Ontogenetic variation in morphology and mortality rate of the galler *Baccharopelma dracunculifoliae* (Hemiptera: Psyllidae)

Variação ontogenética na morfologia e taxa de mortalidade do galhador *Baccharopelma dracunculifoliae* (Hemiptera: Psyllidae)

Milton Barbosa[1]
Bruno Gini Madeira[2]
G. Wilson Fernandes[3]

ABSTRACT

The study of three-trophic level interactions is crucial for the understanding of population dynamics of insect herbivores, especially for many gall-inducing species. We aimed to determine the developmental pattern of the nymphs of *Baccharopelma dracunculifoliae* and its relationship with gall size and natural enemies in Belo Horizonte, Brazil (19°30´S, 44°00´W). We sampled galls from the same cohort in two distinct surveys (June and August 1998). The galls were collected from 10 randomly selected individuals of *Baccharis dracunculifolia* in each survey. We then estimated their volume before dissecting them. Following, we counted the number of nymphs and the survivorship, also recording the mortality factors of the nymphs. The results indicate that the mean number of nymphs per *B. dracunculifoliae* gall did not differ between June and August, while the mean number of live nymphs was significantly higher in June than in August. Additionally, we found a weak correlation between the mean number of nymphs per gall and gall volume in both months of the study ($r_{June} = 0.11$; $r_{August} = 0.17$). We found higher nymph survivorship rates in June (95.0%) than in August (40.4%). Parasitism was responsible for the demise of 56.6% of all larvae in August and the rate of nymph survivorship did not vary with gall volume. Our findings suggest that during the development of *B. dracunculifoliae* the variation

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[1] Laboratório de Ecologia Evolutiva e Biodiversidade, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte MG – Brasil.

[2] Laboratório de Ecologia Evolutiva e Biodiversidade, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte MG – Brasil.

[3] Laboratório de Ecologia Evolutiva e Biodiversidade, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte MG – Brasil. E-mail: gwilson@icb.ufmg.br.

in gall size is more associated with nymph size than number of nymphs in a gall. The attack by natural enemies in *B. dracunculifoliae* is high, and parasitism is a strong force in the structure and regulation of the population, although it does not appear to be a selective force that acts on the oviposition behaviour of the female gallers since parasitism was not associated with gall and nymph size or with the clutch size.

KEYWORDS: Insect galls, insect-plant interactions, parasitism, parasitoid wasp.

RESUMO

O estudo de interações tri-tróficas é crucial para o entendimento da dinâmica populacional de insetos herbívoros, especialmente para muitas espécies indutoras de galhas. Nosso objetivo foi determinar o padrão de desenvolvimento das ninfas de *Baccharopelma dracunculifoliae* e sua relação com tamanho de galha e inimigos naturais em Belo Horizonte, Brasil (19, 30'S, 44°00'W). Nós amostramos galhas da mesma coorte em dois períodos distintos (junho e agosto de 1998). As galhas foram coletadas de 10 indivíduos selecionados aleatoriamente de *Baccharis dracunculifolia* em cada estudo. Então, estimamos seu volume antes de dissecá-las. A seguir, contamos o número de ninfas e a sobrevivência, também registrando os fatores de mortalidade das ninfas. Os resultados indicam que o número médio de ninfas por galha de *B. dracunculifolia* não diferiu entre junho e agosto, enquanto o número médio de ninfas vivas foi significativamente maior em junho do que em agosto. Além disso, encontramos correlação fraca entre o número médio de ninfas por galha e volume da galha nos dois meses do estudo ($r_{junho} = 0,11$; $r_{agosto} = 0,17$). Encontramos maiores taxas de sobrevivência de ninfas em junho (95,0%) do que em agosto (40,4%). O parasitismo foi responsável pela mortalidade de 56,6% de todas as larvas em agosto e a taxa de sobrevivência de ninfas não variou com o volume da galha. Nossos resultados sugerem que durante o desenvolvimento do galhador a variação no tamanho da galha está mais associada ao tamanho da ninfa do que ao número de ninfas em uma galha. O ataque de inimigos naturais em *B. dracunculifoliae* é alto e o parasitismo é uma força importante na estruturação e regulação da população, embora não pareça ser uma força seletiva que atua sobre o comportamento de oviposição por parte das fêmeas dos galhadores já que a taxa de parasitismo não estava associada ao tamanho da galha e da ninfa ou ao tamanho da ninhada.

