Research

Postharvest Population Reservoirs of Coffee Berry Borer (Coleoptera: Curculionidae) on Hawai'i Island

Melissa A. Johnson, 1,2,4,* Samuel Fortna, 1,3,* Robert G. Hollingsworth, 1,1 and Nicholas C. Manoukis 1,0

¹Daniel K. Inouye US Pacific Basin Agricultural Research Center, United States Department of Agriculture—Agricultural Research Service, 64 Nowelo Street, Hilo, HI 96720, ²Oak Ridge Associated Universities, Oak Ridge Institute for Science and Education, Oak Ridge, TN 37831, ³College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa, Honolulu, HI 96822, and ⁴Corresponding author, e-mail: melissa.johnson@ars.usda.gov

*Equal first-author contributions.

tDeceased.

Subject Editor: Rizana Mahroof

Received 23 May 2019; Editorial decision 8 July 2019

Abstract

Coffee berry borer, Hypothenemus hampei Ferrari (Coleoptera: Curculionidae: Scolytinae), is the most damaging insect pest of coffee worldwide. Old coffee berries (raisins) are widely acknowledged as coffee berry borer reservoirs, yet few studies have attempted to quantify coffee berry borer populations in raisins remaining on farms postharvest. We collected ground and tree raisins at six coffee farms on Hawai'i Island to assess raisin density, infestation, coffee berry borer abundance, and adult mortality in three areas of each farm: trees, driplines (ground below the tree foliage), and center aisles (ground between tree rows). We also assessed infestation of the new season's crop by conducting whole-tree counts of infested green berries. Mean raisin density was significantly higher in the dripline compared to the center aisle and trees (131 vs 17 raisins per m² and 12 raisins per tree, respectively). Raisin infestation was significantly higher in samples from trees (70%) relative to those from the dripline (22%) and center aisle (18%). Tree raisins had significantly higher coffee berry borer abundance compared to both areas of the ground (20 vs 3-5 coffee berry borer per raisin). Adult mortality was significantly higher on the ground (63-71%) compared to the trees (12%). We also observed a significant positive correlation between ground raisin density and infestation of the new season's crop. Across all farms, we estimated that 49.5% of the total coffee berry borer load was present in dripline raisins, 47.3% in tree raisins, and 3.2% in center aisle raisins. Our findings confirm the importance of whole-farm sanitation in coffee berry borer management by demonstrating the negative impact that poor postharvest control can have on the following season's crop.

Key words: Coffea arabica, cultural control, Hawaii, Integrated Pest Management, farm sanitation

Coffee (Coffea spp., L. (Gentianales: Rubiaceae)) is the most important agricultural commodity in more than 70 countries in the humid tropics worldwide (Jaramillo et al. 2006). While coffee production has increased in recent decades through the heavy use of fertilizers, higher yielding varieties, and high-density plantings (Baker et al. 2002), production is simultaneously being negatively impacted by a number of pests (e.g., root-knot nematode Meloidogyne spp., black twig borer Xylosandrus compactus) and diseases (e.g., coffee leaf rust Hemileia vastatrix, coffee berry blotch Cercospora coffeicola). The spread of these coffee pests and diseases follows global trends of growing trade and movement of goods, with attendant serious impacts on agricultural and other systems (Simberloff et al. 2013). Coffee berry borer, Hypothenemus hampei

Ferrari (Coleoptera: Curculionidae: Scolytinae), is the most destructive insect pest of coffee, causing serious economic losses through decreased yield and quality of coffee (Le Pelley 1968). Hawaii was one of the last coffee-growing regions in the world without an established population of coffee berry borer, until its invasion, establishment, and detection in 2010 (Burbano et al. 2011).

Coffee berry borer completes its entire life cycle within the coffee berry, making control of this pest very difficult. Adult females bore into the central disc of the developing green berries and into the coffee bean itself, where they excavate galleries in which to lay their eggs. Offspring develop in the coffee bean over a period of 1–2 mo, depending on temperature and berry moisture (Bustillo et al. 1998, Vega et al. 2015). Male offspring inseminate female

siblings, and the mated females leave and search for a new berry in which to lay eggs or remain in the natal berry and begin reproduction (Bustillo et al. 1998, Vega et al. 2015). Flight activity of female coffee berry borer is driven by a combination of environmental cues (i.e., increased temperature and relative humidity; Baker et al. 1992, Aristizabal et al. 2017a) and coffee plant physiology (i.e., availability of coffee berries with <20% dry matter content; Alonzo 1984, Ruiz and Baker 2010). Insecticide sprays must be precisely timed with peak flight activity of female beetles, as they are most susceptible when they are out looking for new berries to infest and are not protected within their natal berries.

With an increasing number of countries banning the use of toxic insecticides such as endosulfan and chlorpyrifos, effective and sustainable strategies are urgently needed to control coffee berry borer (Jaramillo et al. 2006). In Latin America, an important part of Integrated Pest Management (IPM) for coffee berry borer involves the collection and removal of all ripe and overripe berries (termed 'Re-Re' in Spanish for 'Recolleción' and 'Repase') from the trees and ground after the main harvest and during the inter-harvest period to reduce sources of reinfestation (Baker 1999, Bustillo et al. 1999, Jaramillo et al. 2009). This cultural control practice works by removing the mature berries that are still suitable for oviposition, as well as removing the old berries ('raisins') that harbor existing populations of coffee berry borer. Although tedious and time-intensive, this practice has been shown to be very effective at reducing coffee berry borer populations between seasons (Aristizábal et al. 2002, Benavides et al. 2002). The labor required to conduct this type of sanitation was estimated to account for 2% of the total production costs in Colombia (Aristizábal et al. 2011) and 6% of total production costs in Hawaii (L. F. Aristizábal, unpublished data).

