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Rickettsia OCCURRENCE IN COMMERCIAL PAPAYA (*Carica papaya* L.) PLANTATIONS WITH BUNCHY TOP DISEASE IN COLIMA, MEXICO

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ABSTRACT

Phytoplasmas, viruses, and rickettsiae (*Rickettsia* spp.) are the etiological agents of the bunchy top disease (BT) in papaya (*Carica papaya* L.) in several Caribbean countries. In Mexico, phytoplasmas have been reported in papaya plants with BT-like symptoms, but the incidence of *Rickettsia* is unknown. Considering that *Rickettsia* is associated with BT in other countries, it was hypothesized that these bacteria are also present in Colima, Mexico, where this disease is a phytosanitary concern. The objective of this work was to determine the incidence of *Rickettsia* in commercial papaya plantations with BT, as well as weeds and insects related to this crop in Colima. Using polymerase chain reaction (PCR) and sequencing of the rickettsial-specific flavoprotein subunit of the succinate dehydrogenase (*sdh*A) gene, 28 % (54 out of 192) symptomatic and 23.43 % (15 out of 64) asymptomatic papaya samples, as well as 9.77 % (17 out of 174) and 5.95 % (11 out of 185) weeds and insect morphospecies, respectively, tested positive for *Rickettsia*. The presence of *R. bellii* in *sdh*A-positive samples was confirmed by PCR with *R. bellii*-specific primers, sequencing and phylogenetic analysis of the citrate synthase (*glt*A) gene in 5.79 % of symptomatic papaya plants, 82.35 % of weeds, and 45.45 % of insects. Weeds positive for *R. bellii* were *Amaranthus palmeri* S. Watson, *Euphorbia hirta* L., *E. hyssopifolia* L., *Anoda cristata* (L.) Schltdl., *Zinnia maritima* Kunth, *Parthenium hysterophorus* L., *Echinochloa colona* (L.) Link., and *Richardia scabra* L. Insects positive for *R. bellii* were *Balclutha mexicana* Blocker (Hemiptera: Cicadellidae) and *Chlorotettix emarginatus* Baker (Hemiptera: Cicadellidae). This is the first time that *Rickettsia* species have been reported in commercial papaya plantations with BT in Mexico.

Keywords: *Rickettsia*, *sdh*A gene, *glt*A gene, bunchy top disease.

INTRODUCTION

Papaya (*Carica papaya* L.) is the most economically important plant species in the Caricaceae family. It is cultivated in 64 countries around the world, with Mexico being the third major producer and the main supplier to the US and Canadian markets (FAO, 2020; SIAP, 2020). Papaya production in Mexico is concentrated in the south-southeast and central-occident regions, where Oaxaca, Colima, and Chiapas are the top producer states (SIAP, 2020). In Mexico, several viruses and species of *Colletotrichum* limit the papaya industry, but recently, the bunchy top disease (BT) has emerged as an important phytosanitary concern, particularly in producing areas of Colima.

Cook (1931) was the first to report the BT, which has since become of economic importance in the Dominican Republic, Cuba, Haiti, Jamaica, and Puerto Rico (Martorell and Adsuar, 1952; Arocha *et al*., 2003; Luis-Pantoja *et al*., 2015). BT-affected papaya plants exhibit a typical shortening of internodes of apical younger leaves, resulting in a 'bunchy' appearance. Affected leaves display yellowing, crinkling, chlorosis, mottling, mosaic, and/or marginal necrosis and curved petioles (Story and Halliwell, 1969; Acosta *et al*., 2013). Etiological agents of BT include viruses (Bird and Adsuar, 1952) and phytoplasmas (Story and Halliwell, 1969). Later, it was confirmed that bacteria of the genus *Rickettsia* were present in papaya plants with BT in Costa Rica, Puerto Rico (Davis *et al*., 1998), and Cuba (Arocha *et al*., 2003; Luis-Pantoja *et al*., 2015).

