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Field persistence of *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) following augmentative releases against the millet head miner, *Heliocheilus albipunctella* (de Joannis) (Lepidoptera: Noctuidae), in the Sahel

A. Kabore [a,b], N.M. Ba [c,a,*], C.L. Dabire-Binso [a], A. Sanon [b]

[a] Institut de l'Environnement et de Recherches Agricoles, CREAF de Kamboinsé, 01 BP 476 Ouagadougou 01, Burkina Faso

[b] Laboratoire d'Entomologie Fondamentale dt Appliquée, Unité de Formation et de Recherches en Sciences de la Vie et de la Terre, Université Ouaga I Pr Joseph Ki-Zerbo, 06 BP 9499 Ouagadougou 06, Burkina Faso

[c] International Crops Research Institute for the Semi-Arid Tropics, BP 12404 Niamey, Niger.

HIGHLIGHTS

- *H. hebetor* parasitism of MHM remains high one year after release.
- Releases of *H. hebetor* in two successive years slightly reduced MHM damage.
- *H. hebetor* host feeding contributed additional MHM mortality.
- Augmentative releases of *H. hebetor* every two years may be sufficient.

GRAPHICAL ABSTRACT

1.Parasitoid bags attached to a tree | 2. MHM 4th instar larva Within pearl millet spike | 3. *H. hebetor* larvae over MHM larva

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ABSTRACT

Biological control by augmentative releases of the parasitoid wasp *Habrobracon hebetor* Say (Hymenoptera: Braconidae) is a promising strategy for controlling the millet head miner (MHM), *Heliocheilus albipunctella* (de Joannis) (Lepidoptera: Noctuidae). A current biological control program in the Sahel region involves inoculative releases of the parasitoid each growing season, but this is prohibitively expensive. The present study aimed to quantify residual parasitism of MHM in years after augmentative release. We also investigated the impact of two successive annual releases of *H. hebetor* on MHM parasitism. Two successive releases did not increase parasitism, but slightly reduced MHM damage in terms of number of mines and their length. Parasitism levels decreased in subsequent years if no additional parasitoids were released. Nevertheless, in the first year after release, parasitism levels in release villages remained significantly higher than in control villages. These findings suggest that augmentative releases could be carried out biennially instead of annually. Possible means of enhancing parasitoid survival between seasons are discussed.

1. Introduction

Pearl millet is the world's hardiest warm-season cereal crop, surviving even on the poorest soils in the driest regions, and in the hottest climates. Despite this extreme climatic adaptation, pearl millet suffers from many biotic constraints including insect pests (Nwanze and Harris, 1992). Among these, the millet head miner (MHM), *Heliocheilus albipunctella* (de Joannis) (Lepidoptera: Noctuidae), is a key pest of millet in the Sahel region of Africa. *H. albipunctella* is a univoltine species that diapauses from October to June (Gahukar et al., 1986) and attacks pearl millet during the rainy season from June to October. In Burkina Faso, infestations

* Corresponding author at: International Crops Research Institute for the Semi-Arid Tropics, BP 12404 Niamey, Niger.

E-mail addresses: adamskab9@gmail.com (A. Kabore), b.malick@cgiar.org (N.M. Ba).

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of *H. albipunctella* are more severe in drier northern zones (Nwanze and Harris, 1992). Damage of *H. albipunctella* is due to larvae that feed on the panicle and prevent grain formation (Ndoye, 1991; Nwanze and Harris, 1992). Outbreaks of the MHM are observed almost every year in the Sahel, especially on early planted millet or early maturing material (Eisa et al., 2007) and yield losses range from 40 to 85% (Gahukar et al., 1986; Nwanze and Sivakumar, 1990; Krall et al., 1995; Youm and Owusu, 1998).

Control strategies that involve the use of insecticides, host-plant resistance, and cultural management practices (Gahukar, 1990, 1992; Nwanze and Sivakumar, 1990) have been tested with limited success and applicability (Nwanze and Harris, 1992). In the early 1980s, natural parasitism of MHM by *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) in the Sahel was reported to be as high as 95% towards the end of the season, after crop damage had already occurred (Gahukar et al., 1986; Bhatnagar, 1987; Nwanze and Harris, 1992). The first augmentative releases of *H. hebetor* against MHM were attempted in Senegal in 1985 (Bhatnagar, 1989), and subsequently in Niger in the early 2000s (Garba and Gaoh, 2008). In recent years, the potential for augmentative releases of *H. hebetor* to cause significant MHM mortality has been demonstrated (Payne et al., 2011; Ba et al., 2013, 2014). The parasitoids are released from small jute bags containing a mixture of millet grains and flour, together with 25 larvae of the rice meal moth, *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae), and two mated *H. hebetor* females (Ba et al., 2013, 2014). Emerging wasps escape through the jute mesh and disperse to parasitize MHM larvae in millet fields (Ba et al., 2013, 2014). These bags typically produce up to 70 parasitoids in 14 days with a 60:40 (male: female) sex ratio (Ba et al., 2014).

