	5.50	$9.58 \pm 1.50^{f–l}$	2.00	$4.29 \pm 0.80^{f–j}$	3.03	100.00 ± 0.00^{a}	4.60
VI033477	87.50 ± 6.90^{cde}	2.50	$5.21 \pm 0.49^{b–e}$	1.09	$2.29 \pm 0.33^{b–f}$	1.62	100.00 ± 0.00^{a}	4.60
VI033479	100.00 ± 0.00^{e}	11.50	$9.38 \pm 0.99^{e–l}$	1.96	$4.63 \pm 0.60^{g–l}$	3.26	100.00 ± 0.00^{a}	4.60
VI033487	95.83 ± 4.17^{e}	5.50	$10.79 \pm 1.19^{i–m}$	2.25	$5.33 \pm 0.86^{i–n}$	3.76	100.00 ± 0.00^{a}	4.60
VI036225	$83.33 \pm 7.77^{b–e}$	1.90	$11.71 \pm 1.82^{k–n}$	2.44	$3.33 \pm 0.88^{d–i}$	2.35	95.83 ± 4.17^{a}	2.20
VI036227	58.33 ± 10.28^{ab}	0.59	3.50 ± 0.66^{abc}	0.73	1.38 ± 0.31^{ab}	0.97	91.67 ± 5.76^{a}	1.40
VI044367	100.00 ± 0.00^{e}	11.50	$11.13 \pm 1.02^{j–m}$	2.32	$5.29 \pm 0.59^{i–m}$	3.74	100.00 ± 0.00^{a}	4.60
VI044369	100.00 ± 0.00^{e}	11.50	11.54 ± 1.33^{klm}	2.41	$6.04 \pm 0.96^{j–n}$	4.26	100.00 ± 0.00^{a}	4.60
VI044388	87.50 ± 6.90^{cde}	2.50	$7.54 \pm 0.88^{d–k}$	1.57	$3.08 \pm 0.48^{c–i}$	2.18	100.00 ± 0.00^{a}	4.60
VI044432	100.00 ± 0.00^{e}	11.50	16.38 ± 1.84^{no}	3.42	8.17 ± 1.09^{no}	5.76	100.00 ± 0.00^{a}	4.60
VI044437-A	91.67 ± 5.76^{de}	3.50	$7.08 \pm 0.68^{d–j}$	1.48	$2.25 \pm 0.30^{b–e}$	1.59	100.00 ± 0.00^{a}	4.60
VI044473	$79.17 \pm 8.47^{a–e}$	1.50	$5.96 \pm 0.78^{c–f}$	1.24	$2.08 \pm 0.43^{a–d}$	1.47	95.83 ± 4.17^{a}	2.20
VI046233-A	91.67 ± 5.76^{de}	3.50	$6.67 \pm 1.14^{d–i}$	1.39	$3.33 \pm 0.88^{d–i}$	2.35	100.00 ± 0.00^{a}	4.60
VI047517-B	54.17 ± 10.39^{a}	0.50	1.46 ± 0.29^{a}	0.30	0.75 ± 0.18^{a}	0.53	79.17 ± 8.47^{a}	0.60
VI047555-B	87.50 ± 6.9^{cde}	2.50	$10.13 \pm 1.87^{g–l}$	2.11	$5.04 \pm 1.10^{i–m}$	3.56	91.67 ± 5.76^{a}	1.40
VI048076	62.50 ± 10.09^{abc}	0.70	$6.50 \pm 1.36^{d–h}$	1.36	$2.25 \pm 0.51^{b–e}$	1.59	83.33 ± 7.77^{a}	0.76
VI048864-A	100.00 ± 0.00^{e}	11.50	$10.33 \pm 1.13^{h–l}$	2.16	$4.50 \pm 0.58^{g–k}$	3.18	100.00 ± 0.00^{a}	4.60
VI048919	95.83 ± 4.17^{e}	5.50	$6.08 \pm 0.63^{c–g}$	1.27	$2.83 \pm 0.35^{b–h}$	2.00	100.00 ± 0.00^{a}	4.60
VI049242	100.00 ± 0.00^{e}	11.50	$9.38 \pm 1.07^{e–l}$	1.96	$4.42 \pm 0.59^{g–k}$	3.12	100.00 ± 0.00^{a}	4.60
VI049502	100.00 ± 0.00^{e}	11.50	$9.50 \pm 0.74^{f–l}$	1.98	$4.58 \pm 0.50^{g–l}$	3.24	100.00 ± 0.00^{a}	4.60
VI049504	100.00 ± 0.00^{e}	11.50	$7.21 \pm 0.89^{d–j}$	1.50	$3.33 \pm 0.39^{d–i}$	2.35	100.00 ± 0.00^{a}	4.60
VI049530	100.00 ± 0.00^{e}	11.50	$13.17 \pm 1.33^{l–o}$	2.75	$7.17 \pm 0.97^{l–o}$	5.06	100.00 ± 0.00^{a}	4.60
VI049639	95.83 ± 4.17^{e}	5.50	$9.88 \pm 1.16^{g–l}$	2.06	$4.83 \pm 0.73^{h–l}$	3.41	100.00 ± 0.00^{a}	4.60
VI049698	100.00 ± 0.00^{e}	11.50	14.88 ± 1.31^{o}	3.10	7.67 ± 0.95^{mno}	5.41	100.00 ± 0.00^{a}	4.60
VI050609-A	$79.17 \pm 8.47^{a–e}$	1.50	$6.13 \pm 0.99^{c–g}$	1.28	$2.54 \pm 0.68^{b–g}$	1.79	100.00 ± 0.00^{a}	4.60
VI050609-B	$83.33 \pm 7.77^{b–e}$	1.90	$7.21 \pm 1.29^{d–j}$	1.50	$3.38 \pm 0.69^{d–i}$	2.38	91.67 ± 5.76^{a}	1.40
VI054569	100.00 ± 0.00^{e}	11.50	17.54 ± 2.94^{o}	3.66	9.42 ± 1.89^{o}	6.65	100.00 ± 0.00^{a}	4.60

