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Ecology

Incidence of galls on fruits of *Parkinsonia praecox* and its consequences on structure and physiology traits in a Mexican semi-arid region

Incidencia de agallas en frutos de *Parkinsonia praecox* y sus consecuencias sobre atributos morfológicos y fisiológicos en una zona semiárida de México

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Abstract

Galls are atypical plant growths that provide nourishment, shelter, and protection to the inducer or its progeny. Fruit and flowers are poorly represented as host organs for gall-forming insects. Our main question was: Do morphological traits, anatomical features and physiological characteristics differ between galled and healthy fruits of *Parkinsonia praecox*? Galled and healthy fruits of *P. praecox* were characterized in terms of morphological traits (length, diameter, thickness, water and biomass content); anatomical features (trichomes, stomatal and pavement cells), and physiological characteristics (stomatal conductance, g_s). We found that galled fruits were induced by *Asphondylia* sp. (Diptera: Cecidomyiidae). Thickness, diameter, and water content values of galled fruits were greater compared to healthy fruits. Length, biomass, and pavement cells density of healthy fruits were higher. The density of trichomes on galled fruits was higher, while the stomatal density and pavement cell size were not statistically different between galled and healthy fruits. Furthermore, the g_s rates of galled fruits were almost 3 times higher than in healthy fruits. Incidence of galls on fruits on *P. praecox* modified the original morphology and anatomy of healthy fruits that stimulate physiological mechanisms to increase the water continuum from the host plant to the gall.

Keywords: Fabaceae; Pods; Gall-forming insects; Dipteran; Morphology

Resumen

Las agallas son estructuras complejas de las plantas que presentan crecimiento anormal y proveen alimento, refugio y protección al organismo inductor. Flores y frutos están escasamente reportados como órganos hospederos. Nuestra pregunta central fue: ¿los atributos morfológicos, anatómicos y fisiológicos, difieren entre frutos con agallas y sanos de *Parkinsonia praecox*? Los frutos con agallas y sanos fueron caracterizados en términos de atributos: morfológicos (longitud, diámetro, grosor, contenido de agua y biomasa); anatómicos (tricomas, estomas y células del pavimento) y fisiológicos (conductancia estomática, g_s). Encontramos que los frutos con agallas son inducidos por *Asphondylia* sp. (Diptera: Cecidomyiidae). El grosor, diámetro y contenido de agua fue mayor en frutos con agallas. La longitud, biomasa y densidad de células del pavimento fue mayor en frutos sanos. La densidad de tricomas en frutos con agallas fue mayor, pero la densidad de estomas y el tamaño de las células del pavimento no presentaron diferencias. La g_s de los frutos con agallas fue 3 veces mayor que en los sanos. La incidencia de agallas en frutos de *P. praecox* modifica la morfología y anatomía original de éstos, estimulando mecanismos fisiológicos que incrementan el continuo de agua de la planta hospedera hacia la agalla.

Palabras clave: Fabaceae; Vainas; Insectos agalladores; Díptero; Morfología

Introduction

Estimates of galling insect richness calculates ~133,000 species distributed around the world (Espírito-Santo & Fernandes, 2007). The galling habit is widely spread among insects and is mostly comprised of Diptera, Hymenoptera, Hemiptera, Thysanoptera, Lepidoptera, and Coleoptera (Fernandes & Carneiro, 2009). These organisms induce abnormal structures on the plant, known as galls, cecidias or plant tumors (Fernandes & Carneiro, 2009). These structures are composed of plant tissue characterized by the increase in the number of cells (hyperplasy) and/or the increase in cell size (hypertrophy) (Mani, 1964).

Galls can be induced on any vegetative structure (leaves, stems, branches and roots) or reproductive organ (flowers, fruits and seeds) (Mani, 1964). The growth mechanisms of the plant organs are modified in response to stimuli from the galling insects (e.g., salivary secretion during feeding or maternal secretion in the oviposition), which alters the architecture and physiology of the plant in order to benefit it or its progeny (Oliveira et al., 2016; Raman, 2007; Stone & Schönrogge, 2003). The gall provides food, shelter, and protection against natural enemies for the galling insects (Fernandes & Santos, 2014; Price et al., 1987; Stone & Schönrogge, 2003).

Galling insects are found on specific host plants in natural communities across most biogeographical regions (Fernandes & Price, 1991; Price et al., 1998). However, their species richness has been reported to be higher in tropical regions (Fernandes & Price, 1988; Gonçalves-Alvim & Fernandes, 2001), with more species occurring in xeric environments (Price et al., 1998) than in temperate and cold regions. At the global scale, most studies addressing the richness of galling insects have been carried out in the Cerrado (Brazilian savanna) (Araújo et al., 2014; Carneiro et al., 2009; Coelho et al., 2009; Fernandes et al.,

1997; Gonçalves-Alvim & Fernandes, 2001), but also in tropical savanna (Blanche, 2000) and humid subtropical forests (Blanche & Westoby, 1995) in Australia, tropical humid and dry forests in Panama (Medianero et al., 2003) and in montane forest and shrublands in Texas, USA (Blanche & Ludwig, 2001). In Mexico, there is a scarcity of research studies on the ecology of galling insects. There are only a few studies reporting galling insect richness in 2 tropical rainforests (Los Tuxtlas Biosphere Reserve and in Lacandonia rainforest; Oyama et al., 2003) and in a tropical dry forest (Chamela-Cuixmala Biosphere Reserve; Cuevas-Reyes et al., 2004).

Buds, flowers, and fruits are poorly represented as host organs for galling insects, since these structures depend on the phenological stage of the plant (i.e., they may be unavailable to gallers throughout the year). The phenological dependence is more evident in tropical dry forests and xeric environments (Pezzini et al., 2014). Despite the low number of studies reporting galls on reproductive organs (Fernandes & Santos, 2014), the effects of galling on these organs could pose serious threats to the plants due to the potential impact they would have on plant performance and fitness (Fernandes, 1987). Galls on fruits exhibit noteworthy morphotypes, such as irregular (Santos et al., 2016), spherical (Quintero et al., 2014), amorphous, fusiform, globoid, ovoid, swollen or triangular (Isaias et al., 2014).

