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ORIGINAL CONTRIBUTION

Estimating effect of augmentative biological control on grain yields from individual pearl millet heads

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Abstract

Pearl millet is the principal staple food crop in large portions of Western Sub-Sahelian Africa and the millet head miner (*Heliocheilus albipunctella*) is one of its most devastating insect pests. Since 2006, augmentative mass releases of the larval ectoparasitoid, *Habrobracon hebetor,* have been conducted in Mali, Burkina Faso and Niger as part of minimizing pearl millet grain losses imposed by millet head miners. These ongoing mass releases are based on low-cost mass-rearing of both host larvae and parasitoids. A release of parasitoids consists of placing jute bags containing pearl millet grain and flour and parasitized host larvae near pearl millet fields. The total production costs of a single jute bag with parasitized rice moth larvae are US$ 3–4. Based on a study of 6634 individual pearl millet heads collected at harvest in 12 farmers' fields in southern Niger in 2010, we demonstrated (i) a strong negative correlation between pearl millet head damage (mining) and grain yield and (ii) that parasitism by *H. hebetor* reduced grain losses by, on average, 34% (comparison of infested millet heads with/without parasitism) within the given growing season. Additional benefits may include reduction in millet head miners in subsequent generations. Data from 900 pearl millet heads collected in nine farmers' fields in 2011 were used to confirm data trends observed in the 2010 data and to characterize the dispersal of parasitoids in upwind and downwind directions from a release site. This study provided a quantitative description of the negative impact of millet head miner infestations on pearl millet grain yields and of benefits on grain yield of parasitism by *H. hebetor*. Our findings strongly support (i) intensification of mass-rearing of *H. hebetor,* (ii) expansion of educational activities to increase local empowerment and understanding of the potential of augmentative biological control and (iii) optimization of *H. hebetor* mass release programmes among smallholders in Sub-Sahelian Africa.

Introduction

Pearl millet [*Pennisetum glaucum* (L) R. BR] is the principal staple food crop in large portions of the Western Sub-Sahelian Africa between 12°N and 16°N latitude. In Niger, pearl millet accounts for about 55% of the annual grain and legume production (http://www.stat-niger.org/statistique/). A typical Sub-Sahelian pearl millet farmer grows 3–10 ha of pearl millet and produces 250–600 kg shelled pearl millet per ha (http://www.stat-niger.org/statistique/). As many as 100 arthropod pests are known to infest pearl millet (Gahukar 1989a,b), but the millet stem borer [*Coniesta ignefusalis* (Hampson) (Lepidoptera: Pyralidae)] and the millet head miner [*Heliocheilus albipunctella* de Joannis (Lepidoptera: Noctuidae)] cause the most economic damage (Gahukar 1984; Payne 2006). The first reports of millet head miners causing economic damage occurred in 1972–1974 (Vercambre 1978; Gahukar 1984), when Sub-Sahelian Africa experienced severe droughts. In Niger, some of the earliest reports of millet head miner infestation reported 15% yield loss in 1974 (Vercambre 1978). The millet head miner is univoltine and has a geographical distribution between 11° and 15° N latitudes within the Southern Sahel and Sudan bioclimatic zones (Nwanze and Sivakumar 1990). Damage to pearl millet is caused by developing millet head miner larvae feeding on flowers and seeds during the entire plant reproductive phase. Gahukar (1990) showed that millet head miners lay 70–90 eggs in individual pearl millet heads and that the density of young larvae (1st and 2nd instars) was about 10–40 individuals per millet head. In the weeks before grain maturity (September/November), 4th instar millet head miner larvae descend and pupate in the soil and diapause until the onset of the subsequent growing season after the first seasonal rainfall.

