

The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae): a short review, with recent findings and future research directions

Fernando E. Vega^{1,*}, Francisco Infante², Alfredo Castillo² and Juliana Jaramillo^{3,4}

¹Sustainable Perennial Crops Laboratory, U. S. Department of Agriculture, Agricultural Research Service, Bldg. 001, BARC-W, Beltsville, MD 20705, USA

²El Colegio de la Frontera Sur (ECOSUR), Carretera Antiguo Aeropuerto km 2.5, Tapachula, 30700 Chiapas, México

³International Center of Insect Physiology and Ecology (ICIPE), P.O. Box 30772-00100, Nairobi, Kenya

⁴Institute of Plant Diseases and Plant Protection, Leibniz Universität Hannover, Herrenhaeuser Str. 2, 30419 Hannover, Germany

*Corresponding author; e-mail: Fernando.Vega@ars.usda.gov

Received: 5 February 2009; accepted 26 March 2009

Summary

The coffee berry borer, *Hypothenemus hampei* (Ferrari), is the most devastating insect pest of coffee throughout the world. Adult females bore a hole in the coffee berry, where they deposit their eggs; upon hatching, larvae feed on the coffee seeds inside the berry, thus reducing yield and quality of the marketable product. The insect spends most of its life inside the coffee berry, making it extremely difficult to control. This paper presents a short review of the literature dealing with natural enemies of the coffee berry borer, on the possible use of fungal endophytes as a biocontrol strategy, and on factors that might be involved in attracting the insect towards the coffee plant. The paper identifies some areas where research efforts should be focused to increase the chances of successfully developing an effective pest management strategy against the coffee berry borer.

© Koninklijke Brill NV, Leiden, 2009

Keywords

Biological control; broca; *Coffea*; Rubiaceae; entomopathogens; parasitoids; predators; Scolytinae

Introduction

The genus *Coffea* (Rubiaceae) comprises 103 species (Davis et al., 2006), but only two of these are commercially traded: *C. arabica* L. and *C. canephora* Pierre ex A. Froehner (also referred colloquially to as “robusta”). The significance of coffee in the world economy is staggering. It is grown in more than 10 million hectares in over 80 developing

countries (<http://faostat.fao.org/>), and approximately 20 million families depend on this plant for their subsistence (Osorio, 2002; Gole et al., 2002; Vega et al., 2003; Lewin et al., 2004). Arabica coffee has a lower caffeine level than robusta, and arabica is an allotetraploid ($2n=4x=44$), while robusta is a diploid ($2n=22$); furthermore, arabica coffee grows best at high elevations, while robusta is grown at lower elevations (Wintgens, 2004; Vega 2008a; Vega et al., 2008a). Both species of *Coffea* can either be grown at full sun, or under different levels of shade (Muschler 2004; Perfecto et al., 2007).

One of the major constraints to coffee production throughout the world is the damage caused by the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae). This small beetle (Figure 1) is endemic to Central Africa (Le Pelley, 1968), and can now be found throughout every coffee-producing region, with the exception of Hawaii, Nepal, and Papua New Guinea. Adult females bore a hole in the coffee berry and lay their eggs in internal galleries, with larvae feeding on the coffee seed (Figure 1). Feeding damage reduces yields, lowers the quality of the seed, and can result in the abscission of the berry. There is a 10:1 female to male sex ratio, most likely due to the presence of *Wolbachia* (Vega et al., 2002), and once the insects moult into adults inside the berry, there is sibling mating, with the emerging females being already inseminated and ready to search for a berry in which they can start ovipositing. Thus, most of the life cycle is spent inside coffee berries, making this cryptic insect quite difficult to control both by chemical and non-chemical strategies.

The availability of artificial diets that allow for the production of thousands of specimens and multiple generations has made it possible to conduct research in the laboratory (Villacorta and Barrera, 1993; Portilla and Streett, 2006). Recently, Jaramillo et al. (2009a) developed a new technique that allows researchers to use infested-coffee berries in the laboratory for extended periods of time. In this paper, we present a concise review on the coffee berry borer, focusing on biocontrol methods, and identify areas in need of research.

Natural enemies

Many natural enemies of the coffee berry borer have been reported, including parasitoids, predators, nematodes, and fungal entomopathogens (see below). Recent findings serve to point out the many lacunae in the field, and the need for innovative thinking.

Parasitoids

The first coffee berry borer parasitoid reported in the literature was the bethylid *Prorops nasuta* (Waterston) (Hargreaves, 1926). It can be found throughout most coffee-producing countries in Africa (Le Pelley, 1968) and has been introduced to Latin America, the Caribbean, Oceania, and Asia (Klein-Koch et al., 1988; Barrera et al., 1990a; Infante, 1998; Baker, 1999). Even though *P. nasuta* can be mass-reared using coffee berry borer-infested coffee berries (Abraham et al., 1990; Barrera et al., 1991;

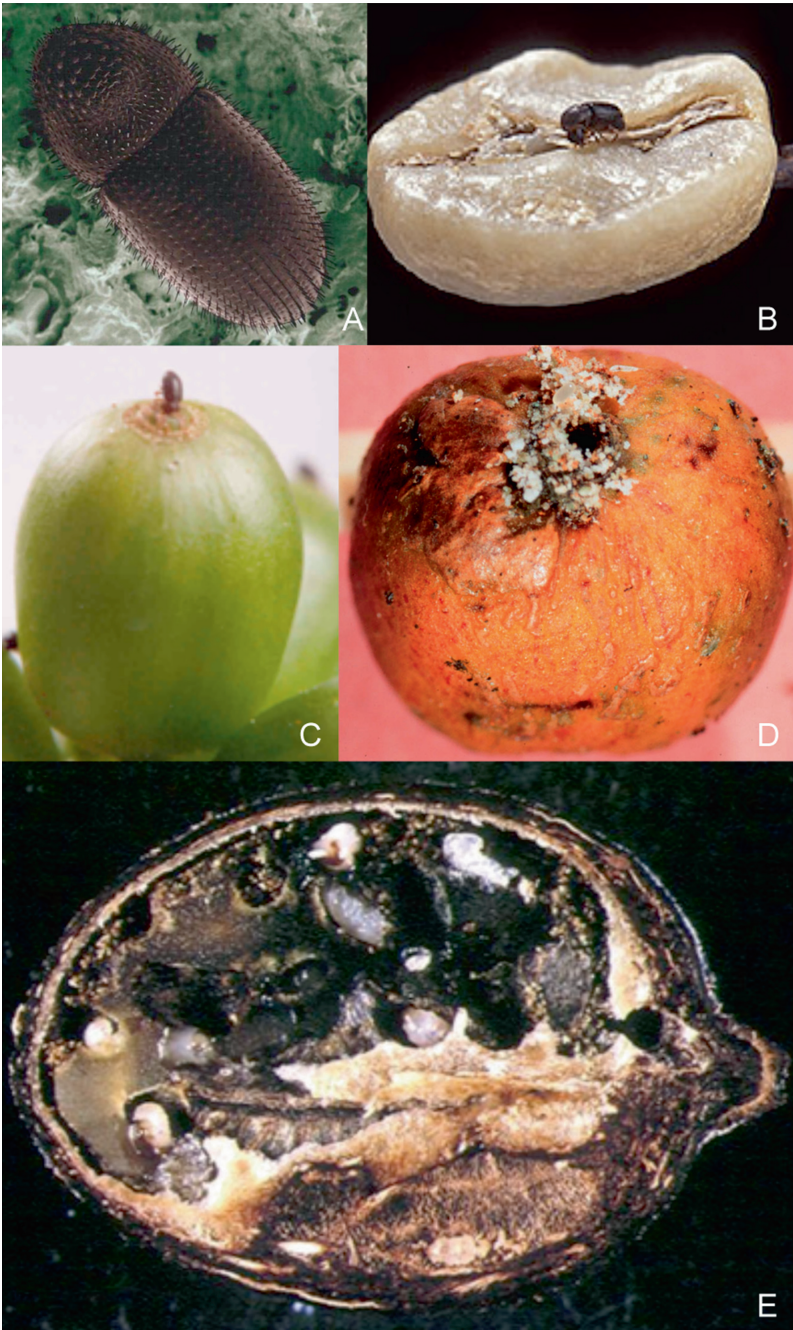


Figure 1. Female coffee berry borer (A) walking over a coffee seed (B) to show the small size of the insect (ca. 2 mm long, 1mm wide). Female coffee berry borer boring a hole in a coffee berry (C) with characteristic symptom of infestation revealing frass on the entrance hole (D). Damage caused by larval feeding inside the coffee berry (E). Credits: (A) E. Erbe, USDA, ARS; (B) P. Greb, USDA, ARS; (C) and (E) G. Hoyos, Cenicafé; (D) G. Mercadier, USDA, ARS.