The impact of galling insects on their host plants is variable. Galling insects are known to stimulate the metabolism of nearby sources by increasing the sink demand relative to source supply (Fay et al., 1993). This leads to negative effects on the plant, such as a reduction in branch length (Fernandes et al., 1993; Kurzfeld-Zexer et al., 2010; Silva et al., 1996), lower quality seeds that affect germination (Santos et al., 2016; Silva et al., 1996), decrease in CO₂ assimilation (Haiden et al., 2012; Larson,

1998), limitations on flower and fruit production (Fernandes et al., 1993; Silva et al., 1996), and a reduction of entire plant biomass (McCrea et al., 1985). Galls on leaves of *Acer sacharum* (Sapindaceae) diminish approximately 60% of the stomatal conductance (Patankar et al., 2011). In contrast, the stomatal conductance of leaf galls on *Acacia longifolia* (Mimosoideae) shows no change in response to light intensity, but the immature galls had higher rates of stomatal conductance (Haiden et al., 2012). To our knowledge, beyond these reports, there are no studies that quantify the stomatal conductance in fruit with galls. Since these structures are physiological sinks and could have a negative effect on the fruit set, studies related to fruit galls become particularly important in order to understand how the presence of galls affects the reproductive input and fitness of the plant. The approach of this study involves the anatomical and physiological features in galled and healthy fruits.

We investigated the effects of galls on fruits of *Parkinsonia praecox* (Ruiz & Pav. ex Hook.) Hawkins based on morphological traits (length, diameter, thickness, water content and biomass content); anatomical features (trichomes, stomatal, and pavement cells), and physiological characteristics (stomatal conductance, g_s).

Materials and methods

The study was conducted in the Zapotitlán Salinas Valley, located in the Tehuacán-Cuicatlán Biosphere Reserve, Puebla, Mexico. The data sampling was carried out in the nearby surroundings of the “Helia Bravo-Hollis” Botanical Garden (18°20' N, 97°28' W, at 1,500 m asl). The main plant association is the *tetechera*, dominated by the columnar cactus *Neobuxbaumia tetetzo* (Zavala, 1982); the vegetation corresponds to semi-arid scrubland (Rzedowski, 2006). The mean annual precipitation is 381.21 mm, and the annual mean temperature is 18.04 °C. The dry season is from September to April, and the rainy season is from May to August (Zavala, 1982). The climatic data were obtained from Conagua (2010) for the period 1964-2010.

Parkinsonia praecox (Fabaceae-Caesalpinoideae) is known in the study area as “manteco” or “palo verde”, it is a 7 m tall tree (Fig. 1A). In Mexico, it is distributed in the Northwest (Baja California Sur, Sonora, Chihuahua, Sinaloa, Durango, Zacatecas and Nayarit), East Center (Jalisco, Colima, Michoacán, Guanajuato, Morelos, Guerrero, Puebla, México), East (Tamaulipas and Veracruz), and South (Oaxaca and Chiapas) (Villaseñor, 2016). It is a common species in some vegetal associations in the Zapotitlán Salinas Valley (López-Galindo et al., 2003; Montaña & Valiente-Banuet, 1998). *P. praecox* fruits

are flattened brown pods 10 cm length and 1 cm width, arranged in racemes, generally in pairs (Fig. 1B). Seeds are shiny-brown color and 7 mm mean length (Pennington & Sarukhán, 2005). The flowering season occurs between December-May, and the fruiting period is between January-September (Arias et al., 2001; Pennington and Sarukhán, 2005). Infructescences of *P. praecox* showed an important incidence of galls (Fig. 1C). Galled fruits had 1 larval chamber located at the center surrounded by parenchymatous tissue (Fig. 1D) (Contreras-Varela pers. obs.). *Asphondylia* sp. (Diptera: Cecidomyiidae) is the galling insect. From November to March, the branches are leafless when flowering and fruit set occurs (Pavón & Briones, 2001), indicating that it is a totally deciduous species during this period.

The number of fruits affected by galls was determined in 30 randomly selected branches with galls and fruits of 50 cm long (2 per tree) in 15 different trees. In 10 individuals of *P. praecox* it was determined macroscopical characteristics of galled and healthy fruits, 50 pairs of a galled and a healthy fruit were randomly selected. A digital caliper (CD-s6, Mitutoyo Corp., Kawasaki, Japan) was used to measure length, diameter (distance considered starting in the abscission line in the middle of the fruit) and thickness of galled and healthy fruits. Additionally, in transversal sections of galled fruits we measured parenchymatous tissue, and larval chamber size. In healthy and galled fruits, we quantified the water and biomass content by recording the fresh weight (FW), and then these were oven-dried for 36 hours at 70 °C. Later, the dry weight (DW) was quantified using a weighing scale (CP-225D, Sartorius, Germany, 0.01 g of accuracy). The water content was calculated as (FW-DW)/FW. The biomass content was defined as DW/FW. The water and biomass contents are expressed as a percentage.

In 3 individuals of *P. praecox*, 5 galled fruits ($n = 15$) and 5 healthy fruits ($n = 15$) were used to determine trichomes, stomatal, and pavement cell density, as well as stomata and pavement cell size. We applied a thin layer of clear nail varnish on the surface of the galled and healthy fruits in order to obtain permanent impressions of trichomes, stomata, and pavement cells. The area covered by the varnish layer was approximately 1 cm². We determined the area of the 150 stomata and 150 pavement cells by measuring microphotographs of the samples with the software ImageJ (Rasband, 2017). The trichomes, stomatal, and pavement cell density were calculated in 2.7 mm² in 3 randomly selected visual fields of an optical microscope per varnish layer (Carl Zeiss Inc., Thornwood, N.Y.).

Measurements of g_s were determined in galled and healthy fruits in field using a porometer (SC-1, Decagon Devices Inc., Washington, USA). The sensor head of the



Figure 1. *Parkinsonia praecox* at the Zapotitlán Salinas Valley in Tehuacán-Cuicatlán Biosphere Reserve, México. A) Panoramic view of the study site; B) tree in flowering associated with *Neobuxbaumia tetetzo*; C) galled and healthy fruits; D) transversal cut of a gall. The black arrow indicates the position of the larval chamber.

porometer was situated in the middle section of the samples. Galled and healthy fruits were carefully placed on the sensor head without pressing, to avoid an overestimation of the g_s . Seven measurement periods of g_s were made between 07:00 h and 21:00 h on 3 different pairs of galled ($n = 21$) and healthy fruits ($n = 21$); 1 pair per individual of *P. praecox*.