Rickettsia is the causal agent of several important human diseases, but its occurrence in commercial crop plantations is little known. In addition to papaya, *Rickettsia* has only been associated with strawberry (*Fragaria* × *ananassa* Dutch.) asymptomatic plants or showing lethal yellows disease in Australia (Streten *et al*., 2005). Caspi-Fluger *et al*. (2012) stated that cotton (*Gossypium hirsutum* L.), basil (*Ocimum basilicum* L.), and black nightshade (*Solanum nigrum* L.) can be infected with *Rickettsia* under controlled conditions by viruliferous whiteflies (*Bemisia tabaci* Genn.). Among arthropods (mites, ticks, and insects), *Rickettsia* appears to be a common endosymbiont (Caspi-Fluger *et al*., 2012; Ishii *et al*., 2013), indicating that these animals are natural hosts for these bacteria. Transmission into plants has only been proved successfully for papaya leafhopper (*Empoasca papayae* Oman) (Acosta *et al*., 2017) and whitefly (Caspi-Fluger *et al*., 2012; Shi *et al*., 2021).

Considering that phytoplasmas have only been detected in papaya plants exhibiting BT-like symptoms in Mexico (Poghosyan *et al*., 2004; Rojas-Martínez *et al*., 2011) and that *Rickettsia* is associated with BT in other countries (Davis *et al*., 1998; Arocha *et al*., 2003), it was hypothesized that these bacteria are also involved in commercial papaya plantations with BT and that it is present in papaya-associated weeds and insects. Therefore, this study aims to determine the occurrence of *Rickettsia* species in commercial papaya plantations with BT incidence, as well as in weeds and insects associated with this crop in Colima, Mexico.

MATERIALS AND METHODS

Biological sampling

In November and December 2019, foliar samples were collected from 64 commercial papaya plantations in Tecomán, Colima, Ixtlahuacán, and Armería municipalities, which have the largest cultivated area of papaya in the state of Colima, Mexico (Figure 1). The samples showed dieback or apical leaves with shortening of internodes, yellowing, chlorosis, marginal necrosis, and curved petioles, indicating BT (Story and Halliwell, 1969; Acosta *et al*., 2013).

During sampling in each plantation, the leaf blade and petiole of four papaya plants (three symptomatic and one asymptomatic) were collected. Furthermore, 174 weeds (the three most frequent species) located within a one-meter radius of the sampled papaya plants, as well as 185 insect morphospecies, were collected from either papaya or weeds. Insects were captured using beating entomological nets and preserved in 96 % ethanol at room temperature until further analysis.

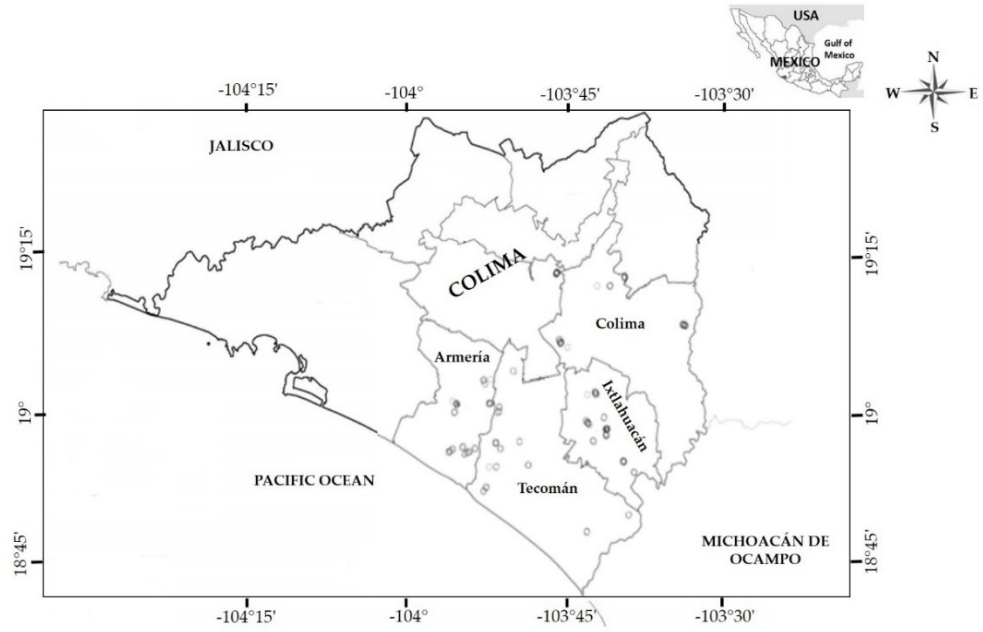

Figure 1. Geographic map of Colima, Mexico. In 2019, papaya plants (*Carica papaya* L.), weeds, and insects with asymptomatic and bunchy top disease were gathered from Tecomán, Colima, Ixtlahuacán, and Armería municipalities in Colima, Mexico. Circles denote collection points in each municipality.