Although *H. hebetor* provides good control of the MHM, it has been assumed that the parasitoid population would not survive the nine month long off-season when the host is in diapause. Thus, the current biological control program encourages inoculative releases each growing season. However, there is little evidence to date that supports this view. Given that annual releases of parasitoids become prohibitively expensive over large scales, we investigated the persistence of *H. hebetor* populations in the years following a single release in a given location. In parallel, we investigated the effect of two successive annual parasitoid releases on the MHM population. These data will help improve recommendations regarding the frequency of *H. hebetor* releases that are required to control the MHM in the Sahel.

2. Material and methods

2.1. Study location

The research sites consisted of 14 villages with endemic infestations of the MHM in the Oudalan and Seno provinces of Burkina Faso. These locations are situated in the Sahel agroecological zone which has a unimodal rainfall pattern, the rainy season extending from June to October. Pearl millet is the main cereal crop and covers almost 80% of the cultivated area, usually in association with cowpea. Pearl millet is cultivated between June and October under rain-fed conditions, followed by small patches of irrigated vegetables from November to February, and a dry season between March and May. Total annual rainfalls during the study period were: 446 mm in 2010; 528 mm in 2011; 609 mm in 2012; 466 mm in 2013; 513 mm in 2015; and 497 mm in 2016. Maximum relative humidity reaches 92% during the millet season, averages 34% during the vegetable production season, and drops to 26% during the dry season. Temperatures ranged from 24 to 39 °C during the rainy season, 15 to 38 °C in the vegetable season, and 22 to 43 °C in the dry season. The region is mostly covered with annual grass species, with areas of woodland and shrubland in which the dominant trees are *Acacia* species, *Balanites aegyptiaca*, *Faidherbia albida*, *Combretum glutinosum*, *Guiera senegalensis*, *Boscia senegalensis* and *Piliostigma reticulatum* (Lykke et al., 2004).

2.2. Parasitoid rearing

A colony of *H. hebetor* was established from field-collected larvae of the MHM and maintained in the laboratory on the rice meal moth, *C. cephalonica*, at the Institut de l'Environement et de Recherches Agricoles at Kamboinse, Burkina Faso. Both insects are routinely cultured in the laboratory at room temperature (mean = 26 ± 2 °C) with wild insects added to the colonies once a year. The rice moth is reared on a mixture of pearl millet grain and flour in wooden cages (20 × 20 × 13 cm) and the parasitoid is reared on third and fourth instar larvae of *C. cephalonica* using the technique described by Ba et al. (2013, 2014).

2.3. Persistence of H. hebetor populations following single releases

This experiment was carried out with a group of eight villages selected for endemic infestations of the MHM with over 60% of panicles infested (Ba et al., 2010). Typical villages have a diameter of 2 km with over 70% of the cultivated land in pearl millet. The eight villages were divided into two groups of 4 and assigned to one of the following treatments: 1) four 'release villages' that were each supplied with 15 parasitoid bags and, 2) four 'control villages' that did not receive parasitoids. All villages were separated by at least 5 km and all control villages were at least 40 km away from release villages (Ba et al., 2014). For release villages, the parasitoid wasps were released using jute bags of 15 cm × 25 cm containing 200 g of millet grains, 100 g of millet flour, 25 *C. cephalonica* larvae (a mixture of third and fourth instars) and two mated *H. hebetor* females. In each release village, the parasitoid bags were evenly distributed among five millet farms (three bags/farm) using the method described by Ba et al. (2014). The augmentative releases were carried out in release villages in the 2010 rainy season without further releases in those villages from 2011 to 2016. Data on MMH damage (number and length of mines) and parasitism levels were recorded 30 days after parasitoid releases in 2010; the same data were recorded in the same villages and the same fields in each subsequent rainy season from 2011 to 2013; and in 2016. For this purpose, 100 millet panicles were randomly selected from each of five millet farms in each village and dissected. The numbers of live (unparasitized) and parasitized larvae were recorded. Larvae parasitized by *H. hebetor* were easily distinguished by the presence of cocoons (Garba and Gaoh, 2008). We also recorded the number of dead host larvae without *H. hebetor* cocoons present.