Due to challenging socioeconomic conditions, effective and widespread use of insecticides is not an option for most smallholder farmers in Sub-Sahelian Africa. Cultural practices [i.e. late planting (Youm and Gilstrap 1993), intercropping and planting density (Gahukar 1989a,b), and use of fertilizer (Tanzubil et al. 2004)] have been examined experimentally as possible management options, but they have not been developed further. Since the 1980s, considerable international research resources have been allocated into screening and development of pearl millet resistant to the millet head miner (Gahukar 1987; Youm and Owusu 1998; Youm et al. 2001). However, these efforts have so far produced few tangible results and have not been made available to smallholders throughout the region (Payne et al. 2011).

Habrobracon hebetor Say (Hymenoptera: Braconidae) is a well-known, gregarious ectoparasitoid of larvae from a wide range of economically important moth families, including Pyralidae (Eliopoulos and Stathas 2008; Ghimire and Phillips 2010a,b), Gelechiidae (Jackson and Butler 1984; Ghimire and Phillips 2010a,b), Tineidae (Ghimire and Phillips 2010a,b), Geometrids (Ghimire and Phillips 2010a,b), and Noctuidae (Ghimire and Phillips 2010a,b; Rabie et al. 2010), including the millet head miner (Youm and Gilstrap 1993). There are several studies describing the use of commercially available *H. hebetor* populations in biological control, especially of pyralid pests in stored products (Brower et al. 1996; Prozell and Schöller 2002). Also detailed life table studies have been developed for this important parasitoid (Eliopoulos and Stathas 2008). The first experimental augmentative releases of *H. hebetor* into farmers' pearl millet fields were conducted in 1985 in Senegal (Bhatnagar 1987). In Niger, experimental mass-rearing of *H. hebetor* began in 1998 (Payne et al. 2011) and continued on a small/experimental basis until 2006. Based on research since 2008, a mass-rearing and augmentative release programme has been ongoing with involvement of over 300 villages in Niger, Mali and Burkina Faso.

The main purpose of this study was to provide the first quantitative analysis of pearl millet head yield losses due to millet head miner and of the impact of millet head miner parasitism by *H. hebetor* on yield loss. This analysis was based on careful examination of individual heads to obtain detailed information about the relationship between 'mining' by millet head miners, levels of parasitism imposed by *H. hebetor* (as indicated by parasitized cadavers and distinct cocoons) and grain yield. A total of 6634 individual pearl millet heads were collected in 12 farmers' fields in 2010 with an additional 900 collected in nine farmers' fields in southern Niger in 2011. In addition to confirming trends identified in 2010, the data collected in growing season 2011 were used to examine dispersal of *H. hebetor* from a release site. With this analysis, we demonstrate the significant potential of low-input, locally produced augmentative biological control agents in reducing losses incurred by the millet head miner in smallholders' pearl millet fields.