Infante et al., 2005), the results of introductions have not been promising due to a lack of establishment, problems with its production, or negligible parasitism rates (De Ingunza, 1964; Heinrich, 1965; Murphy and Moore, 1990; Ruales, 1997; Infante, 1998; Infante et al., 2001).

Some recent and very interesting papers related to *P. nasuta* illustrate how much we still need to learn about coffee berry borer parasitoids. For example, Chiu-Alvarado et al. (2009) have shown that *P. nasuta* is attracted to coffee berry borer-infested coffee berries, as well as to larvae/pupae and frass removed from the infested berries, but not to uninfested berries, or to larva/pupae and frass obtained from artificial diets. These results indicate that an unidentified attractant produced by the interaction between the insect and the berry is critical for *P. nasuta* to locate its host. Overall, the long- and short-range host location strategies of *P. nasuta* – as well as the other parasitoids mentioned below – are poorly understood.

Jaramillo et al. (2009b) showed that 97% of the *P. nasuta* collected in the field originate from berries collected on the ground, in contrast to 2.7% originating from berries on the tree. This is an important finding because it reveals that a common cultural practice in the Americas, involving the collection of berries on the ground to reduce coffee berry borer levels (Bustillo et al. 1998), would also be removing an important biocontrol agent, i.e., *P. nasuta*. Jaramillo et al. (2009b) have suggested a screened enclosure that allows parasitoids to escape, but keeps the coffee berry borer confined, to determine if this would increase parasitism levels in the field.

Another bethylid, *Cephalonomia stephanoderis* Betrem (Figure 2), was discovered as a solitary larval and pupal ectoparasitoid of the coffee berry borer in the Ivory Coast (Ticheler, 1961; Betrem, 1961), and has been reported in various coffee-producing countries in western Africa (Koch, 1973; Damon, 1999; Barrera et al., 2000), but not in East Africa. In the Ivory Coast and Togo, *C. stephanoderis* can cause parasitism rates approaching 50% (Ticheler, 1961; Koch, 1973). This parasitoid can be mass-reared using coffee berry borer-infested coffee berries (Abraham et al., 1990; Barrera et al., 1991), and has been imported to more than 20 countries, and in most of these, it has become established (Klein-Koch, et al. 1988; Barrera et al., 1990a, 1990b, 2000; Bustillo et al., 1998; Baker, 1999). However, where follow-up studies have been conducted (e.g., Mexico and Colombia), the results have been disappointing (Barrera et al., 1990c; Bustillo et al., 1998; Damon, 1999). *Cephalonomia stephanoderis* has been reported to produce a yet unidentified marking pheromone after it oviposits on the coffee berry borer (Barrera et al., 1994).

Phymastichus coffea LaSalle (Hymenoptera: Eulophidae; Figure 2) was discovered in Togo (Borbón-Martínez, 1989; LaSalle, 1990). It has been reported in many coffee-producing countries in Africa (Lopez-Vaamonde and Moore, 1998), and has been introduced to many countries in Latin America (Baker, 1999) and to India, but there is to date no evidence that it has become established. Even though releases in Mexico resulted in relatively high levels of parasitism (up to 55%), it was not possible to recover the parasitoid 8–12 months after it was released (Galindo et al., 2002). Rojas et al. (2006) have shown that the parasitoid is attracted to coffee berries that have been mechanically damaged or that are infested with the coffee berry borer, but the wasps

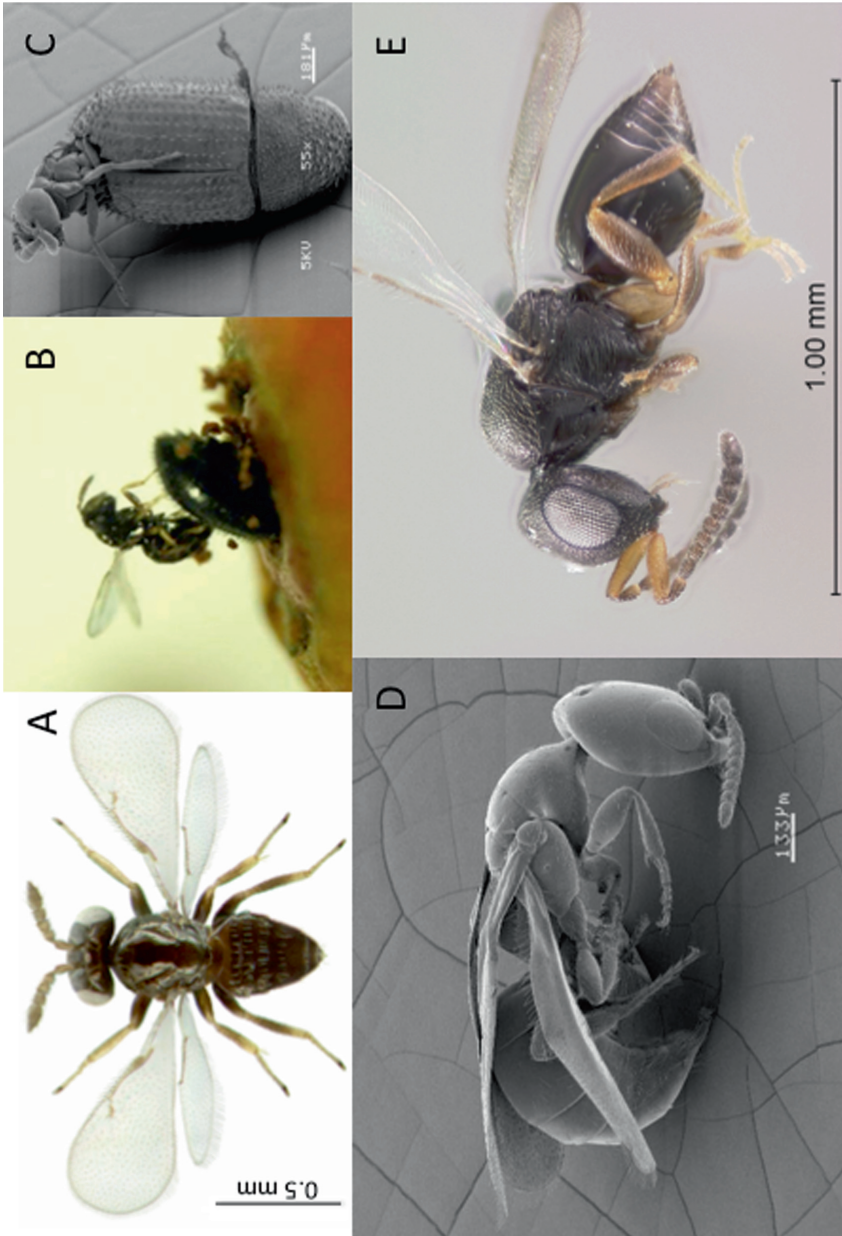


Figure 2. Adult *Phymastichus coffea* (A) ovipositing in the coffee berry borer (B) with one adult parasitoid emerging from the insect (C). Adult *Cephalonomia stephanoderis* (D), and *Aphanogmus dicycyna* (E), a hyperparasitoid of *Prorops nasuta*. Credits: (A) G. Goergen, IITA; (B) A. Castillo and F. Infante, ECOSUR; (C) and (D), G. Nieto, ECOSUR; (E) M. Buffington and A. Simpkins, USDA, ARS.

are more attracted to the mixture of frass and coffee berry particles produced when the female bores galleries. As for *P. nasuta*, these results indicate that the berry-coffee berry borer association results in an unidentified attractant for the parasitoid. Rearing methodologies for *P. coffea* using infested coffee berries have been described by Infante et al. (1994, 2003).