Generalized linear mixed models (GLMMs) were used to evaluate the relationship between galled and healthy fruits in each of the morphological traits (length, diameter, thickness, water content, biomass content) and anatomical features (trichomes, stomata, pavement cells). As fixed effects, we entered the galled and healthy fruits into the model. As random effect, we used intercepts for individuals of *P. praecox*, as well as random slopes for the effect of galled and healthy fruits.

A GLMM was used to assess the effects of the time of the day, galled and healthy fruits on the g_s . The fixed effects were the galled fruits, healthy fruits and the time of the day (07:00 to 21:00 h), while the random effects were the individuals of *P. praecox*, as well as random slopes for the effect of galled and healthy fruits. We assumed a gamma distribution for the model.

Visual inspection of residual plots indicates there was no deviation of homoscedasticity or normality. *P*-values were obtained by a likelihood ratio test of the full model

with the effect against the model without the effect (Zuur et al., 2009). All statistical analyses were performed in R version 3.2.2 (R Development Core Team, 2017) with the package lme4 (Bates et al., 2015) and multcomp (Hothorn et al., 2008). For all statistical analyses, we reported the mean $\pm$ SE and the differences in magnitude (i.e., mm², %, and density) between galled and healthy fruits, referred as estimated values calculated in the GLMMs.

Results

Twenty percent of the *P. praecox* fruits had galls, although some affected fruits had a few seeds in the apical portion of the fruit. The branches with only healthy fruits had on average 28.1 ± 1.38 fruits per branch ($n = 299$), while branches with galled fruits had 21.5 ± 2.04 fruits (fruits $\pm$ SE) per branch ($n = 138$). Galled fruits had a spherical shape and were green-reddish. Each galled fruit was composed of parenchymatous tissue with 0.4 ± 0.06 cm (cm $\pm$ SE) of thickness. This tissue surrounds a larval chamber, which was 0.1 ± 0.01 cm of diameter that holds only 1 galling insect larva.

The morphological traits of galled and healthy fruits (length, diameter, thickness, water content, and biomass content) exhibited significant differences. The galled fruits were 2.91 ± 0.17 cm shorter than the healthy fruits ($\chi^2 =$

51.8, $p < 0.001$; Fig. 2A). On the other hand, galled fruits had 0.28 ± 0.04 cm larger diameter ($\chi^2 = 23.2$, $p < 0.001$; Fig. 2B) and were 0.87 ± 0.03 cm thicker ($\chi^2 = 53.1$, $p < 0.001$; Fig. 2C) than the healthy fruits. The water content was $4.24 \pm 1.2\%$ higher in the galled fruits ($\chi^2 = 7.1$, $p < 0.01$; Fig. 3), while healthy fruits had $4.2 \pm 1.3\%$ higher biomass content ($\chi^2 = 7.16$, $p < 0.01$; Fig. 3).

The stomatal density (0.28 ± 0.81 stomata mm^2 , $\chi^2 = 0.12$, $p = 0.72$; Fig. 4A) did not differ between galled and healthy fruits. Contrarily, trichome density (4.76 ± 1.42 trichomes mm^2 , $\chi^2 = 7.43$, $p = 0.006$; Fig. 4C) and pavement cell density (19.4 ± 8.19 pavement cells mm^2 , $\chi^2 = 4.34$, $p < 0.05$; Fig. 4D) were statistically different between galled and healthy fruits. The area of pavement cells did not differ between galled and healthy fruits (0.005 ± 0.005 μm^2 , $\chi^2 = 0.77$, $p = 0.37$), while the stomatal size was 70.13 ± 21.51 μm^2 larger in galled fruits than in healthy fruits ($\chi^2 = 5.05$, $p < 0.05$; Fig. 4B).

The g_s was higher in galled fruits than in healthy fruits ($\chi^2 = 12.6$, $p = 0.001$). The interaction of daytime and the gall presence had a negative effect on the g_s of galled fruits ($\chi^2 = 36$, $p < 0.001$). In the galled fruits, the highest values of g_s were recorded at 07:00 h, while the lowest values were found in healthy fruits at 16:00 hrs. Likewise, the g_s exhibited differences during the daytime ($\chi^2 = 30$, $p < 0.001$). Values of g_s in galled and healthy fruits decreased throughout the day, with a slight increase in the last 2 records at night (18:00 to 20:00 h) (Fig. 5).

Discussion

In this study, we showed the incidence of galls in *P. praecox* fruits and its consequences on morphology and physiology. This is the first report of gall incidence on fruits in this semi-arid region of Central Mexico. In general, studies on galled fruits are scarce in the literature. We reviewed studies that report the presence of galls on reproductive structures, and we found 128 host plant species; Fabaceae was the most abundant host family (78 species), followed by Asteraceae (9 species), Boraginaceae (6) and Rubiaceae (6). The 2 most representative genera were *Acacia* (58 species) and *Prosopis* (14 species). Of the total number of host plant species found in our revision, 85.15% had galls on flowers (achene, buds, capitula, flowers, inflorescences) and the remaining 14.84% on fruits and seeds (Appendix).

Some species in South America have been reported as hosts of fruit-gall inducing insects, such as *Conostegia xalapensis* (Melastomataceae) (Chavarría et al., 2009); and *Miconia calvescens* (Melastomataceae) (Badenes-Perez & Johnson, 2007). Curiously, most studies are developed in the Costa Rican tropical dry forest (Janzen, 1982); Australian seasonally tropical forest (Kolesik et al., 2010),

