DOI: 10.1079/BER2006434

### **REVIEW ARTICLE**

## Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): searching for sustainable control strategies

J. Jaramillo<sup>1,2</sup>, C. Borgemeister<sup>2\*</sup> and P. Baker<sup>3</sup>

<sup>1</sup>Institute of Plant Diseases and Plant Protection, University of Hanover, Herrenhäuser Str. 2, 30419 Hanover, Germany: <sup>2</sup>International Centre of Insect Physiology and Ecology, PO Box 30772-00100, Nairobi, Kenya: <sup>3</sup>CABI Bioscience, Silwood Park, Ascot, Berks, SL5 7TA, UK

#### Abstract

The coffee berry borer *Hypothenemus hampei* (Ferrari) is the most serious pest of the world's most valuable tropical export crop. Since the last review on this insect was published six years ago, many new studies have contributed to an improved insight into the biology and ecology of the beetle, and have indicated new avenues for integrated and biological control. The latest developments in research, both laboratory and field, on the pest, its natural enemies and their implications for integrated control of *H. hampei* are summarized, with a particular focus on the situation in The Americas. Lately, the global coffee industry has changed radically; it has suffered a long cycle of lowest-ever world market prices caused by overproduction and technological change. At the same time, the advent of sustainable certification schemes has had a major impact on the industry. The role of integrated pest management and biological control of *H. hampei* in an era of changes in the coffee industry is discussed.

Keywords: coffee, biological control, integrated pest management, *Hypothenemus hampei*, parasitoids

#### Introduction

In 70 countries in the humid tropics, coffee (*Coffea* spp., Rubiaceae) is the most important agricultural commodity. Its production has increased over the last decades through the use of high yielding varieties, fertilizers and high density planting (Baker *et al.*, 2002). However, in many countries coffee production is severely threatened by a number of pests and diseases. The most important of the insect pests is the coffee berry borer *Hypothenemus hampei* 

\*Author for correspondence Fax: +254 20 8561690 E-mail: dg@icipe.org (Ferrari) (Coleoptera: Curculionidae: Scolytinae), (Le Pelley, 1968; Damon, 2000). *Hypothenemus hampei* causes serious economic losses and affects the economy of more than 20 million rural families in the world (fig. 1) (Vega *et al.*, 2003a). Extremely high levels of infestation in untreated plantations have been reported, e.g. Uganda 80%, Colombia 60%, Jamaica 58–85%, Tanzania 90%, Malaysia 50–90% and Mexico 60% (Vega, 2004). Presently many coffee farmers rely on the application of synthetic insecticides for control of *H. hampei*. Yet, endosulfan and chlorpyrifos, the two most commonly used insecticides against *H. hampei*, are highly toxic and a threat to the environment, the farmers who use them, and the communities living adjacent to treated coffee plantations (Baker *et al.*, 2002). Growing environmental concerns and increasing problems with insecticide

J. Jaramillo et al.

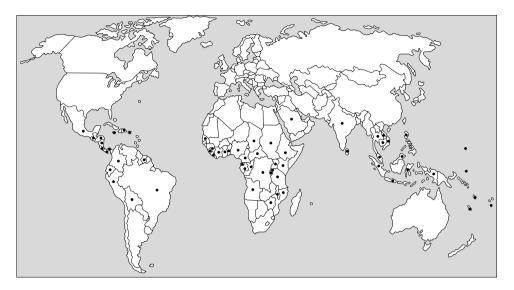


Fig. 1. Countries with known records of *Hypothenemus hampei*. Note: dots do not indicate the precise location where the pest was initially recorded or its present area of distribution within the respective countries.

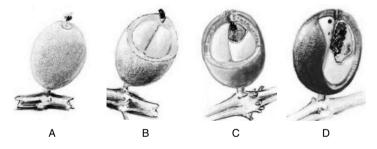


Fig. 2. Positions of the coffee berry borer Hypothenemus hampei in coffee berries (Bustillo et al., 1998; drawing by Gonzalo Hoyos, CENICAFE).

resistance in H. hampei (Brun et al., 1989; Gongora et al., 2001) have stimulated the search for environmentally more friendly control strategies against the pest. Since the most recent review on H. hampei (Damon, 2000) many new reports have contributed to a better understanding of the biology and ecology of H. hampei, as well as indicating new avenues for biological pest control. During this same period, the coffee industry has changed radically; it has suffered a long cycle of lowest-ever world market prices caused by overproduction and technological change (Varangis et al., 2003). At the same time the advent of sustainable certification schemes (Giovannucci & Koekok, 2003) has also had a major impact on the coffee industry. This review focuses on the latest discoveries on the biology and genetics of the beetle, with special emphasis on new findings on biological control of H. hampei primarily in The Americas. Finally, the role of integrated pest management (IPM) and biological control of *H. hampei* in an era of changes in the coffee industry is discussed.

#### Basic biology of H. hampei

The basic biology and ecology of H. hampei has been extensively reviewed by Damon (2000). Females (1.4–1.6 mm

long) attack developing coffee berries from about eight weeks after flowering up to harvest time (>32 weeks) (Baker, 1999). They bore galleries into the endosperm of the coffee berries (fig. 2), causing two types of damage, i.e. premature fall of young berries, and qualitative and quantitative losses in coffee through feeding of the gregarious larvae inside the berries (Le Pelley, 1968). Each berry is attacked by a single female (often referred to as the 'colonizing female'), and oviposition inside the galleries takes place over a period of 20 days; the female daily lays two to three eggs inside the berry (Bergamin, 1943). The population dynamics of, and the infestation pattern by *H. hampei* are closely related to climatic factors such as precipitation and relative humidity (Baker et al., 1992), as well as to the physiology of the coffee plant (Salazar et al., 1993; Ruiz, 1995). The dry matter content of the endosperm is the most crucial factor determining the attack by H. hampei and its speed of penetration into the coffee berry. Seeds with < 20% dry matter content are either abandoned after an initial attack, or the female waits in a tunnel bored into the exocarp until the endosperm has accumulated the sufficient amount of dry matter content for the development of her offspring (Alonzo, 1984). The female stays with her brood and does not leave the berry (Baker et al., 1992). Females of the first brood either leave

the berry after having mated with their male siblings inside the berries (Bustillo *et al.*, 1998), or after mating stay permanently in the berry and egg-laying resumes (Baker *et al.*, 1992). The males do not abandon the berry (Ticheler, 1961). The emergence of the searching females from the berries is triggered by high temperature and relative humidity (Baker *et al.*, 1992).

#### Recent advances in *H. hampei* biology

#### Wolbachia in H. hampei

Wolbachia are cytoplasmatically inherited proteobacteria found in the reproductive tissue of a wide range of arthropods, i.e. insects, isopods and mites; they can cause sex ratio distortions (Werren, 1997). Wolbachia cause the induction of parthenogenesis, cytoplasmatic incompatibility, male-killing and the conversion of male individuals into functional females (Stouthamer et al., 2002). In 2002 a species of Wolbachia was detected in H. hampei populations from Brazil, Colombia, Ecuador, India, Nicaragua, El Salvador, Benin, Honduras, Mexico and Uganda (Vega et al., 2002). These investigations suggest that the presence of Wolbachia might be one reason behind previous findings on the female-biased sex ratio of H. hampei (≈10:1) and on its functional haplodiploidy, i.e. the fact that both sexes are diploid but that only males transmit their maternally derived chromosomes to the offspring (Brun et al., 1995). However, in spite of its skewed sex ratio, no Wolbachia was detected in H. hampei populations from East Africa, the probable centre of origin of the pest (Vega et al., 2002). Though haplodiploid organisms often have female-biased sex ratios without any involvement of Wolbachia; this includes pseudoarrhenotokous species such as predatory mites that probably have similar genetic mechanisms of sex determination to H. hampei like paternal genome loss (Sabelis et al., 2002).