IPM recommendations for coffee berry borer in Hawaii include strip-picking all remaining coffee berries from the trees at the end of the harvest season, stump-pruning by block, monitoring fields for coffee berry borer activity using alcohol-baited traps and the 30-tree sampling method, and spraying the entomopathogenic pesticide Beauveria bassiana (Kawabata et al. 2017). The management of ground raisins is not a typical component of the IPM strategies used by growers in Hawaii, aside from urging pickers to be careful not to drop berries on the ground. As part of a USDA-ARS-funded Area-Wide coffee berry borer monitoring program, efforts were undertaken to quantify the efficacy of each currently recommended component of coffee berry borer IPM to operationally define the order of importance for control measures. Because strip-picking is perhaps the most expensive IPM component in Hawaii due to high labor costs (Aristizábal et al. 2016, 2017b), there is a need to determine the extent to which raisins act as coffee berry borer reservoirs, particularly under the highly variable climate and soil conditions that characterize Hawaii's coffeegrowing regions. Additionally, there is a need to quantify coffee berry borer populations in raisins left on the trees versus those dropped on the ground, so that collection and removal efforts can be targeted to maximize coffee berry borer control while minimizing labor costs.

The major goals of this study were to 1) quantify the density of raisins remaining in the trees and on the ground after the main harvest, 2) estimate raisin infestation, coffee berry borer abundance per raisin, and adult coffee berry borer mortality in ground and tree raisins during the inter-crop season, and 3) estimate the relationship between raisin density and infestation of the new season's crop.

Materials and Methods

Study Sites

Six commercial coffee farms were selected for the study based on the following criteria at the start of the study: 1) ≥90% of the coffee trees were completely devoid of green berries, and 2) no berries past the mature green stage were present on the farm. Farms were located in three coffee-growing districts on Hawai'i Island that experience varying environmental conditions. Two farms were located in the Kona district on the west side of Hawai'i Island (Fig. 1; Table 1), which is characterized by hot sunny mornings and cool, cloudy afternoons with an average annual temperature of 24°C. Winter temperatures and rainfall in Kona are low relative to the rest of Hawai'i Island, resulting in a period of dormancy in the coffee (Bittenbender and Smith 2008). Flowering typically occurs from late February to April following heavy rainfall events, with the harvest season running from August through December. Three farms were located in Ka'u on the southeast side of Hawai'i Island (Fig. 1; Table 1), which experiences relatively constant temperatures (average annual temperature of 22°C) and rainfall, resulting in year-round flowering and fruiting of coffee trees (Bittenbender and Smith 2008). A single farm was located in Hilo on the northeast side of Hawai'i Island (Fig. 1; Table 1), where cloud cover and rainfall are typically high, and the average annual temperature is 23°C.

Establishing Sampling Zones

Perimeters of the coffee farms were established using Garmin Rhino handheld GPS receivers (Rino 650t, Garmin Ltd., Olathe, KS). Field coordinates were imported into QGIS (Quantum Geographic Information Systems; Open Source Geospatial Foundation, Chicago, IL) and a map was generated of each coffee farm. Farms were divided into polygons (hereafter referred to as zones) of approximately 335 m² and were used to ensure a systematic random sampling throughout the field following the method of Johnson et al. (2018).

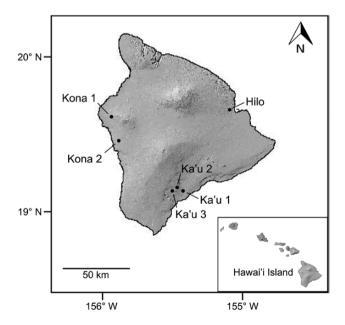


Fig. 1. Location of the six commercial coffee farms used as study sites on Hawai'i Island. Sites were distributed across the districts of Kona, Ka'u, and Hilo. Inset map shows the position of Hawai'i Island within the Hawaiian archipelago.

Ground and Tree Sampling

Ground and tree raisins (old berries with or without exocarp intact) were sampled at 3- to 4-wk intervals from February to June 2017. For each farm/sampling date, tree and ground raisins were collected

from 10 sampling points. Sampling points were selected by alternating every other or every few zones to ensure even sampling across each farm, and to more accurately capture the distribution of infestation hotspots. Each sampling point consisted of two trees located at

Table 1. Characteristics of the six farms included in the present study, including elevation, predominant ground cover, sampled area in hectares, number of trees in the sampled area, total number of trees per hectare, mean distance between trees, mean tree radius, mean center aisle width, and mean row width

Farm	Elev (m)	Ground cover	Sampled area (ha)	Trees	Trees per ha	Distance b/t trees (cm)	Tree radius (cm)	Center width (cm)	Row width (cm)
Hilo	183	Grass	0.93	1,423	1,524.55	163.42	52.98	190.64	296.60
Ka'u 1	279	Soil	1.32	1,190	900.99	200.94	68.66	262.28	399.60
Ka'u 2	484	Soil	0.65	1,147	1,773.62	172.93	76.13	160.25	312.51
Ka'u 3	488	Soil	0.81	1,159	1,436.08	189.38	88.81	200.46	378.08
Kona 1	454	Grass	1.15	1,616	1,409.20	205.56	67.76	172.56	308.08
Kona 2	488	Grass	0.49	759	1,543.36	193.50	78.84	188.42	346.10