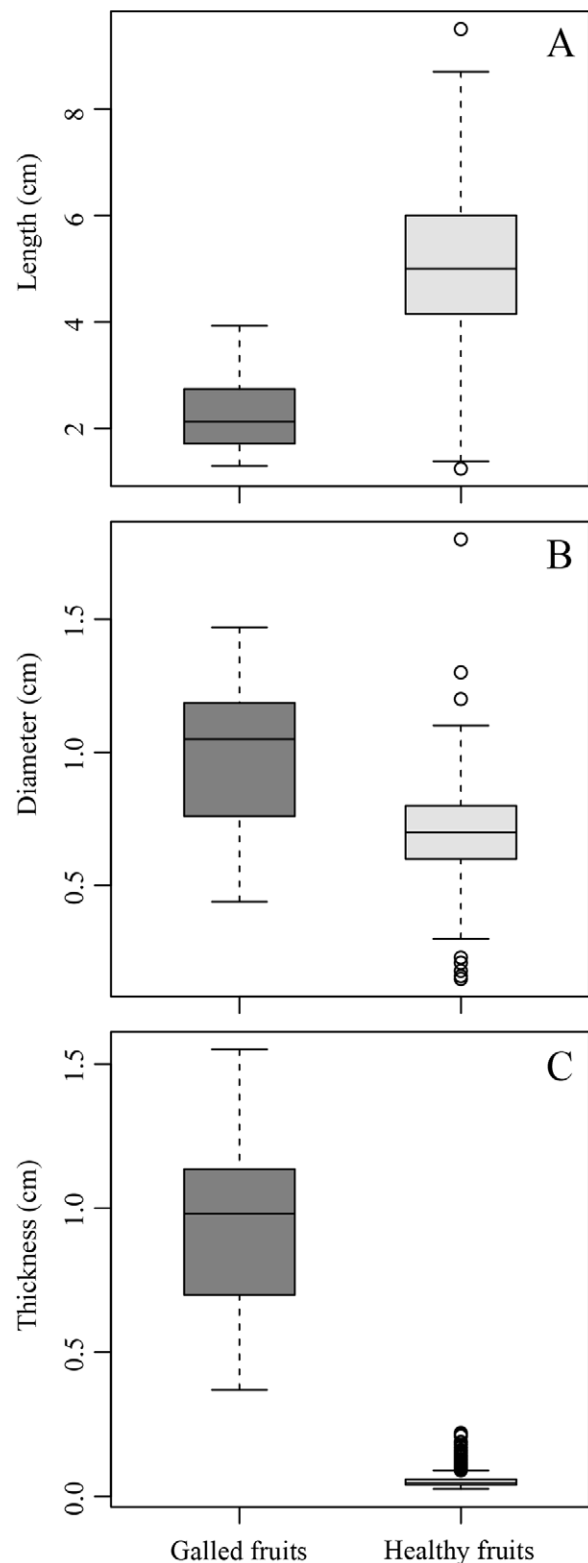


Figure 2. Morphological traits of galled and healthy fruits of *Parkinsonia praecox*. A) The length of a fruit from the base to the apex ($p < 0.001$); B) the diameter of fruits on the middle region ($p < 0.001$), and C) the thickness on the middle region ($p < 0.001$).

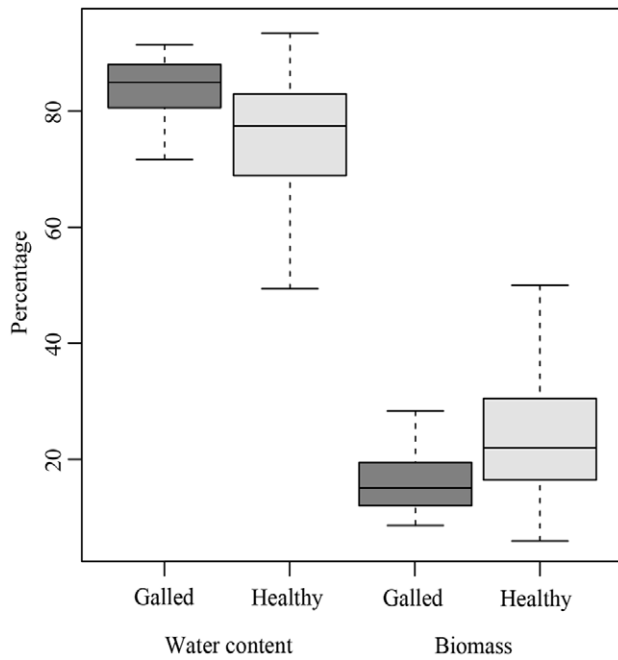


Figure 3. Comparison between galled and healthy fruits of *Parkinsonia praecox* in water content ($p < 0.01$) and biomass ($p < 0.01$).

and Brazilian savanna (Santos et al., 2016). There are few studies on xeric environments that report the presence of galls on fruits, i.e. in Brazilian Restinga, *Pithecellobium tortum* have galls in seeds (de Macêdo & Monteiro, 1989). In our work we reported galls on *P. praecox* fruits and this is a pioneer study related to the study of galls in this area (Tehuacán-Cuicatlán, Mexico).

The galling insect *Asphondylia* sp. modifies the natural development of *P. praecox* fruits and negatively affects the fruit set of the host plant. In our bibliographical revision we found that the most representative taxonomic level of gall-forming insects on reproductive structures corresponded to the order Diptera (92.96%; 119 species) followed by Hymenoptera (6.25%; 8 species). The most important families of dipteran galling insects were Cecydomiidae (89.06%; 114 spp.) and Tephritidae (3.9%, 5 spp.); of Coleoptera was Curculionidae (0.78%; 1 spp.); of Hymenoptera were Braconidae (3.12%; 4 spp.), Agaonidae (0.78%; 1 spp.), Pteromalidae (0.78%; 1 spp.), Chalcidoidea (0.78%; 1 spp.) and Eurytomidae (0.78%; 1 spp.). The most representative genus of galling insects was *Asphondylia* (44.87%; 60 spp.); followed by *Dasineura* (23.43%; 30 spp.), *Allorhgas* (3.12%; 4 spp.), *Clinodiplosis* (3.12%; 4 spp.), *Urophora* (3.12%; 4 spp.),

