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# Hemiparasitism effect on *Baccharis dracunculifolia* DC. and consequences to its major galling herbivore

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## ABSTRACT

Mistletoes obtain nutrients and water from their hosts, with varying effects among those hosts. We assessed the factors that influence the colonization of the mistletoe *Struthanthus flexicaulis* on *Baccharis dracunculifolia* and the subsequent effects on host performance. We evaluated the incidence of *S. flexicaulis* according to size (height classes) and architecture of the host as well as its effects on various physiological parameters of the host. Furthermore, we assessed the occurrence of insect galls induced by *Baccharopelma dracunculifoliae* (Psyllidae), including the number of leaves infected, and the mortality of infected and non-infected branches. Taller hosts had a higher abundance of mistletoes (60%, $p > 0.05$). Physiological parameters of hosts were not affected by parasitism, although galling occurred more often ($p < 0.05$) and leaf loss increased ($p > 0.05$) on infected branches. Taller individuals are more colonized by mistletoes and more architecturally complex hosts support a greater number of mistletoes. Mistletoe causes a *top-down* effect on host-associated organisms on parasitized branches. Mistletoes had a strong *top-down* effect on *B. dracunculifolia* due to a reduction in the number of leaves on parasitized branches and the replacement of the bush crown, as well as an increased incidence of insect galls. Furthermore, the occurrence of a heavy parasite load increased the mortality rate of the host branches.

**Keywords:** *Baccharopelma dracunculifoliae*, insect galls; mistletoe; rupestrian grasslands, *Struthanthus flexicaulis*

## Introduction

Mistletoes are a taxonomically diverse group of flowering plants, widely distributed in terrestrial ecosystems that depend on host plants to acquire water and nutrients (Press & Phoenix 2005; Westwood *et al.* 2012). Mistletoes colonize different taxa of vascular plants and, in most cases, are harmful to their hosts, reducing growth and fertility and sometimes causing the host death (Press *et al.* 1999; Aukema 2003). These parasites depend on animals for both pollination and fruit dispersion (Aukema & Martínez-del-Rio 2002; Aukema 2003; García *et al.* 2009); thus, despite their negative effect on their hosts, they play an important role in structuring the community (Watson 2001; Aukema 2003; Kelly *et al.* 2004). The high potential for colonization, along with the ability to modify the structure and dynamics of communities via direct effects on the physiology and behavior of host species, make mistletoes a relevant group for ecological studies (Lei 2001; Press & Phoenix 2005).

Low host specificity is a key factor in mistletoes success in heterogeneous environments (Aukema 2003; Arruda *et al.* 2012). In these environments, specificity is primarily determined by the ability of the mother plant and the dispersal agents to find potential hosts (Arruda *et al.* 2006). Consequently, two factors that affect the colonization process by mistletoes are local abundance and exposure time in the host environment (Norton & Carpenter 1998; Norton & De Lange 1999). Furthermore, chemical, anatomical, morphological and physiological host factors are important in the mistletoe colonization process (Marvier 1998; Press & Phoenix 2005; Arruda *et al.* 2006). During the ontogenetic development of the host there is a variation in the availability and quality of resources (Fonseca & Benson 2003). Aukema & Martínez-del-Rio (2002) reported an increased mistletoe abundance with host plant development. The architecture of the host can also affect mistletoe colonization. Larger and more branched hosts represent the most attractive perch for birds, and therefore, increase

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the likelihood of seed deposition in these individuals (see Monteiro *et al.* 1992; Aukema & Martínez-del-Rio 2002; Mourão *et al.* 2009).

Mistletoes cause several negative effects on their hosts (Aukema 2003; Press & Phoenix 2005; Cuevas-Reyes *et al.* 2011). Effects can vary from lower reproductive vigor, water and nutrient balance interference, malfunction of woody tissues, reduction of photosynthetic rates, mortality of infected branches and even, in extreme cases, host death (Lüttge *et al.* 1998; Press *et al.* 1999; Aukema 2003; Schwartz *et al.* 2003; Cuevas-Reyes *et al.* 2011; Westwood *et al.* 2012). In addition to impact the fitness of their hosts, mistletoes also may influence the host's interaction with their associated organisms. Therefore, plant parasites may exert a *top- down* effect to their hosts; increasing susceptibility to natural enemies, including insect herbivores and even augmenting the chances of colonization by other parasites (Aukema 2003; Schwartz *et al.* 2003).