#### Biogeography of the coffee berry borer

Benavides et al. (2005), using amplified fragment length polymorphism (AFLP) DNA fingerprints, studied the diversity and biogeography of *H. hampei* and revealed low levels of genetic variability in beetles of different geographic origins, confirming previous findings by Andreev et al. (1998). These low levels of genetic variability of H. hampei have important pest control implications as they suggest that resistance to chemicals, if it were to emerge, would presumably become widespread much faster due to high levels of inbreeding (Brun & Suckling, 1992; Brun et al., 1995). Similar to Bergamin (1946), Benavides et al. (2005) also hypothesized that all accidental introductions of H. hampei into The Americas derived from West African source populations. They found the greatest match between fingerprints from South America and Africa in samples taken in Cameroon. However, the authors only sampled in two geographically rather adjacent locations in Cameroon, whereas for example in Uganda samples were taken in 11 different sites. Moreover, the authors strangely attributed Cameroon to be part of West and not Central Africa, and in previous reports H. hampei was believed to originate from Central and Eastern Africa (see review by Ticheler, 1961).

#### Fungal associations in H. hampei

A mutualistic interaction between some members of the weevil subfamilies Scolytinae and Platypodinae (i.e. bark and ambrosia beetles) (Farrell et al., 2001) and asexual fungi has been extensively studied. In such interactions, the fungi may contribute to the death of the host tree, or the beetles may benefit from the association by feeding on the fungi (Paine et al., 1997). A possible interaction between H. hampei and fungi has been hypothesized for many years. Waterson & Norris (1989) speculated that when H. hampei first-instar larvae feed on frass produced by their mothers they might acquire a symbiotic fungus. Subsequently, Rojas et al. (1999) and Morales-Ramos et al. (2000) reported a symbiosis of the beetle with Fusarium solani (Martius) (Moniliales: Tuberculariaceae), and the latter authors hypothesized that *H. hampei* obtains ergosterol, a key substance for the reproduction of the beetle, from the fungus. The study by Morales-Ramos et al. (2000) was the first to report a mutualistic relationship between H. hampei and a microbe. More recently Peterson et al. (2003) identified Penicillium brocae (Deuteromycotina: Hyphomycetes) in *H. hampei* populations from Mexico. In addition, Carrion & Bonet (2004), studying the mycobiota associated with H. hampei and its galleries, reported 13 different fungi. However, seven of them were saprophytes and one was the entomopathogenic fungus Beauveria bassiana (Balsamo) Vuillemin (Deuteromycotina: Hyphomycetes), the latter commonly reported infecting H. hampei in the field (Baker, 1999). In a similar study, Pérez et al. (2003) identified 40 fungal and two yeast species from H. hampei and its galleries. Also, Vega et al. (2003b) found a yeast species, Pichia burtonii Boidin, associated with H. hampei. They suspected that the yeast is involved in the breakdown of caffeine, but had to reject this hypothesis of a mutualistic relationship after subsequent laboratory studies. Moreover, most recently Pérez et al. (2005) demonstrated that F. solani and the yeast Candida fermentati (Saito) have no effect on reproduction and survival of H. hampei, thereby ruling out any mutualistic relationship between H. hampei and the fungus and the yeast. Hence, unlike in other scolytids (Paine et al., 1997), currently there is no evidence to suggest that H. hampei has mutualistic associations with fungi or yeasts.

#### Biological control of H. hampei

#### Parasitoids for H. hampei control

Cephalonomia spp. and Prorops nasuta

Classical biological control through introductions of the two bethylid wasps of African origin, *Cephalonomia stephanoderis* Betrem and *Prorops nasuta* Waterston in South and North America in the 1980s and 1990s (Barrera *et al.*, 1990; Baker, 1999), have not proven entirely successful. After quarantine in England and studies under laboratory conditions (Barrera *et al.*, 1989; Abraham *et al.*, 1990; Murphy & Moore 1990), the parasitoids were released in the field. Although both parasitoids established in North, Central and South American countries, their impact on field populations of *H. hampei* has been rather limited (Damon, 2000; Baker *et al.*, 2002). After these initial introductions, another *Cephalonomia* sp. native to North America was found naturally attacking field populations of *H. hampei* in

#### J. Jaramillo et al.



Fig. 3. Female Phymastichus coffea. Photo by Dr Georg Goergen, International Institute of Tropical Agriculture, Benin.

Chiapas province of southern Mexico (Pérez-Lachaud, 1998). It was later identified as C. hyalinipennis Ashmead, and has a very similar biology to C. stephanoderis and P. nasuta. All three species are larval-pupal ectoparasitoids of H. hampei and usually prey on H. hampei eggs; C. stephanoderis also attacks and feeds on the adult female H. hampei, whereas *P. nasuta* does not attack the beetle for feeding but does use their bodies (abdomens) to block the entrance to infested coffee berries (Lauziere et al., 1999; Infante et al., 2005). Moreover, unlike the two other bethylids that lay only one egg per host, C. hyalinipennis lays one to four or five eggs per host, and more eggs may be laid in other host species (Pérez-Lachaud, 1998; Pérez-Lachaud & Hardy, 2001). Female C. hyalinipennis can live for up to 95 days and their mean fecundity is higher than that of C. stephanoderis (Pérez-Lachaud & Hardy, 1999). In laboratory studies considerable inter- and intraspecific competition among C. stephanoderis, P. nasuta and C. hyalinipennis has been recorded (Pérez-Lachaud et al., 2002; Batchelor et al., 2005, 2006). In general, the wasps exhibited aggressive brood and host guarding behaviour, with C. stephanoderis being the most successful competitor and often killing its opponents (Batchelor et al., 2005). Additionally, when C. hyalinipennis was provided with immature stages of C. stephanoderis and P. nasuta (but not with the mother of the immature brood), the wasp behaved like a hyperparasitoid (Pérez-Lachaud et al., 2002, 2004). These authors concluded that C. hyalinipennis is a facultative hyperparasitoid of C. stephanoderis and P. nasuta, and results of their laboratory studies indicate that coexistence among the three parasitoid species might be unlikely based only on fighting behaviour recorded in the laboratory (Pérez-Lachaud & Hardy, 1999; Pérez-Lachaud et al., 2002; Batchelor et al., 2005), but might be possible under field conditions (Batchelor et al., 2006). However, even repeated augmentative releases of only one bethylid species yield levels of parasitism below 5% (Baker, 1999), suggesting that under field conditions the effect of inter- and intraspecific competition in reducing the efficacy of the parasitoids would

be insignificant. Nevertheless, even such a small impact of these bethylids on *H. hampei*, when integrated over an entire region, implies a positive economic effect, especially at times of low coffee prices when farmers often limit their more costly control measures. Anecdotal evidence suggests that when coffee plots are abandoned and the berries not harvested, the populations of bethylid parasitoids increase significantly (P.S. Baker, personal observation), which might limit the invasive impact of the pest on surrounding coffee farms.