PALAVRAS-CHAVE: Galhas de insetos, interações inseto-planta, parasitismo, vespas parasitoides.

INTRODUCTION

The study of three-trophic level interactions is crucial for the understanding of population dynamics of insect herbivores (Price *et al.* 1980), especially for many gall-inducing species (Price & Clancy 1986, Craig *et al.* 1990). Many galling herbivores are heavily attacked by natural enemies perhaps due to their larvae living within their host-plant tissues, which makes them an easier target for natural enemies (Rossi *et al.* 1992). However, female parasitoid must first penetrate the gall wall and locate the host insect within gall tissue to be able to parasitize it (Craig *et al.* 1990). Therefore, gall traits resulting from the interaction between the gall former and plant genotypes (see Weis & Abrahamson 1985), have the potential to determine parasitoid success (Price & Clancy 1986). Several hypotheses about the adaptive nature of galls have been proposed (Price *et al.* 1987). One of those, the enemy hypothesis, proposes that the galling habit offers the insect a protective refuge against the attack by natural enemies (Weis *et al.* 1985).

The performance of galling insects is influenced by several factors, such as female oviposition preference (Price *et al.* 1990), plant quality (Anderson *et al.* 1989), resistance (Fernandes 1990, Fernandes & Negreiros 2001, Barbosa & Fernandes 2014), and attack by parasitoids (Weis & Abrahamson 1985, Craig *et al.* 1990, Rossi *et al.* 1992). However, a factor that has received little attention is the occurrence of competition among the larvae of galling insects, which occupy the same space in the gall. If there is any asymmetry on the acquisition of resources among the larvae in a gall, the determination of the performance and population dynamics of galling insects might be altered.

The importance of clutch size as a fitness component and the trade-offs between parent and offspring has been demonstrated in many studies (e.g., Stearns 1992). These studies have documented the existence of an optimum between clutch size and larval size: larger offspring tend to present smaller larvae and therefore, less competitive ability (Freese & Zwölfer 1996, de Souza *et al.* 2001). Optimal allocation of eggs in relation to the available breeding places seems particularly complicated for specialized phytophagous insects in tri-trophic systems. Under these conditions, the reproductive fitness of a female depends on oviposition decisions, which allows the offspring an optimal exploitation of their host plant and at the same time provide a maximum of protection against natural enemies (Freese & Zwölfer 1996).

Gall size is sometimes correlated with increased larval survival, adult weight and fecundity, because larger galls offer more breeding sites, providing better nutritional quality to the larvae (Whitham 1978). Furthermore, parasitism levels are reduced in galls of larger diameter, because they often exceed the length of the parasitoid ovipositor (Weis *et al.* 1985).

Baccharis dracunculifolia De Candole (Asteraceae) (heretofore called *B. dracunculifolia*) is a widespread dioecious perennial shrub, 2-3 m in height, that occurs in southeastern and southern Brazil, Argentina, Uruguay, Paraguay, and Bolivia (Barroso 1976). *B. dracunculifolia* grows throughout the year continuously producing leaf buds, and produces flowers twice a year from March to June and from November to December (Espírito-Santo & Fernandes 1998). *Baccharopelma dracunculifoliae* Burckhardt (Sternorrhyncha: Psyllidae) is the commonest gall inducer found on *B. dracunculifolia* (Araújo *et al.* 1995). The galls induced by this psyllid are elliptical, green, glabrous, one-chambered, and are induced throughout the year, showing two peaks of abundance, which coincide with the periods of plant flowering (Espírito-Santo & Fernandes 1998). Females of *B. dracunculifoliae* oviposit on the borders of leaves of the host plant. Initially, the leaf tissue swells, bending over itself until joining its borders and thereby forming an elliptical capsule (Lara & Fernandes 1994, Arduin *et al.* 2005). Nymphs develop inside the inner chamber of this capsule. Gall walls are succulent throughout the development of the psyllid (Espírito-Santo & Fernandes 1998). The galls of *B. dracunculifoliae* contain from one to 21 nymphs inside the gall chamber (Espírito-Santo & Fernandes 2002). The development of the nymph inside the gall can take up to six months (Espírito-Santo & Fernandes 2002) but is usually much shorter than that (Barbosa *et al.* 2017). The adult galler psyllid is free-leaving and length of the adult stage is unknown (Espírito-Santo & Fernandes 2002). Twelve parasitoid genera are known to attack *B. dracunculifoliae* (Barbosa *et al.* 2017): *Aphelinus* and *Paraphytis* (Hymenoptera: Aphelinidae), *Metaphycus*, *Psyllaephagus*, and *Zaplatycerus* (Hymenoptera: Encyrtidae), *Brasema* (Hymenoptera: Eupelmidae), *Caraphractus* and *Mymaridae* (Hymenoptera: Mymaridae), *Platygastridae* (Hymenoptera: Platygastridae), *Lyrcus* (Hymenoptera: Pteromalidae), *Rileya* (Hymenoptera: Eurytomidae), and *Tetrastichinae* (Hymenoptera: Eulophidae). The parasitic hymenopterans leave their pupae inside the gall and exit holes in the gall wall after emergence, facilitating the identification of the mortality caused by parasitoid.