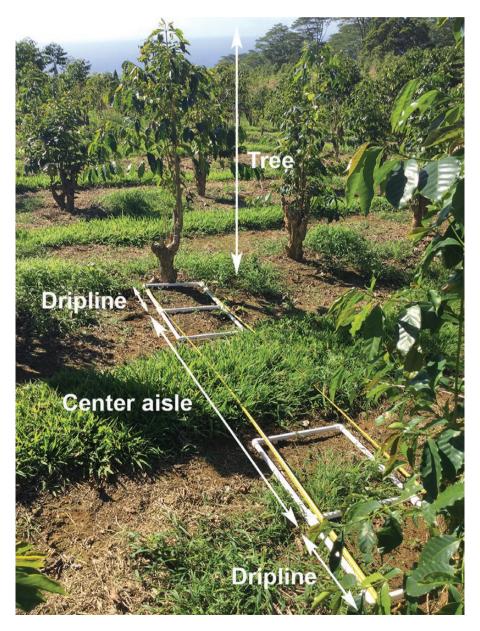


Fig. 2. Coffee raisins were sampled in three distinct areas of each coffee farm: trees, dripline (ground below the tree foliage), and center aisles (ground between tree rows).

the same point of adjoining rows and included the ground between the two trees from tree trunk to tree trunk (Fig. 2). This approach allowed us to sample both ground and tree raisins in a given area, and also accounted for terrain differences such as slope and substrate.

To sample ground berries at each collection point, we used two 0.5 m × 1 m quadrats made from 0.5-inch PVC pipe. The 0.5 m side of the quadrat was centered at the base of each tree so that the 1-m side lined up with the paired quadrat across the aisle. Each sampling quadrat had a sliding bar that was adjusted to the edge of the tree foliage (see Fig. 2). The distance from the edge of the tree foliage to the base of the tree was classified as the dripline, and the two dripline samples from the base of each tree were combined into a single sample. The space between the trees that fell outside of the dripline was classified as center aisle. The sampling area of the center aisle was established by extending the two lateral borders of each quadrat until it met with the paired quadrat across the aisle. All raisins were collected from within the dripline and center aisle quadrats and placed in separate Ziploc bags (SC Johnson & Son, Racine, WI) labeled with sample date, farm name, and sample area (dripline or center aisle) for dissection. Area measurements were taken for the tree driplines, the center aisle, and the total sampling area from tree trunk to tree trunk.

A random number generator was used to select which of the two trees would be used for raisin collection. All raisins were removed from the selected tree and placed in a Ziploc bag labeled with sample date, farm name, and sample area (tree) for dissection. Collected raisins were stored at 14°C to suspend beetle development. In instances where a tree was randomly selected but only a stump was present, the sample was recorded as 'NA'. Following ground and tree sample collection, the tree from which the raisins were collected was flagged on the side of the tree from which the sample plot was set up, and the sample date was recorded on the flag to avoid resampling the same area in the future. The average distance between trees across rows was estimated by adding all ground sampling distances taken from tree trunk to tree trunk and dividing by the total number of samples. The average distance between trees within a row was estimated by measuring the distance from tree trunk to tree trunk for 10 trees in a row, then dividing by nine. Lastly, the number of trees in all sampling zones was summed on each farm and divided by the total area sampled. The number of sampled trees per hectare (ha) was multiplied by the total farm area to estimate the total number of trees per farm.

Raisin Density, Infestation, Coffee Berry Borer Abundance, and Adult Mortality

For each farm/sampling date, raisin samples were separated by sample plot number (1-10) and collection location (center aisle, dripline, or trees). The total number of raisins from each sample plot was then counted and recorded for each collection location. For each of the 10 sample plots, we dissected a maximum of 30 raisins from each collection location (i.e., if less than 30 raisins were collected from a given sample plot/collection location, then all raisins were dissected). Because tree raisins were generally uniform in character with the exocarp intact, raisins were randomly selected from each of the 10 sample plots for dissection without segregation. Ground raisins were further sorted into piles with similar characteristics (i.e., exocarp intact, exocarp partially intact, or bare bean). From the center aisle and dripline piles, raisins for dissection were selected from each of the 10 sample plots in proportion to the total distribution of characteristics of all ground samples. For example, if 300 ground samples were collected and 50 of those had the exocarp

intact, 100 had partial exocarp intact, and 150 were bare beans, the sample of 30 used for dissection would be 5 exocarp intact, 10 partial exocarp intact, and 15 bare beans. This was done because we speculated that ground raisins with more exocarp intact fell more recently from the trees, and were therefore less degraded and more likely to be a suitable habitat for coffee berry borer. Within 24 h of collection, raisins were dissected under a dissecting microscope at 30-50x (Leica Microsystems GmbH, Wetzlar, Germany), and the number of eggs, larvae, pupae, teneral adults (young adults that have recently emerged from the pupa stage and are pale in color with a soft exoskeleton), and mature adults (dark in color with a hardened exoskeleton) was counted. Teneral and mature adults were recorded as alive or dead for each raisin. Given that our sampling units consisted of raisins, each of which comprises two beans, for samples that consisted of bare beans we randomly selected two beans of similar size to comprise a single raisin for dissection. Only raisins that contained at least one life stage of coffee berry borer were counted as infested, since the high level of decomposition of many raisins made it difficult to determine if bean damage was caused by coffee berry borer or other organisms.

Estimation of Coffee Berry Borer Load in Raisins

The average coffee berry borer load was calculated for each sampling area using the following variables: R = mean number of raisinsper m^2 ; I = mean proportion of infested raisins; <math>C = mean numberof coffee berry borer in each infested raisin; S = mean proportionof adult coffee berry borer that survive in each infested raisin. We calculated a conservative estimate based on adult coffee berry borer only, and a high estimate based on the total coffee berry borer population (the sum of all life stages). Given that we did not track mortality of eggs, larvae, or pupae, we assumed that these immature life stages had the same survival rate as adults. The average coffee berry borer load per m² (L) was: $L = (R \times I) \times (C \times S)$. We then converted these estimates to the number of coffee berry borer per ha by first multiplying the number of coffee berry borer per m² by 10,000 m²/ ha. Finally, we multiplied this number by the proportion of sampled ground area comprised of either dripline or center aisle (for ground raisins), or the number of trees per ha (for tree raisins).