#### Phymastichus coffea

A third parasitoid species introduced to The Americas, and subsequently also to India, for classical biological control of H. hampei is the eulophid Phymastichus coffea LaSalle (fig. 3). It was first discovered in Togo in 1987 (Borbón-Martinez, 1989) and later described by LaSalle in 1990. The latter author placed it taxonomically in the subfamily Tetrastichinae. Initially, Feldhege (1992) believed it to be the only species in the genus Phymastichus, though later LaSalle (1995) described P. xyleborii LaSalle, a parasitoid of the Hawaiian scolytid Xyleborus perforans (Wollaston). The distribution of P. coffea ranges from West (e.g. Togo, Benin and Ivory Coast), over Central (Cameroon and Uganda) to East Africa (Burundi and Kenya) (Lopez & Moore, 1998). It is a gregarious endoparasitoid of H. hampei adult females (Borbón-Martinez, 1989). Lopez et al. (1997) described P. coffea as an idiobiont and oligophagous parasitoid, though recently Shaw (2004) proposed the term imagobiont for parasitoids of adult insects. Under laboratory conditions, in addition to H. hampei, P. coffea parasitizes other Hypothenemus spp. such as H. seriatus (Eichhoff), H. obscurus (F.) (Lopez & Moore, 1998), H. eruditus Westwood and H. crudiae (Panzer) (Castillo et al., 2004a). Phymastichus coffea females start to search for their hosts immediately after emerging from the H. hampei mummy; parasitization of H. hampei can occur within the first hours

after emergence. According to Infante et al. (1994), P. coffea females lack a pre-oviposition period, whereas Feldhege (1992) reported pre-oviposition periods between 5 min and 4 h, with 20 min as the most frequent duration. *Phymastichus* coffea females possess a short and concealed ovipositor (LaSalle, 1990), which obliges them to assume a more or less vertical position on top of the host during oviposition. Oviposition takes 1-7 min. A P. coffea female can oviposit into the abdomen, thorax or between the thorax and the abdomen of the beetle (Feldhege, 1992) and usually lays two eggs per host, one female and one male. (For more detailed information on superparasitism see below.) A single female offspring develops in the abdomen of the beetle, whereas towards the end of its larval development the male migrates to the head and completes its development there (Lopez et al., 1997). After parasitization, the mobility of the female beetle is greatly impaired; moreover, parasitized females stop ovipositing and usually die after 12 days (Borbón-Martinez, 1989; Feldhege, 1992; Infante et al., 1994). Published data on the duration of the life cycle of P. coffea vary to a great extent: Lopez et al. (1997) reported 43 days at 24°C, Feldhege (1992) 30 days at 27°C, and Infante et al. (1994) 27.5 days at 26°C. Under field conditions in Colombia, the duration of the life cycle was 46 days at 22°C and 76% relative humidity (Vergara et al., 2001a,b). Likewise, published data on the lifespan of adult males and females vary considerably. Feldhege (1992) reports 30h for honeywater fed females and <22 h for males at  $25\pm2^{\circ}$ C, whereas Lopez et al. (1997) and Orozco (1997) reported 2-3 and 3–4 days for males and females at  $24 \pm 1^{\circ}$ C, respectively. In the latter two studies longevity of the females could be extended to up to 5 days in the laboratory when the parasitoids were fed with a honey-water solution.

*Phymastichus coffea* mass-rearing and releases in the field were first carried out in Colombia. Parasitoids were introduced and subsequently released in 1996 and 1997, respectively, and *P. coffea* establishment was reported in 1998 (Baker, 1999). Further releases followed and according to Aristizabal *et al.* (2004) the parasitoid has established to date on 41 farms in Colombia. Baker *et al.* (2002) documented additional successful cases of establishment of *P. coffea* in North, Central and South America. Under field conditions in Colombia, Jaramillo *et al.* (2005) observed that parasitism of *H. hampei* by *P. coffea* was significantly affected by the developmental stage of the coffee berries and by the position of the beetles inside the berries at the time of the parasitoid releases (fig. 2).

The population dynamics of, and the infestation pattern by H. hampei are closely related to climatic factors and the dry matter content of the coffee berries (see section on basic biology of H. hampei). Jaramillo et al. (2005) recorded highest levels of parasitism (85%) in berries younger than 160 days, which equals position B in fig. 2, thus preventing the H. hampei females from reaching the endosperm and hence damaging the coffee berries. Based on the results of their study Jaramillo et al. (2005) suggested that the timing of P. coffea mass releases in coffee plantations should depend on the age of the berries, to assure that the majority of the beetles have not yet reached the endosperm of the coffee berries at the time of the parasitoid releases. This can be comparatively easily determined through site-specific data on the major blossoming period and also on long-term climatic data since a heavy rain followed by a prolonged dry period usually triggers the blossoming of the coffee tree

(de Alvim, 1960). In Colombia, the well-distributed rainfall pattern leads to many flowerings and may present greater difficulties in assessing control points based on the fruiting phenology of the coffee plant.

In laboratory choice experiments, Castillo et al. (2004b) observed that P. coffea discriminates between parasitized and unparasitized hosts. These authors hypothesized that a marking pheromone is involved in this process and concluded that the ability to discriminate would increase the efficiency of the parasitoid in the field by avoiding superparasitism. However, Jaramillo et al. (2006) recorded considerable levels of superparasitism by P. coffea under field conditions in Colombia. For instance, often more than six P. coffea larvae were found in a single host, and these authors showed that the decision of the female to superparasitize is complex and affected by the age of the coffee berries, i.e. their dry matter content, which influences the ratio of available female hosts to searching parasitoids by providing refuges to the herbivore. Thus, in summary, though many aspects of the basic biology of the parasitoid are still unknown, P. coffea so far appears to be a candidate for biological control of H. hampei, especially because it primarily attacks adult female H. hampei outside the berries before they have started ovipositing into the endosperm, i.e. before the coffee beans have been damaged.

Compatibility of P. coffea with other H. hampei control methods. Within an IPM context, H. hampei control methods are divided into two main categories: (i) methods targeting H. hampei populations when they start to penetrate the coffee berries (positions A and B in fig. 2), such as applications of synthetic or microbial insecticides; and (ii) methods that aim at H. hampei stages inside the coffee berries, such as releases of the bethylid parasitoids C. stephanoderis and P. nasuta (Bustillo et al., 1998). Studies on P. coffea so far indicate that the parasitoid prefers to attack H. hampei females that are just starting to penetrate the coffee berries. Hence, other H. hampei control methods that target females in positions A and B (fig. 2) will most likely negatively affect P. coffea. Studies on releases/ applications of P. nasuta and B. bassiana and/or synthetic insecticides suggest that the timing of the releases/applications is of utmost importance and can considerably reduce negative effects on the parasitoids (Mejia et al., 2000; de la Rosa et al., 2000). Comparable studies with P. coffea and microbial and/or synthetic insecticides are needed to evaluate their compatibility and/or incompatibility as control agents of *H. hampei*.

*Mass rearing of* P. coffea. *Phymastichus coffea* is presently mass-released in South, Central and North American countries following an augmentative approach that requires high numbers of parasitoid females for field releases. To date, the major bottleneck for a high-output rearing of *P. coffea* is the production of large numbers of healthy *H. hampei* females. So far, two mass-rearing protocols for *P. coffea* have proven successful. The first one was developed by Infante *et al.* (1994) in México, and the second by the Centro Nacional de Investigaciones de Café (CENICAFE) in Colombia (Orozco, 2002).

Infante *et al.* (1994) proposed the use of healthy unripe berries for parasitoid rearing. Following their artificial infestation by the beetles, the *H. hampei*-infested berries are then exposed to *P. coffea* females. After approximately 30 days the parasitoids commence to emerge from the mummies.

CENICAFE's mass-rearing technique is slightly more complex and involves two steps: (i) H. hampei infestation of premium quality parchment coffee with an initial moisture content of 45%; and (ii) their later parasitization by P. coffea. During this latter step a gradual reduction in temperature and simultaneous increase in relative humidity is desirable. Using this methodology a complete life cycle of P. coffea takes at least 45 days, which is considerably longer than reported by Infante et al. (1994). However, the gradual decrease of temperatures, in addition to a rigorous cleaning of the beans, and the slowly rising relative humidity levels assure that fungal infection and desiccation of the beans are prevented, which would otherwise harm the development of the immature stages of *P. coffea* inside the beetles/berries. Using this methodology 16 million P. coffea adults were produced in CENICAFE's laboratories between 1996 and 2001 (Orozco, 2001).