DNA isolation and quality validation

DNA was extracted from 10 g of fresh tissue consisting of midribs and petioles from papaya and weed leaves following the protocol described by Ahrens and Seemüller (1992). Insect DNA was extracted from 1 to 5 specimens of each morphospecies using the method described by Stillson and Szendrei (2020). Plant and insect DNA quality was evaluated by PCR amplification of the chloroplast ribosomal protein S16 gene (*rps16*) (Oxelman *et al*., 1997) or mitochondrial cytochrome c oxidase subunit I gene (*COI*) (Folmer *et al*., 1994), respectively.

Rickettsia spp. identification

Rickettsia in papaya, weeds, and insects was detected by PCR amplification of a 705-bp fragment of the rickettsial-specific flavoprotein subunit of the succinate dehydrogenase gene (*sdh*A) with primers PBTF1/PBTR1 (Davis *et al*., 1998). A clone of the *Rickettsia sdh*A gene in pGEM-T Easy vector (Promega, USA), provided by the National Phytosanitary Reference Center, was used as a positive control. DNA extracted from *Rickettsia*-free papaya leaves (confirmed as negative by PCR for the *sdh*A gene) was used as negative control. Amplicons of three positive papaya samples were purified with the Wizard SV Gel and PCR Clean-Up System (Promega, USA), according to the manufacturer's instructions, and sequenced at Macrogen Inc. (Seoul, South Korea). The resulting sequences were analyzed with the MEGA X program (Kumar *et al*., 2018) and the BLASTn function of the National Center for Biotechnology Information (NCBI) (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and registered at the GenBank (NCBI). The obtained sequences (Accession numbers MT103330–MT103332) were similar to *R. bellii sdh*A gene isolates.

To verify whether all positive samples that were amplified for the *sdh*A gene belonged to the *R. bellii* species, PCR reactions with *R. bellii*-specific primers [which amplify a 338-bp fragment of the citrate synthase gene (*glt*A)] (Szabó *et al*., 2013) were carried out. Additionally, the *glt*A sequences of three randomly selected samples (one for each papaya, weeds, or insects) were sequenced at Macrogen Inc. (Seoul, South Korea), registered at the GenBank, and used for phylogenetic inference analysis utilizing the neighbor-joining method with 1000 bootstrap replicates using MEGA X (Kumar *et al*., 2018), as well as the *glt*A gene sequences of other *Rickettsia* species (Table 1).

Weeds and insects positive for *R. bellii* were further identified at the species level by Carlos L. Leopardi-Verde (Colima University, Mexico) and Edith Blanco-Rodríguez (Postgraduate College, Mexico).

RESULTS AND DISCUSSION

Rickettsia was shown to be associated with BT in Colima, Mexico, by evaluating two different rickettsial-specific genes (*sdh*A and *glt*A) in DNA matrices from papaya and papaya-associated weeds and insects. The *Rickettsia sdh*A was detected in 54 out of 192

Table 1. *Rickettsia* spp. *glt*A gene sequences used for phylogenetic analysis.