2.4. Impact of successive parasitoid releases on the MHM

This experiment was carried out in a different set of six villages. Parasitoids were released twice in these villages, first in the 2015 rainy season, and again in the 2016 rainy season, each time in the same pearl millet fields. There were three 'release villages' that each received 15 parasitoid bags in 2015 and again in 2016, and three 'control villages' that did not receive parasitoids in either year. The selection of villages, releases of parasitoids, and data collection were all as described in Section 2.3.

2.5. Data analysis

Data were subjected to an independent *t*-test to compare release villages with control villages using SAS software version 9.1 (SAS, 2003). The number of mines and numbers of parasitized larvae were both log (n + 1) transformed prior to analysis. For the field persistence experiment, comparisons were made for each year. For the experiment with successive releases, comparisons between release and control villages were made annually, but release villages were also compared between 2015 and 2016.

3. Results

3.1. MHM damage following a single release of H. hebetor

Numbers of MHM mines fluctuated over years (Fig. 1). Parasitoid releases in millet fields significantly reduced the number of mines caused by the MHM in 2010, the year of the releases ($t_{1,526}$ = *8.53*, $P < 0.0001$). However, no significant difference was observed between control and release villages in 2011, a year after parasitoid releases ($t_{1,714}$ = 1.20, P = 0.22). The following year (2012), the number of mines was significantly higher in release villages than in control villages ($t_{1,1011}$ = 2.83, P = 0.004). Conversely, in 2013, three years after parasitoid releases, significantly higher numbers of mines were recorded in control villages ($t_{1,549}$ = 3.23, P = 0.001). In 2016, six years after the initial releases, damage by MHM was as high as in 2010, with no significant difference between the two types of villages ($t_{1,2248}$ = 1.22, P = 0.21, Fig. 1).

The mean length of mines, which reflects the extent of MHM damage, was significantly lower in villages that received parasitoids in 2010 than in control villages ($t_{1,526}$ = 6.42; $P < 0.0001$). The same trend was noted the following years in 2011 ($t_{1,714}$ = 7.36; $P < 0.0001$) and 2012 ($t_{1,1011}$ = 2.44, P = 0.01) without any additional parasitoid releases (Fig. 2). However, three years after parasitoid releases in 2013, the lengths of mines were similar for both types of villages ($t_{1,549}$ = 1.36, P = 0.17). In 2016, six years after initial releases, MHM mines were once again as long as they were initially in 2010, but with a significant difference between the two types of villages ($t_{1,2248}$ = 2.24, P = 0.02, Fig. 2).

3.2. Parasitism of MHM following a single release of H. hebetor

Parasitoid releases in 2010 significantly increased MHM parasitism by *H. hebetor* compared with control villages ($t_{1,526}$ = 9.49, $P < 0.0001$). Parasitism decreased the following year but remained significantly higher in release villages ($t_{1,714}$ = 6.56, $P < 0.0001$, Fig. 3). However, parasitism levels did not differ significantly between release and control villages in either 2012 ($t_{1,1011}$ = 0.20, P = 0.83), 2013 ($t_{1,549}$ = 1.18, P = 0.23), or 2016 ($t_{1,2248}$ = 1.65, P = 0.09, Fig. 3).

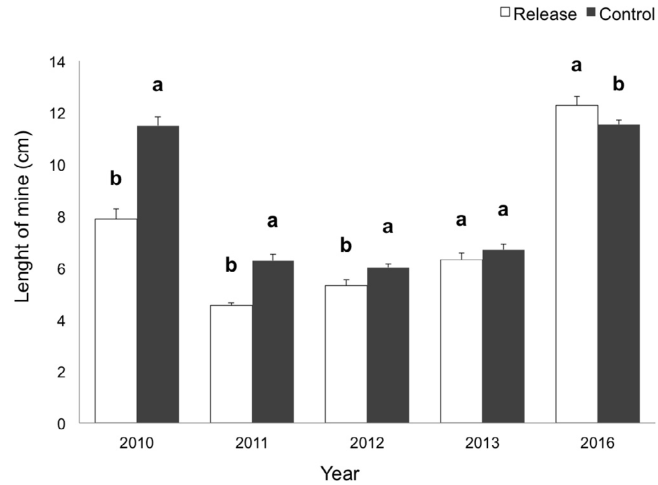

Fig. 2. Mean (+SE) length of *H. albipunctella* mines in release and control villages in five different years after single releases of *H. hebetor* in 2010. Columns bearing different letters were significantly different (independent *t*-test, α = 0.05).