The purpose of this study was to determine the ontogenetic variation in size and number of nymphs of *B. dracunculifoliae* and its relationship with gall size, besides assessing the frequency of mortality by natural enemies and its relationship with gall size.

Material and Methods

The study was performed in the Campus of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (19°30´S, 44°00´W) at an altitude of 805 m above sea level. The population of *B. dracunculifolia* studied was located in an area of extremely heterogeneous and disturbed vegetation, composed of natural, introduced, ornamental and fruit-bearing species (Espírito-Santo & Fernandes 1998), and the native adjacent vegetation is composed of savannah and cerrado species (Ferrari 1977). The plants studied were located in a 2 ha area, predominantly occupied by *B. dracunculifolia*, *B. ramosissima*, grass species, herbaceous plants and shrubby Leguminosae (Araújo *et al.* 1995, Espírito Santo *et al.* 2004).

Two gall samples with galls belonging to the same cohort were taken, with a two-month interval between the samples (June and August 1998), in order to evaluate the temporal variation in the growth and survivorship of *B. dracunculifoliae* galls. All galls found on 10 randomly selected individuals of *B. dracunculifolia* were collected and taken to the laboratory in June (n = 240). In August, all galls from another 10 individuals were collected (n = 94). The sex of *B. dracunculifolia* was not taken into account in the analyses since the abundance of *B. dracunculifoliae* galls, as well as their survivorship and mortality factors, are not influenced by the sex of the host plant (Lara & Fernandes 1994, Espírito-Santo & Fernandes 1998, Faria & Fernandes 2001).

All galls had their length and diameter measured (0.01 mm precision), and gall size was estimated by calculating its volume as an ellipsoid ($4/3\pi.\text{width}^2.\text{length}$), which is an ellipse rotated on its own axis, and which roughly describes the shape of a *B. dracunculifoliae* gall (see Preszler & Price 1988). Later, the galls were dissected and the number of nymphs was counted and the survivorship and/or mortality factors (parasitoid attack and other factors – e.g., plant resistance, fungal attack, and predation) were determined according to Fernandes & Price (1992) and Ribeiro-Mendes *et al.* (2002). Then, the nymphs from each gall had the following morphometric features measured: body size, the distance between eyes, and cephalic capsule width.

The analyses of temporal variation on the number of nymphs per gall, number of live nymphs per gall, survivorship and mortality rates were performed independently for each month, by using Mann-Whitney *U* test, since the data did not follow a normal distribution (Zar 1996). The analyses of the relationship between larval mortality rates and the number of nymphs per gall, and nymphal survivorship rates and the gall volume classes were performed through Mann-Whitney *U* test using the data from August, due to the high parasitoid attack rates observed in this month.

The distance between eyes of the nymphs was the morphometric feature used for the analysis of temporal variation on larval body size since it provided a good estimate of larval body size, it was more precise than the other measurements and followed a normal distribution. Therefore, this analysis was performed using Student *t*-test (Zar 1996). For the relationship between cephalic capsule width and distance between eyes, only the nymphs from galls collected in August were used, due to the great number of small-sized larvae on the June sample, which would hinder the differentiation of the instars.

Results

The mean volume of the galls induced by *B. dracunculifoliae* was significantly higher in August (1,933.76 ± 984.85 mm^3 [mean ± sd]) than in June (473.11 ± 475.65 mm^3; Mann-Whitney *U* test = 1,488, $p < 0.001$).