The braconid *Heterospilus coffeicola* Schmiedeknecht was discovered by Hargreaves (1926, 1935) in Uganda, and is believed to be distributed throughout most coffee-producing countries in Africa (Le Pelley, 1968). This insect has a life-style that resembles a predator, and not a parasitoid. The female lays an egg inside the gallery made by the female coffee berry borer, and upon hatching, the larvae feeds for 18–20 days on eggs and immature states of its host, consuming 10–15 individuals throughout its life cycle (Hargreaves, 1926, 1935; da Fonseca and Araujo, 1939; Le Pelley, 1968; Murphy and Moore, 1990). A rearing technique for this parasitoid has not yet been developed; this makes it difficult to import the parasitoid to other countries for field release.

Two parasitoids not reported from Africa have been identified as natural enemies of the coffee berry borer in the Americas: *Cryptoxilos* sp. and *Cephalonomia hyalinipennis* Ashmed. The braconid *Cryptoxilos* sp. was reported by Bustillo et al. (2002) in Colombia. Various species of *Cryptoxilos* are known to attack members of the Scolytinae (Jordal and Kirkendall, 1998; Kenis et al., 2004), and consequently, it is likely that their main host is not the coffee berry borer.

Pérez-Lachaud (1998) reported on a new bethylid parasitoid of the coffee berry borer in Mexico. It was tentatively identified as *Cephalonomia* sp. near *waterstoni*, and later identified conclusively as *C. hyalinipennis* Ashmed (Pérez-Lachaud and Hardy, 1999). This species attacks various species in the Curculionidae and Anobiidae (Evans 1964, 1978) and has also been found to be a facultative hyperparasitoid of *C. stephanderis* and *P. nasuta* (Pérez-Lachaud et al., 2004) thus bringing into doubt its potential as a coffee berry borer biocontrol agent.

Predators

Ants

Ants are quite common in coffee plantations, and shade-grown coffee has been reported to have higher ant diversity than non-shaded coffee (Armbrecht and Gallego 2007). Several authors have shown a close association of ants with the coffee berry borer (Vélez et al., 2000, 2003; Gallego-Ropero and Armbrecht, 2005; Vélez-Hoyos et al., 2006; Philpott and Armbrecht 2006; Armbrecht and Gallego 2007) but so far there is no hard evidence, for instance through molecular gut content analysis, on whether ants play an important role as predators of the insect. It is important to consider that impressive findings of ant predation in the laboratory might not necessarily be replicated in the field (Varón et al. 2004). Manipulating ants to increase coffee berry borer predation would be quite difficult, not to mention that ants can be a serious nuisance to coffee pickers.

Birds

Coffee grown under shade has increased levels of biodiversity when compared to non-shaded coffee (Perfecto et al., 1996; Greenberg et al., 1997a, 1997b; Moguel and Toledo, 1999; Hietz, 2005; Armbrecht and Gallego, 2007; Philpott et al., 2008). This increased diversity can include higher levels of birds, which have been shown to reduce coffee berry borer levels. For example, Kellermann et al. (2008) identified 17 species of birds as potential predators of the coffee berry borer in Jamaica. Using coffee berry borer-infested plants from which birds were excluded and contrasting them to plants to which birds had access, Kellermann et al. (2008) reported that birds reduce coffee berry borer infestation levels, resulting in reduced berry damage. Similar results were also reported for Jamaica by Levy (2007). Sherry (2000) also reports on birds as predators of the coffee berry borer. Similarly, Greenberg et al. (2000) and Perfecto et al. (2004) have shown increased bird predation of other types of insects in coffee plantations with increased shade.

Thrips

Jaramillo (2008) and Chapman et al. (2009) have reported on the black thrips, *Karnyothrips flavipes* (Jones) (Phlaeothripidae), as a predator of egg and larvae of the coffee berry borer in Kenya. Molecular gut analyses have confirmed that *K. flavipes* feeds on coffee berry borer (Jaramillo et al., submitted; Chapman et al., 2009). Sampling for predatory thrips in other coffee growing areas throughout the world might reveal whether this widely distributed thrips species is present, or whether other thrips might be preying on the coffee berry borer.

Other predators

In a survey of natural enemies of the coffee berry borer in Togo and Ivory Coast, Vega et al. (1999) reported on a *Leptophloeus* sp. near *punctatus* (Coleoptera: Laemophloeidae) preying on larvae. There have been no further reports of this possible coffee berry borer predator. Spiders have also been observed to prey on the coffee berry borer, although their preference for this insect is low (Henaut et al., 2001).

Nematodes

Laboratory research has shown that the coffee berry borer can be infected by nematodes in the genus *Steinernema* and *Heterorhabditis* (Allard and Moore, 1989; Castillo and Marbán-Mendoza, 1996; Molina and López, 2002; Sánchez and Rodríguez, 2007). These are commercially produced in many countries as insect biocontrol agents, but whether they would be economically feasible in coffee producing countries is yet to be seen. What remains a relatively unexplored area is natural nematode infections in the field. Varaprasad et al. (1994) have reported an unidentified species in the genus *Panagrolaimus* (Rhabditida: Panagrolamidae) attacking the coffee berry borer in India. Castillo et al. (2002) and Poinar et al. (2004) have reported on a new nematode species, *Metaparasitylenchus hypothenemi* (Nematoda: Allantonematidae) attacking the

coffee berry borer in Mexico (Figure 3); the nematode has also been found in Honduras (Poinar et al., 2004). This was the first report for a nematode attacking the coffee berry borer in the Americas. It is essential for coffee researchers to sample coffee-growing areas throughout the world for the presence of other nematodes infecting the coffee berry borer.

Fungal entomopathogens

Various entomopathogenic hypocrealean fungi (Ascomycota) have been reported infecting the coffee berry borer: *Beauveria bassiana* (Balsamo) Vuillemin, *Metarhizium anisopliae* (Metschn.) Sorokin, *Isaria farinosa* (Holmsk.) Fr. (formerly known as *Paecilomyces farinosus*), *Isaria fumosorosea* Wize (formerly known as *Paecilomyces fumosoroseus*), *Lecanicillium lecanii* (Zimm.) Zare and Gams (formerly known as *Verticillium lecanii*), *Nomurae rileyi* (Farl.) Samson, and *Ophiocordyceps entomorrhiza* (Dicks) Sung et al. (formerly known as *Hirsutella eleutheratorum*) (Bustillo et al. 1998, 2002; Vega et al., 1999). By far, *B. bassiana* (Figure 4) has been the most commonly reported throughout the world. Few studies have been conducted to assess coffee berry borer mortality levels in the field due to natural *B. bassiana* infections (i.e., not based on field bioassays with introduced isolates). One such study reported up to 30% mortality in Venezuela (Klein Koch et al., 1988), 60% in India (Balakrishnan et al., 1994), <10% in Mexico (Méndez-López, 1990; Córdova-Gómez, 1995), and <1% in Brazil (Costa et al., 2002). Field studies have assessed coffee berry borer infection with *B. bassiana* after spraying conidial suspensions in the field (Velez-Arango and Benavides-Gómez, 1990; Bustillo et al., 1991; Bustillo et al., 1999), but long-term studies in these sites are lacking.



Figure 3. Infective juveniles of *Metaparasytlenchus hypothenemi* emerging from an infected coffee berry borer (left), and detail of the infective juvenile (right). Credits: (A) A. Castillo, ECOSUR; (B) G. Nieto, ECOSUR.



Figure 4. Coffee berry borers infected with the fungal entomopathogen *Beauveria bassiana*. Credits: left, A. Ramírez, Puerto Rico Department of Agriculture; right, F. Posada.