Though the CENICAFE methodology to mass-produce the wasps has been successful, it is rather costly (Baker, 1999). Hence attempts to mass-produce the hosts using artificial diets have been undertaken. Based on previous work by Villacorta (1985) and Villacorta & Barrera (1996) in Brazil and Mexico, respectively, Portilla (1999a,b) developed in Colombia an easy to produce and significantly cheaper artificial diet for H. hampei called 'Cenibroca'. Presently, using Cenibroca artificial diet, hundreds of generations of the beetle hosts and its parasitoids have been mass-produced at low cost at an experimental level, with no significant decline in the fecundity of the insects. Preliminary calculations suggest that augmentative mass releases of P. coffea could be economically viable (Baker et al., 2002) if the parasitoid is effective at keeping low populations under control, though this remains to be tested in the field.

#### Heterospilus coffeicola

Damon (2000) mentioned field observations from Africa that suggest *Heterospilus coffeicola* Schmiedeknecht (Hymenoptera: Braconidae) to be an important natural enemy of *H. hampei*, thus a potentially promising classical biological control agent. Studies by Murphy *et al.* (2001) in Uganda indicate that *H. coffeicola* females lay only one egg per berry, and that the emerging larva consumes immature stages of *H. hampei*, consequently acting as a predator. However, to date, the wasp has not been used in biological control programmes against *H. hampei* due to, among others, the so far insurmountable difficulties in rearing the wasps under laboratory or even field conditions (Murphy *et al.*, 2001).

#### Predators for H. hampei control

So far, the only known predators of *H. hampei* are ants (Hymenoptera: Formicidae). According to Vega *et al.* (1999) in Africa *Leptophloeus* sp. near *punctatus* could be a specific predator of *H. hampei*. However, no further studies have been conducted to confirm such specificity. In Colombia, Armbrecht *et al.* (2005) studied ant diversity in shaded coffee plantations where one or several different shade trees were used and compared it to non-shaded coffee. They found that the number of ant species and their ecological associations and complexity decreased with intensification of coffee

production, i.e. less diverse shaded- and non-shaded coffee. In non-shaded coffee plantations Solenopsis picea Emery and Pheidole radoszkowski Mayr could out-compete and exclude other ant species and were found in great numbers and widely distributed in such a production system. In Colombia, seven ant genera have been observed attacking H. hampei, i.e. Solenopsis, Pheidole, Wasmannia, Paratrechina, Crematogaster and Brachymyrmex, with S. picea being often the most efficient predator of H. hampei in coffee plantations (Bustillo et al., 2002; Armbrecht et al., 2005). They penetrate the infested coffee berries, take out the immature stages of the beetles and transport them to their nests (Bustillo et al., 2002). Additionally, in Mexico Infante et al. (2003) observed that several ant species, for instance Pseudomyrmex, Azteca and Tapinoma spp. (all Hymenoptera: Formicidae), also prey on P. nasuta, one of the bethylid parasitoids of H. hampei.

#### Entomopathogenic nematodes for control of H. hampei

The paper by Allard & Moore (1989) constitutes the first report of entomopathogenic nematodes for H. hampei control. In laboratory experiments they demonstrated that a Heterorhabditis sp. (Rhabditida: Heterorhabditidae) causes mortality in adults and larvae of H. hampei, and suggested its use mainly against populations of the beetles attacking fallen berries on the soil. Later, Molina & Lopez (2002) demonstrated in the laboratory that H. bacteriophora Poinar and Steinernema feltiae (Filipjev) (Rhabditida: Steinernematidae) have the ability to locate, penetrate and attack H. hampei inside coffee berries, causing high levels of mortality inside ripe berries. More recently, Lara et al. (2004) found that the two nematode species not only can locate the hosts in the berries, but also are able to reproduce inside the immature stages and adults of *H. hampei*, thus having the potential to reduce pest populations in the field.

In addition to *H. bacteriophora* and *S. feltiae*, Castillo *et al.* (2002) discovered a species of *Sphaerulariopsis* (Tylenchida: Sphaerularioidea) attacking immature and adult stages of *H. hampei* in the field in Mexico. Poinar *et al.* (2004) reclassified this nematode species as *Metaparasitylenchus hypothenemi* (Nematoda: Allantonematidae). The nematode does not cause high mortality of *H. hampei* stages, but substantially reduces the fecundity of females (Poinar *et al.*, 2004).

#### Entomopathogenic fungi for control of H. hampei

Control of H. hampei using entomopathogenic fungi, and specifically B. bassiana, has been reviewed in great detail by Damon (2000). In more recent experiments in Colombia B. bassiana effectively controlled H. hampei in the field using a dose of  $1 \times 10^{10}$  to  $1 \times 10^{12}$  spores per coffee tree (Posada, 1998). Moreover, efforts have been undertaken to design more realistic bioassays to quantify the effectiveness of B. bassiana as an H. hampei biocontrol agent. For instance, Posada et al. (2002), using a leaf spraying bioassay, concluded that not only the virulence of the isolate has to be taken into account, but also factors like formulation, number of drops per leaf surface and number of spores per drop of solution are critical features that might affect the degree in *H. hampei* mortality. However, a concentration like the one used by Posada (1998) is at present economically not feasible. An enhancement of the virulence of the

fungus, however, would permit the use of a reduced dose rate. Recent studies at CENICAFE focus on the genetic diversity of *B. bassiana* with the aim of future genetic modifications (Gongora, 2005), building on previous successful experiences with Metarhizium anisopliae (Metsch.) Sorokin (Deuteromycotina: Hyphomycetes) (Rodríguez & Góngora, 2005). However, a great deal of work would need to be done before releasing a genetically modified fungus into the field. The main obstacle is that the above fungal species have wide host ranges and their biology and ecology in the coffee environment is almost completely unknown. To our knowledge, so far there are no convincing long-term studies that show the economic feasibility and the practical use of entomopathogenic fungi at farm level. In a study on the adoption of H. hampei IPM components in the Antioquia department in Colombia, 50.6% of the interviewed farmers had used entomopathogenic fungi for H. hampei control in the past, yet 71.1% of them had recently stopped using them because of, among other reasons, their lack of efficacy (Mejia & Lopez, 2002).

#### Implications for H. hampei IPM

# Cultural control of H. hampei: the importance of post-harvest management

A complete removal of all ripe berries after the harvest and during the inter-harvest period is an important control measure as it reduces vital sources of H. hampei reinfestations. Rigorous collection of berries from the trees and from the ground, termed in Colombia the 'Re-Re' strategy (for 'Recoleccion' and 'Repase', i.e. harvesting of berries and immediately thorough re-collection of remaining berries in the same field), can substantially reduce infestations in the field because ripe and dry berries harbouring H. hampei are removed, thereby reducing the source population of the beetles in the plantation (Bustillo et al., 1998). In addition to such a rigorous removal of ripe coffee berries, careful handling of H. hampei-infested berries after the harvest must be implemented, as this will prevent emergence of H. hampei females from infested berries and their return to the plantation. Castro et al. (1998) calculated that during harvest between 66 and 74% of the H. hampei population present in the plantation ends up in the processing area, and, if the coffee is not properly handled, a high proportion of the pest will return to the plantation to re-infest new berries.