Some dead MHM larvae were found without *H. hebetor* cocoons or evidence of any other natural enemy. These comprised between 3 and 26% of total dead larvae, with no significant differences in their occurrence between release and control villages in most years (2010: $t_{1,526}$ = 0.86, P = 0.38; 2011: $t_{1,714}$ = 0.47, P = 0.63; 2012: $t_{1,1011}$ = 0.59, P = 0.55; 2013: $t_{1,549}$ = 0.70, P = 0.48). However in 2016, there were significantly more larvae died of unknown causes in control villages than in release villages ($t_{1,2248}$ = 6.46, $P < 0.0001$).

3.3. MHM damage after two successive years of H. hebetor releases

Releases of parasitoids in millet fields in 2015 significantly resulted in fewer mines per panicle (mean ± SE = 2.32 ± 0.02) in the same cropping season compared with control villages (mean ± SE = 2.48 ± 0.03, $t_{1,2998}$ = 3.46, P = 0.0005). In contrast, despite subsequent releases of parasitoid wasps in 2016, the number of mines per panicle was higher in release villages than in control villages (mean ± SE = 2.66 ± 0.04 vs. 2.35 ± 0.03, respectively,

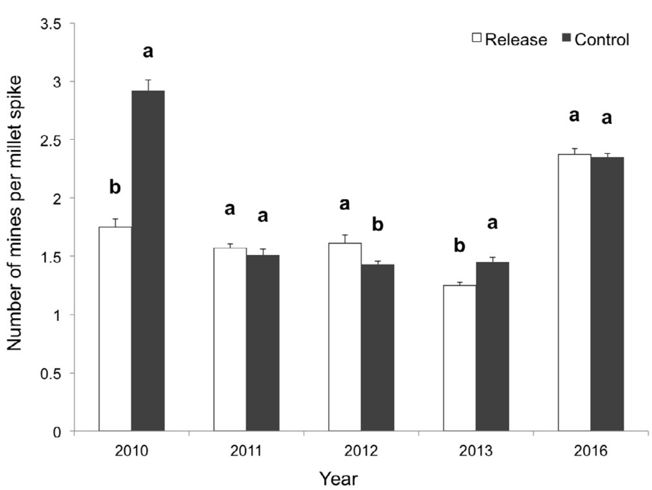

Fig. 1. Mean (+SE) number of *H. albipunctella* mines per millet spike in release and control villages in five different years after single releases of *H. hebetor* in 2010. Columns bearing different letters were significantly different (independent *t*-test, α = 0.05).

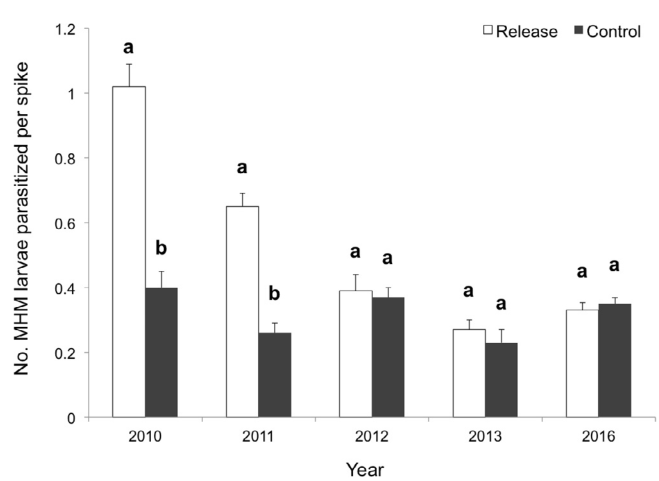

Fig. 3. Mean (+SE) numbers of *H. albipunctella* larvae parasitized by H. hebetor per millet spike in release and control villages in five different years after single releases of H. hebetor in 2010. Columns bearing different letters were significantly different (independent *t*-test, α = 0.05).