New Crop Infestation

Infestation estimates for the season's new crop were conducted once green berries became available on the majority of trees, starting in March 2017 and ending in June 2017. Infestation estimates were conducted at 3- or 4-wk intervals, and usually coincided with sampling dates for ground/tree raisins. Sampling methods were similar to ground and tree zone sampling, though a greater number of samples were taken per sampling date. For farms with <30 zones, an infestation estimate was taken from each zone. For farms with >30 zones, approximately half of the zones were selected for infestation estimates. Upon entering a zone, a tree was selected haphazardly and the total number of green berries, as well as the total number of infested green berries were counted and recorded. All green berries larger than the size of a pea were counted, as this is the minimum size that was determined to be infestable. After the tree was sampled, it was flagged to prevent resampling it in the future. To estimate the new season's crop infestation for each farm/sampling date we first divided the total number of trees on the farm by the number of trees sampled, then multiplied by the total number of infested berries. We assumed that there was only one adult per entrance hole, given that the berries were generally too high in moisture content for the beetle to begin developing new life stages (Hamilton et al. 2019).

Statistical Analysis

To account for non-normal data and random effects we used generalized linear mixed models (GLMMs) to determine if different areas of the farm (center aisle, dripline, and tree) are good predictors of: 1) raisin density, 2) raisin infestation, 3) coffee berry borer abundance, and 4) adult coffee berry borer mortality. We ran four separate GLMMs, each having one of the four continuous response variables (raisin density, infestation, coffee berry borer abundance, and adult mortality). Each analysis included sampling area (three levels as categorical variables) as a fixed effect. To control for random differences among farms and sampling dates we included these variables as random effects. The GLMM for raisin density was run using a Poisson distribution (ideal for count data), with an offset to specify that the number of raisins is proportional to the sampling area. For coffee berry borer abundance we also used a Poisson distribution and analyzed each of the four life stages separately. The GLMMs for raisin infestation and adult mortality were run using a binomial distribution (ideal for proportion data). GLMMs and model comparisons using likelihood ratio tests were implemented in the lme4 package (Bates et al. 2015) in the R statistical environment (R Core Team 2018). Each GLMM analysis was followed by pairwise Tukey contrasts in the package emmeans (Lenth 2018) in R. Lastly, we conducted a Pearson correlation test in R to estimate the relationship, if any, between raisin density and green berry infestation in the new season's crop.

Results

Raisin Density

The total area sampled at each of the farms ranged from 0.65 to 1.32 ha (Table 1). We collected a total of 37,940 raisins across all six farms; 74% of the raisins collected were from the dripline, 19% from the center aisle, and 7% from the trees. Results from the GLMM suggested that sampling area was a good predictor of raisin density ($X^2 = 41.99$, df = 2, P < 0.001). Raisin density was significantly higher in the dripline (mean ± 1 SE; 131.80 ± 24.77 raisins per m²) compared to the center aisle (17.07 ± 2.52 raisins per m²) and trees (12.41 ± 4.20 raisins per tree) (Table 2; Fig. 3). Raisin density in the center aisle was also significantly higher than the density of raisins in the trees (Table 2; Fig. 3).

Raisin Infestation

Sampling area was a good predictor for raisin infestation according to the GLMM ($X^2 = 54.17$, df = 2, P < 0.001). Trees had a significantly higher mean proportion of infested raisins across all farms (0.70 \pm 0.13) compared to the dripline (0.22 \pm 0.06) and center

Table 2. GLMM estimates for raisin density, raisin infestation, coffee berry borer per infested raisin (separated into four life stages), and adult coffee berry borer mortality as explained by farm sampling area (center aisle, dripline, and trees)

Model variable		Tukey contrasts				
Raisin density	Estimate	SE	z-ratio	P-value		
Center vs dripline	-2.119	0.015	-141.556	***		
Center vs tree	0.233	0.021	10.905	* * *		
Dripline vs tree	2.353	0.018	134.791	爷爷爷		
Raisin infestation	Estimate	SE	z-ratio	P-value		
Center vs dripline	-0.000	1.44	0.000	1.000		
Center vs tree	-4.512	1.11	-4.081	* * *		
Dripline vs tree	-4.512	1.11	-4.081	* * *		
Eggs/raisin	Estimate	SE	z-ratio	P-value		
Center vs dripline	-0.606	0.352	-1.722	0.197		
Center vs tree	-1.313	0.319	-4.110	* * *		
Dripline vs tree	-0.707	0.256	-2.759	*		
Larvae/raisin	Estimate	SE	z-ratio	P-value		
Center vs dripline	-0.916	0.338	-2.712	*		
Center vs tree	-2.356	0.299	-7.879	* * *		
Dripline vs tree	-1.439	0.201	-7.156	非非非		
Pupae/raisin	Estimate	SE	z-ratio	P-value		
Center vs dripline	-0.916	0.588	-1.559	0.264		
Center vs tree	-2.495	0.518	-4.819	* * *		
Dripline vs tree	-1.578	0.346	-4.559	斧斧斧		
Adults/raisin	Estimate	SE	z-ratio	P-value		
Center vs dripline	-0.395	0.159	-2.491	*		
Center vs tree	-1.726	0.134	-12.919	* * *		
Dripline vs tree	-1.331	0.114	-11.700	非异环		
Adult mortality	Estimate	SE	z-ratio	P-value		
Center vs dripline	0.217	0.661	0.329	0.942		
Center vs tree	3.832	0.875	4.381	하는 하는 하는		
Dripline vs tree	3.615	0.851	4.246	* * *		

^{*}Significant at P < 0.05, ***significant at P < 0.001.