The *Struthanthus flexicaulis* – *Baccharis dracunculifolia* system is a good system to determine factors that promote colonization and to assess the impact of mistletoe on the host plant and possible *top-down* effects. Mistletoes are very common in tropical mountain grassland environments (Monteiro *et al.* 1992; Lüttge *et al.* 1998; Mourão *et al.* 2006; 2009; Cuevas-Reyes *et al.* 2011). Mistletoes can have various effects on this community and are known to infect at least 65 species of eudicot plants in Serra do Cipó, Brazil (Guerra & Pizo 2014). *Baccharis dracunculifolia* is common in the area and supports a high galling insect fauna (Lara & Fernandes 1994; Espírito-Santo & Fernandes 1998). Here, we assess the factors that influence the colonization by *S. flexicaulis* on *B. dracunculifolia* and their effects on host performance and report the direct effect that hemiparasitism may have on the major galling herbivore on the host plant. In this study we test the following hypotheses: (i) larger and architecturally more complex hosts support a greater number and larger mistletoes compared to smaller hosts; (ii) parasitism by mistletoes negatively affect the physiological performance of the host plant by reducing their photosynthetic rate and increasing their water stress and branch mortality; (iii) mistletoe causes a *top-down* effects on the hosts associated organisms with parasitized branches supporting a greater abundance of galling insect herbivores compared to healthy branches.

# Materials and methods

## Study area

This study was conducted in the Private Reserve Vellozia (19°16'54" S, 43°35'45" W) in Serra do Cipó, Minas Gerais, Brazil. The predominant physiognomy of this area is rupestrian grasslands, that are characterized by disperse shrubs and herbaceous vegetation. The climate type is tropical of altitude with cool summers and a well-defined dry season from May to September. The average annual temperature is 21.27 °C with an average annual rainfall of 1247 $mm^3$ (INMET 2015).

## Species

*Struthanthus flexicaulis* (Mart.) Mart. (Loranthaceae) is one of the most common hemiparasitic species from Brazil. It has a wide distribution, occurring in several phytophysiognomies of the Cerrado landscape (Rizzini 1980). Its seeds are covered by a sticky substance that adheres to the host branch (Norton & Carpenter 1998), and is dispersed by birds (Guerra & Pizo 2014). Once the attached seeds of the mistletoe germinate, they insert their haustorium into the xylem of their host plant (Norton & Carpenter 1998). According to Guerra & Pizo (2014), *S. flexicaulis* is a generalist hemiparasite, occurring on 65 species within 20 plant families. Mistletoe leaves usually have greater stomatal conductance and greater transpiration than its hosts, providing these parasitic plants a greater competitive physiological advantage than their hosts (Lüttge *et al.* 1998). The highest attack rate by *S. flexicaulis* is usually on the dominant plants on the landscape (Lüttge *et al.* 1998; Mourão *et al.* 2006).

*Baccharis dracunculifolia* DC. (Asteraceae) is a Brazilian native shrub, common in the Cerrado region; perennial, dioecious, measuring between 0.5 - 4.0 m tall, with flowering at the end of the rainy season (Espírito-Santo & Fernandes 1998). Due to the large number of achenes and the frequent occurrence in disturbed areas, the species show a great colonization capacity (Gomes & Fernandes 2002). The host *B. dracunculifolia* serves as a perch for several species of birds, such as *Elaenia cristata* Pelzeln, 1868 (Passeriformes: Tyrannidae), the major seed disperser of the mistletoe *S. flexicaulis* in the study region (Mourão *et al.* 2006; Guerra & Pizo 2014). *Baccharis dracunculifolia* supports a rich fauna of galling insects (Espírito-Santo & Fernandes 1998). The psyllid, *Baccharopelma drancunculifoliae* Burckhardt (Hemiptera, Psylloidea) has great host specificity within the genus *Baccharis* (Fernandes *et al.* 1996; Burckhardt *et al.* 2004). The leaf galls produced by *B. baccharidis* are green, spindle, and in the oviposition point the leaf tissue undergoes swelling, bends and forms a fusiform capsule, showing a single nymph per gall (Lara & Fernandes 1994).