In Colombia, several post-harvest control strategies have been developed and, since 1998, implemented in a participatory manner with small-scale coffee growers (Baker et al., 2002). Fibre bags with a 1mm mesh size are used, instead of plastic containers, to contain the freshly picked coffee berries, thereby preventing the escape of H. hampei females (Bustillo et al., 1998). This also allows air exchange that reduces the relative humidity inside the bags (Bustillo et al., 1998) since high levels of relative humidity are a strong trigger for the emergence of H. hampei (Baker et al., 1992). Containers with freshly harvested berries are covered in the washing stations with oil-smeared plastic covers to trap emerging H. hampei females (Bustillo et al., 1998). In a participatory research programme with 115 small-scale coffee growers in Colombia, Salazar et al. (2003) during one harvest period recorded the mean number of H. hampei

females trapped in such a manner ranging from 1576 to 20,266 per m<sup>2</sup> of lid. After the pulping the coffee beans are washed and the remaining pulp is usually composted. To prevent an escape of *H. hampei* females that have survived the pulping process, the piles of pulp are sprayed with *B. bassiana* (Bustillo *et al.*, 1998). Modification of the coffee dryers through addition of a muslin cover, helps to prevent the return of *H. hampei* to the plantation (Velez, 2000; Velez *et al.*, 2002).

Though these strategies of cultural and post-harvest control of *H. hampei* are extremely laborious and consequently very costly, especially for small-scale coffee growers (Baker, 1999), a recent study by Aristizabal *et al.* (2002) on the adoption of IPM strategies against *H. hampei* in Colombia reported that with an adoption rate of 89%, 'Re-Re' is by far the most frequently implemented control method, followed by post-harvest control with 40%.

The problem, however, with the emphasis on crop sanitation using 'Re-Re' is that biological control agents are removed along with *H. hampei*, thus reducing their effect and this therefore effectively removes a potential central pillar of an IPM strategy. In practice, crop sanitation is mostly carried out as a routine measure rather than based on a threshold decision because of the difficulty of accurately sampling pest levels on trees and on trees and ground (Baker, 1999). It seems that many farmers have arrived at a combination of sanitation and spraying that is at best only a rudimentary form of IPM. With the advent of high-density plantings (up to 10,000 trees ha<sup>-1</sup>) the human contamination during spraying is high, though we know of no published studies on this aspect.

#### Traps as an IPM component

In 1991, a study by Mendoza-Mora documented for the first time that a 1:1 mixture of methanol and ethanol could act as an attractant to coffee berry borer females (Mendoza-Mora, 1991). Subsequently, Mathieu et al. (1997) showed that visual stimuli are also important in host location by H. hampei. They tested white and red multi-funnel traps (Lindgren, 1983), baited with a 1:1 mixture of ethanol and methanol at three dose rates (i.e. 0.5, 1.5 and  $20 \text{ g day}^{-1}$ ) and concluded that red traps baited with low doses are more attractive to *H. hampei* females. They were able to catch 45% of the initially released H. hampei females. The volatile composition of C. arabica berries of different ages is highly dominated by different alcohols (Ortiz et al., 2004). Using ethanol:methanol baited traps, Dufour et al. (1999) conducted field studies in El Salvador and achieved a reduction in H. hampei infestations by 34.8% which subsequently led to the development of the commercial H. hampei trap BROCAP<sup>®</sup> (Dufour et al., 2001). Its validation under field conditions in commercial coffee plantations in El Salvador resulted in reductions in infestations levels of up to 80% (Dufour et al., 2004).

#### Some issues surrounding coffee, H. hampei, IPM and sustainability

We believe that in recent years IPM in coffee has lost ground to 'sustainability'. The latter covers matters related to farming and labour relations, marketing, water conservation and other aspects that are often subsumed under economic, environmental and social subheadings. With this concept of sustainability, IPM becomes merely one element among many others that the farmer has to comply with to achieve certifications for their produce (e.g. Fair Trade, Rainforest Alliance schemes). Such certifications in general can offer coffee growers (large plantation owners as well as small-scale farmers) significant economic benefits through higher prices.

Sustainability has undeniably become a force that has tackled some major issues and through certification brands, has brought these issues into the public domain. In this sense the advent of sustainable schemes can be seen as a way to increase IPM implementation. At a practical level though, there is a risk that available IPM information is incorporated into a farm management plan for the purposes of certification, and that this then becomes regarded as standard practice, even though the IPM schemes in question, for instance the use of entomopathogenic fungi and augmentative mass releases of the bethylid parasitoids of H. hampei (Fischerworring & Rosskamp, 2001), are still in a research and development stage. On the other hand, sustainable schemes stress the safety aspects of pest control such as restrictions on the use of the most toxic compounds and this should lead to increased demands for biological control solutions.

These two aspects together suggest that researchers need to review the current recommendations for sustainable schemes. This should: (i) include an evaluation of the efficacy of some of the current recommendations to avoid misconceptions and inconsistencies in some of the advice provided; and (ii) formulate a new research agenda to find answers to enduring problems in coffee such as H. hampei. Thus we believe that there is an urgent need to develop clear and effective IPM-related guidelines for the increasing number of certification bodies to whom IPM of pests is but one of many tasks. However, IPM scientists also need to consider broadening their research mandates to include sustainability themes, such as insect indicators for biodiversity, or long-term studies of organic farms. Another future challenge will be to bring in small-scale coffee growers into the sustainable domain, and this should be seen as a chance to re-evaluate the role of IPM for the underprivileged sector. The latter implies a necessity to make IPM practices easier to implement and more realistic at the farm level.

During recent years, research on control of *H. hampei*, and the development and implementation of IPM programmes, in general has not advanced markedly and reasons may involve a shortage of funds due to the coffee price crisis and the advent of the sustainable coffee schemes that have attracted much attention from donors who previously funded IPM research. Thus we believe it is time for a coordinated approach involving all parties concerned with the coffee berry borer problem, i.e. IPM researchers, certification bodies, the coffee industry, extensionists and of course the coffee farmers themselves, to re-assess the role of research and how to employ it to best effect in the future.

#### References

Abraham, Y.J., Moore, D. & Godwin, G. (1990) Rearing and aspects of biology of *Cephalonomia stephanoderis* and *Prorops nasuta* (Hymenoptera: Bethylidae) parasitoids of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* 80, 121–128.

