Population dynamics of the gall inducer *Eriogallococcus isaias* (Hemiptera: Coccoidea: Eriococcidae) on *Pseudobombax grandiflorum* (Malvaceae)

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Eriogallococcus isaias Hodgson and Magalhães is a Neotropical species of gall-inducing scale insect (Coccoidea: Eriococcidae), whose phenological synchrony with its host plant, *Pseudobombax grandiflorum*, is fundamental to the maintenance of its population. Furthermore, *E. isaias* is unusual among gall-inducing Eriococcidae because its galls are not sexually dimorphic and are induced by the second-instar nymphs. We studied the life cycles of the host plant and the galling insect, and followed the development of the insects and the structure of the gall. The results showed that gall induction is synchronous with leaf flushing, and that the galls and leaves mature concomitantly. Males have a 36–48-day life cycle within the gall, whereas females have a 75–100-day life cycle.

Keywords: insect galls; insect–plant interaction; phenological synchrony; conservation biology

Introduction

The establishment of gall-inducing insects on their host plants generally requires active responses from the plant tissues to succeed. After the establishment, a specific gall morphotype (*sensu* Isaias et al. 2013) develops and is dependent on particular determining factors, such as, the sex of the inducer and the duration of the life cycle in the case of Eriococcidae-induced galls. When gall dimorphism is present, as in many eriococcid gall inducers, male-induced galls can be distinguished from female-induced ones by their external shape (Linsenmaier 1972; Meyer 1987; Gullan and Kosztarab 1997; Gonçalves et al. 2005; Gullan et al. 2005; Gullan and Martin 2009). The time of development of male and female eriococcids is also important because males have five instars (four nymphal and adult), whereas females are neotenic, with only three instars (two nymphal and adult). Male Eriococcidae are delicate, alate, ephemeral insects, without functional mouth parts. They leave their galls to find and fertilize the females. Females are apterous, sessile, have a nymph-like appearance, and never leave their galls (Gullan et al. 2005). New gall cycles are induced by the first-instar nymphs (crawlers), or more rarely by the second-instar nymphs (Gonçalves et al. 2009). The longer the gall cycle, the more differentiated are the cells within the galls, and consequently their structural complexity is greater. For instance, the Brazilian

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eriococcid *Pseudotectococcus rollinae* Hodgson and Gonçalves has two gall morphotypes on the same host plant, *Rollinia laurifolia*, each one with its own distinct patterns of cell responses. The population overwinters (through the dry season) as the first-instar nymphs in stem galls, which are much simpler than the leaf galls (Gonçalves et al. 2009). In stem galls, the feeding activity of the nymph causes the cells around the insect's body to differentiate into a lenticel-like gall, and, when the insect enters dormancy, the stimuli for gall differentiation stop. During the summer (wet season), the second-instar nymphs induce complex leaf galls with several layers of specialized tissues (Gonçalves et al. 2005).

The present study focused on the phenology of *Eriogallococcus isaias* Hodgson and Magalhães (Hemiptera: Eriococcidae)–*Pseudobombax grandiflorum* (Cav.) A. Robyns (Malvaceae), two Neotropical species. The morphological aspects of the male-induced and female-induced galls were followed through two annual life cycles. As *P. grandiflorum* is deciduous, the life cycle of *E. isaias* should present a strategy similar to that of *Ps. rollinae* (Gonçalves et al. 2009) to survive the period of leaf absence. A phenological synchrony between the life cycles of the host plant and of the gall-inducer is clearly crucial for the maintenance of the system.

Material and methods

Study area and plant population

The study was carried out on a plateau formed by a limestone outcrop. The vegetation is located above the Gruta da Lapinha (19°33'67" S, 043°57'54" W) in the Parque Estadual do Sumidouro, in the municipality of Lagoa Santa, Minas Gerais state, Brazil. The region has distinct dry (April to September) and rainy (October to March) seasons, with minimum temperatures of 14–26°C in the dry season, and 18–29°C in the rainy season.