Table 8 continued

Gene bank code	Stem weevil incidence	Relative risk	Tunneling mines	Relative risk	Stem weevil abundance	Relative risk	Stem weevil damage incidence	Relative risk
VI054798	100.00 ± 0.00^{e}	11.50	$12.88 \pm 1.29^{l–o}$	2.69	$6.92 \pm 1.17^{k–o}$	4.88	100.00 ± 0.00^{a}	4.60
VI055127	100.00 ± 0.00^{e}	11.50	$12.38 \pm 1.23^{k–n}$	2.58	$6.08 \pm 0.85^{j–n}$	4.29	100.00 ± 0.00^{a}	4.60
VI055128	100.00 ± 0.00^{e}	7.50	$12.56 \pm 1.52^{k–o}$	2.62	$5.63 \pm 0.64^{i–n}$	3.97	100.00 ± 0.00^{a}	3.00
VI055135	100.00 ± 0.00^{e}	11.50	$12.00 \pm 0.81^{k–n}$	2.50	$5.83 \pm 0.43^{j–n}$	4.12	100.00 ± 0.00^{a}	4.60
VI056563	62.50 ± 10.09^{abc}	0.70	3.21 ± 0.79^{ab}	0.67	1.33 ± 0.33^{ab}	0.94	83.33 ± 7.77^{a}	0.76

*Susceptible check

Mean ± SE followed by the same lower-case letter within a column are not significantly different at $P < 0.05$ (Tukey's test) with VI054798, VI049530, VI049698, VI044432 and VI054569 recording the highest number of tunnels whereas VI047517-B, VI056563 and VI036227 had the lowest number of tunnels (Table 8). There was a significant positive correlation between the number of stem weevils and corresponding number of tunnels ($r = 0.96$; $df = 34$; $P < 0.001$).

Discussion

There is a broad diversity of insect pests that have been reported on amaranth in several parts of the world (Clarke-Harris et al. 1998; James et al. 2010; García et al. 2011; Aderolu et al. 2013; Mureithi et al. 2015). This is contrary to the popular belief and knowledge that amaranth and other AIVs are seldom attacked by pests (Dinssa et al. 2016). Clarke-Harris and Fleischer (2003), Aderolu et al. (2013), Mureithi et al. (2015) and James et al. (2010) indicate that Lepidopteran pests are the most damaging to cultivated amaranths. Our results indicate a similarly high diversity of the lepidopteran pests attacking amaranths in Tanzania. With 14 different lepidopteran species recorded from amaranth during two seasons, the leaf-webber *S. recurvalis* was the most predominant. Our results are similar to reports from Nigeria (Aderolu et al. 2013), Kenya (Mureithi et al. 2015), India (Arivudainambi et al. 2010: Batra and Bhattacherjee 1960; Pande 1972) and Jamaica (Clarke-Harris et al. 1998, 2004) where *S. recurvalis* has been reported to be the most destructive pest of amaranth.