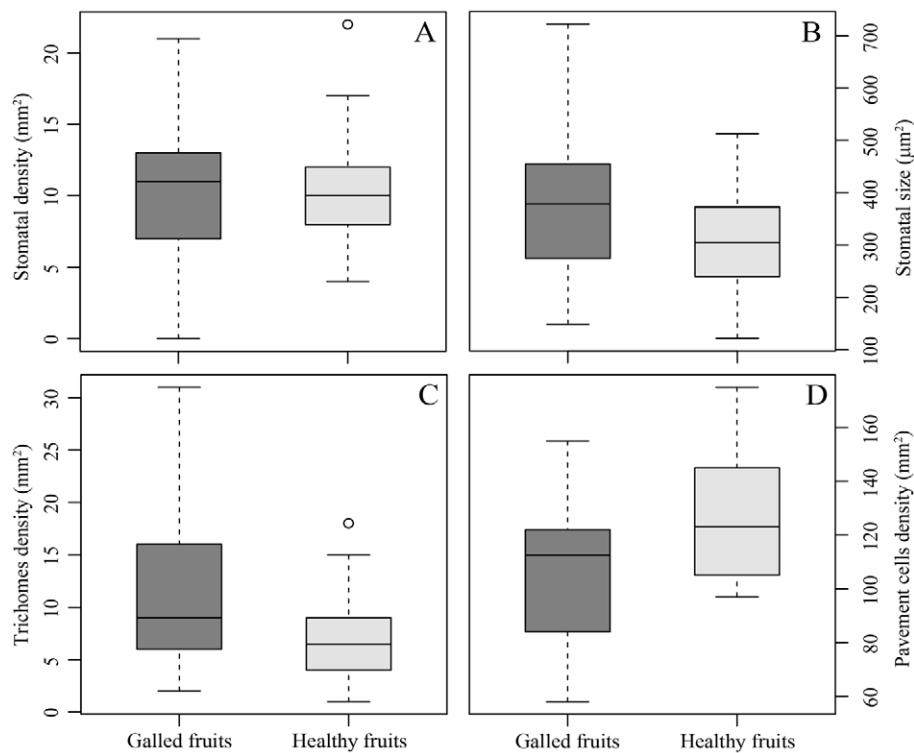


Figure 4. Anatomical features of galled and healthy fruits of *Parkinsonia praecox*. A) Stomatal density per area unit ($p = 0.72$); B) stomatal size ($p < 0.05$); C) trichomes density per area unit ($p = 0.006$), and D) pavement cells density per area unit ($p = 0.37$).

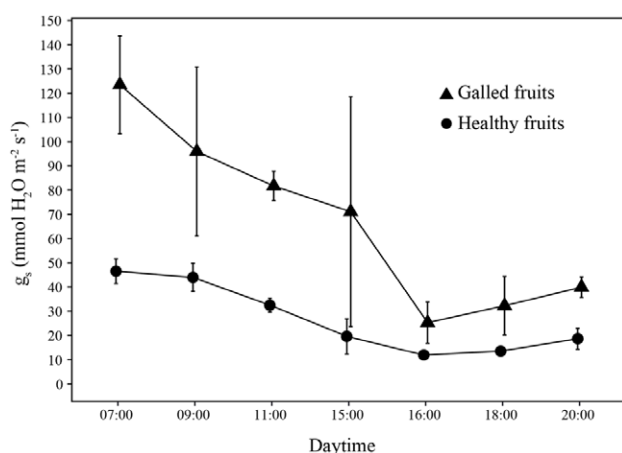


Figure 5. Stomatal conductance (g_s) of galled and healthy fruits ($p = 0.001$) of *Parkinsonia praecox* at different times of the day.

Bruggmanniella (2.34%; 3 spp.), *Eschizomia* (1.56%; 2 spp.), and 13 genera correspond to 10.93%, each one represented by 1 species (Appendix).

Branches of *P. praecox* had 20% of gall incidence, indicating a high impact on fruit production. In association with pre-dispersal seed predation by coleopterans (Contreras-Varela, pers. obs.) and seed viability (Flores & Briones, 2001) the performance of *P. praecox* should be largely reduced.

Gall induction on *P. praecox* fruits should start inside the ovary where the cells are not yet differentiated, consequently the normal structure of the fruit is modified thus producing galls of spherical shape mainly without seeds (Fig. 1C). In general, gall-forming insects require totipotent and undifferentiated tissues to induce galls development (Fernandes & Carneiro, 2009; Fernandes & Santos, 2014).

Galled fruits on *P. praecox* are mainly composed of parenchymatous tissue surrounding the larval chamber. We found that the biomass was greater in healthy fruits than in galled fruits. The water content in galled fruits (ca. 84.16%) suggests that galls are indeed important adaptations to live under harsh environments (Fernandes & Price, 1988; Price et al., 1987). The volumetric growth of fleshy fruits is the result of water and solutes accumulation that involves differences in water potential between the pedicel of the fruit and the rest of the plant (Matthews & Shackel, 2005). The gall formation in *P. praecox* involves the differentiation of a wide range of tissues that make the fleshy galls to superimpose an overall size. The water storage of galled fruits should be associated to solutes accumulation and to the increase of parenchyma cells turgor, these 2 conditions induce the cell hypertrophy and hyperplasia (Cosgrove, 2000). The parenchyma plays an important role for water and nutrient storage (Evert,

2006). To our knowledge, there is no information about the role of solutes content on the water movement to galls or if the chemical signals from the gall-forming insects regulate the accumulation of solutes in galls. It has been reported that gall formation in vegetative structures comprise mainly the cellular elongation, however, cellular division and elongation has been associated to galls formation in reproductive structures (dos Santos et al., 2014). The sclerified tissue in galls and the high trichome density provide mechanical protection, the parenchymatous layer serves as a water and nutrient reservoir (Oliveira et al., 2014, 2016; Stone & Schönrogge, 2003).

The density of trichomes found on galled fruits of *P. praecox* was 1.5 times higher than on healthy fruits. In xeric environments, an increase of leaf pubescence leads to reduced water vapor transpiration and increases the thickness of the boundary layer (Evert, 2006; Pallardy, 2008). It has been reported that the pubescence of fruits significantly reduces water loss (Fernández et al., 2011). In *P. praecox* galled fruits, the high density of trichomes could prevent excessive moisture loss in the larval chamber and may maintain the internal temperature (Oliveira et al., 2014; Price et al., 1987). In addition, an elevated density of trichomes could reduce the vulnerability of the gall-forming insects to potential natural enemies (Fernandes et al., 1987; Stone & Schönrogge, 2003; Woodman & Fernandes, 1991).

Galling insects do not only affect plant architecture and host organ morphogenesis, but also can modify physiological conditions such as stomatal conductance (Fay et al., 1996; Florentine et al., 2005; Larson, 1998), transpiration and CO_2 assimilation (Dorchin et al., 2006). Those modifications influence positively to the gall (Fay et al., 1996) or negatively to the host (Florentine et al., 2005; Larson, 1998). Galled fruits of *P. praecox* increase the g_s and stomatal size but had lower density of pavement cells in relation to healthy fruits; thus, it is possible that the increase in trichome density is the result of a compensatory mechanism to the high gas exchange of the galls with the environment; otherwise, the g_s could be even higher (Fernández et al., 2011). Stomatal conductance estimates the rate of gases exchange through the stomata; it involves the density and aperture of stomata (Pietragalla & Pask, 2012) to infer transpiration and photosynthesis (Hiyama et al., 2005). According to Lemos-Filho and Isaias (2004), the fruits of *Dalbergia miscolobium* (Fabaceae) have a photosynthetic activity that contributes to the carbohydrates required for the fruit development. The g_s in both galled and healthy fruits of *P. praecox* exhibited a similar pattern throughout the day, the higher values were recorded after the sunrise, indicating that the variation in g_s of galls is due to water conditions in stem. The stomatal opening

regulates the transpiration and prevents excessive water loss in the environment (Farquhar & Sharkey, 1982).