Pseudobombax grandiflorum is a 15–25 m high tree, with compound digitate deciduous leaves with glabrous and leathery leaflets. The species is monoecious, and occurs in Brazilian semi-deciduous forest (Lorenzi 1998). All individual plants of *P. grandiflorum* on the plateau were infested by galls, and their phenological cycles were followed during 2008 and 2009. In 2008, the observations were made under field conditions, so as not to interfere with the gall cycle. In 2009, galled leaflets were sampled at 3-day intervals and examined in the laboratory. A voucher specimen of *P. grandiflorum* was deposited in the BHCN herbarium of the Instituto de Ciências Biológicas of the Universidade Federal de Minas Gerais, under registration number 133730.

Morphology and levels of infestation

The colour, covering features, shape, size, and location of the galls on the leaflets were observed in the field. The levels of infestation were calculated as the ratio of the number of non-galled to galled leaflets. The following equation was applied for each individual plant, and the final result is expressed as mean infestation in the population:

$$\text{Infestation} = \frac{\text{number of galled leaflets} \times 100}{\text{total number of leaflets}}$$

Phenology

Host plant

Leaf phenology was monitored during 2008 and 2009 on 12 plants selected at the study site. The observations were carried out using a phenological observation sheet. The presence or absence of leaf flushing was evaluated for each plant, and the activity index for each phenophase was calculated by estimating the percentage of individual plants in the population showing phenological synchrony in each season (Bencke and Morellato 2002; Torezan-Silingardi and Oliveira 2004). The phenophases were divided into five categories: 0 = absence of the phenophase; 1 = 1–25% of the phenophase; 2 = 26–50%; 3 = 51–75% and 4 = 76–100% (Fournier and Carpannier 1975). Leaf flushing extended from the appearance of the first leaves until their complete expansion, as proposed by Pedroni et al. (2002). The beginning of leaf fall was based on the percentage categories for the canopy covering. During 2008, the presence of leaf flushing, and the number of mature and senescent leaves were observed for each plant twice a month. To estimate the synchrony of each stage of leaf expansion on individual plants, an index of activity of these phenological phases was calculated (Bencke and Morellato 2002). Each phenological datum generated a phenological sheet and the data on the population were obtained from the means of all data points.

Galls

The phenology of the galls was evaluated during 2008 on six individual plants in the population (a total of 24 branches and 613 leaflets were evaluated per year). Twice a month, the development of the galls (mean 870, minimum 225, and maximum 1443) was monitored by counting the number of galls in each phase directly in the field, i.e. growth and development, maturation and senescence. The growth and development phase is characterized by a slight projection of the leaflet around the body of the nymph. In the maturation phase, the gall assumes the aciculate shape. The senescent phase is characterized by the empty chamber. Once the crawlers are microscopic, the induction phase, i.e. the initial appearance of the second-instar nymphs on the leaflets, was not estimated in the field.

Gall-inducing insects

1. During 2009, the development of *E. isaias* was evaluated in the laboratory, from samples collected from six plants. Leaf flushing (when the leaflets were 0.5 cm long) was defined as the beginning of the cycle. The leaflets were first harvested 3 days after flushing and then at 3-day intervals, with 12 leaflets harvested (two per plant) on each plant (a total of 641 galls). These galls were isolated from the leaflet laminae and fixed in Karnovsky's solution in 0.1 M phosphate buffer (pH 7.2) (O'Brien and McCully 1981) for subsequent anatomical studies (data not shown). The galls were dissected under a stereomicroscope

to separate the insects by instar and gender. The identification of the instars was based on the morphological descriptions of galling Eriococcidae (Gullan et al. 2005), and of *E. isaias* (Hodgson et al. 2011). Male and female first- and second-instar nymphs were separated by using the measurement of the length of each hind trochanter + femur. This sclerotized part of the leg was chosen according to Daly (1985), mounted in microscope slides, and measured under a light microscope. The lengths of hind trochanter + femur of nymphs harvested from leaf galls with adult females, nymphs from stems, and nymphs from young leaflets at the beginning of gall induction were compared. According to Hodgson et al. (2011), the crawlers (sex not determined) have the trochanter + femur 43–50 μm long, whereas those of the second-instar male nymphs are 65–73 μm long.

The life cycle of *E. isaias* was estimated from leaflet flushing until the emergence of the crawlers and adult males from the galls.