Such studies are necessary to determine whether *B. bassiana* becomes established in the field, causing increased insect mortality in subsequent seasons when compared to plots where it was not sprayed. In addition, it is important to develop cost-effective ways to spray it. One particularly interesting concept involving *B. bassiana* involves its possible use as a fungal endophyte in biological control programs (see below).

The search for natural enemies

It is imperative that sampling for natural enemies be conducted in a methodical manner throughout the entire coffee-producing regions of the world. This sampling should be based on long-term collections in different sites, and not in the traditional short-term visits approach. This approach has resulted in the discovery of *Aphanogmus* sp. (Hymenoptera: Ceraphronidae; Figure 2), a previously unreported hyperparasitoid of *P. nasuta* in Kenya (Jaramillo and Vega, 2009); the predatory thrips *Karnyothrips flavipes* in Kenya (discussed above); and the new nematode species *Metaparasitylenchus hypothenemi* in Mexico (Poinar et al., 2004). It is possible that previously unrecorded natural enemies might be found, and these could become important components of biocontrol programs against the coffee berry borer.

Fungal endophytes

One innovative research area recently being explored against the coffee berry borer, involves fungal endophytes in coffee plants (Posada and Vega, 2006; Posada et al. 2007; Vega et al. 2008b, 2008c; Vega 2008b). The goal is to introduce *B. bassiana* as a fungal endophyte; this would ideally result in the establishment of a systemic biocontrol agent inside the plant. If effective, such a technique could become a very valuable pest management strategy.

Various fungal entomopathogens have already been reported as endophytes (Vega et al., 2008b) and the various methods used to inoculate coffee plants with *B. bassiana*

were partially effective (Posada et al., 2007), as recovery was confirmed but establishment was not long lasting. This lack of establishment was hypothesized to be due to the presence of other fungal endophytes that outcompeted *B. bassiana* (Posada et al., 2007). For coffee, where seedlings are constantly being grown in nurseries to be subsequently transplanted in the field, it would be ideal to develop a methodology to inoculate these seedlings in a manner that results in permanent and systemic establishment of *B. bassiana* as an endophyte.

The research also revealed the presence of bacterial endophytes (Vega et al., 2005), and that coffee plants growing in the field in Hawaii, Colombia, Mexico, and Puerto Rico can harbor hundreds of fungal endophytes (Vega et al., 2010), including *B. bassiana* (isolated in Colombia). These results bring to the forefront three interesting questions: (1) How does the fungal endophyte diversity in Africa compare to that of Hawaii, Colombia, Mexico, and Puerto Rico? (2) Can the presence of specific fungal endophytes be correlated to reduced coffee berry borer damage?; and (3) Is it possible that the dissemination of coffee from its center of origin left behind an important coevolved fungal endophyte biodiversity?

Insect attraction towards the coffee plant

Insect attraction to plants can be influenced by kairomones and plant color, among others factors (Vinson, 1976; Prokopy and Owens, 1983; Miller and Strickler, 1984; Vet and Dicke, 1992; Vet, 1999). Knowledge on kairomones and colors that are attractive to the insect are of critical importance in the development, design and implementation of lures and traps that can be used against the coffee berry borer.

Kairomones

The specific cues used by the coffee berry borer to localize the berry have not been elucidated, but various studies have directly or indirectly examined the composition of volatiles produced by the berries. Direct chemical analyses of berry-produced volatiles (using gas chromatography, etc.) have been conducted by Mathieu et al. (1991, 1996, 1998) and Ortiz et al. (2004). These studies have identified various volatiles that should be tested for their possible effectiveness in attracting the coffee berry borer. Ortiz et al. (2004) found alcohols – mainly ethanol – as the dominant components in the volatile composition. This might explain why the commonly used coffee berry borer trapping mixture of ethanol:methanol is effective (see below).

In an example of unidentified volatiles that attracted the coffee berry borer, Velasco Pascual et al. (1997) extracted homogenized berries in 80 ml methanol and 120 ethanol, followed by field studies in which the extracts were placed in dispensers. Their results are interesting because they show significant differences in insect capture based on the coffee variety used. This indicates the presence of a berry component that attracts the insect when compared to ethanol, methanol, or a combination of ethanol and methanol. In similar studies, Gutiérrez-Martínez et al. (1990, 1996) used various solvents to extract different parts of *C. canephora* plants and tested these extracts in the

field and the laboratory. The highest attraction was obtained from a methylene chloride extract in which caffeine was detected as the main component. Giordanengo et al. (1993) have reported on upwind attraction by the coffee berry borer to unidentified volatiles obtained from coffee berry extracts.

Based on the previous discussion, it is clear that the literature on coffee plant volatiles and their attraction to the coffee berry borer is quite limited. This is an area in which there is ample room for testing new possible attractants that would ideally be an improvement over the currently used methanol:ethanol mixtures. This mixture has been widely used in coffee berry borer trapping devices (Mendoza-Mora, 1991; Brun and Mathieu, 1997; Mathieu et al., 1999; Cárdenas, 2000; Borbón Martínez et al., 2000; Saravanan and Chozhan, 2003; Dufour and Frérot, 2008) and even though the coffee berry borer captures can be quite high, they are still a low percentage of the total population. It is important to ask whether a different attractant might result in significantly higher insect capture, while keeping in mind that plant-derived attractants used in a trap won't solve the infestation problem.

Similarly, groundbreaking research on volatiles that act as repellents would also be quite useful as part of the arsenal of control strategies against the coffee berry borer. The only article on coffee berry borer repellents is by Borbón Martínez et al. (2000), in which they report Z-3 hexenol, 3-methylcyclohex-2-en-1-one, and verbone as coffee berry borer repellents. Thus, there is ample room for research in this area.

Color

Concerning color preferences, laboratory studies have used green, yellow, red, and black berries, as well as artificial berries made of spherical polystyrene to determine which one's are preferred by the insect (Mendoza et al., 2000). The results indicate a preference for red and black berries, both in the real berries and the artificial berries. In the field, it is the norm to find insects starting to penetrate the coffee berry in the green stage, and the determining factor for the progress of the penetration is the dry matter content, which has to be over 20% (Bustillo et al., 1998). Thus, the results in the laboratory indicating preference for a berry that is red or black, are not likely to have any significance in the field, because by the time the berry reaches those colors, it has already been attacked by the insect. In trapping devices, it has been shown that red traps result in higher insect capture (Dufour and Frérot, 2008), but the role that the coffee berry color plays by itself, or in combination with volatiles, remains to be elucidated.

Other areas that would benefit from increased research efforts

Some basic aspects of the insect's biology need further research. For example, as mentioned before, the proteobacterium *Wolbachia*, believed to be responsible for the skewed sex ratio favoring females, has been detected in the coffee berry borer (Vega et al., 2002). To confirm whether *Wolbachia* is actually responsible for the skewed sex ratio, research aimed at eliminating it from the insect (e.g., using antibiotics) needs to

be conducted, followed by determinations of ensuing sex ratios, which should then be close to 1:1. Additional studies would then be needed to determine if there is any possible mechanism to eliminate *Wolbachia* in field populations, as this would drastically reduce the number of females.

Recently, Jaramillo et al. (2009c) conducted research on the potential effects of global warming on the coffee berry borer and reported lower and upper thresholds for development estimated at 14.9 and 32°C, respectively. The results reveal that the previous absence of the insect in some locations in Ethiopia might have been simply due to the low temperatures prevalent in the area, which would not allow full development of the insect. The paper also focuses on how to use shade to mitigate the higher coffee berry borer pressure expected as a result of the predicted higher seasonal temperatures in coffee production areas.