Materials and Methods

Farmers' fields and releases of *H. hebetor*

In the 2010 growing season, we selected three fields in each of four villages [Kochima (14°00′ 14.25″N and 5°45′ 59.99″E), Tounga Yacouba (13°54′ 50.98″N and 5°26′ 10.48″E), Tsaouna Gomma (13°57′ 52.94″N and 5°21′ 00.13″E) and Tamaka (13°53′ 14.10″N and 5°20′ 56.86″E)] located within a 20 by 50 km area near the border between Niger and Nigeria. These data were used to characterize the relationships between millet head miner occurrence and damage and the adverse effect of this pest on grain yield. We also quantified the relative importance of parasitism by *H. hebetor* of millet head miners. At harvest (September–October), 400–600 individual pearl millet heads were sampled haphazardly within each field and carefully examined for damage (see below). All fields were local pearl millet varieties planted in May–June at densities ranging from 4000–6000 plants per ha. No quantitative information was available concerning pearl millet genotypes, soil types, planting space and these variables may even have varied considerably within individual fields. Consequently, 'field' was included as a random component in the statistical analyses. Fields were not irrigated and no fertilizer was applied to any of them. *H. hebetor* populations are reared on rice moth larvae [*Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae)], which are widely used host species for mass-rearing of both egg and larval parasitoids. Rice moths are pests on stored rice, pearl millet, and other cereals, and they are widely available from farmers' granaries in Niger and other Sub-Sahelian countries. Rice moth larvae are easily reared under relatively simple laboratory conditions, so they constitute an ideal mass-rearing host of *H. hebetor*. We used a larval host rearing procedure similar to that described by Nathan et al. (2006), in which jars of pearl millet flour are maintained at 28–30°C and 65% RH, with a 14 : 10 light regime. Adult *H. hebetor* individuals are exposed to fifth instar host larvae, which are subsequent transferred to locally produced 15 jute bags (15 cm by 25 cm), each containing about 100 g pearl millet flour, parasitized rice moth larvae and 200 g pearl millet grains. For mass releases near pearl millet fields, these jute bags were placed inside a plastic bucket mounted in a tree canopy to provide shade. The total production costs of a single jute bag with parasitized rice moth larvae are US$ 3–4. *H. hebetor* populations were released in mid August in each village. The choice of releasing parasitoids from a point in a village was to offer maximum biological control service to fields scattered around the villages, and in the 2010, growing season data were collected from fields within 1 km from parasitoid release points. Preliminary studies (I.B. Baoua, unpublished data) have shown that each jute bag releases about 80 *H. hebetor* individuals daily during the first 2–3 weeks or the equivalent of about 1200 *H. hebetor* individuals from each release site. With a developmental time of about 13 days (Eliopoulos and Stathas 2008), 140–190 parasitoid progeny being produced from 50 host larvae by 2–4 parasitoid pairs (Ghimire and Phillips 2010a,b), and population doubling times within 3.5–4.5 days (Eliopoulos and Stathas 2008) – even fairly low density releases can lead to considerable parasitoid population densities developing in farmers fields near release points.

In the 2011 growing season, the same augmentative release procedure was used with *H. hebetor* individuals being released in mid August from a release point in Bazaga in southern Niger (13°47′ 29.37″N and 5°06′ 10.28″E). We used data from the 2011 growing season to assess the level of *H. hebetor* dispersal in upwind and downwind directions as a function of distance from the augmentative release site in Bazaga At harvest, 100 pearl millet heads were collected in each of nine farmers' fields (N = 900) along a 30 km transect in an east–west direction (prevailing winds from west to southwest) with Bazaga as the centre of a transect. We sampled fields located 0, 3, 5, 10 and 15 km in either direction from Bazaga. These data were used to confirm trends observed in the 2010 data set and to assess parasitoid dispersal of *H. hebetor* in upwind and downwind directions.

Data collection

Pearl millet plants have multiple tillers, but only the main head was sampled on individual plants. In both growing seasons, we collected the following agronomic data from individual pearl millet heads at harvest: length (length) and diameter (diameter) of each pearl millet head (cm), total length of millet head miner mines (cm) in each head (mine length), and presence/absence of parasitism by *H. hebetor*. In addition, in the 2010 growing season, we obtained weight of shelled grain (gram) from each sampled pearl millet head (yield). Level of parasitism was quantified based on number of parasitized millet head miner larval cadavers in each pearl millet head: all millet head miner cadavers in each head were carefully examined, and they were considered to have succumbed due to parasitism incurred by *H. hebetor* if distinct braconid cocoons were observed on the cadaver. We are unaware of any other braconid species parasitizing pearl millet head miners in this region. If the millet head miner cadaver was absent and/or the parasitized cadaver did not have the distinct *H. hebetor* cocoon, we presumed it had either left the pearl millet head to diapause in the soil, or it had died due to causes other than parasitism by *H. hebetor*.