During both seasons, *S. recurvalis* occurrences were preceded by different species of leaf-webber pests; *P. basalis* which folds apical leaves of amaranths into characteristic leaf shelters and *E. impactella* which webs leaves that are near the soil. These also inflict substantial amount of damage to amaranth and in cases where *P. basalis* infestations occurred, apical growth was hindered. The other pests of economic importance in amaranth production in the region were the leaf-worms, *S. littoralis* and *S. exigua,* which are known to be polyphagous in nature and extremely voracious feeders and can feed on entire foliage. It is apparent that the pests of amaranths occur as a complex array of species that contribute to substantial foliage loss. Similar observations were made by Aderolu et al. (2013) in Nigeria where 17 different species of lepidopteran defoliators were reported to infest and damage amaranth during two seasons. In East Africa, this is probably the first extensive study to document such a broad diversity of lepidopteran defoliators of amaranths, however further studies are warranted to assess changes in pests and natural enemies' diversity over a longer period.

Associated with the lepidopteran defoliators was a rich diversity of 14 indigenous parasitoids species which had varying parasitism levels per accession in the two seasons. Indigenous parasitoids if conserved optimally can play an important role in keeping the pest populations under check. Othim et al. (2017) through laboratory trials reported parasitism rates of up to 90% by an indigenous parasitoid *Apanteles hemara* Nixon (Hymenoptera: Braconidae) on the amaranth leaf-webbers *S. recurvalis* and *U. ferrugalis*. Open field parasitism rates ranging from 11 to 62% caused by *Apanteles* sp. on *S. recurvalis* have been reported in parts of India (Narayanan et al. 1957; Bhattacherjee and Ramdas-Menon 1964; Peter and Balasubramanian 1984; Kedar and Kumaranag 2013; Arivudainambi et al. 2010). In addition, *A. hemara* has been reported from various countries across Africa, Asia, Europe and Oceania (Kedar and Kumaranag 2013; Madl and van Achterberg 2014; Yu et al. 2016; Fernandez-Triana et al. 2017). However, the performance (parasitism, development and reproduction) of a parasitoid has been reported to be differentially affected by its host plant (Turlings and Benrey 1998). The variations in the levels of parasitism recorded in our study suggest an effect of the different accessions on the parasitoids. The variation in the number of lepidopteran hosts and interspecific competition may also affect parasitism levels. With the rich diversity of parasitoids reported from this study, it is recommended that further studies be conducted to assess their individual performance on selected resistant accessions and possibility of having them incorporated in conservation and/or augmentative biological control of the lepidopteran defoliators of amaranth.

The Eulophid wasp *Entedon* sp. was also found on amaranth stem weevils causing low levels of parasitism on the immature stages during both seasons. The first case of parasitism on amaranth stem weevils was reported in South Africa two decades ago by Louw et al. (1995). This study becomes the second to report such parasitism in Africa and the first in East Africa. Due to the dearth of information regarding this parasitoid, further studies are recommended to assess the biology and performance of *Entedon* sp. with an aim of integrating it with HPR in an Integrated Pest Management (IPM) package for amaranth pests.

Amaranth stem weevils belonging to four different species were observed to cause damage to amaranth alongside the lepidopteran defoliators. According to Torres-Saldaña et al. (2004), Tara et al. (2009), Garcia et al. (2011), Aderolu et al. (2013), Kagali et al. (2013), Mureithi et al. (2015), the amaranth stem weevil, *H. truncatulus* is classified among the major pests of amaranths that can cause significant amounts of damage to the crop. Our study also shows high abundance of *H. truncatulus* in Tanzania compared to other species of stem weevils.