The g_s in galled fruits was 2.5 times higher than in healthy fruits. Stomatal conductance can vary due to environmental (e.g., light intensity, CO_2 concentration, relative humidity, temperature, wind, atmospheric pressure), anatomical (e.g., foliar area, pubescence, size and stomatal density), and/or endogenous factors (e.g., phytohormones) (Farquhar & Sharkey, 1982; Pallardy, 2008). In our study, the environmental conditions were similar in galled and healthy fruits. We found that galled fruits increased significantly the g_s rates, although the stomatal density was not statistically different. This could be influenced by the production of signaling molecules, like phytohormones that promote the stomata opening and water movement to galls, in order to favor the water and nutrient continuum from host plant to gall. A revision of the abscisic acid (ABA) role in gall formation made by Tooker and Helms (2014) indicates that this phytohormone promotes gall growth. Even though the exact function of this hormone has not been yet fully recognized in gall tissues, ABA has been acknowledged as an endogenous regulator of the transpiration rate that controls the stomatal closing (Xiong & Zhu, 2003). We also suggest that similar endogenous regulation may occur on *P. praecox* galled fruits, but further phytochemical analysis will be necessary to determine the presence of ABA.

In conclusion, we found an important incidence of galled fruits on *P. praecox* that negatively affect morphological features of the fruits, with consequences on performance of the fruits. In addition, galled fruits are water sinks for this host plant that inhabits xeric environments. Future research is required to evaluate if the incidence of galled fruits negatively affects the plant fitness at the population level, in the different environmental conditions that occur in the Tehuacán-Cuicatlán Biosphere Reserve.

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Appendix. Studies related to galls incidence in reproductive structures in plants, highlighting several aspects to the host plants, morphological traits of galls, as well as data of galling insects.

Host		Galls			Galling insect	Order/family	Reference
Family plant	Species	Organ	Shape	Color			
Anacardiaceae	<i>Mangifera indica</i>	Flower	Elliptical	unknown	<i>Procontarina mangiferae</i>	Diptera-Cecidomyiidae	Tavares, 1917; Gagné, 2004; Carneiro et al., 2009
Apocynaceae	<i>Peplonia asteria</i>	Flower	Ovoid	Green	<i>Asphondylia peploniae</i>	Diptera-Cecidomyiidae	Gagné, 2004; Carneiro et al., 2009
Apocynaceae	<i>Oxypetalum banksii</i>	Flower bud	-	-	<i>Asphondylia peploniae</i>	Diptera-Cecidomyiidae	Gagné, 2004; Flor & Maia, 2017
Arecaceae	<i>Geonoma cuneata</i>	Inflorescence	Cylindrical	Green-reddish	<i>Contarinia geonomae</i>	Diptera-Cecidomyiidae	Gagné et al., 2018
Asteraceae	<i>Porophyllum</i> sp.	Stem/flower	Elliptical	Purple	<i>Zalepidota itiensis</i>	Diptera-Cecidomyiidae	Tavares, 1917; Gagné, 1994, 2004; Carneiro et al., 2009
Asteraceae	<i>Chromolaena odorata</i>	Achene	Swollen	unknown	<i>Asphondylia corbulae</i>	Diptera-Cecidomyiidae	Möhn, 1959; Gagné, 1994, 2004; Carneiro et al., 2009
Asteraceae	<i>Fleischmannia microstemon</i>	Achene	Swollen	unknown	<i>Asphondylia corbulae</i>	Diptera-Cecidomyiidae	Möhn, 1959; Gagné, 1994, 2004; Carneiro et al., 2009
Asteraceae	<i>Chromolaena odorata</i>	Bud	Swollen	unknown	<i>Perasphondylia reticulata</i>	Diptera-Cecidomyiidae	Möhn, 1959; Gagné, 1977; Carneiro et al., 2009

Appendix. Continued

Host		Galls				Reference
Family plant	Species	Organ	Shape	Color	Galling insect	
Asteraceae	<i>Sonchus arvensis</i>	Flower heads	-	-	<i>Tephritis dilacerata</i>	Diptera-Tephritidae Harris & Shorthouse, 1996
Asteraceae	<i>Centaurea maculosa</i>	Floral receptacle	-	-	<i>Urophora affinis</i>	Diptera-Tephritidae Crowe & Bouchier, 2006
Asteraceae	<i>Carduus nutans</i>	Flower heads	-	-	<i>Urophora solstitialis</i>	Diptera-Tephritidae Groenteman et al., 2007
Asteraceae	<i>Centaurea stoebe</i> subsp. <i>micranthos</i>	Flower heads	-	-	<i>Urophora quadrifasciata</i>	Diptera-Tephritidae Duguma et al., 2009
Asteraceae	<i>Centaurea solstitialis</i>	Flower heads	-	-	<i>Urophora sirunaseva</i>	Diptera-Tephritidae Woods et al., 2008
Botaginaceae	<i>Cordia alba</i>	Flower	Swollen	unknown	<i>Asphondylia cordiae</i>	Diptera-Cecidomyiidae Gagné, 1994, 2004; Carneiro et al., 2009
Botaginaceae	<i>Cordia dentata</i>	Flower	Swollen	unknown	<i>Asphondylia cordiae</i>	Diptera-Cecidomyiidae Gagné, 1994, 2004; Carneiro et al., 2009
Botaginaceae	<i>Cordia verbenacea</i>	Flower	Ovoid	Green	<i>Asphondylia cordiae</i>	Diptera-Cecidomyiidae Maia, 2001; Carneiro et al., 2009
Botaginaceae	<i>Tournefortia angustifolia</i>	Fruit	Elongated sheroïd	unknown	<i>Asphondylia tournefortiae</i>	Diptera-Cecidomyiidae Houard, 1933; Möhn, 1960; Gagné 1994, 2004; Carneiro et al., 2009
Botaginaceae	<i>Tournefortia volubilis</i>	Fruit	Elongated sheroïd	unknown	<i>Asphondylia tournefortiae</i>	Diptera-Cecidomyiidae Houard, 1933; Möhn, 1960; Gagné 1994, 2004; Carneiro et al., 2009
Botaginaceae	<i>Varronia curassavica</i>	Inflorescence	Ovoid, hairy	Green-yellow	<i>Asphondylia</i> cf. <i>cordia</i>	Diptera-Cecidomyiidae Gagné, 1994; Maia et al., 2008; Flor & Maia, 2017
Brassicaceae	<i>Cakile maritima</i>	Bud	Swollen	Brown	<i>Gephyraulus zewaili</i>	Diptera-Cecidomyiidae Elsayed et al., 2017
Calophyllaceae	<i>Kielmeyera coriacea</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Calophyllaceae	<i>Kielmeyera rosea</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Calophyllaceae	<i>Kielmeyera petiolaris</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Calophyllaceae	<i>Kielmeyera variata</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Calophyllaceae	<i>Kielmeyera speciosa</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Calophyllaceae	<i>Kielmeyera rubiflora</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Calophyllaceae	<i>Kielmeyera corymbosa</i>	Flower bud	Swollen	unknown	<i>Arcivena kielmeyera</i>	Diptera-Cecidomyiidae Gagné, 2004; Carneiro et al., 2009
Celastraceae	<i>Maytenus obtusifolia</i> var. <i>obovata</i>	Fruit	Ovoid	Red	<i>Bruggmanniella maytenuse</i>	Diptera-Cecidomyiidae Maia, 2001; Gagné, 1994, 2004; Carneiro et al., 2009