Data analysis

All data processing and analyses were conducted in R software (R Development Core Team 2007) and ASREML-R (Butler et al. 2009). To quantify the relative impact of millet head miner damage, pearl millet heads were divided into three treatment categories: no damage to millet heads (N = 2384) ('no damage'), damage by millet head miner but no parasitism by *H. hebetor* (N = 2949) ('damage'), and damage by millet head miner and parasitism by *H. hebetor* (N = 1301) ('parasitized'). Linear mixed models (LMM) were developed and fitted for responses of *length* and *diameter* of pearl millet heads and of *grain* yield per pearl millet head. Due to the nature of the data (counts) for the response variable *mines*, a generalized linear mixed model (GLMM) with Poisson model for the error and log link function was used. In general, all of the models had the following structure:

$$\text{Response} \sim \text{Fixed Effects} + \text{Random Effects} + \text{Error}$$

The random effect component for all of the fitted models was 'field', which accounted for the variation among the sampled fields. The fixed effect component was, treatment with three levels: no damage, damage and parasitized. All models showed very good fit, including the model for *mines*. An important issue in fitting GLMMs is over-dispersion. The variance heterogeneity factor or also called variance inflation factor c is used to assess over-dispersion. Ideally, c should be around 1 to assume that there is no over-dispersion. The model fitted for *mines* showed $c = 1.12$, which confirmed good specification of the model. A polynomial regression fit was used to analyse the relationship between mine length intervals and grain yield in millet heads without parasitism.

Results and Discussion

Millet head variability

The standard pearl millet harvest technique in the region is to cut each millet head individually by hand, and the current analysis was based on careful evaluation of heads on main stems of individual pearl millet plants. Pearl millet head data varied markedly within fields and among villages and fields, and the extent of the data heterogeneity is illustrated by the ranges of response variables among the 12 fields (Table 1). The obvious consequence of this data heterogeneity is that detection of trends, such as, quantification and characterization of agronomic responses, including effects of augmentative biological control, in smallholders' fields will only be possible when large numbers of observations are acquired.

Assessment of yield loss in response to millet head miner damage and parasitism

Parasitism by *H. hebetor* initially paralyses the host before oviposition, and the host will eventually succumb in the pearl millet head. Due to pupal diapause in the soil, pearl millet heads do not contain any millet head miner individuals at harvest, unless they were parasitized or succumbed due to causes other than parasitism by *H. hebetor*. The exact contribution of *H. hebetor* to the mortality of developing millet head miner larvae is obviously important, and the data presented here suggested that it may exceed 75%. That is, on average, 75% of millet head miner cadavers in pearl millet heads were associated with cocoons of *H. hebetor*, while no visible cocoons were detected on the remaining 25%. The 6634 millet heads were divided into three treatment categories (non-infested, damaged without parasitized millet head miner larvae and damaged with parasitized millet head miner larvae). In the context of LMM or GLMM, a Wald test is most commonly used to assess the significance of the fixed terms. Using this approach, the treatment effect was significant ($P < 0.001$) for all responses. Table 2

Table 1 Average agronomic data (length, diameter and grain yield) and millet head miner mortality from individual pearl millet spikes collected in 12 fields in southern Niger

		Length (cm)		Diameter (cm)		Grain yield (gram)		Cadavers	
Village	Field number	Non-infested	Infested	Non-infested	Infested	Non-infested	Infested	B.h.	Other
Kochima	1	57.80	57.91	7.58	7.18	38.88	19.24	1.17	0.55
	2	59.17	62.18	8.08	7.83	41.37	25.93	0.97	0.54
	3	58.30	58.69	8.04	7.17	37.43	17.71	1.01	0.36
Tamaka	1	71.65	65.88	9.14	7.70	52.26	21.44	0.93	0.59
	2	62.44	67.86	8.26	8.01	43.07	32.18	1.10	0.22
	3	61.72	60.89	7.88	7.68	32.63	19.01	0.99	0.31
Tounga Yacouba	1	63.83	60.75	8.30	7.55	41.28	13.09	0.99	0.18
	2	58.95	53.96	7.72	6.91	31.59	11.11	0.96	0.22
	3	65.39	63.37	7.59	7.33	30.66	18.76	0.99	0.25
Tsaouna Gomma	1	72.11	66.63	8.55	7.59	43.98	21.91	0.81	0.32
	2	67.70	62.70	7.90	7.05	34.43	18.43	1.04	0.27
	3	62.28	62.79	7.52	7.21	32.92	18.44	1.02	0.28
		63.44	61.97	8.05	7.43	38.37	19.77	0.99	0.34