Species	Origin	Host source	GenBank accession number
R. tarasevichiae	Russia	*Ixodes persulcatus* Schulze	AM418460
R. Helvetica	Russia	*I. persulcatus*	AM418450
R. Helvetica	Italy	*I. ricinus* L.	AJ427878
R. tamurae	Japan	Ticks	AB114796
R. conorii	Russia	*Homo sapiens* L.	MT667397
R. prowazekii	Spain	*H. sapiens*	U14334
R. aeschlimannii	Russia	*H. sapiens*	MT667402
R. sibirica	Russia	*H. sapiens*	MT667386
R. typhi	USA	*H. sapiens*	U20245
R. rickettsia	Panama	*H. sapiens*	MT814706
R. rickettsia	Brazil	*H. sapiens*	MF988097
R. felis	Taiwan	*Ctenocephalides felis* Bouche	U33922
R. canadensis	Russia	*Haemaphysalis japonica* Warburton	MG545038
R. akari	Taiwan	*C. felis*	U41752
R. akari	Taiwan	*I. granulatus* Supino	MT847612
R. bellii	Argentina	*I. loricatus* Neumann	MT407576
R. bellii	Brazil	*Amblyomma dubitatum* Neumann	MW293870
R. bellii	Mexico	*Carica papaya* L. (this study)	ON303294
R. bellii	Mexico	*Euphorbia hyssopifolia* L. (this study)	ON303295
R. bellii	Mexico	*Balclutha mexicana* Blocker (this study)	ON303296

papaya plants (28.12 %) with shortened apical leaf internodes. These plants showed chlorosis, yellowing, and marginal necrosis (Figure 2A and 2B). Detection of this gene also occurred in asymptomatic papaya plants (15 out of 64, 23.43 %), papaya-associated weeds (17 out of 174, 9.77 %), and insects (11 out of 185, 5.95 %) (Table 2). Intriguingly, these results on *Rickettsia* detection in papaya differ from those reported by Davis *et al*. (1998), Acosta *et al*. (2013), and Luis-Pantoja *et al*. (2015), who found, respectively, 100, 100, and 95 % incidence of *Rickettsia* (*sdh*A gene) in BT-diseased plants from Costa Rica, Puerto Rico, and Cuba but did not register *Rickettsia* DNA in asymptomatic plants. A possible explanation for this could consider that other pathogens, such as phytoplasmas or viruses, which are known etiological agents of BT (Bird and Adsuar, 1952; Story and Halliwell, 1969), are responsible for the symptoms. However, a low detection percentage of the *Rickettsia sdh*A gene was also reported in strawberry plants with lethal yellows disease in Australia, since only 32.23 % of evaluated symptomatic samples tested positive (Streten *et al*., 2005). Another plausible explanation is that *Rickettsia* cells were present in lower numbers given their short lifespan inside plant tissues, which has been reported as two weeks in cotton under artificial inoculation conditions (Shi *et al*., 2021), but is unknown for papaya or other plants. This could result in insufficient *Rickettsia* DNA to be detected using molecular techniques.