$t_{1,2998} = 4.51$, $P < 0.0001$). Comparing release villages only, significantly more mines were recorded in 2016 than in 2015 ($t_{1,2998} = 4.68$, $P < 0.0001$). However, mine length was significantly reduced by parasitoid releases in both 2015 (mean ± SE = 10.74 ± 0.14 vs. 11.56 ± 0.17, respectively, $t_{1,2998} = 3.57$, $P = 0.0004$) and 2016 (mean ± SE = 9.96 ± 0.16 vs. 11.76 ± 0.17, respectively, $t_{1,2998} = 7.60$, $P < 0.0001$). Furthermore, additional releases of parasitoids in 2016 significantly reduced mine length compared to 2015 ($t_{1,2998} = 3.57$, $P < 0.0001$).

3.4. Parasitism of MHM after two successive years of H. hebetor releases

Parasitoid releases significantly increased *H. hebetor* parasitism of MHM in both 2015 ($t_{1,2998} = 15.87$, $P < 0.0001$) and 2016 ($t_{1,2998} = 15.49$, $P < 0.0001$) compared with control villages (Fig. 4). Successive releases of parasitoids in the same villages in 2015 and 2016 did not significantly increase parasitism across years ($t_{1,2998} = 1.83$, $P = 0.06$, Fig. 4).

The number of MHM larvae dead from unknown causes accounted for 10–30% of total larval mortality and was not significantly affected by parasitoid releases in either 2015 ($t_{1,2998} = 0.50$, $P = 0.61$) or 2016 ($t_{1,2998} = 0.51$, $P = 0.60$). However, there were more dead MHM larvae without *H. hebetor* cocoons in release villages in 2015 than in 2016 ($t_{1,2998} = 5.87$, P < 0.0001).

4. Discussion

Apart from the impact of *H. hebetor*, differences in MHM damage among years are at least partly a consequence of yearly variation in pest abundance. The relative abundance of MHM could be influenced by pearl millet planting dates and flowering periods (Youm and Gilstrap, 1993; Sastawa et al., 2002), the varieties planted by farmers (Gahukar, 1990), and rainfall patterns (Nwanze and Sivakumar, 1990). In the present study, a single augmentative release of *H. hebetor* significantly increased parasitism of MHM in that cropping season and the following year. The number of MHM larvae killed by *H. hebetor* was twice as high in release villages than in controls, suggesting that half the parasitism recorded in released villages could be attributed to released wasps, similar to previous findings (Ba et al., 2013, 2014; Baoua et al., 2013). Augmentation also resulted in lower spike damage by MHM, but without additional releases, *H. hebetor* parasitism remained low in

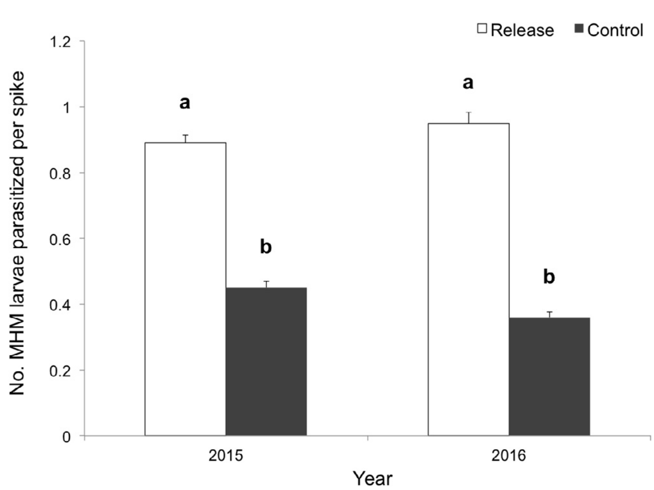

Fig. 4. Mean (+SE) numbers of *H. albipunctella* larvae parasitized per millet spike by *H. hebetor* in release and control villages after two successive releases of *H. hebetor* in 2015 and 2016. Columns bearing different letters were significantly different (independent *t*-test, $\alpha = 0.05$).

subsequent years. Consequently, parasitoid releases reduced MHM damage in the first two years following release, but not in subsequent years. Likewise, parasitoid releases in two successive years resulted in similar levels of parasitism in both years, which suggests no cumulative impact of two sequential releases. Similarly, parasitoid releases in two successive years did not reduce MHM damage more than did a single release. In addition to MHM larval mortality inflicted by *H. hebetor* wasps, substantial numbers of larvae were killed with no sign of any obvious natural enemy. When the cause of larval mortality was unknown, the dead larvae were similar in appearance as those killed by *H. hebetor* except for the absence of cocoons. Similar findings were reported in Niger (Baoua et al., 2013. Additional natural enemies of MHM in the Sahel include predators, eggs parasitoids and a larval parasitoid (Chalcidae) (Gahukar et al., 1986). The unknown larval mortality could not be attributed to predators, as they would have consumed the larvae, or at least part of it. Nor were larvae parasitized by another parasitoid, as cocoons or pupae would have been found. However, *H. hebetor* adults sometimes feed on host larvae (Hagstrum and Smittle, 1977), so some of this mortality might be attributed to *H. hebetor* host-feeding activity.