Table 2 Predicted means with the standard errors (SE) for the three treatment categories

Group	Grain (SE)	Length (SE)	Diameter (SE)	Mines (SE)
No damage	38.3 (1.35)	63.5 (1.12)	8.04 (0.098)	NA
Damaged	17.9 (1.34)	61.5 (1.12)	7.35 (0.097)	4.3 (0.26)
Parasitized	23.9 (1.39)	62.7 (1.16)	7.64 (0.100)	3.5 (0.22)
AVSED	0.508	0.371	0.039	

AVSED: the overall averaged standard error of differences of means. For response Mines, the AVSED is not presented as all comparisons should be done on the transformed log scale.

presents the predicted means for the three treatment categories. As expected, the average grain yield of millet heads with parasitism fell in between the averages of undamaged and damaged millet heads, and the positive effect of parasitism was about 34% (difference between average of damaged millet heads and average of those with parasitism). Additional benefits may include reduction in millet head miners in subsequent generations. The highly significant differences among millet head categories are particular noteworthy when the heterogeneity among fields is taken into account. Furthermore, all 12 data sets contained at least 8% (average = 20% and maximum = 30%), so the significant differences among millet head categories were not attributed to a bias caused by parasitism predominantly occurring in a only few of the 12 fields. This is important, because it supports the argument that differences in grain yield between the treatment classes (no damage, damage but no parasitism and parasitized by *H. hebetor*) is likely a combination of head miner infestation severity and level of parasitism.

The highest number of individual mines in a single millet head was 25. Such high infestation levels are corroborated by findings of 10–40 developing larvae in each millet head (Gahukar 1990). However in this study, only a few millet heads contained more than 10 mines. Figure 1a reveals an interesting pattern in the relationship between number of millet mines and grain yield for millet heads with damage or with damage and parasitism. There was a strong decreasing trend in grain yield as the number of mines increases millet heads with damage, while average grain yield from millet heads with and parasitism fluctuate around the overall mean. The difference in trends between the two categories clearly demonstrates the positive effect of parasitism on grain yields. Based on a highly significant regression fit of average grain yield to mine length divided into millet head length intervals (adjusted R^2-value = 0.96; d.f. = 3,20, F-value = 237.04, P-value < 0.0001), we found that (fig. 1b): (i) non-infested pearl millet heads yielded, on average, 38.4 g of grain, (ii) the grain yield was reduced by about 50%, when the mine length reached 25–30 cm and (iii) there was an almost linear decrease in grain yield with mine length between 40–80 cm. Figure 2 clearly demonstrated that: (i) millet head mine damage caused a marked decrease in grain yield in all fields and in all millet head length intervals and (ii) that parasitism reduced the negative effect of millet head mine damage. We are unaware of any previous studies providing insight into the quantitative relationship between millet head miner damage