Still, reports of effects of shade on the coffee berry borer and its natural enemies are conflictive. For example, da Fonseca (1939) presents anecdotal evidence for increased coffee berry borer damage in shaded plantations in Uganda and Brazil, which he ascribes to increased moisture and protection from the wind; at the same time he doubts that shaded habitats will lead to increased parasitism levels by *H. coffeicola* and *P. nasuta* based on their presence in Ugandan plantations and the still high coffee berry borer infestation levels. Similarly, Wrigley (1988) states that heavy shade leads to severe infestations, but does not present any data to support this claim. Graner and Godoy (1959) conducted a six-year study in Brazil and found higher infestation levels in shaded coffee. In contrast, in a study conducted in Mexico, Soto-Pinto et al. (2002) found no correlation between coffee berry borer population levels and several variables, including shade levels. Even though Crowe and Gebremedhin (1984) briefly indicate that heavy shade is unfavorable towards natural enemies (without specifying which one's they are referring to), one would expect that heavy shade would be favorable towards entomopathogenic fungi due to the ensuing reduction in ultraviolet light and likely increase in humidity levels. To our knowledge, there are no studies correlating shade with increased coffee berry borer mycoses due to entomopathogenic fungi. This entire area of the insect response and its natural enemies to shade levels needs additional research.

One other area that has remained elusive, is whether the coffee berry borer produces pheromones. It could be argued that their biology precludes the need for pheromones, as there is sibling mating inside the berry. Even though under high infestation levels it is possible to find a berry that has been infested by two females (based on two entrance holes), it is the norm to find berries with only one female. This suggests that it might be possible for colonizing females to be producing a marking pheromone once they enter the berry. If such a chemical were identified, it might be possible to install dispensers in the field that might end up confusing and/or repelling colonizing females.

Conclusion

The coffee berry borer is an extremely difficult pest to control, mostly due to its cryptic nature. Some of the research areas outlined in this paper should lead to new knowledge

on the coffee berry borer, which might increase our chances of developing successful biocontrol strategies against this insect.

References

- Abraham, Y.J., D. Moore, and G. Godwin. 1990. Rearing and aspects of biology of *Cephalonomia stephanoderis* and *Prorops nasuta* (Hymenoptera: Bethyridae) parasitoids of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). Bulletin of Entomological Research 80:121–128.
- Allard, G. B. and D. Moore. 1989. *Heterorhabditis* sp. nematodes as control agents for coffee berry borer, *Hypothenemus hampei* (Scolytidae). Journal of Invertebrate Pathology 54:45–48.
- Armbrecht, I. and M. C. Gallego. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. Entomologia Experimentalis et Applicata 124:261–267.
- Baker, P. S. 1999. The coffee berry borer in Colombia. Final report of the DFID- Cenicafé - CABI Bioscience IPM for coffee project. Chinchiná (Colombia), DFID - CENICAFÉ. 154 pp.
- Balakrishnan, M. M., K. Sreedharan, and P. Krishnamoorthy Bhat. 1994. Occurrence of the entomopathogenic fungus *Beauveria bassiana* on certain coffee pests in India. Journal of Coffee Research 24:33–35.
- Barrera, J. F., P. S. Baker, A. Schwarz, and J. Valenzuela. 1990a. Introducción de dos especies de parasitoides africanos a México para el control biológico del la broca del cafeto *Hypothenemus hampei* (Ferr.) (Coleoptera: Scolytidae). Folia Entomológica Mexicana 79:245–247.
- Barrera, J. F., F. Infante, M. Vega, O. González, E. Carrillo, O. Campos, R. Muñoz, A. Serrano, J. J. Osorto, B. Decazy, and D. Moore. 1990b. Introducción de *Cephalonomia stephanoderis* (Hymenoptera: Bethyridae) a Centroamérica para el control biológico de la broca del cafeto, *Hypothenemus hampei* (Coleoptera: Scolytidae). Turrialba 40:570–574.
- Barrera, J. F., D. Moore, Y. J. Abraham, S. T. Murphy, and C. Prior. 1990c. Biological control of the coffee berry borer *Hypothenemus hampei* in Mexico and possibilities for further action. pp. 391–396. *In*, Brighton Crop Protection Conference: Pest and Diseases, Brighton, England, November 19–22, 1990.
- Barrera, J. F., F. Infante, A. Castillo, W. De la Rosa, and J. Gómez. 1991. Cría y manejo de *Cephalonomia stephanoderis* y *Prorops nasuta*, parasitoides de la broca del café. Miscelánea de la Sociedad Colombiana de Entomología 18:76–86.
- Barrera, J. F., F. Infante, W. de la Rosa, A. Castillo, and J. Gómez. 2000. Control biológico de broca del café. pp. 211–229. *In*, M. H. Badii, A. E. Flores, and L. J. Galán Wong (Editors). Fundamentos y perspectivas de control biológico. Universidad Autónoma de Nuevo León, Monterrey, México. 462 pp.
- Barrera, J. F., G. Gómez, and C. Alauzet. 1994. Evidence for a marking pheromone in host discrimination by *Cephalonomia stephanoderis* (Hym.: Bethyridae). Entomophaga 39:363–366.
- Betrem, J. G. 1961. *Cephalonomia stephanoderis* nov. spec. (Hymenoptera: Bethyridae). Entomologische Berichten 21:183–184.
- Borbón-Martínez, O. 1989. Bioécologie d'un ravageur des baies de caféier, *Hypothenemus hampei* Ferr. (Coleoptera: Scolytidae) et de ses parasitoides au Togo. Ph.D. thesis, Université Paul-Sabatier, Toulouse, France. 185 pp.
- Borbón-Martínez, O., O. Mora Alfaro, A. Cam Oehlschlager, and L. M. González. 2000. Proyecto de trampas, atrayentes y repelentes para el control de la broca del fruto de cafeto, *Hypothenemus hampei* L. (Coleoptera: Scolytidae). pp. 331–348. *In*, Memorias del XIX Simposio Latinoamericano de Caficultura. San José, Costa Rica. 514 pp.
- Brun, L. O. and F. Mathieu. 1997. Utilisation d'un piège a attractif kairomonal pour le suivi des populations du scolyte du café en champ. pp. 714–717. *In*, 17th International Scientific Colloquium on Coffee. Nairobi, Kenya. 828 pp.