## Sampling

To assess whether there is a relationship between host size and the incidence of mistletoes, we sampled 110 individuals that were grouped into 11 classes -30 cm height each. The study was conducted in September of 2012. Sampling of hosts was performed in 1000 meter transects haphazardly located in the study area. We recorded the number of parasites per host and we measured the diameter (mm) of each branch of the host at which the haustorium of each mistletoe was inserted. Subsequently, based on the diameter of each branch, parasites were also grouped according to four diameter classes (0.1-0.2 cm; 0.3-0.5 cm; 0.6-1 cm; and >1.1 cm) to evaluate whether mistletoe size is related to the size of their host. The level of branching (1-7 levels) of each individual of *B. dracunculifolia* was also assessed to determine whether more architecturally complex plants are more colonized by mistletoes (see Espírito-Santo *et al.* 2012 for details). The number of parasites on each host branch level was also recorded.

To evaluate whether *Struthanthus flexicaulis* affects the host physiological parameters such as water potential and total leaf number, 10 individual plants were randomly selected to analyze parasitized and non-parasitized branches. The following parameters were measured using an IRGA®: stomatal conductance (gs - mol $m^{-1} s^{-1}$); transpiration rate (E - mol $H_2O$ $m^{-2} s^{-1}$); $CO^2$ absorption (e -μmol $mol^{-1}$); and photosynthetic rate (A -μmol $m^{-2} s^{-1}$). For the water potential, we used the Scholander® pressure chamber. In addition, we also evaluated if the parasite can cause the mortality of parasitized branches, by calculating the size of the parasite (diameter in the insertion point) and the branch survival condition, "dead" or "alive".

To assess whether the parasite mediates a *top-down* effect by the organisms associated with *Baccharis dracunculifolia*, the number of galls induced by *B. dracunculifolia* was quantified in 102 parasitized and 102 non-parasitized branches (204 branches in total), at the different architecture levels of the host.

### *Statistical analyses*

The effect of host size on the abundance and size of *Struthanthus flexicaulis* was evaluated using total mistletoe abundance per plant and abundance by size classes as response variables and the size classes per host as explanatory variables. To test the effect of host architecture on mistletoe abundance, the total abundance of *S. flexicaulis* per host was used as the response variable, while the number of branching levels and host height represented the explanatory variables. Additionally, to assess the branching levels where *S. flexicaulis* prevail, we use the number of parasites in each level as response variable and, the ramification level as the explanatory variable.

To determine the effect of mistletoes on host performance, absorption of $CO_2$, stomatal conductance, transpiration rate and water potential were used as response variables, while the state of the branch (parasitized or non-parasitized) was used as the explanatory variable (see Lüttge *et al.* 1998). We also evaluated the effect of parasite size on branch mortality. To assess whether the parasite causes a top-down effects on hosts, we used the number of insect galls as response variable, and the branch condition (parasitized or non-parasitized) as the explanatory variable.

Data were analyzed using the R software (R Development Core Team 2008). We conducted multiple regression tests, using a Generalized Linear Models (GLM) (Sólymos 2009). For each model we used a suitable distribution of errors for each response variable, according to the critical model (Crawley 2007). All the models created were compared with the null model, and adjusted to the minimum adequate model with the omission of non-significant terms. The adequacy of the models was tested through residuals analysis (Crawley 2007).

## Results

Individuals of *Baccharis dracunculifolia* had a high level of parasitism by *Struthanthus flexicaulis*. Among the 110 plants sampled, 63 (60%) had at least one mistletoe per plant. A total of 440 mistletoes were recorded in this survey. As expected, taller plants showed more parasites than shorter plants ($X^2 = 609.53$, $P < 0.001$, Fig. 1A). We did not observe parasites on hosts with less than 90 cm tall. Taller hosts also presented statistically larger mistletoes (Tab. 1, Fig. 1B).