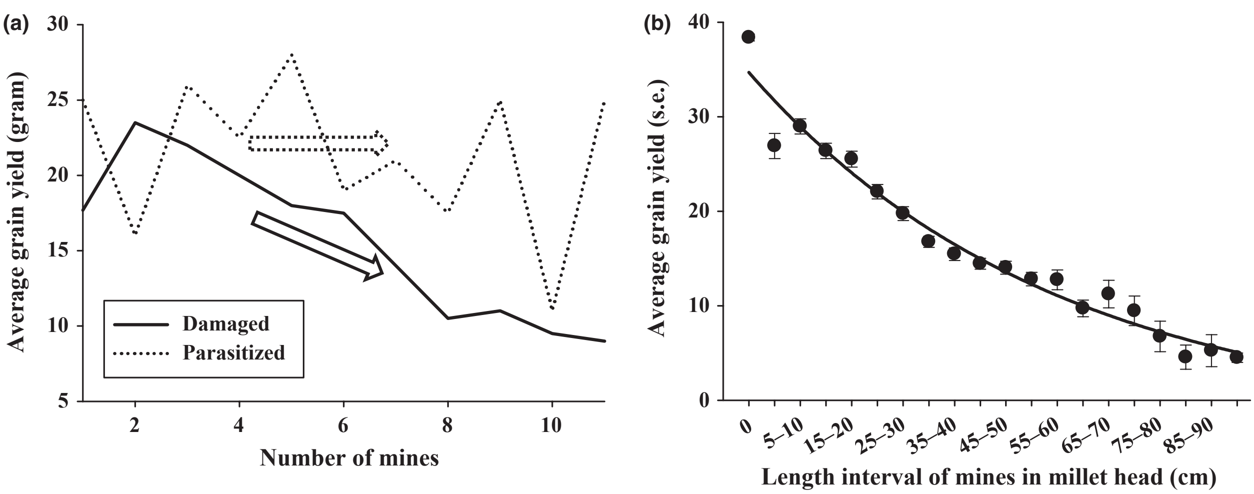

Fig. 1 Relationship between number of mines and grain yield in millet heads damaged by millet head miners and with/without parasitism (a). The arrows indicate general trends for the two treatment categories. Relationship between total length of mines and grain yield in millet heads (b).