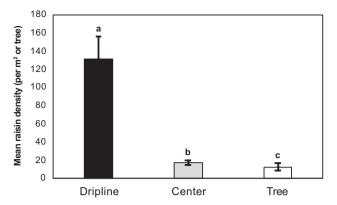


Fig. 3. Mean (\pm 1 SE) raisin density across six coffee farms on Hawai'i Island. Density is reported as the mean number of raisins collected per m² (for dripline and center aisle ground sampling areas) and per tree. Lowercase letters represent significant differences in the means.

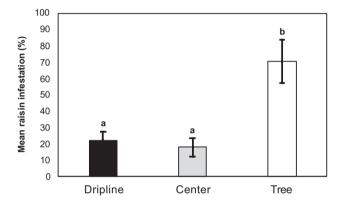


Fig. 4. Percent (mean ± 1 SE) raisin infestation across six coffee farms on Hawai'i Island. Infestation is reported as the mean percentage of raisins that had at least one life stage of coffee berry borer. Lowercase letters represent significant differences in the means.

aisles (0.18 \pm 0.06) (Table 2; Fig. 4). Mean infestation was not significantly different between the dripline and center aisles (Table 2; Fig. 4).

Coffee Berry Borer Abundance Per Infested Raisin

Results of the GLMM revealed that sampling area was a good predictor of coffee berry borer abundance per infested raisin $(X^2 = 41.11, df = 2, P < 0.001)$. Trees had a significantly higher mean number of eggs, larvae, pupae, and adults per infested raisin compared to raisins in the dripline and in the center aisle (Table 2; Fig. 5), and this trend held constant through the entire inter-crop season (Supp Fig. 1 [online only]). Coffee berry borer abundance in the dripline was significantly higher than in the center aisle for the larval and adult life stages (Table 2; Fig. 5). The mean coffee berry borer population (sum of all life stages) per infested raisin was 20.06 individuals in the trees, 5.42 in the dripline, and 3.06 in the center aisle (Fig. 6). When averaged across all six farms, mean coffee berry borer abundance in dripline raisins trended down slightly until leveling off in May, while center aisle raisins trended down from February to March and then remained stable (Fig. 7). For five of six farms, the highest ground population estimate was in either February or March. In contrast, mean coffee berry borer abundance in tree raisins peaked from March to April, and then showed a second peak in June (Fig. 7).

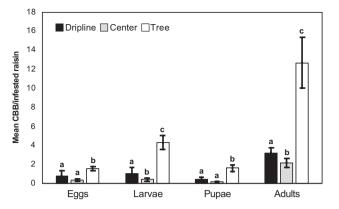


Fig. 5. Mean (± 1 SE) number of four main life stages of coffee berry borer (eggs, larvae, pupae, and adults) per infested raisin across six coffee farms on Hawai'i Island. Lowercase letters represent significant differences in the means.

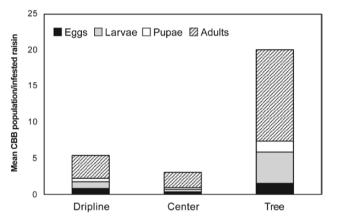


Fig. 6. Mean number of coffee berry borer per infested raisin across six coffee farms on Hawai'i Island. The total coffee berry borer population per raisin is separated into the four main life stages: eggs, larvae, pupae, and adults.

Adult Mortality

Results of the GLMM revealed that sampling area was a good predictor of adult mortality in infested raisins ($X^2 = 36.90$, df = 2, P < 0.001). Mean adult coffee berry borer mortality was significantly higher in the center aisle (0.71 ± 0.11) and dripline (0.64 ± 0.10) relative to the trees (0.12 ± 0.03 ; Table 2; Fig. 8). Mortality was not significantly different between the dripline and center aisle (Table 2; Fig. 8).

Coffee Berry Borer Load Estimates

Our calculation of mean coffee berry borer load in raisins across all six farms revealed that 49.5% of the coffee berry borer on a given farm during the inter-crop season were in dripline raisins, 47.3% were in tree raisins, and 3.2% were in center aisle raisins. Across all farms and sampling dates, we estimated 140,616–237,384 coffee berry borer per ha in dripline raisins, 143,257–227,357 coffee berry borer per ha in tree raisins, and 10,846–15,428 coffee berry borer per ha in center aisle raisins.

New Crop Infestation

Green berry infestation during the sampling period from March to June 2017 ranged from 1 to 48% across all six farms. Infestation was generally higher earlier in the season, although this varied among

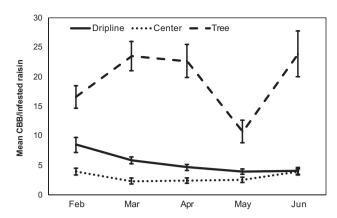


Fig. 7. Mean (± 1 SE) coffee berry borer per infested raisin over time across six coffee farms on Hawai'i Island. All four life stages are combined to represent the total population per infested raisin.

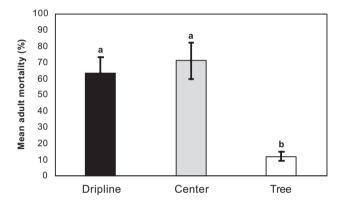


Fig. 8. Percent (mean \pm 1 SE) adult mortality across six coffee farms on Hawai'i Island. Mortality is reported as the mean percentage of dead adults out of the total number of adults (teneral and mature) recovered in infested raisins. Lowercase letters represent significant differences in the means.

farms due to the ongoing development of new green berries. Results of the Pearson correlation test indicated that there was a significant positive association between the number of ground raisins/ m^2 and percent infestation in green berries (r = 0.84, P < 0.001; Fig. 9). No significant association was found between the number of raisins per tree and percent infestation in green berries (r = 0.03, P = 0.90).