- Buffington, M. L., and A. Polaszek. 2009. Recent occurrence of *Aphanogmus dictynna* (Waterston) (Hymenoptera: Ceraphronidae) in Kenya – an important hyperparasitoid of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae). *Zootaxa* 2214:62-68.
- Bustillo, A., H. Castillo, D. Villalba, E. Morales, and P. Vélez. 1991. Evaluaciones de campo con el hongo *Beauveria bassiana* para el control de la broca del café, *Hypothenemus hampei* en Colombia. pp. 679-686. *In*, 14th International Scientific Colloquium on Coffee. San Francisco, California. 710 pp.
- Bustillo P., A. E., R. Cárdenas M., D. A. Villalba G., P. Benavides M., J. Orozco H., and F. Posada. 1998. Manejo integrado de la broca del café *Hypothenemus hampei* (Ferrari) en Colombia. Centro Nacional de Investigaciones de Café (Cenicafé). Chinchiná, Colombia. 134 pp.
- Bustillo, A. E., M. G. Bernal, P. Benavides, and B. Chaves. 1999. Dynamics of *Beauveria bassiana* and *Metarhizium anisopliae* infecting *Hypothenemus hampei* (Coleoptera: Scolytidae) populations emerging from fallen coffee berries. *Florida Entomologist* 82:491-498.
- Bustillo, A. E., R. Cárdenas, and F. J. Posada. 2002. Natural enemies and competitors of *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae). *Neotropical Entomology* 31: 635-639.
- Cárdenas, M., R. 2000. Trampas y atrayentes para monitoreo de poblaciones de broca del café *Hypothenemus hampei* (Ferrari) (Col., Scolytidae). pp. 369-379. *In*, Memorias del XIX Simposio Latinoamericano de Caficultura. San José, Costa Rica. 514 pp.
- Castillo, A. and N. Marbán-Mendoza. 1996. Evaluación en laboratorio de nematodos entomopatógenos para el control biológico de la broca del café *Hypothenemus hampei*. *Nematropica* 26:101-109.
- Castillo, A., F. Infante, J. Barrera, L. Carta, and F. E. Vega. 2002. First field report of a nematode (Tylenchida: Sphaerularioidae) attacking the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) in the Americas. *Journal of Invertebrate Pathology* 79:199-202.
- Chapman, E. G., J. Jaramillo, F. E. Vega, and J. Harwood. 2009. Biological control of coffee berry borer: the role of DNA-based gut-content analysis in assessment of predation. pp. 475-484. *In*, P. G. Mason, D. R. Gillespie, and C. Vincent (eds.), *Proceedings of the 3rd International Symposium on Biological Control of Arthropods*, February 8-13, 2009. Christchurch, New Zealand. 636 pp.
- Chiu-Alvarado, P., J. F. Barrera, and J. C. Rojas. 2009. Attraction of *Prorops nasuta* (Hymenoptera: Bethyilidae), a parasitoid of the coffee berry borer (Coleoptera: Curculionidae), to host-associated olfactory cues. *Annals of the Entomological Society of America* 102:166-171.
- Córdova-Gámez, G. 1995. Plan de trabajo del Centro Reproductor de Entomopatógenos y Entomófagos (CREE), para 1995. Instituto Técnico Agropecuario de Oaxaca No. 23. 15 pp.
- Costa, J. N. M., R. B. da Silva, P. de Araújo Ribeiro, and A. Garcia. 2002. Ocorrência de *Beauveria bassiana* (Bals.) Vuill. em broca-do-café (*Hypothenemus hampei*, Ferrari) no Estado de Rondônia, Brasil. *Acta Amazonica* 32:517-519.
- Crowe, T. J. and T. Gebremedhin. 1984. Coffee pests in Ethiopia. Their biology and control. Institute of Agricultural Research, Addis Abeba, Ethiopia. 44 pp.
- da Fonseca, J. P. 1939. A “bróca” e o sombreamento dos cafezais. *Biologico* (Sao Paulo) 5:133-136.
- da Fonseca, J. P. and R. L. Araujo. 1939. Insetos inimigos do *Hypothenemus hampei* (Ferr.) (“Broca do Café). *Boletim Biológico* 4:486-504.
- Damon, A. A. 1999. Evaluation of current techniques and new approaches in the use of *Cephalonomia stephanoderis* (Hymenoptera: Bethyilidae) as a biological control agent of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae), in Chiapas, México. Ph.D. thesis, Imperial College, University of London. 327 pp.
- Davis, A. P., R. Govaerts, D. M. Bridson, P. Stoffelen. 2006. An annotated taxonomic conspectus of the genus *Coffea* (Rubiaceae). *Botanical Journal of the Linnean Society* 152:465-512.
- De Ingunza, S. M. A. 1964. La “broca del café” *Hypothenemus hampei* (Ferrari, 1867) (Col.: Ipinæ) en el Perú. *Revista Peruana de Entomología* 7:96-98.
- Dufour, B. P. and B. Frérot. 2008. Optimization of coffee berry borer, *Hypothenemus hampei* Ferrari (Col., Scolytidae), mass trapping with an attractant mixture. *Journal of Applied Entomology* 132:591-600.

- Evans, H. E. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology* 132:1-222.
- Evans, H. E. 1978. The Bethylidae of America north of Mexico. *Memoirs of the American Entomological Institute* 27:1-332.
- Galindo, V. H., F. Infante, A. Castillo, J. F. Barrera, E. Pinson, G. González, and J. C. Espinoza. 2002. Establecimiento preliminar del parasitoide *Phymastichus coffea* (Hymenoptera: Eulophidae) en Chiapas, México. pp. 44-46. *In*, Memorias del XXV Congreso Nacional de Control Biológico. Hermosillo, Sonora, México.
- Gallego Roper, M. C. and I. Armbrrecht. 2005. Depredación por hormigas sobre la broca del café *Hypothenemus hampei* (Coleoptera: Scolytinae) en cafetales cultivados bajo dos niveles de sombra en Colombia. *Revista Manejo Integrado de Plagas y Agroecología* 76:1-9.
- Giordanengo, P., L. O. Brun, and B. Frérot. 1993. Evidence for allelochemical attraction of the coffee berry borer *Hypothenemus hampei*, by coffee berries. *Journal of Chemical Ecology* 19:763-769.
- Gole, T. W., M. Denich, D. Teketay, and P. L. G. Vlek. 2002. Human impacts on the *Coffea arabica* gene pool in Ethiopia and the need for its *in situ* conservation. pp. 237-247. *In*, J. M. M. Engels, V. Ramanatha Rao, A. H. D. Brown, and M. T. Jackson (eds.). *Managing plant genetic diversity*, CABI Publishing. Oxon, United Kingdom. 487 pp.
- Graner, E. A. and C. Godoy Junior. 1959. Sombreamiento dos cafêzais. I. Resultados de três ciclos bienais (1953/1958) obtidos na Escola “Luiz de Queiróz.” *Anais da Escola Superior de Agricultura “Luiz de Queiroz”* 16:139-165.
- Greenberg, R., P. Bichier, and J. Sterling. 1997a. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, Mexico. *Biotropica* 29:501-514.
- Greenberg, R., P. Bichier, A. Cruz Angon, and R. Reitsma. 1997b. Bird populations in shade and sun coffee plantations in central Guatemala. *Conservation Biology* 11:448-459.
- Greenberg, R., P. Bichier, A. Cruz Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology* 81:1750-1755.
- Gutiérrez-Martínez, A., R. Haro-González, and S. Hernández Rivas. 1990. Kairomona responsable de la atracción de la broca del café *Hypothenemus hampei* Ferrari (Coleoptera: Scolytidae) al grano de café. pp. 28-36. *In*, Congreso Nacional MIR, Managua, Nicaragua.
- Gutiérrez-Martínez, A. and R. N. Ondarza. 1996. Kairomone effect of extracts from *Coffea canephora* over *Hypothenemus hampei* (Coleoptera: Scolytidae). *Environmental Entomology* 25:96-100.
- Hargreaves, H. 1926. Notes on the coffee berry borer (*Stephanoderes hampei*, Ferr.) in Uganda. *Bulletin of Entomological Research* 16:347-354.
- Hargreaves, H. 1935. *Stephanoderes hampei* Ferr., coffee berry borer in Uganda. *The East African Agricultural Journal* 1:218-224.
- Heinrich, W. O. 1965. Aspectos do combate biológico as pragas do café. *Biológico (Sao Paulo)* 31:57-62.
- Henaut, Y., J. Pablo, G. Ibarra-Núñez, and T. Williams. 2001. Retention, capture and consumption of experimental prey by orb-web weaving spiders in coffee plantations in Southern Mexico. *Entomologia Experimentalis et Applicata* 98:1-8.
- Hietz, P. 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. *Conservation Biology* 19:391-399.
- Infante, F. 1998. Biological control of *Hypothenemus hampei* (Coleoptera: Scolytidae) in Mexico, using the parasitoid *Prorops nasuta* (Hymenoptera: Bethylidae). Imperial College, University of London. 173 pp.
- Infante, F., S. T. Murphy, J. F. Barrera, G. J. Gómez, W. de la Rosa, and A. Damon. 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., J. Mumford, and I. Méndez. 2001. Non-recovery of *Prorops nasuta* (Hymenoptera: Bethylidae), an imported parasitoid of the coffee berry borer (Coleoptera: Scolytidae) in Mexico. *Southwestern Entomologist* 26:159-163.