Scanning electron microscopy analyses

To check whether the crawlers had migrated to the stems during the dry season, when the trees had no leaves, samples of terminal branches ($n = 5$) from five different trees were fixed in Karnovsky's solution in 0.1 M phosphate buffer (pH 7.2), gradually dehydrated in an ethanol series, dried in a CO_2 critical-point-drier, sputter-coated with 35 nm gold (O'Brien and McCully 1981), and observed in a scanning electron microscope (Leo Evo 40 XVP), similarly to the procedures described for *Ps. rollinae* (Gonçalves et al. 2009).

Results

Host plant

Pseudobombax grandiflorum has definite vegetative phenophases (Figure 1A, B). The vegetative period lasts from the beginning of August to the end of March, with leaf flushing from August to October, with maximum activity (100%) and intensity (80%) in September, i.e. when all but 20% of the trees show leaf flushing, (Figure 2A). In October, all plants had fully expanded leaves (Figure 2B), and the

Figure 1. Habitus of *Pseudobombax grandiflorum*. (A) tree with expanded leaves; (B) tree in deciduous stage.

Figure 2. Representation of the vegetative phenology of *Pseudobombax grandiflorum*, from March 2008 to February 2009, according to two methods of data analyses: index of activity and percentage of intensity of Fournier. (A) leaf flushing; (B) expanded leaves; (C) senescent leaves; (D) leaf fall.

greatest intensity (85%) occurred concomitantly with the highest percentage of activity, i.e. all plants had some expanded leaves but 15% of the leaves were still immature. At the end of February, the leaves entered senescence (Figure 2C) and by May, 100% of the trees were leafless (Figure 2D).

Galls

The crawlers dispersed to the branches in December, before leaf fall, and hid within the stem bark, where they entered dormancy until the next spring. In August of the following year, they moulted on the branches to second-instar nymphs, and dispersed to the young leaflets of *P. grandiflorum* (Figure 3A, B) to start a new leaf-gall cycle (Figure 3C, D). This dispersal coincided with the appearance of the first young leaflets. The leaf galls are green, glabrous and intralaminar, with an aciculate projection on the adaxial surface. At maturity, they are 7.8 ± 2.1 mm tall (from the ostiole to the projection) and 3.0 ± 0.5 mm (greatest width) (Figure 3E). Each gall contained one nymphal chamber, and the ostiole faced the abaxial surface (Figure 3F). *Eriogallococcus isaias* is univoltine, and induces morphologically similar galls regardless of the sex of the gall-inducer. The only difference noted between the male (Figure 4A) and female (Figure 4B) galls, was the shape of the chamber, which was significantly wider in the female-induced galls in order to accommodate the expanded abdomen. At maturation, all galls have a one-layered epidermis and a cortex of homogeneous parenchyma with phloematic bundles and mucilaginous cells in the

Figure 3. Features of *Eriogallococcus isaias* and of its galls on *Pseudobombax grandiflorum*. (A) crawlers (red nymphs), second-instar nymphs (pale yellow nymphs), and a moult on stem bark. Detail in minor square; (B) second-instar nymph (arrow) on a young leaf surface seen with scanning electron microscopy; (C, D) young leaflets with galls in the phase of growth and development; (E, F) mature leaflets with mature galls. Detail of gall with the aciculate projection towards the adaxial surface; (G) mature leaflet with mature gall. Senescent gall on detail, opening towards the abaxial surface.

outer region (Figure 4C, D). The cortex is divided into the outer cortex (Oc), the median cortex (Mc), and the inner cortex (Ic) (Figure 4C, D). The leaflet infestation levels were 98.2% in 2008 and 79.7% in 2009, with the oldest leaves on the branches escaping gall induction.

Leaf flushing of *P. grandiflorum* took place in the first half of August, and the growth and development phase of the gall (Figure 3C, D) occurred from the second half of August (100%) until the second half of October (~ 20%) (Figure 5). The first galls in the maturation phase (Figure 3E) were observed at the beginning of September (~ 20%) with a maximum in October (80%) (Figure 5). Galls in the senescent phase (Figure 3F) appeared at the beginning of November (~50%) and reached their maximum occurrence in December (100%) (Figure 5).

The entire growth cycle of the galls was synchronous with the vegetative phase of the host plant, i.e. both gall induction and the growth and development phases were concomitant with leaf flushing and expansion (Figure 6). Gall maturation and senescence occurred on mature leaflets (Figure 6).