Amaranth accessions tested differed significantly in the incidence (infestation), abundance and damage caused by lepidopteran defoliators, compared to the susceptible check. The level of pest incidence or abundance on any given accession portrays its level of non-preference by/resistance to the pest. Several accessions exhibited non-preference to amaranth lepidopteran defoliators with VI036227, VI049698, RVI00027, VI054569, VI033487, VI044432, VI048076, VI049639 and VI036225 showing high to moderately high levels of non-preference during the long rainy season. VI036227, VI049530 and VI049698 were the least preferred during the short rainy season and 22 others showed moderately high levels of resistance. During both seasons, VI036227 and VI049698 were highly resistant to lepidopteran defoliators. Low pest abundance in the resistant accessions could be due to antixenosis or antibiosis traits. Antixenosis involves behavioural factors that compel the pest to avoid the plant for feeding or laying its eggs while antibiosis involves adverse effects that the crop may have on the pest because of chemicals (secondary metabolites) or structures the plant possesses (Kogan and Ortman 1978; Kishore et al. 2007). Further studies are thus recommended to explore these (antixenosis and antibiosis) resistance traits and the dynamics involved in host-pest interactions among the resistant amaranth accessions. In addition, the possibilities of transferring these resistance traits into susceptible or locally grown varieties of amaranth by methods such as introgression also need further study, especially in instances where the susceptible varieties are the most preferred by consumers.

Extremely high infestation of stem weevils and their corresponding damage was recorded during both seasons with infestation rates of up to 100% on certain accessions. This is concurrent with the findings of Torres-Saldaña et al. (2004) and García et al. (2011) in Mexico and Tara et al. (2009) in India who reported infestation rates of up to 100, 92 and 82.3%, respectively on amaranth by the stem weevils. Whereas Torres-Saldaña et al. (2004) did not find significant effect of stem weevil abundance and tunnelling on grain yield reduction and biomass production, Phogat et al. (1994) and García et al. (2011) have demonstrated that substantial losses in grain yields occur due to stem weevil infestations. The high levels of infestation and tunnelling damage by the stem weevils in our study points to the importance of these pests in amaranth production, particularly grain amaranths. However, whether this heavy presence of stem weevil grubs causes a reduction in the yield of leaves is still not clear and further studies are recommended to show whether presence of stem weevil grubs will affect yield of leaves of resistant accessions and enhance other negative attributes such as lodging. Since the stem weevil pests cause damage both to the foliage (as adults) and within the stems and roots (as grubs), sustainable management strategies are of utmost need. VI047517-B, VI036227 and VI056563 had the least stem weevil infestations (below 62.5%) and consequently the least tunnels as a result of weevil feeding during both seasons suggesting that they possess low levels of resistance against the stem weevil pests. Whether this resistance is due to antixenosis, antibiosis, or tolerance is still unclear and further studies are recommended to unravel the mechanisms involved.

In conclusion, our study identified two highly resistant amaranth accessions against lepidopteran defoliators and 24 moderately resistant accessions to lepidopteran defoliators attacking amaranth. Three accessions with low levels of resistance against stem weevils were also identified. VI036227 had the highest resistance to the complex of defoliators and weevils. Several species of lepidopteran defoliators and stem weevils of amaranth predominated by the leaf-webber *S. recurvalis* and the stem weevil *H. truncatulus* were found to cause high levels of damage to the crop in Tanzania. The populations of *S. recurvalis* on amaranth gradually increased as the populations of other leaf-webber species declined with time. Extremely high incidence and abundance of amaranth stem weevils in the open fields stresses the need for an alternative management strategy that would work in synergy with the identified resistant accessions. There is also a rich diversity of indigenous parasitoids of both lepidopteran defoliators and amaranth stem weevils which have a potential to offer significant control for these pests and synergize the resistant accessions. This study is perhaps the first to report on the incidence of amaranth stem weevil parasitoids in East Africa. In addition to the accession with the highest resistance to the complex of defoliators and weevils, VI036227, the 24 moderately resistant accessions are also recommended for advancement for release to farmers.

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Author contributions STOO, RS, RK, TD, FFD, SE and KKMF conceived research. STOO conducted experiments. RS, RK, TD, FFD, SE and KKMF provided research materials, tools and intellectual support during research execution. STOO and RK analysed data and conducted statistical analyses. STOO, RS, RK, TD, FFD, SE and KKMF wrote the manuscript. RS and KKMF secured funding. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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