- Infante, F., A. Castillo, J. C. Espinoza, V. H. Galindo, M. de J. Ortíz, R. Montes, J. F. Barrera, J. Gómez, and F. E. Vega. 2003. "*Phymastichus*", la avispa que parasita a los adultos de la broca del café. Manual Ilustrado. ECOSUR-SIBEJ. Tapachula, Mexico. 14 pp.
- Infante, F., J. Mumford, and P. Baker. 2005. Life history studies of *Prorops nasuta*, a parasitoid of the coffee berry borer. BioControl 50:259–270.
- Jaramillo, J. 2008. Biology, ecology and biological control of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae). Ph.D. thesis, Faculty of Natural Sciences, Gottfried Wilhelm Leibniz Universität Hannover, Germany. 237 pp.
- Jaramillo, J. and F. E. Vega. 2009. *Aphanogmus* sp. (Hymenoptera: Ceraphronidae): a hyperparasitoid of the coffee berry borer parasitoid *Prorops nasuta* (Hymenoptera: Bethyilidae) in Kenya. Biocontrol Science and Technology 19:113–116.
- Jaramillo, J., A. Chabi-Olaye, H. M. Poehling, C. Kamonjo, and C. Borgemeister. 2009a. Development of an improved laboratory production technique for the coffee berry borer *Hypothenemus hampei*, using fresh coffee berries. Entomologia Experimentalis et Applicata 130:275–281.
- Jaramillo, J., A. Chabi-Olaye, C. Borgemeister, C. Kamonjo, H.-M. Poehling, and F. E. Vega. 2009b. Where to sample? Ecological implications of sampling strata in determining abundance of natural enemies of the coffee berry borer, *Hypothenemus hampei*. Biological Control 49:245–253.
- Jaramillo, J., A. Chabi-Olaye, C. Kamonjo A. Jaramillo, F. E. Vega, H.-M. Poehling, and C. Borgemeister 2009c. Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change on a tropical insect pest. PLoS ONE 4(8): e6487. doi:10.1371/journal.pone.0006487
- Jordal, B. H. and L. R. Kirkendall. 1998. Ecological relationships of a guild of tropical beetles breeding in *Cecropia* petioles in Costa Rica. Journal of Tropical Ecology 14:153–176.
- Kellerman, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. Conservation Biology 22:1177–1185.
- Kenis, M., B. Wermelinger, and J.-C. Grégoire. 2004. Research on parasitoids and predators of Scolytidae - a review. pp. 237–290. *In*, F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire, and H. F. Evans (Editors). Bark and wood boring insects in living trees in Europe. A synthesis. Kluwer Academic Publishers. Dordrecht, The Netherlands. 569 pp.
- Klein-Koch, C., O. Espinoza, A. Tandazo, P. Cisneros, and D. Delgado. 1988. Factores naturales de regulación y control biológico de la broca del café (*Hypothenemus hampei* Ferr.). *Sanidad Vegetal* (Quito, Ecuador) 3:5–30.
- Koch, V. M. J. 1973. Abundance de *Hypothenemus hampei* Ferr., scolyte des graines de café, en fonction de sa plante hôte et de son parasite *Cephalonomia stephanoderis* Betrem, en Côte d'Ivoire. *Mededelingen Landbouwhogeschool Wageningen* 73:1–85.
- 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 80:7–10.
- Le Pelley, R. H. 1968. Pests of coffee. Longmans, Green and Co., Ltd., London. 590 pp.
- Levy, N. J. 2007. Bird predation decreases arthropod abundance and biomass in three coffee farms in the Blue Mountains, Jamaica. Unpublished article. Available online: <http://socrates.berkeley.edu/~es196/projects/2007final/Levy.pdf>
- Lewin, B., D. Giovannucci, and P. Varangis. 2004. Coffee markets: New paradigms in global supply and demand. The International Bank for Reconstruction and Development, Agriculture and Rural Development Discussion Paper 3. 150 pp.
- López-Vaamonde, C. and D. Moore. 1998. Developing methods for testing host specificity of *Phymastichus coffea* La Salle (Hym.: Tetrastichinae), a potential biological control agent of *Hypothenemus hampei* (Ferrari) (Col.: Scolytidae) in Colombia. Biocontrol Science and Technology 8:397–411.
- Mathieu, F., L. Brun, and B. Frérot. 1991. Preliminary results on comparative GC analyses of volatiles produced by the coffee berries. pp. 687–689. *In*, 14th International Scientific Colloquium on Coffee. San Francisco, California. 710 pp.

- Mathieu, F., C. Malosse, A. H. Cain, and B. Frerot. 1996. Comparative headspace analysis of fresh red coffee berries from different cultivated varieties of coffee trees. *Journal of High Resolution Chromatography* 5:298-300.
- Mathieu, F., L. O. Brun, B. Frérot, D. M. Suckling, and C. Frampton. 1999. Progression of field infestation is linked with trapping of coffee berry borer, *Hypothenemus hampei* (Col., Scolytidae). [Journal of Applied Entomology](#) 123:535-540.
- Mathieu, F., C. Malosse, and B. Frérot. 1998. Identification of volatile components released by fresh coffee berries at different stages of ripeness. *Journal of Agriculture and Food Chemistry* 46:1106-1110.
- Méndez-López, I. 1990. Control microbio de la broca del fruto del cafeto *Hypothenemus hampei* Ferrari (Coleoptera: Scolytidae), con el hongo *Beauveria bassiana* (Bals.) Vuill. (Deuteromycetes) en el Soconusco, Chiapas. M.S. thesis, Colegio de Postgraduados, Departamento de Entomología y Acarología, Chapingo, México. 135 pp.
- Mendoza Mora, J.R. 1991. Resposta da broca-do-café, *Hypothenemus hampei*, a estímulos visuais e semi-químicos. M.S. thesis, Universidade Federal de Viçosa, Brasil. 44 pp.
- Mendoza, J. R., J. O. Gomes de Lima, E. F. Vilela, and C. J. Fantón. 2000. Atractividade de frutos a broca-do-café, *Hypothenemus hampei* (Ferrari): estímulos visuais e olfativos. pp. 313-315. In, Anais do 3º Seminário Internacional sobre Biotecnologia na Agroindústria Cafeeira. Londrina (Brasil), Maio 24-28, 1999. UFPR-IAPAR-IRD.
- Miller, J. R. and K. L. Strickler. 1984. Finding and accepting host plants. pp. 127-157. In, W. J. Bell and R. T. Cardé (Editors). *Chemical ecology of insects*. Chapman & Hall, London. 524 pp.
- Moguel, P. and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. [Conservation Biology](#) 13:11-21.
- Molina, A., J. P. and J. C. López N. 2002. Desplazamiento y parasitismo de entomonematodos hacia frutos infestados con la broca del café *Hypothenemus hampei* (Coleoptera: Scolytidae). *Revista Colombiana de Entomología* 28:145-151.
- Murphy, S. T. and D. Moore. 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.
- Muschler, R. G. 2004. Shade management and its effect on coffee growth and quality. pp. 391-418. In, J. N. Wintgens (Editor). *Coffee: growing, processing, sustainable production*. Wiley-VCH Verlag, Weinheim, Germany. 984 pp.
- Ortiz, A., A. Ortiz, F. E. Vega, and F. Posada. 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.
- Osorio, N. 2002. The global coffee crisis: a threat to sustainable development. International Coffee Organization, London. Available online: <http://www.ico.org/documents/globalcrisis.pdf>
- 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. and I. C. W. Hardy. 1999. Reproductive biology of *Cephalonomia hyalinipennis* (Hymenoptera: Bethylinidae), a native parasitoid of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae), in Chiapas, Mexico. [Biological Control](#) 14:152-158.
- Pérez-Lachaud, G., T. P. Batchelor, and I. C. W. Hardy. 2004. Wasp eat wasp: facultative hyperparasitism and intra-guild predation by bethylid wasps. [Biological Control](#) 30:149-155.
- Perfecto, I., R. A. Rice, R. Greenberg, and M. E. Van der Voort. 1996. Shade coffee: a disappearing refuge for biodiversity. *BioScience* 46:598-608
- Perfecto, I., J. H. Vandermeer, G. López Bautista, G. Ibarra Nuñez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: the role of neotropical birds. [Ecology](#) 85:2677-2681.
- Perfecto, I., I. Armbrecht, S. M. Philpott, L. Soto-Pinto, and T. V. Dietsch. 2007. Shaded coffee and the stability of rainforest margins in northern Latin America. pp. 227-263. In, T. Tscharntke, C. Leuschner, M. Zeller, E. Guhardja, and A. Bidin (Editors). *Stability of tropical rainforest margins: linking ecological, economic and social constraints of land use and conservation*. Springer Verlag, Berlin. 515 pp.