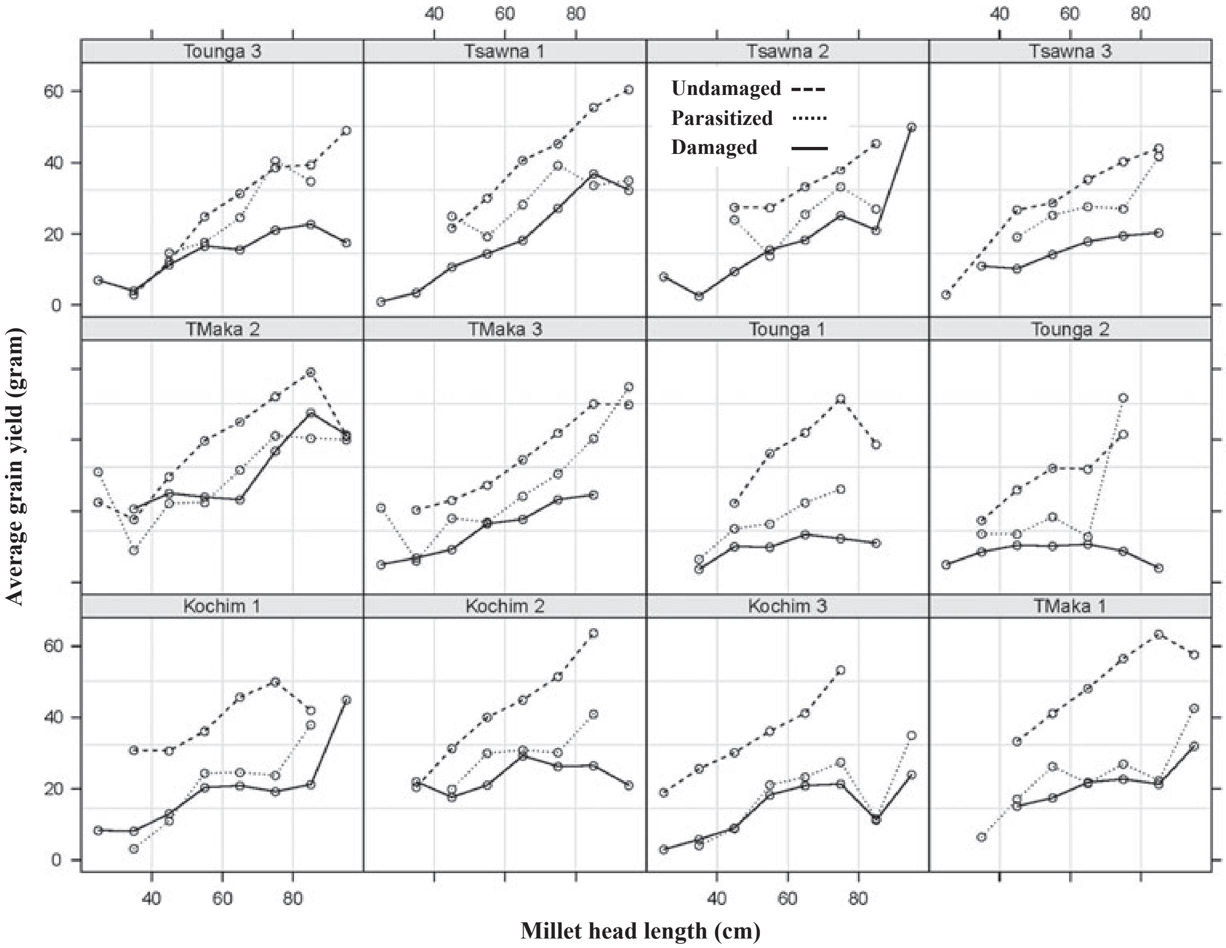

Fig. 2 Relationship between average total length of mines and average grain yield for damaged millet heads with/without parasitism, and average grain pearl millet grain yield of pearl millet heads with: no damage to millet heads in all 12 fields.

and grain yields from individual pearl millet heads. Our analysis therefore shows the quantitative importance of millet head miner damage, and it enabled us to estimate the potential importance and benefit of parasitism.

H. hebetor dispersal in response to predominant wind direction

In the 2011 growing season, the average total length of millet head mines ranged from 2.00–20.88 cm and the average number of mines per pearl millet head per field ranged from 0.32–3.75. Of the 900 pearl millet heads collected, 514 were infested with at least one millet head miner and with infestation percentages per field ranging from 2 to 88%. We did not collect yield damage data in the 2011 growing season, so it was not possible to validate the correlation between millet head miner infestation and grain yield. However, we found a similar relationship between number of mines and total length of mines as was observed for the 2010 growing (fig. 3). With only one directional transect and no information on naturally occurring *H. hebetor* population density, and alternate host availability, there are clearly numerous confounding variables and a statistical analysis was not considered appropriate. Despite these constraints, we found that levels of both parasitism and millet head miners were highest in upwind direction from the release site (fig. 4a). The percentage of parasitism was markedly highest in the upwind direction (fig. 4b), but within the 30 km transect, there was a clear negative trend, which suggested that other factors (other than distance from release site) may have influenced the obtained pattern. Furthermore, these findings highlight the importance of continued research into factors affecting establishment, persistence and performance of *H. Hebetor* as control agent of millet head miners.

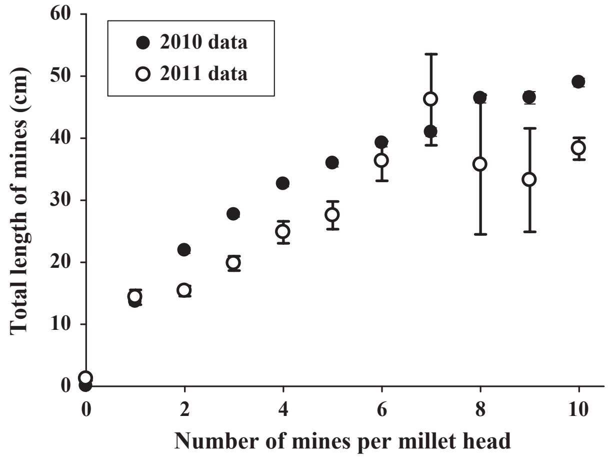

Fig. 3 Relationship between number of mines per head and average total length of mines in two growing seasons.