Mean number of nymphs per *B. dracunculifoliae* gall did not differ between June (1.76 ± 1.2) and August (1.59 ± 0.98; Mann-Whitney *U* test = 10,518, p = n.s.). The mean number of live *B. dracunculifoliae* nymphs was significantly higher in June (1.68 ± 1.2) than in August (0.66 ± 0.86; Mann-Whitney *U* test = 17,474, $p < 0.001$, Figure 1). The relationship between the mean number of *B. dracunculifoliae* nymphs and gall volume was weak in both months of the study (Spearman correlation, $r_{June} = 0.11$; $r_{August} = 0.17$). There was a slight tendency of increasing the number of nymphs with the increase in gall volume (Figure 2).

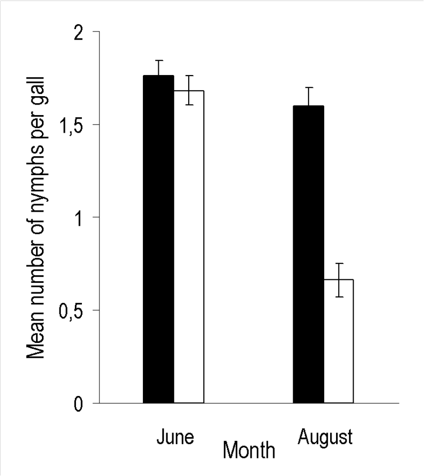

Figure 1 - Mean number of *B. dracunculifoliae* nymphs per gall (mean ± se) (dark bars) and mean number of living nymphs per gall (clear bars) on *B. dracunculifolia* (mean ± se) in June and August, 1998.

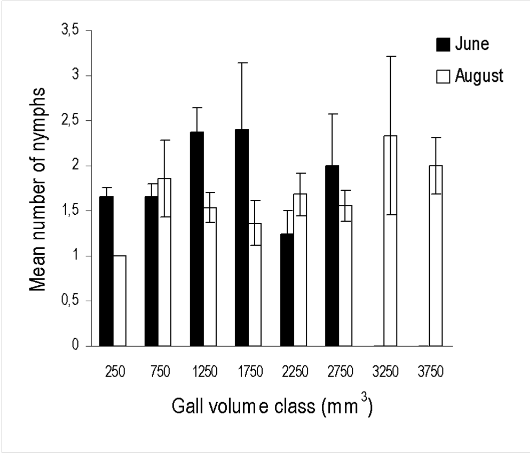

Figure 2 - Mean number of *B. dracunculifoliae* nymphs of *B. dracunculifolia* (mean ± se) per gall volume class in June and August, 1998.

The rates of nymph survivorship were very high in June (approx. 95.0% of the nymphs), whereas parasitoid attack accounted for the mortality of approximately 4.0% of the nymphs. On the other hand, in August, nymph survivorship was reduced to 40.4%. Once again, parasitism was the most important factor determining *B. dracunculifoliae* nymphal mortality, being responsible for the death of 56.6% of all nymphs in August. The other factors (e.g., plant resistance, fungal attack, and predation) together contributed with only 3.0% to the total death of the nymphs (Figure 3). The differences between survivorship rates, parasitoid attack and other factors were statistically significant between the months of June and August (Mann-Whitney *U* test, $p < 0.05$ all).

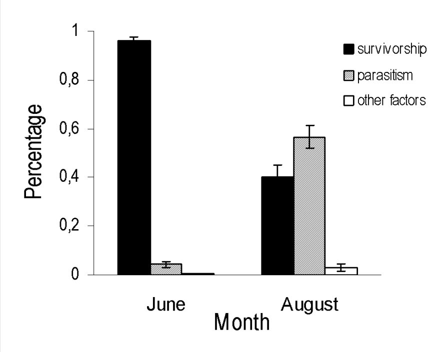

Figure 3 - Percentage of survivorship, mortality due to parasitoids and other factors of *B. dracunculifoliae* nymphs on *B. dracunculifolia* (mean ± se) in June and August, 1998.