Our results indicate that *H. hebetor* populations do not persist for more than two years after augmentative release. The host species, *H. albipunctella*, develops only during the rainy season and remains in diapause for more than 10 months (Gahukar et al., 1986). Even though *H. hebetor* is endemic to the region (Gahukar et al., 1986; Bhatnagar, 1987; Nwanze and Harris, 1992), it must either develop on an alternative host species or enter diapause in order to survive the period of MHM scarcity. Reproductive diapause can be induced in *H. hebetor* by a combination of photoperiod and low temperature (Chen et al., 2012) but there are no reports of *H. hebetor* diapausing naturally in the Sahel region and it is believed to develop throughout the year on a wide range of stored product moths, most commonly *C. cephalonica* in the cereal stocks of northern Burkina Faso (Waongo et al., 2013, 2015). In addition to stored-product moths, *H. hebetor* develops on several field pests, including *Helicoverpa armigera* (Hübner), *Spodoptera* spp., *Earias* spp. and *Maruca vitrata* (F.), all of which are present in Burkina Faso (Nibouche, 1992; Ba et al., 2009). However, these potential host species are either sporadically present or rare in the region.

Environmental conditions can be critical for parasitoid establishment (Naranjo, 2001; Wright et al., 2005). In the Sahel, daily outdoor temperatures above 45 °C and relative humidity as low as 15% are common in the off-season, and these are unfavorable conditions for *H. hebetor* development and survival (Farghaly and Ragab, 1984; Forouzan et al., 2008; Zhong et al., 2009). In India, *H. hebetor* populations decrease as temperatures increase and increase when relative humidity is high (Dabhi et al., 2011). Furthermore, *H. hebetor* populations in India are able to shift from field hosts in the rainy season to stored-product hosts in the off-season. It is also possible that the source of our *H. hebetor* population is significantly limiting its fitness in the released location (Saadat et al., 2014, 2016; Borzoui et al., 2016).

Taken together, these factors might explain why MHM parasitism by *H. hebetor* tended to decrease in the years following a single augmentative release. Perhaps massive parasitoid releases, sufficient to reduce the number of diapausing hosts that survive to trigger infestations the following year, could lead to better suppression of the pest in subsequent years. Successive annual releases of parasitoids has led to the suppression of some insect pests (Greathead, 2003; Collier and van Steenwyk, 2004; Harris et al., 2010; van Lenteren, 2012). However, this strategy would require an area-wide, large-scale biological control program that covered the whole affected area of northern Burkina Faso and the neighboring countries of Mali and Niger, otherwise the pest would be able to migrate from infested areas to non-infested areas. In annual crops, the annual inoculation of natural enemies may be required for effective biological control simply because of annual habitat disruptions caused by agricultural activities (Obrycki et al., 1997). Hence, one might consider a conservation biological control strategy with habitat manipulation to assist parasitoid survival during the off-season (Altieri and Letourneau, 1982; Obrycki et al., 1997). The adoption of agro-forestry systems that increase biological diversity in the agricultural landscape could also create more ecological niches in time and space for MHM biocontrol agents (Brévault et al., 2014). Natural enemies would benefit from additional resource availability, especially during the dry season. Shrubs and trees could harbor alternative host insects and provide floral resources such as nectar for the *H. hebetor* population before MHM larvae become available in pearl millet fields, as they have done in other cropping systems (Frank, 2010; Simpson et al., 2011; Sivinski, 2013; Morgan et al., 2016). Additional vegetation would also create a more favorable microclimate for *H. hebetor* during the hot, dry season. Investigations should address the commonly available *Faidherbia albida* (Delile) A. Chew on which *H. hebetor* occurs (Lale and Igwebuikew, 2002). In the meantime, parasitoids releases could be limited to once every two years in the Sahel to reduce the cost of the program without compromising its effectiveness.

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