- Philpott, S. M. and I. Armbrrecht. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology* 31:369-377.
- Philpott, S. M., W. J. Arendt, I. Armbrrecht, P. Bichier, T. V. Dietsch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams-Linera, J. Valenzuela, and J. M. Zolotoff. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conservation Biology* 22:1093-1105.
- Poinar, G., F. E. Vega, A. Castillo, I. E. Chavez, and F. Infante. 2004. *Metaparasitylenchus hypothenemi* n. sp. (Nematoda: Allantonematidae), a parasite of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Curculionidae: Scolytinae). *Journal of Parasitology* 90:1106-1110.
- Portilla, R., M. and D. Streett. 2006. Nuevas técnicas de producción masiva automatizada de *Hypothenemus hampei* sobre la dieta artificial Cenibroca modificada. *Cenicafé (Manizales, Colombia)* 57:37-50.
- Posada, F. and F. E. Vega. 2006. Inoculation and colonization of coffee seedlings (*Coffea arabica* L.) with the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales). *Mycoscience* 47: 284-289.
- Posada, F., M. C. Aime, S. W. Peterson, S. A. Rehner, and F. E. Vega. 2007. Inoculation of coffee plants with the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales). *Mycological Research* 111:748-757.
- Prokopy, R. J. and E. D. Owens. 1983. Visual detection of plants by insects. *Annual Review of Entomology* 28:337-364.
- Rojas, J. C., A. Castillo, and A. Virgen. 2006. Chemical cues used in host location by *Phymastichus coffea*, a parasitoid of coffee berry borer adults, *Hypothenemus hampei*. *Biological Control* 37:141-147.
- Ruales, C. 1997. Aspectos generales sobre la broca del café en Ecuador. *Café y Cacao: Noticias (Ecuador)* 2:7-11.
- Sánchez, L. and M. G. Rodríguez. 2007. Potencialidades de *Heterorhabditis bacteriophora* Poinar cepa HC1 para el manejo de *Hypothenemus hampei* Ferr. I. Parasitismo y capacidad de búsqueda. *Revista de Protección Vegetal (Habana, Cuba)* 22:80-84.
- Saravanan, P. A. and K. Chozhan. 2003. Monitoring and management of coffee berry borer, *Hypothenemus hampei* Ferrari (Scolytidae: Coleoptera). *Crop Research* 26:154-158.
- Sherry, T. W. 2000. Shade coffee: a good brew even in small doses. *The Auk* 117:563-568.
- Soto-Pinto, L., I. Perfecto, and J. Caballero-Nieto. 2002. Shade over coffee: its effects on berry borer, leaf rust and spontaneous herbs in Chiapas, Mexico. *Agroforestry Systems* 55:37-45.
- Ticheler, J. H. G. 1961. Étude analytique de l'épidémiologie du scolyte des graines de café, *Stephanoderes hampei* Ferr., en Cote d'Ivoire. *Mededelingen Landbouwhogeschool Wageningen* 61:1-49.
- Varaprasad, K. S., S. Balasubramanian, B. J. Diwakar, and C. V. Rama Rao. 1994. First report of an entomogenous nematode, *Panagrolaimus* sp. from coffee berry borer, *Hypothenemus hampei* (Ferrari) from Karnataka. *Plant Protection Bulletin* 46:42.
- Varón, E. H., P. Hanson, O. Borbón, M. Carballo, and L. Hilje. 2004. Potencial de hormigas como depredadores de la broca del café (*Hypothenemus hampei*) en Costa Rica. *Manejo Integrado de Plagas y Agroecología (Costa Rica)* 73:42-50.
- Vega, F. E. 2008a. The rise of coffee. *American Scientist* 96:138-145.
- Vega, F. E. 2008b. Insect pathology and fungal endophytes. *Journal of Invertebrate Pathology* 98: 277-279.
- Vega, F. E., G. Mercadier, A. Damon, and A. Kirk. 1999. Natural enemies of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) in Togo and Ivory Coast, and additional entomofauna associated with coffee beans. *African Entomology* 7:243-248.
- Vega, F. E., P. Benavides, J. Stuart, and S. L. O'Neill. 2002. *Wolbachia* infection in the coffee berry borer (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 95:374-378.
- Vega, F. E., E. Rosenquist, and W. Collins 2003. Global project needed to tackle coffee crisis. *Nature* 435:343.
- Vega, F. E., M. Pava-Ripoll, F. Posada, and J. S. Buyer. 2005. Endophytic bacteria in *Coffea arabica* L. *Journal of Basic Microbiology* 45:371-380.

- Vega, F. E., A. Ebert, and R. Ming. 2008a. Coffee germplasm resources, genomics, and breeding. *Plant Breeding Reviews* 30:415-447.
- Vega, F. E., F. Posada, M. C. Aime, S. W. Peterson, and S. A. Rehner. 2008b. Fungal endophytes in green coffee seeds. *Mycosystema* 27:75-84.
- Vega, F. E., F. Posada, M. C. Aime, M. Pava-Ripoll, F. Infante, and S. A. Rehner. 2008c. Entomopathogenic fungal endophytes. *Biological Control* 46:72-82.
- Vega, F. E., A. Simpkins, M. C. Aime, F. Posada, S. W. Peterson, S. A. Rehner, F. Infante, A. Castillo, and A. E. Arnold. 2010. Fungal endophyte diversity in coffee plants from Colombia, Hawai'i, Mexico, and Puerto Rico. *Fungal Ecology*, *in press*.
- Velasco Pascual, H., J. M. Llavén Gómez, and A. F. Velásquez Velásquez. 1997. Respuesta a extractos de cerezas de café utilizados como atrayente para hembras inter cosecha de la broca del fruto *Hypothenemus hampei* Ferr. pp. 349-352. In, *Memorias XVIII Simposio Latinoamericano de Caficultura*. San José, Costa Rica. 524 pp.
- Vélez, M., A. E. Bustillo, and F. J. Posada. 2000. Predación sobre *Hypothenemus hampei*, (Ferrari) de las hormigas *Solenopsis* spp., *Pheidole* spp. y *Dorymyrmex* spp. durante el secado del café. p. 17. In, *Resúmenes XXVII Congreso Sociedad Colombiana de Entomología*, Medellín, Colombia.
- Vélez, M., A. E. Bustillo, and F. Posada. 2003. Depredación de *Hypothenemus hampei* por *Solenopsis geminata* y *Gnamptogenys* sp. (Hymenoptera: Formicidae). p. 26. In, *Libro de Resúmenes XXX Congreso, Sociedad Colombiana de Entomología*. Universidad Autónoma, Cali, Colombia.
- Vélez-Arango, P. E. and M. Benavides-Gómez. 1990. Registro e identificación de *Beauveria bassiana* en *Hypothenemus hampei* en Anyuca, Departamento de Nariño, Colombia. *Cenicafé* (Manizales, Colombia) 41:50-57.
- Vélez-Hoyos, M., A. E. Bustillo-Pardey, and F. Posada-Flórez. 2006. Depredación de *Hypothenemus hampei* por hormigas, durante el secado solar del café. *Cenicafé* 57:198-207.
- Vet, L. E. M. 1999. From chemical to population ecology infochemical use in an evolutionary context. *Journal of Chemical Ecology* 25:31-49.
- Vet, L. E. M., and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* 37:141-172.
- Villacorta, A. and J. F. Barrera. 1993. Nova dieta meridica para criação de *Hypothenemus hampei* (Ferrari, 1867). *Anais da Sociedade Entomológica do Brasil* 22:405-409.
- Vinson, S. B. 1976. Host selection by insect parasitoids. *Annual Review of Entomology* 21:109-133
- Wintgens, J. N. (Editor). 2004. *Coffee: Growing, processing, sustainable production*. Wiley-VCH. Weinheim, Federal Republic of Germany. 976 pp.
- Wrigley, G. 1988. *Coffee*. Longman Scientific & Technical. Essex, England. 639 pp.