The distance between eyes of the nymphs was greater in August (1.04 ± 0.04 mm, n = 270) than in June (0.49 ± 0.09 mm, n = 70, $t = 20.869$, $p < 0.001$), indicating larval growth through time and a possible change of nymph stage. However, no relationship between the number of nymphs in the gall (or clutch size) and the distance between eyes was found in June ($y = 10.241 – 0.156x$, df = 258, r^2

= 0.004, p = n.s.) or in August (y = 21.439 – 0.297x, df = 68, r^2 = 0.004, p = n.s.)

The probability of a nymph being attacked in galls with different numbers of nymphs did not differ between June (x^2 = 3.011, df = 4, p = n.s.) and August (x^2 = 6.087, df = 4, p = n.s.). Nymphal survivorship rate did not vary with gall volume in August (Mann-Whitney *U* test = 10.094, p = n.s.); the month when the highest mortality rates were observed (Figure 4).

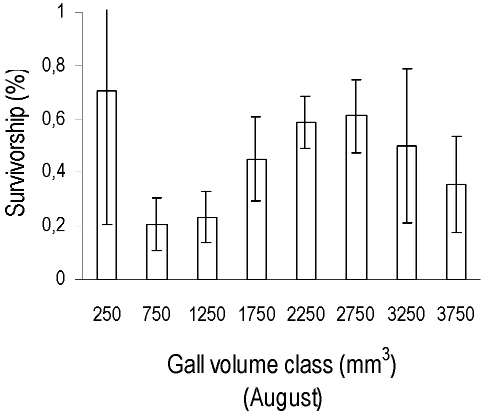

Figure 4 - Survivorship of *B. dracunculifoliae* nymphs on *B. dracunculifolia* (mean ± se) by gall volume class in the third month of the experiment, August 1998.

The positive relationship between the distance between eyes and cephalic capsule width showed the existence of three different-size instars, with cephalic capsule width varying between 0.2 and 0.9 mm (Figure 5). Nymphs of different instars were found in approximately 40.0% of all galls with more than one nymph.

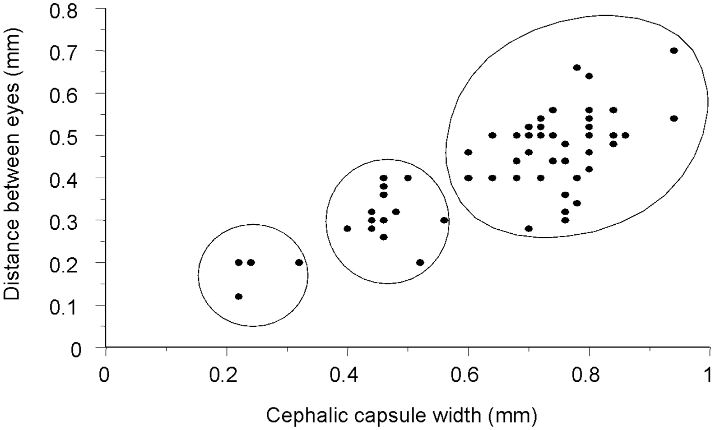

Figure 5 - Ordination between distance between eyes and cephalic capsule width of *B. dracunculifoliae* nymphs on *B. dracunculifolia*.

Discussion

During the development of the galler *B. dracunculifoliae*, the increase in gall size was as a result of the increase in nymph size. Moreover, gall size was not directly determined by clutch size, meaning that larger galls do not necessarily have more nymphs than smaller ones. The fact that the mean number of *B. dracunculifoliae* nymphs did not differ between the two months of the study should be expected since clutch size is determined at the time of oviposition. However, it could still have varied between the two months if, for instance, galls with more nymphs were for some reason negatively selected over time, persisting only those galls with a lower number of nymphs - or vice-versa. Thus, gall size can be used as an indirect measure of nymph fitness for the galler *B. dracunculifoliae*. The number of nymphs per gall, on the other hand, is determined by the female's physiology and oviposition behaviour, both of which can be affected by environmental conditions as well as local interactions – e.g. interference with ants (Neves *et al.* 2011). Furthermore, the parasitic wasps do not seem to show a preference for gall with more or fewer nymphs inside.