Gall-inducing insects

Both the crawler and the second-instar nymphs males of *E. isaias* could be recognized by their morphology (see drawings in Hodgson et al. 2011). The length of the trochanter + femur of the nymphs before crawler dispersal ($48.0 \pm 1.0 \mu\text{m}$) from galls with adult females inside, of the nymphs on the stems ($48.0 \pm 3.0 \mu\text{m}$), and of nymphs from the galls just induced on young leaflets ($64.2 \pm 0.7 \mu\text{m}$) proved that this last group of nymphs were second-instar nymphs. The nymphs used for these measurements were randomly sampled and not separated by sex.

The population of insects sampled from 3- to 12-day-old galls on young leaflets were all second-instar nymphs (Figure 7A). However, by days 15–24, a small proportion of the nymphs were third-instar and fourth-instar males (pre-pupae and pupae), and adult females, although most of the nymphs (~80%) were still in the second instar (Figure 7b) (sex undetermined). By days 27–36, approximately equal proportions of individuals were non-adult and adults, including both females containing eggs (Figure 7c) and adult males. In the middle of the sampling period, the population consisted of adult females, females with eggs and adult males, but almost 40% of the galls were empty, probably because the males had emerged (Figure 7D–F), which indicated a high proportion of males in the population. At the end of the sampling period, the proportion of females with eggs and adult males was reduced and the percentage of females with crawlers had increased (30%), whereas almost 50% of the galls were empty (Figure 7G, H). Hence, the cycle within the male galls lasted 36–48 days, whereas the females remained alive within the galls for 75–100 days from gall induction to gall senescence.

Discussion

The induction of leaf galls by *E. isaias* on *P. grandiflorum* is similar to that of *Ps. rolliniae*, another Neotropical Eriococcidae, on *R. laurifolia* (Gonçalves et al. 2005), in that it is the second-instar nymphs that initiate the gall. Although the sexual dimorphism of Coccoidea influences the phenotype of their galls (Gullan and Kosztarab 1997; Gonçalves et al. 2005; Gullan and Martin 2009), the general structure of the galls induced by males and females of *E. isaias* is similar, with a

Figure 5. Phenological cycle of the galls induced by *Eriogallococcus isaias* on *Pseudobombax grandiflorum* from August to December 2008.

Figure 6. Diagram representing the synchrony between the host *Pseudobombax grandiflorum* and the gall stages induced by *Eriogallococcus isaias*.

slight difference in the shape of the nymphal chamber when the adult female contains eggs. The high level of infestation of *E. isaias* on the leaflets of *P. grandiflorum* may be related to the low mobility of the first-instar nymphs, as previously observed for

Figure 4. General structure of the galls induced by *Eriogallococcus isaias* on *Pseudobombax grandiflorum*. (A, C) mature male-induced gall; (B, D) mature female-induced gall; (C, D) anatomical aspects of the galls showing the parenchymatic nature of gall wall, with vascular bundles and secretory ducts interspersed; (C) male-induced gall showing elongated nymphal chamber; (D) female-induced gall showing the round nymphal chamber. IC, inner cortex; MC, middle cortex; NC, nymphal chamber; OC, outer cortex.

Figure 7. Population structure of *Eriogallococcus isaias* during 2009. Each graphic represents four harvests of galls (3-day span) except for (H), which represents five harvests. (A) samples 1–4 ($n = 80$ galls); (B) samples 5–8 ($n = 80$ galls); (C) samples 9–12 ($n = 80$ galls); (D) samples 13–16 ($n = 79$ galls); (E) samples 17–20 ($n = 79$ galls); (F) samples 21–24 ($n = 78$ galls); (G) samples 25–28 ($n = 71$ galls); (H) samples 29–33 ($n = 94$ galls). The first sample was harvested 3 days after flushing, and the last sample, 99 days later. 2nd I, second-instar nymphs; 3rd IM, third-instar male nymphs; 4th IM, fourth-instar male nymphs; AM, adult male; AF, adult female; AF + E, adult female with eggs; AF + C, adult female with crawlers; EG, empty galls.

the *Ps. rollinae*–*R. laurifolia* system (Gonçalves et al. 2005) and for *Tectococcus ovatus* Hempel on *Psidium cattleianum* (Vitorino et al. 2000) in the Neotropics.