- Allard, G.B. & Moore, D. (1989) Heterorhabditis sp. nematodes as control agents for coffee berry borer, Hypothenemus hampei (Scolytidae). Journal of Invertebrate Pathology 54, 45–48.
- Alonzo, P.F. (1984) El problema de la broca (*Hypothenemus hampei* (Ferr).) (Col: Scolytidae) y la caficultura. Aspectos relacionados con importancia. Daño, identificación, biología, ecología y control. 242 pp. IICA PROMECAFE.
- Andreev, D., Breilid, D., Kirkendall, L., Brun, L.O. & Ffrench-Constant, R.H. (1998) Lack of nucleotide variability in a beetle pest with extreme inbreeding. *Insect Molecular Biology* 7, 197–200.
- Aristizabal, L.F., Salazar, H.M. & Mejia, C.G. (2002) Changes in the adoption of the components of coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) integrated management, through participative methodologies. *Revista Colombiana de Entomologia* 28, 153–160.
- Aristizabal, L.F., Salazar, H.M., Mejia, C.G. & Bustillo, A.E. (2004) Introducción y evaluación de *Phymastichus coffea* (Hymenoptera: Eulophidae) en fincas de pequeños caficultores a través de investigación participativa. *Revista Colombiana de Entomología* 30, 219–224.
- Armbrecht, I., Rivera, L. & Perfecto, I. (2005) Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. *Conservation Biology* 19, 897–907.
- Baker, P.S. (1999) The coffee berry borer in Colombia; final report of the DFID-Cenicafé-CABI Bioscience IPM for coffee project (CNTR 93/1536A). 154 pp. Chinchiná (Colombia), DFID-CENICAFE.
- Baker, P.S., Ley, C., Balbuena, R. & Barrera, J.F. (1992) Factors affecting he emergence of *Hypothenemus hampei* (Coleoptera: Scolytidae) from coffee berries. *Bulletin of Entomological Research* 82, 145–150.
- Baker, P.S., Jackson, J.A.F. & Murphy, S.T. (2002) Natural enemies, natural allies. Project completion report of the integrated management of coffee berry borer project, CFC/ICO/02 (1998–2002). The commodities press. CABI commodities, Egham UK and Cenicafé, Chinchiná, Colombia.
- Barrera, J.F., Gomez, J., Infante, F., Castillo, A. & de la Rosa, W. (1989) Biologique de Cephalonomia stephanoderis Betrem (Hymenoptera: Bethylidae) en laboratoire. I. Cycle biologique, capacité d'oviposition et émergence du fruit du caféier. Café Cacao Thé 33, 101–108.
- Barrera, J.F., Baker, P.S., Valenzuela, J.E. & Schwarz, A. (1990) Introduccion de dos especies de parasitoides Africanos a Mexico para el control biologico de la broca del café Hypothenemus hampei (Coleoptera: Scolytidae). Folia Entomologica Mexicana 79, 245–247.
- Batchelor, T.P., Hardy, I.C.W. & Pérez-Lachaud, G. (2005) Insect gladiators II: competitive interactions within and between bethylid parasitoid species of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control* 32, 194–202.
- Batchelor, T.P., Hardy, I.C.W. & Barrera, J.F. (2006) Interactions among bethylid parasitoid species attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control* **36**, 106–118.
- Benavides, P., Vega, F.E., Romero-Severson, J., Bustillo, A.E. & Stuart, J.J. (2005) Biodiversity and biogeography of an important inbred pest of coffee, coffee berry borer (Coleoptera: Curculionidae: Scolytinae). Annals of the Entomological Society of America 98, 359–366.

- Bergamin, J. (1943) Contribuicao ao conhecimento da biología da broca do café (*Hypothenemus hampei*). Ferrari. 1867 (Col: Ipidae). Arquivos do Instituto Biológico 14, 31–72.
- Bergamin, J. (1946) A broca do café no Brasil. Boletim da Superintendencia dos Servicos do Café 33, 21–22.
- Borbón-Martinez, M.O. (1989) Bioecologie d'un ravageur des baies de caféier. *Hypothenemus hampei* Ferr. (Coleoptera: Scolytidae) et de ses parasitoides au Togo. PhD thesis, Université Paul Sabatier de Toulouse, France.
- Brun, L.O. & Suckling, D.M. (1992) Field selection for endosulfan resistance in coffee berry borer (Coleoptera: Scolytidae). *Journal of Economic Entomology* 85, 325–334.
- Brun, L.O., Marcillaud, C., Gaudichon, V. & Suckling, D.M. (1989) Endosulfan resistance in *Hypothenemus hampei* (Coleoptera: Scolytidae) in New Caledonia. *Journal of Economic Entomology* 82, 1311–1316.
- Brun, L.O., Stuart, J., Gaudichon, V., Aronstein, K. & Ffrench-Constant, R.H. (1995) Functional haplodiploidy: a mechanism for the spread of insecticide resistance in an important international insect pest. *Proceedings of the National Academy* of Sciences, USA 92, 9861–9865.
- Bustillo, A.E., Cardenas, R., Villalba, D., Benavides, P., Orozco, J. & Posada, F.J. (1998) Manejo integrado de la broca del café Hypothenemus hampei (Ferrari) en Colombia. 134 pp. Cenicafé, Chinchiná, Colombia.
- Bustillo, A.E., Cardenas, R. & Posada, F.J. (2002) Natural enemies and competitors of *Hypothenemus hampei* (Ferrari) in Colombia. *Neotropical Entomology* **31**, 635–639.
- Carrión, G. & Bonet, A. (2004) Mycobiota associated with the coffee berry borer (Coleoptera: Scolytidae) and its galleries in fruit. Annals of the Entomological Society of America 97, 492–499.
- Castillo, A., Infante, F., Barrera, J.F., Carta, L. & Vega, F.E. (2002) First field report of a nematode (Tylenchida: Sphaerularioidea) attacking the coffee berry borer, *Hypo*thenemus hampei (Ferrari) (Coleoptera: Scolytidae) in the Americas. Journal of Invertebrate Pathology **79**, 199–202.
- Castillo, A., Infante, F., Lopez, G., Trujillo, J., Kirkendall, L.R. & Vega, F.E. (2004a) Laboratory parasitism by *Phymastichus coffea* (Hymenoptera: Eulophidae) upon non-target bark beetles associated with coffee plantations. *Florida Entomologist* 87, 274–277.
- Castillo, A., Infante, F., Vera-Graziano, J. & Trujillo, J. (2004b) Host-discrimination by *Phymastichus coffea*, a parasitoid of the coffee berry borer. *BioControl* 49, 655–663.
- Castro, L., Benavides, P. & Bustillo, A.E. (1998) Dispersion y mortalidad de *Hypothenemus hampei*, durnte la recoleccion y beneficio del café. *Manejo Integrado de Plagas* 50, 19–28.
- **Damon, A.** (2000) A review of the biology and control of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* **90**, 453–465.
- De Alvim, P.T. (1960) Moisture stress as a requirement for flowering of coffee. Science 132, 3423.
- de la Rosa, W., Segura, H.R., Barrera, J.F. & Williams, T. (2000) Laboratory evaluation of the impact of entomopathogenic fungi on *Prorops nasuta* (Hymenoptera: Bethylidae), a parasitoid of the coffee berry borer. *Environmental Entomol*ogy 29, 126–131.
- Dufour, B.P., Gonzalez, M.O. & Frérot, B. (1999) Mass trapping of coffee berry borer *Hypothenemus hampei* Ferr. (Coleoptera: Scolytidae) under field conditions: first results. pp. 480–491 in *Proceedings, Dix-huitieme Colloque Scientifique International sur le Café*, Helsinki, 2–8 August 1999. Helsinki, Finland.