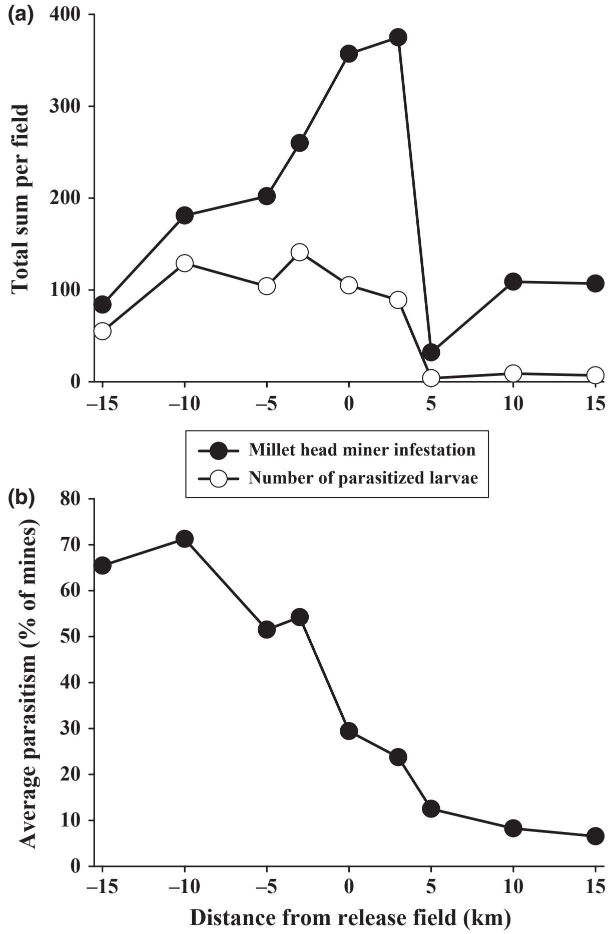

Fig. 4 Sum of mines in infested pearl millet heads (infestation) and parasitized millet head miner larvae (parasitism) (a) and percentage parasitism (b) along an east–west transect according to the prevailing wind (south to southwest). An augmentative release of *H. hebetor* was conducted in the centre of the transect. Negative distances were fields in upwind direction of the release site.

Perspectives

The quantitative analysis presented here corroborates previous reports of: (i) millet head miners causing significant pearl millet losses (Vercambre 1978; Gahukar 1984; Payne 2006), (ii) parasitism by *H. Hebetor* having a highly positive impact on millet grain yields. Between 2006 and 2008, augmentative mass releases of *H. hebetor* were conducted in more than 385 villages or >200 000 ha in southern Niger, and these releases were believed to increase pearl millet yields by as much as 40% (Payne et al. 2011). The factors limiting establishment and persistence of *H. hebetor* are so far unknown and deserve further research attention, but lack of alternative hosts and adverse climate conditions outside the millet growing season are likely constraints. As a consequence, annual augmentative releases of *H. hebetor* appear to be required for control of millet head miner populations. The proposed region-wide increase in pearl millet productivity in response to augmentative mass releases of *H. hebetor* are corroborated by the findings presented in this study, which showed that: (i) there was a strongly negative correlation between damage (mining) and grain yield, (ii) there was a strongly negative correlation between presence of millet head miner cadavers (indication of parasitism by *H. hebetor*) and pearl millet head damage, (iii) millet head miner was detected in 64% of the examined pearl millet heads and caused about 50% grain loss and (iv) parasitism reduced grain losses from individual millet heads by about 41%. Our data suggested that augmentative mass releases of *H. hebetor* disperse within a 5 km range from the release site. Due to considerable within- and between-field variation in pearl millet stands, it is very important to: (i) conduct experimental field work in actual farmers fields and (ii) large data sets are necessary to account for within- and between-field variation. The analysis presented here is encouraging and strongly supports intensification of mass-rearing of *H. hebetor*, expansion of educational activities to increase local empowerment under understanding of the potential of augmentative biological control and optimization of *H. hebetor* mass release programmes.

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