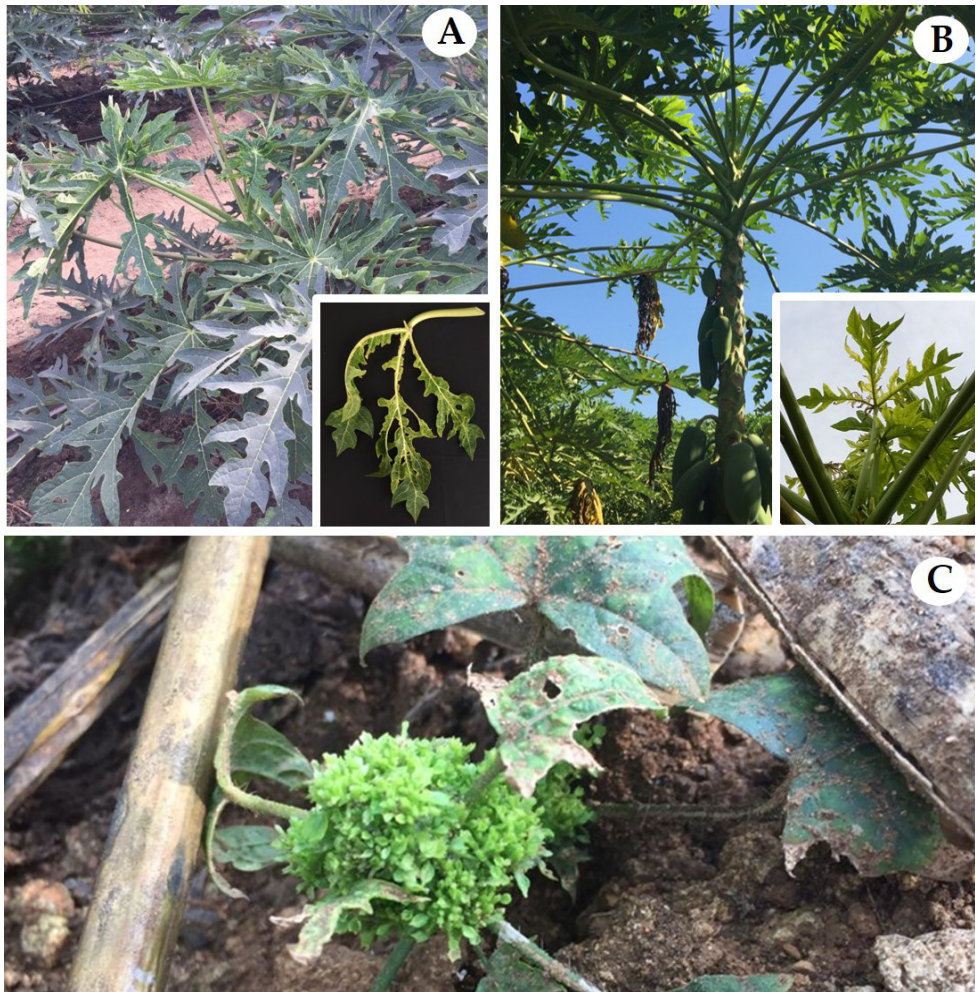

Figure 2. Papaya plants and papaya-associated weeds in Colima, Mexico, exhibiting symptoms associated with *Rickettsia bellii*. A and B: *Carica papaya* L. plants with shortened apical leaf internodes, giving a bunchy appearance, showing chlorosis, yellowing, and marginal necrosis; C: *Anoda cristata* (L.) Schltdl. with vegetative proliferation.

The positive detection of *Rickettsia sdh*A gene in asymptomatic papaya and weed samples can be explained by the fact that these bacteria induce a symptomless phenotype in cotton, basil, and black nightshade plants after its artificial inoculation with viruliferous whiteflies (Caspi-Fluger *et al*., 2012), and further justified positive results reported for asymptomatic strawberry plants in Australia (Streten *et al*., 2005). The similarity between the percentage detection in asymptomatic and symptomatic papaya samples in the present research may also be explained by this observation. Lower *Rickettsia* detection in papaya-associated insects clearly indicates that this bacterium has a limited host range and natural occurrence as an endosymbiont.

Table 2. *Rickettsia* occurrence in commercial papaya (*Carica papaya* L.) plantations with bunchy top disease in Colima, Mexico.

Municipality	Positive samples for *Rickettsia* from the total number of examined samples				Positive samples for *R. bellii* among total positive samples for *Rickettsia*		
	Papaya		Weeds	Insects	Papaya	Weeds	Insects
	Symptomatic	Asymptomatic					
Armería	7 of 48 (14.58 %)	1 of 16 (6.25 %)	3 of 31 (9.68 %)	3 of 60 (5.00 %)	2 of 8 (25.00 %)	2 of 3 (66.66 %)	1 of 3 (33.33 %)
Colima	26 of 48 (54.17 %)	9 of 16 (56.25 %)	10 of 34 (29.41 %)	2 of 32 (6.25 %)	1 of 35 (2.85 %)	9 of 10 (90.00 %)	1 of 2 (50.00 %)
Ixtlahuacán	20 of 48 (41.67 %)	4 of 16 (25.00 %)	1 of 35 (2.86 %)	2 of 46 (4.35 %)	0 of 24 (0.00 %)	1 of 1 (100.00 %)[ǂ]	0 of 2 (0.00 %)
Tecomán	1 of 48 (2.08 %)	1 of 16 (6.25 %)	3 of 74 (4.05 %)	4 of 47 (6.25 %)	1 of 2 (50.00 %)	2 of 3 (66.66 %)	3 of 4 (75.00 %)
Total	54 of 192 (28.12 %)	15 of 64 (23.43 %)	17 of 174 (9.77 %)	11 of 185 (5.95 %)	4 of 69 (5.79 %)[¶]	14 of 17 (82.35 %)	5 of 11 (45.45 %)

[ǂ]Positive weed showed vegetative proliferation. [¶]All positive samples were from bunchy top-diseased plants.