- **Dufour, B.P., Picasso, C. & Gonzalez, M.O.** (2001) Development of a large capacity trap for controlling the coffee berry borer *Hypothenemus hampei* Ferr. (Coleoptera: Scolytidae) in El Salvador. pp. 1–12 in *Proceedings*, 19-eme Colloque Scientifique International sur le Café, Trieste, 14–18 May 2001. Trieste, Italy.
- Dufour, B.P., Gonzalez, M.O., Mauricio, J.J., Chavez, B.A. & Ramirez, R. (2004) Validation of coffee berry borer trapping with Brocap<sup>®</sup> trap. pp. 1243–1247 in *Proceedings*, 20-eme *Colloque Scientifique International sur le Café*, Bangalore, 11–15 October 2004. Bangalore, India.
- Farrell, B.D., Sequeira, A.S., O'Meara, B.C., Normark, B.B., Chung, J.H. & Jordal, B.H. (2001) The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). *Evolution* 55, 2011–2027.
- Feldhege, M.R. (1992) Rearing techniques and aspects of biology of *Phymastichus coffea* (Hymenoptera: Eulophidae) a recently described endoparasitoid of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae). *Café Cacao Thé* 36, 45–54.
- Fischerworring, B. & Rosskamp, R. (2001) *Guía a la caficultura ecológica*. 3rd edn. 153 pp. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), Eschborn, Germany.
- **Giovannucci, D. & Koekoek, K.J.** (2003) *The state of sustainable coffee: a study of twelve major markets.* 199 pp. International Coffee Organization and International Institute of Sustainable Development, London and Winnipeg.
- Gongora, C. (2005) Avances en conocimiento y mejoramiento del hongo entomopatógenos *Beauveria bassiana* para el control de la broca del café, *Hypothenemus hampei*. pp. 27–32 in *Congreso de la Sociedad Colombiana de Entomología*, 32, July 27–29, 2005. Ibague, Colombia.
- Gongora, C.E., Posada, F.J. & Bustillo, A.E. (2001) Detección molecular de un gen de resistencia al insecticida endosulfan en una población de broca *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) en Colombia. pp. 47–48 in *Congreso de la Sociedad Colombiana de Entomología 28*, August 8–10, 2001, Pereira, Colombia.
- Infante, F., Murphy, S.T., Barrera, J.F., Gómez, J.W. & Damon, A. (1994) Cría de *Phymastichus coffea* parasitoide de la broca del café y algunas notas sobre su historia de vida. *Southwestern Entomologist* 19, 313–315.
- Infante, F., Mumford, J. & Garcia-Ballinas, A. (2003) Predation by native arthropods on the African parasitoid *Prorops nasuta* (Hymenoptera: Bethylidae) in coffee plantations of Mexico. *Florida Entomologist* 86, 86–88.
- Infante, F., Mumford, J. & Baker, P. (2005) Life history studies of *Prorops nasuta*, a parasitoid of the coffee berry borer. *BioControl* 50, 259–270.
- Jaramillo, J., Bustillo, A.E., Montoya, E.C. & Borgemeister, C. (2005) Biological control of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae, Scolytinae) by *Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae) in Colombia. *Bulletin of Entomological Research* 95, 467–472.
- Jaramillo, J., Borgemeister, C. & Setamou, M. (2006) Field superparasitism by *Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae), parasitoid of the adult coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae, Scolytinae). *Entomologia Experimentalis et Applicata* (in press).
- Lara, J.C., López, J.C. & Bustillo, A.E. (2004) Effect of entomopathogenic nematodes on populations of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) in

J. Jaramillo *et al.* 

berries on the soil. *Revista Colombiana de Entomologia* **30**, 179–185.

- LaSalle, J. (1990) A new genus and species of Tetrastichinae (Hymenoptera: Eulophidae) parasitic on the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae). *Bulletin of Entomological Research* 80, 1–7.
- LaSalle, J. (1995) A new species of *Phymastichus* (Hymenoptera: Eulophidae) parasitic on adult *Xyleborus perforans* (Coleoptera: Scolytidae) on macadamia trees in Hawaii. *Proceedings* of the Hawaiian Entomological Society **32**, 95–101.
- Le Pelley, R.H. (1968) Pests of coffee. 590 pp. London, Longmans Green and Co.
- Lindgren, B.S. (1983) A múltiple funnel trap for scolytid beetles (Coleoptera). *Canadian Entomologist* **115**, 299–302.
- López, V.C. & Moore, D. (1998) Developing methods for testing host specificity of *Phymastichus coffea* LaSalle (Hymenoptera: Tetrastichinae) a potential biological control agent of *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) in Colombia. *Biocontrol Science and Technology* 8, 397–411.
- López, V.C., Baker, P., Cock, J.W. & Orozco, J. (1997) Dossier on *Phymastichus coffea* (Hymenoptera: Eulophidae Tetrastichinae) a potential biological control agent for *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) in Colombia. 23 pp. CABI, IIBC, Ascot, UK and Cenicafé, Chinchiná, Colombia.
- Lauziere, I., Pérez-Lachaud, G. & Brodeur, J. (1999) Influence of host density on the reproductive strategy of *Cephalonomia stephanoderis*, a parasitoid of the coffee berry borer. *Entomologia Experimentalis et Applicata* 92, 21–28.
- Mathieu, F., Brun, L.O., Marchillaud, C. & Frérot, B. (1997) Trapping of the coffee berry borer *Hypothenemus hampei* Ferr. (Coleoptera: Scolytidae) within a mesh-enclosed environment: interaction of olfactory and visual stimuli. *Journal of Applied Entomology* **121**, 181–186.
- Mejia, J.W. & Lopez, D.F. (2002) Study of the necessity for integrated management of the coffee berry borer in the department of Antioquia. *Revista Colombiana de Entomologia* 28, 167–173.
- Mejia, J.W., Bustillo, A.E., Orozco, J. & Chaves, B.C. (2000) Effect of four insecticides and *Beauveria bassiana* on *Prorops nasuta* (Hymenoptera: Bethylidae) parastoid of the coffee berry borer. *Revista Colombiana de Entomologia* 26, 117–123.
- Mendoza-Mora, J.R. (1991) Resposta da broca do café *Hypothenemus hampei* a estimulos visuais e semioquimicos. MSc thesis, Universidade Federal de Vicosa, Brasil.
- Molina, J.P. & Lopez, J.C. (2002) Desplazamiento y parasitismo de entomonematodos hacia frutos infestados con la broca del café *Hypothenemus hampei* (Coleoptera: Scolytidae). *Revista Colombiana de Entomologia* 28, 145–151.
- Morales-Ramos, J.A., Rojas, M.G., Sittertz-Bhatkar, H. & Saldaña, G. (2000) Symbiotic relationship between Hypothenemus hampei (Coleoptera: Scolytidae) and Fusarium solani (Moniliales: Tuberculariaceae). Annals of the Entomological Society of America 93, 541–547.
- Murphy, S.T. & Moore, D. (1990) Biological control of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae): previous programmes and possibilities for the future. *Biocontrol News and Information* **11**, 107–117.
- Murphy, S.T., Day, R., Orozco, J. & Kucel, P. (2001) Investigations into the use of *Heterospilus coffeicola* for the biological control of the coffee berry borer in Latin America and Africa. 13 pp. Unpublished report for the period November 2000–July 2001, CABI Commodities, Ascot, UK.

- Orozco, H.J. (1997) Ciclo de vida del parasitoide *Phymastichus* coffea LaSalle (Hymenoptera: Eulophidae). pp. 45–46 in *Congreso de la Sociedad Colombiana de Entomología, 24*, Pereira, July 16–18, 1997 Pereira, Colombia.
- **Orozco, H.J.** (2001) Producción de parasitoides para el control de la broca del café, *Hypothenemus hampei* (Ferrari). pp. 101–109 in *Simposio la cría de insectos como una industria rentable. Congreso de la Sociedad Colombiana de Entomología 28.* Pereira, 8–10 August, 2001. Pereira, Colombia.
- **Orozco, H.J.** (2002) Guía para la producción del parasitoide *Phymastichus coffea* para el control de la broca del café. 19 pp. CENICAFE-CFC-CABI Commodities-ICO, Chinchina, Colombia.
- Ortiz, A., Ortiz, A., Vega, F.E. & Posada, F. (2004) Volatile composition of coffee berries at different stages of ripeness and their possible attraction to the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae). *Journal of Agricultural and Food Chemistry* **52**, 5914–5918.
- Paine, T.D., Raffa, K.F. & Harrington, T.C. (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* 42, 179–206.
- Pérez, J., Infante, F., Vega, F.E., Holguin, F., Macias, J., Valle, J., Nieto, G., Peterson, S.W., Kurtzman, C.P. & O'Donnell, K. (2003) Mycobiota associated with the coffee berry borer (*Hypothenemus hampei*) in Mexico. *Mycological Research* 107, 879–887.
- Pérez, J., Infante, F. & Vega, F.E. (2005) Does the coffee berry borer (Coleoptera: Scolytidae) have mutualistic fungi? Annals of the Entomological Society of America 98, 483–490.
- Pérez-Lachaud, G. (1998) A new bethylid attacking the coffee berry borer in Chiapas (Mexico) and some notes on its biology. *Southwestern Entomologist* 23, 287–288.
- Pérez-Lachaud, G. & Hardy, I.C.W. (1999) Reproductive biology of *Cephalonomia hyalinipennis* (Hymenoptera: Bethylidae) a native parasitoid of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) in Chiapas, Mexico. *Biological Control* 14, 152–158.
- Pérez-Lachaud, G. & Hardy, I.C.W. (2001) Alternative hosts for bethylid parasitoids of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control* 22, 265–277.
- Pérez-Lachaud, G., Hardy, I.C.W. & Lachaud, J.P. (2002) Insect gladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control* 25, 231–238.
- Pérez-Lachaud, G., Batchelor, T.P. & Hardy, I.C.W. (2004) Wasp eat wasp: facultative hyperparasitism and intraguild predation by bethylid wasps. *Biological Control* 30, 149–155.
- Peterson, S.W., Pérez, J., Vega, F.E. & Infante, F. (2003) Penicillium brocae a new species associated with the coffee berry borer in Chiapas, Mexico. Mycologia 95, 141–147.
- Poinar, G., Vega, F.E., Castillo, A., Chaves, I.E. & Infante, F. (2004) Metaparasitylenchus hypothenemi n. sp. (Nematoda: Allantonematidae), a parasite of the coffee berry borer Hypothenemus hampei (Curculionidae). Jounal of Parasitology 90, 1160–1110.
- **Portilla, M.** (1999a) Desarrollo y evaluacion de una dieta artificial para la cria de *Hypothenemus hampei*. *Revista CENICAFE* **50**, 24–38.
- Portilla, M. (1999b) Mass rearing technique for *Cephalonomia* stephanoderis (Hymenoptera: Bethylidae) on *Hypothenemus*