Discussion

We examined ground and tree raisins on six commercial coffee farms to determine the importance of raisins as coffee berry borer reservoirs during the inter-crop season on Hawai'i Island. Results showed that for a given farm, raisin density was highest in the dripline, while infestation and coffee berry borer abundance per infested raisin was highest in the trees. We also found that raisins in the center aisle and dripline had significantly higher adult mortality relative to raisins in the trees. For an average farm during the inter-crop season, 49.5% of the total coffee berry borer load was present in dripline raisins, 47.3% in tree raisins, and only 3.2% in center aisle raisins.

The six commercial coffee farms investigated in this study employed strip-picking as a sanitation method following the end of the main harvest in December. For five of the six farms, the mean number of raisins remaining on trees after strip-picking was 1–6 raisins per tree, which is rated 'good' in terms of efficacy of harvesting practice

(Bustillo et al. 1998). One farm had exceedingly high numbers of raisins in trees (mean = 57 raisins per tree), and this likely is related to the fact that this farm had primarily *C. arabica* var. *catuai* planted, as opposed to the other five farms that had *C. arabica* var. *typica* planted. The *typica* variety is tall and low-yielding, while the *catuai* variety is known for its compact shape and high yield, thus requiring increased time and labor to remove all the raisins at the end of the season.

Ground raisins were not managed at any of the study farms, and this was reflected in the high density of raisins in the dripline at all of the farms examined. Additionally, no trends were observed between ground raisin density and ground cover type (data not presented here), although we did not examine farms that had a broad spectrum of ground cover (only farms with bare soil, grass, or a combination of both were included). Of the six farms, the highest ground raisin density was at a farm with bare soil in the dripline and grass in the center aisles. The farm with the second highest raisin density had grass in both the dripline and center aisles. Additional studies are needed to further examine the effects of various ground cover types on raisin decomposition and coffee berry borer survival.

We found that mean infestation in tree raisins was significantly higher than in ground raisins at all six farms (31–98% vs 4–38%). Our infestation results coincide with those of Jaramillo et al. (2009), which examined raisins at a single farm in Western Kenya over a 2-yr period and reported higher infestation in tree raisins relative to ground raisins (60–91% vs 44–84%). Higher infestation in tree raisins may be a result of the closer proximity of these raisins to large numbers of coffee berry borer in other tree raisins and berries. Upon emergence of female coffee berry borer from their natal berries, it is likely that they infest the next nearest berry that is suitable for oviposition in the trees. Similarly, when coffee berry borer emerge from ground berries their natural instinct is to fly up into the tree canopy above to find a suitable berry for oviposition (Baker 1984, Bustillo et al. 1999).

In the present study, the mean number of coffee berry borer individuals in all life stages was significantly higher in tree raisins relative to ground raisins across the entire inter-crop season (Supp Fig. 1 [online only]). Our finding of significantly higher mean coffee berry borer abundance in tree raisins relative to ground raisins (20 coffee berry borer per raisin vs 3–5 coffee berry borer per raisin; Fig. 6) corresponds with results from an earlier field study in Ethiopia, which reported that the number of adult coffee berry borer was significantly higher in tree raisins (~40-120 adults per month) compared to ground raisins (~20-70 adults per month) across the entire year (Mendesil et al. 2004). In contrast, Jaramillo et al. (2009) observed that immature and mature stages of coffee berry borer were similar in terms of abundance in tree and ground raisins at a single farm in Western Kenya, and observed a peak in adult female abundance in March in both ground (~10 females per raisin) and tree raisins (~7 females per raisin) across two seasons. Baker (1984) reported higher adult female abundance in ground raisins compared to tree raisins in Mexico, despite the fact that the number of individuals in immature stages was similar. The author speculated that higher temperatures in the trees may have stimulated female adults to leave the tree raisins, while those on the ground remained and lead to a buildup of females (as many as 50/infested raisin). We observed a substantial decrease in coffee berry borer adults and larvae in tree raisins in May, with high temperatures potentially causing coffee berry borer to evacuate raisins. The varying results reported across these coffee-growing regions suggests that coffee berry borer reproduction is tightly associated with weather conditions, and thus should be assessed for each particular region prior to forming IPM recommendations.

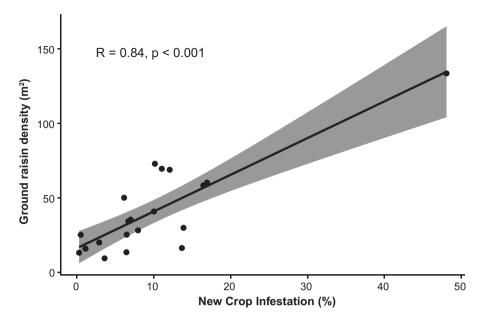


Fig. 9. Significant positive correlation between ground raisin density and infestation of green berries in the new season's coffee crop. Points represent mean ground raisin density and green berry infestation for a given sampling date/farm (3–4 samples from each of six farms from March to June 2017). The shaded area represents the 95% confidence interval.

We observed higher adult mortality in ground raisins relative to tree raisins (64–71% vs 12%), which corresponds with results from Jaramillo et al. (2009) who reported ~10–63% adult coffee berry borer mortality in ground raisins compared to ~3–40% mortality in tree raisins. Additionally, the authors observed that the high coffee berry borer mortality in ground raisins coincided with high numbers of the parasitoid *Prorops nasuta*. Given that this parasitoid is not present in Hawaii, the high coffee berry borer mortality we observed in ground raisins may be the result of natural enemies (e.g., fungal pathogens, bacteria, nematodes) and/or weather conditions that negatively impact coffee berry borer survival (e.g., flooding during rain events, direct exposure to solar radiation; Baker 1984).