Architecturally, hosts that were more complex had greater mistletoe abundance (Tab. 1, Fig. 2A). Plant height and level of branching positively affected mistletoe abundance. There was an interaction between these two explanatory variables, indicating that there is a limit on branching levels (6° and 7°) that affects mistletoe abundances (Fig. 2A). We observed a higher mistletoe frequency on branches of 3º and 4º order (Fig. 2B). Parasitism did not affect the host photosynthetic capacity or the water potential. The $CO_2$ absorption, stomatal conductance, transpiration rate, photosynthetic rate, and water potential did not differ statistically in the presence of *S. flexicaulis* (Tab. 2).

Branches parasitized by *Struthanthus flexicaulis* had approximately 40% less leaves compared to non-parasitized branches (Tab. 3, Fig. 3A), leading to increased mortality of infected branches (Tab. 3). Larger mistletoes increased the probability of host branch mortality (Fig. 3B). Host branches that supported mistletoes with diameter larger than 1.2 cm had a 60% risk of death. Mistletoes caused a positive effect on the most common galling herbivore on *B. dracunculifolia* (Tab. 3). Parasitized branches showed averaged 7.5 galls, ca. 30% more galls compared with non-infected branches (Fig. 4).

## Discussion

We observed a greater incidence of mistletoe on larger host *B. dracunculifolia* plants. There was a positive association between host size and the rate of parasitism, were taller plant individuals with larger diameters were more parasitized by *S. flexicaulis* (higher frequency of hemiparasites). These plants also supported the larger mistletoes as well. Norton & Carpenter (1998) argued that the most important factors to facilitate the colonization and maintenance of mistletoes are specificity and permanence of the host in time

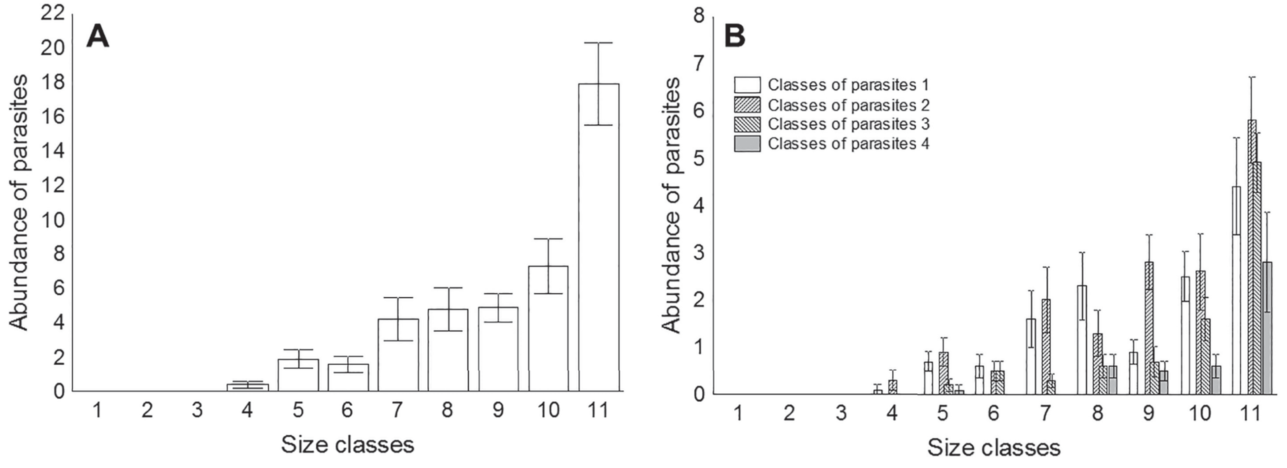

**Figure 1.** Abundance of *Struthanthus flexicaulis* Mart. (Mart.) on *Baccharis dracunculifolia* DC. per size - **A**; and on each host class size – **B**.