232

hampei (Coleoptera: Scolytidae) developed using Cenibroca artificial diet. *Revista Colombiana de Entomologia* **25**, 57–66.

- **Posada, F.** (1998) Production, formulation and application of *Beauveria bassiana* for control of *Hypothenemus hampei* in Colombia. PhD thesis, University of London.
- Posada, F.J., Osorio, E. & Velazquez, E.T. (2002) Evaluation of *Beauveria bassiana* pathogenicity in the coffee berry borer using the leaf spraying method. *Revista Colombiana de Entomologia* 28, 139–144.
- Rodriguez, M.L. & Góngora, C.E. (2005) Transformación de Beauveria bassiana cepa Bb9205 con los genes pr1A, pr1J y ste1 de Metarhizium anisopliae y evaluación de su patogenicidad sobre la broca del café. Revista Colombiana de Entomología 31, 51–58.
- Rojas, M.G., Morales-Ramos, J.A. & Harrington, T. (1999) Association between the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae) and *Fusarium solani* (Moniliales: Tuberculariaceae). *Annals of the Entomological Society* of America 92, 98–100.
- Ruiz, C.R. (1995) Efecto de la fenología del fruto de café sobre los parámetros de la tabla de vida de la broca del café *Hypothenemus hampei* (Ferrari). BSc thesis, University of Caldas, Colombia.
- Sabelis, M.W., Nagelkerke, C.J. & Breeuwer, J.A.J. (2002) Sex ratio control in arrhenotokous and pseudo-arrhenotokous mites. pp. 195–215 in Hardy, I.C.W. (Ed.) Sex ratios: concepts and research methods. Cambridge, Cambridge University Press.
- Salazar, H.M., Aristizabal, L.F. & Mejia, C.G. (2003) Investigacion participativa con caficultores en relacion con el manejo de la broca del café *Hypothenemus hampei* (Coleoptera: Scolytidae) en el proceso del beneficio. *Revista Colombiana de Entomologia* 29, 57–62.
- Salazar, M.R., Arcila, J., Riaño, N. & Bustillo, A.E. (1993) Crecimiento y desarrollo del fruto de café y su relación con la broca. Avance Técnico No 194, Cenicafé, Chinchina, Colombia.
- Shaw, S.R. (2004) Essay on the evolution of adult parasitism in the subfamily Euphorinae (Hymenoptera: Braconidae). *Proceedings of the Russian Entomological Society St. Petersburg* 75, 82–95.
- Stouthamer, R., Hurst, G.D.D. & Breeuwer, J.A.J. (2002) Sex ratio distorters and their detection. pp. 195–215 in Hardy, I.C.W. (Ed.) Sex ratios: concepts and research methods. Cambridge, Cambridge University Press.
- Ticheler, J. (1961) Etude analytique de l'épidémiologie du scolyte des graines de café Stephanoderis hampei Ferr. en Cote d'Ivoire. Mededelingen Landbouwhogeschool Wageningen 61, 1–49.
- Varangis, P., Giovannucci, D. & Lewin, B. (2003) Dealing with the coffee crisis in Central America: impacts and

strategies. World Bank Policy Research Working Paper 2993, Washington, USA.

- Vega, F.E. (2004) Coffee berry borer Hypothenemus hampei (Ferrari) (Coleoptera: Scolytidae). pp. 575–576 in Capinera, J.L. (Ed.) Encyclopedia of entomology, Vol 1. Dordrecht, The Netherlands, Kluwer Academic Publishers.
- Vega, F.E., Mercadier, G., Damon, A. & Kirk, A. (1999) Natural enemies of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) in Togo and Cote d'Ivoire, and other insects associated with coffee beans. *African Entomology* 7, 243–248.
- Vega, F.E., Benavides, P., Stuart, J. & O'Neill, S. (2002) Wolbachia infection in the coffee berry borer (Coleoptera: Scolytidae). Annals of the Entomological Society of America 95, 374–378.
- Vega, F.E., Rosenquist, E. & Collins, W. (2003a) Global project needed to tackle coffee crisis. *Nature* 435, 343.
- Vega, F.E., Blackburn, M.B., Kurtzman, C.P. & Dowd, P.F. (2003b) Identification of a coffee berry borer associated yeast: does it break down caffeine? *Entomologia Experimentalis et Applicata* 107, 19–24.
- Velez, M. (2000) Evaluacion de marquesinas para el control de la broca del café, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae). BSc thesis, National University, Palmira, Colombia.
- Velez, M., Bustillo, A.E. & Alvarez, J. (2002) Secador parabolico modificado para el control de la broca del café. Avance tecnico 306. CENICAFE, Chinchina, Colombia.
- Vergara, J.D., Orozco, J., Bustillo, A.E. & Cháves, B. (2001a) Biología de *Phymastichus coffea* en condiciones de campo. *Revista Cenicafé* 52, 97–103.
- Vergara, J.D., Orozco, H.J., Bustillo, A.E. & Chaves, B. (2001b) Dispersión de Phymastichus coffea en un lote de café infestado de Hypothenemus hampei. Revista Cenicafé 52, 104–110.
- Villacorta, A. (1985) Dieta meridica para criacao de successivas geracoes de Hypothenemus hampei (Ferrari, 1867) (Coleoptera: Scolytidae). Anais da Sociedade Entomologica do Brasil 14, 315–319.
- Villacorta, A. & Barrera, J. (1996) Mass rearing using a meridic diet, of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae) parasitoid of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). 7 pp. ECOSUR, Tapachula, Mexico.
- Waterson, D.F. & Norris, K.R. (1989) Biological control: Pacific prospects. Supplement 1. Australian Centre for International Agriculture Research, Canberra, Australia, pp. 56–75.
- Werren, J.H. (1997). Biology of Wolbachia. Annual Review of Entomology 42, 587–609.

(Accepted 6 March 2006) © CAB International, 2006

Downloaded from https://www.cambridge.org/core. Technische Informationsbibliothek, on 23 Jan 2018 at 08:06:16, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1079/BER2006434