We observed a strong positive association between ground raisin density and infestation of green berries in the new season's crop. Previous research has suggested similar relationships between tree raisin density and green berry infestation on Hawai'i Island (L. F. Aristizábal, unpublished data), but no studies have reported this relationship with ground raisins. In addition, we estimated that after strip-picking 49.5% of the entire coffee berry borer load on a given farm on Hawai'i Island is in dripline raisins, 3.2% is in center aisle raisins, and 47.3% is in tree raisins. From this we conclude that: 1) tree raisins are the main source of coffee berry borer for the following season, since even after strip-picking they account for nearly half of all the coffee berry borer in the inter-season period, 2) ground raisins located in the dripline are a significant secondary source of coffee berry borer, and 3) center aisle raisins are a negligible source of coffee berry borer. Thus, these data suggest that there is a need to incorporate the management of ground raisins in the dripline into current IPM strategies for coffee berry borer in Hawaii, as well as other regions outside of Latin America where this cultural control practice is not currently implemented (e.g., Puerto Rico, Papua New Guinea). The main challenge in implementing ground raisin management is that the labor required to remove fallen raisins is cost-prohibitive for many growers. Duque and Baker (2003) estimated that, on average, labor accounted for 89% of the total cost to manage coffee berry borer in Colombia. Secondarily,

the substrate on many farms makes it difficult or impossible to find and pick up ground raisins. For example, in the Kona coffee-growing district on Hawai'i Island, most coffee farms have very rocky substrates that make ground raisin removal unfeasible. More efficient and cost-effective strategies for ground raisin management need to be evaluated, including: 1) laying down tarps before picking coffee cherries to minimize the number of ground raisins, 2) increasing the frequency of cherry and raisin harvesting to every 2–3 wk to reduce the number of berries that fall to the ground, 3) using vacuums or mechanical collectors (see Constantino Chuaire et al. 2016) to increase efficiency and decrease time required for ground raisin removal, and 4) spraying biopesticides such as B. bassiana (Vera et al. 2011) or entomopathogenic nematodes (Lara et al. 2004, Manton et al. 2012) on ground raisins to reduce coffee berry borer populations. Given that the number of coffee berry borer per infested ground raisin remained high up through the end of the sampling period (June), we recommend that ground raisin management be conducted as early in the inter-crop season as possible to minimize reproduction. Ideally, ground raisins should be removed before the new season's crop develops to an infestable size, which typically occurs approximately 3 mo following the completion of the main harvest at many farms in Hawaii.

Conclusions

To or knowledge, this is the first study that has comprehensively quantified the coffee berry borer load present in ground and tree raisins, and thereby accurately estimated the potential for raisins to act as coffee berry borer reservoirs during the inter-crop season. Our results suggest that while tree raisins are the main coffee berry borer reservoirs during the inter-crop season on Hawai'i Island, ground raisins located in the dripline are a significant secondary source of coffee berry borer that should not be disregarded. The data presented here can be used to form new IPM guidelines for ground raisin management, particularly in regions where coffee berry borer is a recent invader and the connection between whole-farm sanitation and coffee infestation has not been fully explored.

Supplementary Data

Supplementary data are available at Journal of Economic Entomology online.

Acknowledgments

We thank Lindsey Hamilton, Nikki Lew, Emma Tiffan, and Hannah Tucker-Meuse for field and laboratory assistance. We are also grateful to the Kona and Ka'u coffee growers that allowed us to conduct this study on their farms, and to Luis Aristizábal for comments that improved this manuscript. This research was funded through the United States Department of Agriculture. Opinions, findings, conclusions, or recommendations expressed in this publication are those of the authors and do not necessarily reflect the views of the USDA. USDA is an equal opportunity employer.

References Cited

- Alonzo, P. F. 1984. El problema de la broca (Hypothenemus hampei (Ferr).) (Col: Scolytidae) yla caficultura. Aspectos relacionados con importancia. Dano, identificación, biologia, ecologia y control. IICA, PROMECAFE, Guatemala.
- Aristizábal, L. F., H. M. Salazar, and C. G. Mejia. 2002. Changes in the adoption of the components of coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae) integrated management, through participative methodologies. Rev. Colomb. Entomol. 28: 153–160.
- Aristizábal, L. F., M. Jiménez, A. E. Bustillo, and S. P. Arthurs. 2011. Monitoring cultural practices for coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) management in a small coffee farm in Colombia. Fla. Entomol. 94: 685–687.
- Aristizábal, L. F., A. E. Bustillo, and S. P. Arthurs. 2016. Integrated pest management of coffee berry borer: strategies from Latin America that could be useful for coffee farmers in Hawaii. Insects. 7: 6.
- Aristizábal, L. F., S. Shriner, R. Hollingsworth, and S. Arthurs. 2017a. Flight activity and field infestation relationships for coffee berry borer in commercial coffee plantations in Kona and Ka'u districts, Hawaii. J. Econ. Entomol. 110: 2421–2427.
- Aristizábal, L. F., M. A. Johnson, S. Shriner, R. Hollingsworth, N. C. Manoukis, R. Myers, P. Bayman, and S. P. Arthurs. 2017b. Integrated pest management of coffee berry borer in Hawaii and Puerto Rico: current status and prospects. Insects. 8: 123.
- Baker, P. 1984. Some aspects of the behavior of the coffee berry borer in relation to its control in Southern Mexico (Coleoptera, Scolytidae). Folia Entomol. Mex. 61: 9–24.
- Baker, P. 1999. The coffee berry borer in Colombia. DFID-CENICAFE-CABI-BIOSCIENCE, Chinchiná, Colombia.
- Baker, P., J. Barrera, and A. Rivas. 1992. Life-history studies of the coffee berry borer (*Hypothenemus hampei*, Scolytidae) on coffee trees in southern Mexico. J. Appl. Ecol. 29: 656–662.
- Baker, P. S., J. A. F. Jackson, and S. T. Murphy. 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.
- Bates, D., M. Machler, B. Bolker, and S. Walker. 2015. Fitting linear mixedeffects models using lme4. J. Stat. Softw. 67: 1–48.
- Benavides, P., A. Bustillo, E. C. Montoya, R. Cardenas, and C. Mejia. 2002. Participation of cultural, chemical and biological control in the management of the coffee berry borer. Rev. Colomb. Entomol. 28: 161–165.
- Bittenbender, H. C., and V. E. Smith. 2008. Growing coffee in Hawaii. College of Tropical Agriculture and Human Resources, University of Hawai'i, Honolulu, HI.
- Burbano, E., M. Wright, D. E. Bright, and F. E. Vega. 2011. New record for the coffee berry borer, *Hypothenemus hampei*, in Hawaii. J. Insect Sci. 11: 117.