**Table 1.** *Deviance* analysis of the effect of *Struthanthus flexicaulis* Mart. (Mart.) in size and architecture of host *Baccharis dracunculifolia* DC.

| Response variable | Explanatory variable | Error distribution | Deviance | Residual DF | Deviance residual | P |
|---|---|---|---|---|---|---|
| Size of *B. dracunculifolia* individuals (Classes) | Parasite abundances Class 1 | Quasi-Poisson | 166.15 | 99 | 121.05 | < 0.001 |
| | Parasite abundances Class 2 | Negative binomial | 143.78 | 99 | 87.59 | < 0.001 |
| | Parasite abundances Class 3 | Quasi-Poisson | 178.34 | 99 | 71.14 | < 0.001 |
| | Parasite abundances Class 4 | Quasi-Poisson | 114.07 | 99 | 74.71 | < 0.001 |
| Architectural level | Parasite abundances | Negative binomial | 167.927 | 108 | 190.54 | < 0.001 |
| Height | Parasite abundances | Negative binomial | 76.692 | 107 | 113.85 | < 0.001 |
| Architectural level: Height | Parasite abundances | Negative binomial | 16.033 | 106 | 97.82 | < 0.001 |
| Architectural level | By branch level | Negative binomial | 153.28 | 362 | 294.27 | < 0.001 |

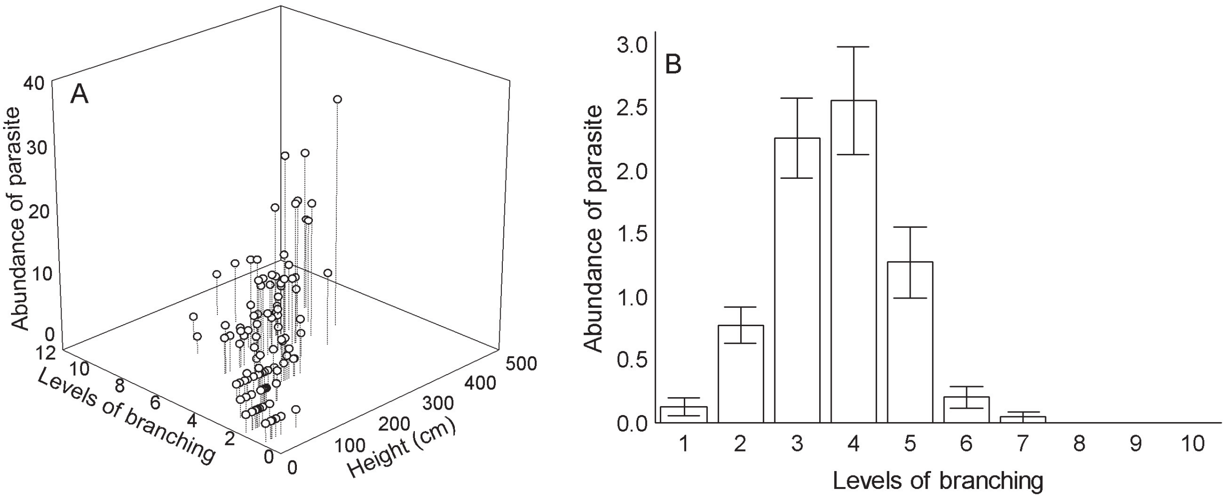

**Figure 2. A**- Abundance of mistletoe *Struthanthus flexicaulis* Mart. (Mart.) in both architectural level and height on *Baccharis dracunculifolia* DC.; **B**- Abundance of mistletoes in different classes of branching.