Regarding the occurrence of *Rickettsia* in the municipalities evaluated, Colima and Ixtlahuacán had the highest number of positive symptomatic and asymptomatic papaya plants (Table 2). Colima also had the highest number of positive insect morphospecies, while incidences of *Rickettsia*-positive weeds were similar in all municipalities (Table 2).

After determining the presence of *Rickettsia* through the *sdh*A gene detection analysis, the *Rickettsia* species in the positive samples were identified. Three *sdh*A amplicons obtained from papaya plants were randomly selected and sequenced (GenBank accession numbers MT103330–MT103332). The *sdh*A sequences had a 97.4–97.6 % similarity to *R. bellii* isolated from the United States (GenBank CP000087, CP000849) and Argentina (GenBank CP015010).

Further analysis of the *glt*A gene revealed the presence of *R. bellii*. However, positive results were obtained in only 5.79, 45.45, and 82.35 % of the *sdh*A-positive symptomatic papaya, insect, and weed samples, respectively, indicating that other *Rickettsia* species are present, particularly in papaya and insect samples (Table 2). In the phylogenetic analysis (Figure 3), *glt*A sequences from three samples (*Carica papaya* (Cpa), *Euphorbia hyssopifolia* (Ehy), and *Balclutha mexicana* (Bme)) (GenBank ON303294–ON303296) had a 99 % similarity to the *glt*A gene of *R. bellii* isolate CMS2 from Brazil (GenBank MW293870) and clustered with *R. bellii* from Argentina (GenBank MT407576) and Brazil (GenBank MW293870).

Weeds positive for *R. bellii* were *Amaranthus palmeri* S. Watson (Amaranthaceae), *Euphorbia hirta* L. and *E. hyssopifolia* L. (Euphorbiaceae), *Anoda cristata* (L.) Schltdl.

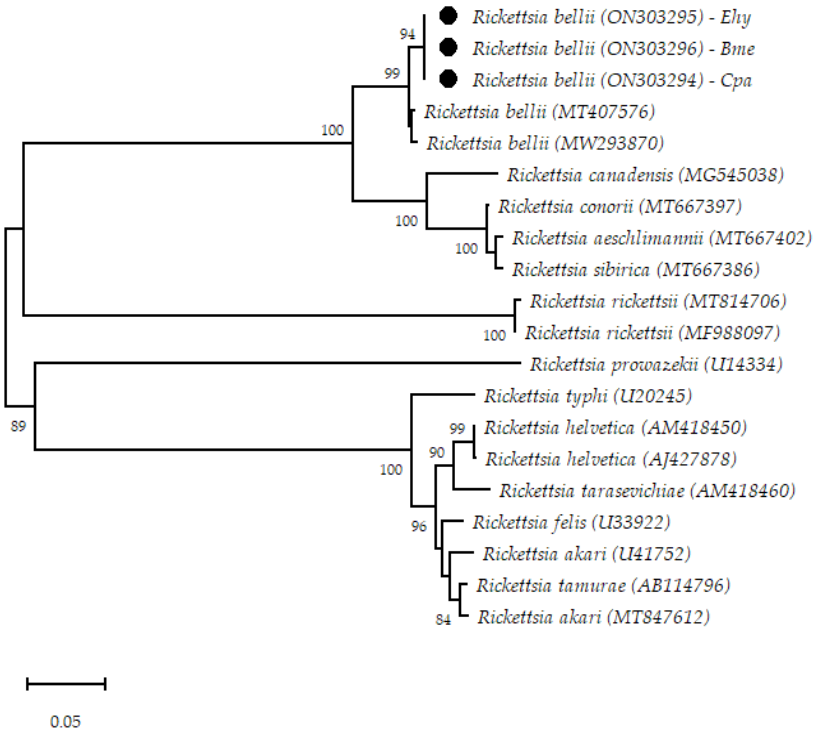

Figure 3. Phylogenetic tree of *Rickettsia bellii* found in papaya (*Carica papaya* L., Cpa), *Euphorbia hyssopifolia* L. (Ehy), and *Balclutha mexicana* Blocker (Bme) (black dots) in Colima, Mexico, as well as other *Rickettsia* species from other parts of the world, using the neighbor-joining method. GenBank identification numbers and bootstrap values (per 1000 replicates, greater than 70 %) are shown in parentheses and tree branches, respectively. The scale bar represents 0.05 nucleotide substitutions per site.