- Bustillo, A. E., M. R. Cardenas, D. Villalba, J. Orozco, M. P. Benavides, and F. J. Posada. 1998. Manejo integrado de la broca del café Hypothenemus hampei (Ferrari) en Colombia. Cenicafé, Chinchiná, Colombia.
- Bustillo, A. E., M. G. Bernal, P. Benavides, B. Chaves. 1999. Dynamics of Beauveria bassiana and Metarhizium anisopliae infecting Hypothenemus hampei (Coleoptera: Scolytidae) populations emerging from fallen coffee berries. Fla. Entomol. 82: 491–498.
- Constantino Chuaire, L. M., C. E. Oliveros Tascon, P. Benavides Machado, J. C. Gomez Soto, C. A. Serna Giraldo, C. A. Ramirez Gomez, R. Medina, and A. Arcila. 2016. Recolecion de frutos café del suelo con canastilla: heramienta para el manejo integrado de la broca, pp. 1–8. In Avances Tecnicos Cenicafe No. 468, Junio de 2016. Gerencia Tecnica/Programa de Investigacion Cientifica Fondo Nacional del Café. Manizales. Caldas. Colombia.
- Duque, O. H., and P. S. Baker. 2003. Devouring profit: the socio-economics of coffee berry borer IPM. The Commodities Press, CABI/CENICAFE, Chinchina, Colombia, pp. 51–63.
- Hamilton, L. J., R. G. Hollingsworth, M. Sabado-Halpern, N. C.Manoukis, P. A. Follett, and M. A. Johnson. 2019. Coffee berry borer (Hypothenemus hampei) (Coleoptera: Curculionidae) development across an elevational gradient on Hawaii Island: Applying laboratory degree-day predictions to natural field populations. PLoS ONE 14: e0218321.
- Jaramillo, J., C. Borgemeister, and P. Baker. 2006. Coffee berry borer Hypothenemus hampei (Coleoptera: Curculionidae): searching for sustainable control strategies. Bull. Entomol. Res. 96: 223–233.
- Jaramillo, J., A. Chabi-Olaye, C. Borgemeister, C. Kamonjo, H.-M. Poehling, and F. E. Vega. 2009. Where to sample? Ecological implications of sampling strata in determining abundance and impact of natural enemies of the coffee berry borer, *Hypothenemus hampei*. Biol. Control. 49: 245–253.
- Johnson, M. A., R. Hollingsworth, S. Fortna, L. F. Aristizábal, and N. C. Manoukis. 2018. The Hawaii protocol for scientific monitoring of coffee berry borer: a model for coffee agroecosystems worldwide. J. Vis. Exp. 133: e57204.
- Kawabata, A. M., S. T. Nakamoto, R. T. Curtiss, S. Shriner, and L. F. Aristizábal. 2017. Recommendations for CBB integrated pest management in Hawaii 2016. UH-CTAHR, IP-41, Honolulu, HI.
- Lara, J. C., J. C. López, and A. E. Bustillo. 2004. Efecto de entomonematodes sobre poblaciones de la broca del café, *Hypothenemus hampei* (Coleoptera: Scolytidae), en frutos en el suelo. Rev. Colomb. Entomol. 30: 179–185.
- Lenth, R. 2018. emmeans: estimated marginal means, aka least-squares means. R package version 1.3.1. https://CRAN.R-project.org/package=emmeans.
- Le Pelley, R. H. E. 1968. Pests of coffee. Tropical science series; Longmans, London, United Kingdom, pp. 590, 147s.
- Manton, J. L., R. G. Hollingsworth, and R. Y. M. Cabos. 2012. Potential of Steinernema carpocapsae (Rhabditida: Steinernematidae) against Hypothenemus hampei (Coleoptera: Curculionidae) in Hawaii. Fla. Entomol. 95: 1194–1197.
- Mendesil, E., B. Jembere, and E. Seyoum. 2004. Population dynamics and distribution of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) on *Coffea arabica* L. in Southwestern Ethiopia. Ethiop. J. Sci. 27: 127–134.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.
- Ruiz, C., and S. P. Baker. 2010. Life tables of *Hypothenemus hampei* (Ferrari) in relation to coffee berry phenology under Colombian field conditions. Sci. Agr. 67: 648–668.
- Simberloff, D., J. L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, B. Galil, E. García-Berthou, M. Pascal, et al. 2013. Impacts of biological invasions: what's what and the way forward. Trends Ecol. Evol. 28: 58–66.
- Vega, F. E., F. Infante, and A. J. Johnson. 2015. The genus *Hypothenemus*, with emphasis on *H. hampei*, the coffee berry borer. *In F. E. Vega and R. W. Hofstetter (eds.)*, Bark beetles, biology and ecology of native and invasive species, 1st ed. Elsevier, London, United Kingdom.
- Vera, J. T., E. C. Montoya, P. Benavides, and C. E. Gongora. 2011. Evaluation of *Beauveria bassiana* (Ascomycota: Hypocreales) as a control of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) emerging from fallen infested coffee berries on the ground. Biocontrol Sci. Techn. 21: 1–14.