In most Coccoidea, the morphological differences between male and female first-instar nymphs are small or not evident; subtle differences occur in the second instar and dimorphism is obvious thereafter, with extreme sexual dimorphism evident in the adults (Hodgson et al. 2011). The males leave their galls to locate and inseminate the sessile females within the gall. *Eriogallococcus isaias* is univoltine, and gall induction is synchronous with bud flushing on *P. grandiflorum*, as observed for *P. rollinae* (Ericoccidae) on *R. laurifolia* (Annonaceae) (Gonçalves et al. 2009). The synchrony between the host plant and the gall is particularly important for univoltine gall inducers (Weis et al. 1988; Gonçalves et al. 2009; Campos et al. 2010) because gall induction depends on the capacity of the young host tissues to respond to the gall-inducing stimuli from the insects (Weis et al. 1988; Gonçalves et al. 2009). Besides their potential reactiveness, the young plant parts function as physiological sinks (Buchanam et al. 2000), with gall development altering phloem translocation so that the gall continues to act as a sink while the inducers are still active (Mani 1964; McCrea et al. 1985; Larson and Whitham 1991; Inbar et al. 1995). Consequently, as proposed by several authors (Yukawa 2000; Mendonça Jr 2001; Castro et al. 2013), large quantities of high-quality nutritional resources are translocated to the gall site. As both *R. laurifolia* (Gonçalves et al. 2009) and *P. grandiflorum* are deciduous for almost half of the year, the synchrony is vital for the survival of the associated gall-inducing herbivores.

In addition to the synchrony with bud flushing, the gall-inducing herbivore needs a strategy to survive during the periods when the host plant is deciduous. When the crawlers of *E. isaias* are dispersed, the host plant has no new leaflets, the sites for gall induction. For the eriococcid *Ps. rollinae*, Gonçalves et al. (2009) reported a second gall morphotype on the stems of host plants, where the gall-inducing first-instar nymphs remained during the deciduous phase of the host. Even though *E. isaias* does not seem to induce stem galls on *P. grandiflorum*, the crawlers do remain on the stem bark during the dry season, suggesting a similar strategy. The crawlers of *E. isaias* have both surfaces somewhat sclerotized and the dorsal dermis is nodulose (Hodgson et al. 2011), characteristics which may avoid desiccation. This can be of great adaptive value for these nymphs once they cannot induce stem galls and be protected by plant tissues. In August, a new sprouting occurs, the nymphs moult in the stems, and the second-instar nymphs move to the new leaflets to induce the leaf galls. This part of the cycle was confirmed by the measurements of the trochanter–femur segment of the nymphs. These nymphs were harvested from leaf galls with adult females inside, from stems, and from young leaflets at the beginning of gall induction. During the second year of study, the first emerging leaflets of *P. grandiflorum* had few or no galls, indicating a brief asynchrony between the insects and its host plant. Gall-inducing herbivores may be susceptible to temporal variations in the phenology of their hosts, and this could increase or decrease the infestation levels (Pilson 2000). Some plants may delay their phenological phases until a period when no herbivores are active (Agrawal 2000). However, in the earlier study on *R. laurifolia*, a second leaf flushing in the same year provided normal healthy leaves for the host plant (Gonçalves 2008). This suggest that a late event of leaf flushing should benefit the host plant.

The population dynamics of *E. isaias* on *P. grandiflorum* showed a phenological synchrony between leaf flushing and gall induction, which is vital for the survival of *E. isaias*. Gall maturation and gall senescence are concomitant to leaf aging. Although the females are longer-lived than the males, the galls are not morphologically dimorphic and their tissue complexity is similar with only a slight difference regarding the nymphal chamber, which assumes the shape of the insect's body. Both of the Neotropical eriococcid species, *E. isaias* and *Ps. rollinae*, have similar strategies to survive the period of leaf absence. *Eriogallococcus isaias* shelters on stem bark but is not capable of inducing stem galls for dormancy, which may be interpreted as a morphogenetic constraint of the host plant, which the galling insect cannot surpass. This may be because a phellogen layer cannot be redifferentiated in these stems.

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