(Malvaceae), *Zinnia maritima* Kunth and *Parthenium hysterophorus* L. (Asteraceae), *Echinochloa colona* (L.) Link. (Poaceae), and *Richardia scabra* L. (Rubiaceae). However, *A. cristata* exclusively showed disease symptoms (Figure 2C). Based on this diversity of the botanical families registered, this result suggests a wide plant host range for *Rickettsia* in commercial papaya plantations. Thus, these plants should be considered alternative (non-crop) hosts and natural inoculum sources of *Rickettsia*. Until now, only the Caricaceae, Rosaceae, Lamiaceae, and Solanaceae had species known as hosts for *Rickettsia* (Davis *et al*., 1998; Streten *et al*., 2005; Caspi-Fluger *et al*., 2012).

Insects positive for *R. bellii* were *Balclutha mexicana* Blocker (Hemiptera: Cicadellidae) and *Chlorotettix emarginatus* Baker (Hemiptera: Cicadellidae). Interestingly, in our study, *E. papayae*, the natural vector of BT-associated *Rickettsia* in papaya in Cuba (Acosta *et al*., 2017), was not found during collecting. Until now, other *Rickettsia*-carrying arthropods included several mites and ticks, whiteflies, and leafhoppers, in

which *Rickettsia* bacteria have a natural occurrence as endosymbionts (Caspi-Fluger *et al*., 2012; Ishii *et al*., 2013; Sánchez-Montes *et al*., 2020; Shi *et al*., 2021; Guzmán-Cornejo *et al*., 2022). Given that *Rickettsia* transmission into plants has only been proved successfully for papaya leafhopper (*E. papayae*) (Acosta *et al*., 2017) and whitefly (*B. tabaci*) (Caspi-Fluger *et al*., 2012; Shi *et al*., 2021), it is possible that the leafhoppers *B. mexicana* and *C. emarginatus* could be responsible for *Rickettsia* transmission from papaya to weeds and vice versa in Colima, Mexico.

In Mexico, the genus *Balclutha* is part of the entomofauna in crops such as blueberry (*Vaccinium corymbosum* L.) (Pérez-Mejía *et al*., 2020), grape (*Vitis vinifera* L.) (Almendra-Paxtlan *et al*., 2021), pepper (*Capsicum* spp.) (Velásquez-Valle *et al*., 2018), and corn (*Zea mays* L.) (Pinedo-Escatel and Moya-Raygoza 2018). *Chlorotettix emarginatus* is a common pest in corn and rice (*Oryza sativa* L.) (Cervantes-Mayagoitia and Huacuja-Zamudio, 2017). However, until now, the presence of *Rickettsia* in these crops has not been addressed.

Altogether, these findings support the hypothesis that *Rickettsia* spp. are involved in commercial papaya plantations with BT in Colima and that they are also present in papaya-associated weeds and insects. In Mexico, the distribution and hosts of *Rickettsia* spp. have been updated recently (Sánchez-Montes *et al*., 2021), but none of the species listed were associated with plants. In the case of *R. bellii*, it has been identified in ticks collected from Jalisco and Hidalgo (Sánchez-Montes *et al*., 2020; Guzmán-Cornejo *et al*., 2022). In Colima, *R. typhi* causing murine typhus in humans has been reported (García-Acosta *et al*., 2017).

CONCLUSIONS

Rickettsia spp. have a natural occurrence in asymptomatic and bunchy top-diseased papaya plants, as well as in papaya-associated weeds and insects in commercial plantations in Colima, Mexico.

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