Appendix. Continued

Host		Galls					Reference
Family plant	Species	Organ	Shape	Color	Galling insect	Order/family	
Convolvulaceae	<i>Jacquemontia holosericea</i>	Flower	Ovoid	Green/reddish	<i>Schizomyia santosi</i>	Diptera- Cecidomyiidae	Maia, 2001; Cameiro et al., 2009
Erythroxilaceae	<i>Erythroxylum ovalifolium</i>	Flower	Ovoid	Greenish	<i>Asphondylia</i> sp.	Diptera- Cecidomyiidae	Maia, 2001; Cameiro et al., 2009
Fabaceae	<i>Senna bicapsularis</i>	Flower	Spherical	Yellow	<i>Asphondylia sennae</i>	Diptera- Cecidomyiidae	Maia et al., 1992; Gagné, 2004; Cameiro et al., 2009
Fabaceae	<i>Mimosa caesalpinifolia</i>	Fruit	Unknown	unknown	<i>Tavaresomyia mimosae</i>	Diptera- Cecidomyiidae	Möhn, 1961; Gagné, 1994, 2004; Cameiro et al., 2009
Fabaceae	<i>Inga vera</i>	Seeds	-	-	<i>Allorehogus</i> sp.	Hymenoptera- Braconidae	Morales-Silva & Modesto-Zampiero, 2018
Fabaceae	<i>Acacia longifolia</i>	Inflorescence	-	-	<i>Trichilogaster acaciaelongifoliae</i>	Hymenoptera- Pteromalidae	Dennill, 1988
Fabaceae	<i>Acacia aneura</i>	Open flowers	-	-	<i>Dasineura glauca</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia baileyana</i>	Open flowers	-	-	<i>Dasineura pilifera</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia baileyana</i>	Flower buds	-	-	<i>Asphondylia pilogerminis</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia cyclops</i>	Flower buds, fruit	-	-	<i>Asphondylia acaciae</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia cyclops</i>	Open flowers	-	-	<i>Dasineura dielsi</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia dealbata</i>	Open flowers	-	-	<i>Dasineura pilifera</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia dealbata</i>	Flower buds	-	-	<i>Asphondylia pilogerminis</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia deanei</i>	Flower buds	-	-	<i>Asphondylia glabrigermis</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia deanei</i>	Open flowers	-	-	<i>Dasineura glomerata</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia deanei</i>	Fruit	-	-	<i>Asphondylia bursicola</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia decurrens</i>	Open flowers	-	-	<i>Dasineura pilifera</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia decurrens</i>	Fruit	-	-	<i>Asphondylia bursicola</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010
Fabaceae	<i>Acacia divergens</i>	Flower buds	-	-	<i>Asphondylia germinis</i>	Diptera- Cecidomyiidae	Kolesik et al., 2010

Appendix. Continued

Host		Galls				Reference
Family plant	Species	Organ	Shape	Color	Galling insect	
Fabaceae	<i>Acacia elata</i>	Open flowers	-	-	<i>Dasineura glomerata</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia floribunda</i>	Flower buds, fruit	-	-	<i>Asphondylia acaciae</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia genistifolia</i>	Flower buds	-	-	<i>Asphondylia germinis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia hakeoides</i>	Open flowers	-	-	<i>Dasineura glomerata</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia implexa</i>	Open flowers	-	-	<i>Dasineura acaciaelongifoliae</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia irrorata</i>	Open flowers	-	-	<i>Dasineura fistulosa</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia irrorata</i>	Fruit	-	-	<i>Asphondylia bursicola</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia irrorata</i>	Flower buds	-	-	<i>Asphondylia pilogerminis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia littorea</i>	Flower buds	-	-	<i>Asphondylia germinis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia littorea</i>	Fruit	-	-	<i>Asphondylia occidentalis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia longifolia</i>	Open flowers	-	-	<i>Dasineura acaciaelongifoliae</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia meamsii</i>	Open flowers	-	-	<i>Dasineura fistulosa</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia meamsii</i>	Flower buds	-	-	<i>Asphondylia glabrigerminis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia meamsii</i>	Open flowers	-	-	<i>Dasineura glomerata</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia meamsii</i>	Fruit	-	-	<i>Asphondylia bursicola</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia meamsii</i>	Flower buds	-	-	<i>Asphondylia pilogerminis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia maidenii</i>	Open flowers	-	-	<i>Dasineura rubiformis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia melanoxylon</i>	Flower buds, fruit	-	-	<i>Dasineura acaciaelongifoliae</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia melanoxylon</i>	Open flowers	-	-	<i>Asphondylia acaciae</i>	Kolesik et al., 2010
Fabaceae					<i>Dasineura furcata</i>	Kolesik et al., 2010