The proportion of mortality due to factors such as plant resistance, fungal attack, and predation was extremely low compared to parasitism, especially in June, which is in accordance with what is reported in previous studies (Fernandes & Price 1992, Ribeiro-Mendes *et al.* 2002). Parasitoid attack was the main factor determining the mortality of *B. dracunculifoliae* nymphs, and its values are comparable to those of many studies involving parasitoid attack (Weis & Abrahamson 1985, Weis *et al.* 1985). Espírito-Santo & Fernandes (1998), for instance, found parasitism rates in *B. dracunculifoliae* galls ranging from 16 to 80%. *B. dracunculifoliae* nymph mortality caused by parasitoid attack varied greatly between the months of the study. It seems, however, that parasitoid attack could have been underestimated in the first month of the study, most likely because parasitism was not detectable at the time. Parasitoid attack occurs in the early stages of gall development changing the colour and shape of the nymphs over time, which aids in the identification of mortality by parasitism (Espírito-Santo *et al.* 2004). Thus, the higher parasitism rates observed at the end of the experiment can be a result of the higher detectability of parasitism, and not a result of a concentrated attack in August.

The absence of a positive relationship between nymph survivorship and gall size may also be intrinsically related to the life histories of the parasitoid that attack *B. dracunculifoliae*. If parasitoid attack nymphs during the gall initial developmental stages, final gall diameter should not influence parasitism rates (Walton 1988, Rossi *et al.* 1992). The results found in this study are contrary to those of Freese & Zwölfer (1996), which relate an increase in gall size with larger chances of larval survivorship since bigger galls seem to provide more protection to the larvae and more space for their development. On the other hand, it could well be that parasitism increased nymph size and, therefore, gall size, but here we found no relationship between gall size and parasitism in *B. dracunculifoliae*.

Nymph size was not influenced by clutch size, despite there being a slight tendency of decreasing body size with clutch size in both months of the experiment. Whitham (1978) and Freese & Zwölfer (1996), on the contrary, found a positive relationship between the increase in the number of larvae per gall and larval weight. The probability of a *B. dracunculifoliae* nymphs being attacked in galls with different numbers of nymphs did not vary between the months, indicating that mortality is not related to clutch size either. Therefore, instant attack rates by parasitoids may vary from place to place, or through time, since some hosts may be more vulnerable than others, or the probability of attack may be a random variable and parasitism occurs by chance (Chesson & Murdoch 1986). Hence, parasitism did not seem to be a force driving the selection of specific oviposition decisions by female gallers. As stated by Preszler & Price (1988), mortality factors (such as predation and parasitism) which is hard to anticipate to, seem to be less important in selecting female behaviour patterns that influence population sizes of herbivores.

Psyllids present five nymph instars, from eclosion of the egg to the adult instar, and it has been reported that it is the fifth instar larvae that leave the gall and moults into the adult free leaving insect immediately (Burckhardt *et al.* 2004). Indeed, in none of all 334 galls examined in this study an adult individual of *B. dracunculifoliae* was found. However, through the relationship that we found, between the distance between eyes and cephalic capsule width, we only identified three distinct instars occurring in *B. dracunculifoliae* galls. Thus, its seems that two of the instars inside galls do not display much difference regarding the body measurements. From all galls which contained more than one nymph, 38% presented nymphs in different developmental stages. A possible explanation for that would be the occurrence of competition among nymphs (Espírito-Santo *et al.* 2004). Small differences in the ability to acquire resources may cause a delay in nymph development (Espírito-Santo & Fernandes 2004). Generally, this is a complex process, which can possibly arise due to the amount of resources allocated to each egg by the parental generation.

To sum up, the present study shows that during the development of the galler *B. dracunculifoliae*, the variation in gall size is associated with nymph size but not clutch size. The attack by natural enemies in B. dracunculifoliae is high. Parasitism is a strong force on the structure and regulation of the population, although it does not seem to be a selective force acting on the oviposition behaviour of female gallers since parasitism rate was not associated with gall size, nymph size or clutch size. The precise determination of the occurrence of parasitism must be assessed by an exclusion experiment, which would allow the exact evaluation of the size of the window of vulnerability (Washburn & Cornell 1981, Craig *et al.* 1990) of the galls to attack by natural enemies. The total understanding of *B. dracunculifoliae* population dynamics on *B. dracunculifolia* requires studies that investigate the biology and natural history of the species. Data such as the time spent on gall formation, female oviposition behaviour, adult life span and developing site of the adult stage, are mandatory for the enlightenment of the interactions between *B. dracunculifoliae* and its host plant and its natural enemies.

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