Appendix. Continued

Appendix. Continued

Host		Galls				Reference
Family plant	Species	Organ	Shape	Color	Galling insect	
Fabaceae	<i>Acacia ulicifolia</i>	Flower buds, fruit	-	-	<i>Asphondylia acaciae</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia urophylla</i>	Flower buds	-	-	<i>Asphondylia germinis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia verticillata</i>	flower buds, fruit	-	-	<i>Asphondylia acaciae</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia xanthina</i>	Flower buds	-	-	<i>Asphondylia germinis</i>	Kolesik et al., 2010
Fabaceae	<i>Acacia cavenia</i>	Bud	-	-	<i>Chalcidoidea</i> sp.	Maia, 2012
Fabaceae	<i>Gourliea decorticans</i>	Bud and stem	-	-	<i>Proseurytoma gallarum</i>	Maia, 2012
Fabaceae	<i>Inga laurina</i>	Fruit	-	-	<i>Allorhogus</i> sp.	Santos et al., 2016
Fabaceae	<i>Enterolobium cyclocarpum</i>	Fruit	-	-	<i>Asphondylia enterolobi</i>	Janzen, 1982
Fabaceae	<i>Prosopis alba</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis caldenia</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis chilensis</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis flexuosa</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis nigra</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis kuntzei</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis ruscifolia</i>	Flower	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis affinis</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis alba</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis caldenia</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis chilensis</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Mc Kay & Gandolfo, 2007

Appendix. Continued

Host		Galls				Order/family	Reference
Family plant	Species	Organ	Shape	Color	Galling insect		
Fabaceae	<i>Prosopis flexuosa</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Diptera- Cecidomyiidae	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis kuntzei</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Diptera- Cecidomyiidae	Mc Kay & Gandolfo, 2007
Fabaceae	<i>Prosopis nigra</i>	Unripened pods	-	-	<i>Asphondylia</i> sp. nr. <i>prosopidis</i>	Diptera- Cecidomyiidae	Mc Kay & Gandolfo, 2007
Lamiaceae	<i>Hyptis</i> sp.	Flower	Spherical	unknown	<i>Asphondylia canastreae</i>	Diptera- Cecidomyiidae	Gagné, 2004; Carneiro et al., 2009
Loranthaceae	<i>Struthanthus</i> sp.	Fruit	Globular	unknown	<i>Asphondylia struthanthi</i>	Diptera- Cecidomyiidae	Gagné, 1994, 2004; Carneiro et al., 2009
Loranthaceae	<i>Psittacanthus robustus</i>	Flower	Unknown	unknown	<i>Schizomyia</i> sp.	Diptera- Cecidomyiidae	Gagné, 1994; Carneiro et al., 2009
Malpighiaceae	<i>Byrsonima sericea</i>	Inflorescence	Ovoid	Brown	<i>Bruggmanniella byrsonimae</i>	Diptera- Cecidomyiidae	Maia, 2001; Gagné 1994, 2004; Carneiro et al., 2009
Malpighiaceae	<i>Byrsonima sericea</i>	Bud	Cylindrical	Green	<i>Bruggmanniella byrsonimae</i>	Diptera- Cecidomyiidae	Guimarães et al., 2014
Malpighiaceae	<i>Heteropteris</i> sp.	Flower	Swelling		<i>Cantarinia</i> sp.	Diptera- Cecidomyiidae	Gagné, 1994; Carneiro et al., 2009
Malpighiaceae	<i>Heteropteris nitida</i>	Flower	Elliptical	Yellow	<i>Clinodiplosis floricola</i>	Diptera- Cecidomyiidae	Maia, 2001; Carneiro et al., 2009
Malvaceae	<i>Waltheria indica</i>	Leaf/ inflorescence	Spherical	yellow/brown	<i>Anisodiplosis praecox</i>	Diptera- Cecidomyiidae	Maia & Fernandes, 2005; Almeida et al., 2006; Carneiro et al., 2009
Melastomataceae	<i>Conostegia xalapensis</i>	Fruit	-	-	<i>Allorhogas conostegia</i>	Hymenoptera- Braconidae	Chavarria et al., 2009
Melastomataceae	<i>Miconia calvescens</i>	Fruit	-	-	<i>Apion</i> sp.	Coleoptera- Curculionidae	Badenes-Perez & Johnson, 2007
Melastomataceae	<i>Miconia calvescens</i>	Fruit	-	-	<i>Allorhogas</i> sp.	Hymenoptera- Braconidae	Badenes-Perez & Johnson, 2007
Moraceae	<i>Chlorophora tinctoria</i>	Flower	Swollen	unknown	<i>Clinodiplosis chlorophorae</i>	Diptera- Cecidomyiidae	Rübsaamen, 1905; Gagné, 1994; Carneiro et al., 2009
Moraceae	<i>Ficus</i> sp.	Flower	-	-	<i>Aganidae</i> sp.	Hymenoptera- Aganotidae	Maia, 2012
Myrtaceae	<i>Eugenia buxifolia</i>	Fruit	Subglobular	Green	<i>Dasineura eugeniae</i>	Diptera- Cecidomyiidae	Gagné, 1994, 2004; Carneiro et al., 2009
Rubiaceae	Undetermined	Flower	Subovoid	Green	<i>Asphondylia bahiensis</i>	Diptera- Cecidomyiidae	Houard, 1933; Gagné 1994, 2004; Carneiro et al., 2009

Appendix. Continued

Host		Galls			Reference
Family plant	Species	Organ	Shape	Color	
Rubiaceae	Undetermined	Flower	Subovoid/ elliptical	Green	Gagné 1994, 2004; Carneiro et al., 2009
Rubiaceae	<i>Diodia gymnocephala</i>	Flower	Elliptical	Green	Maia, 2001; Gagné, 2004; Carneiro et al., 2009
Rubiaceae	<i>Borreria</i> sp.	Flower	Swollen	unknown	Gagné, 1994, 2004; Carneiro et al., 2009
Rubiaceae	<i>Diodia</i> sp.	Flower	Swollen	unknown	Gagné, 1994, 2004; Carneiro et al., 2009
Rubiaceae	<i>Borreria verticillata</i>	Inflorescence	Fusiform	Green	Maia et al., 1992; Carneiro et al., 2009
Solanaceae	<i>Solanum</i> sp.	Fruit	Spherical	Green	Flor & Maia, 2017
Verbenaceae	<i>Lantana</i> sp.	Flower	Ovoid	Pink	Tavares, 1918; Houard, 1933; Gagné, 1994, 2004; Carneiro et al., 2009

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