**Table 2.** Deviance analysis of the effect of *Struthanthus flexicaulis* Mart. (Mart.) on physiological parameters of the host, *Baccharis dracunculifolia* DC.

| Response variable | Explanatory variable | Error distribution | Deviance | Residual DF | Deviance residual | *F* | *P* |
|---|---|---|---|---|---|---|---|
| CO$^2$ Absorption | Branch level | Gaussian | 0.0027 | 10 | 0.2117 | 0.1278 | 0.73 |
| Stomatal conductance | Branch level | Gaussian | 0.0003 | 10 | 0.0656 | 0.0457 | 0.83 |
| Transpiration rate | Branch level | Gaussian | 0.00003 | 10 | 0.0007 | 0.4545 | 0.51 |
| Water potential | Branch level | Gaussian | 6.1838 | 32 | 1763.0 | 0.1122 | 0.74 |

**Table 3.** Deviance analysis of consequences of *Struthanthus flexicaulis* Mart. (Mart.) on individuals of *Baccharis dracunculifolia* DC.

| Response variable | Explanatory variable | Error distribution | Deviance | Residual DF | Deviance residual | *P* |
|---|---|---|---|---|---|---|
| Number of leafs | Branch level | Negative binomial | 5.1499 | 32 | 36.447 | < 0.05 |
| Number of galls | Branch level | binomial | 6.4993 | 946 | 971.15 | < 0.01 |
| Mortality | Parasite size | Binomial | 17.179 | 107 | 129.85 | < 0.001 |

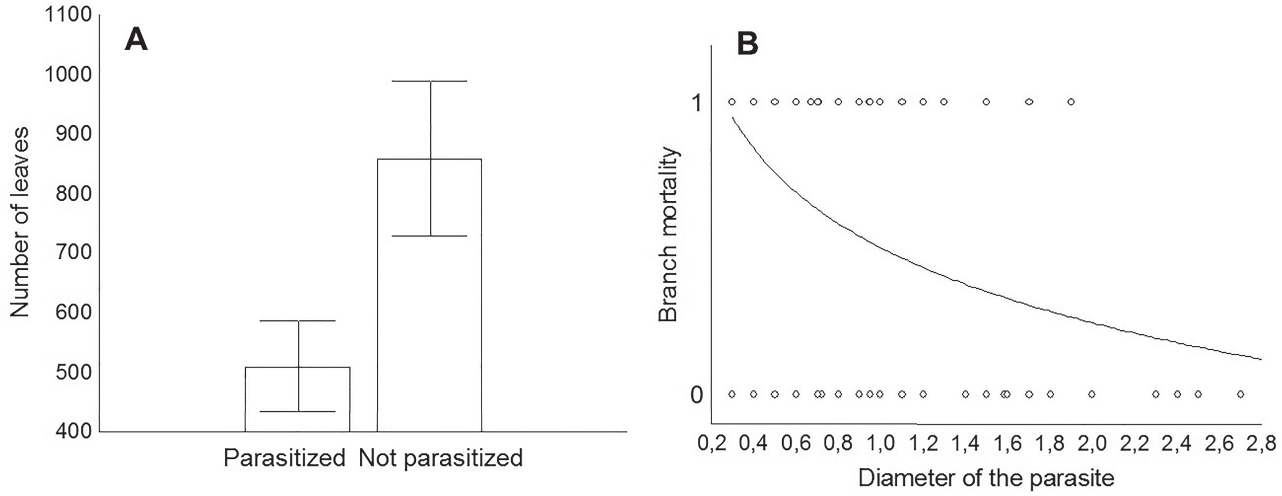

**Figure 3. A**- Number of leaves (mean and SE) on parasitized and non-parasitized branches of *Baccharis dracunculifolia* DC.; **B**- Comparison of mortality of infested branches of *Baccharis dracunculifolia* DC. relative to the size of the parasite. 1.0: alive branch, 0.0: dead branch.

**Figure 4.** Comparison of the occurrence of insect galls between parasitized and non-parasitized branches of *Baccharis dracunculifolia* DC.

and space. Our study supported the idea that the ontogenetic development of he host affects the level of parasitism by mistletoes, in which the availability and quality of resources may change during the life of the hosts (Fonseca & Benson 2003; Boege & Marquis 2006; Murphy *et al.* 2014). During plant ontogeny, many structural changes occur, including architectural differences (Barthélémy & Caraglio 2007).

As shown in other studies (Aukema & Martínez-del-Rio 2002; Roxburgh & Nicolson 2005; Arruda *et al.* 2009), we found that plants with more complex architecture tend also to have greater mistletoe abundance. Mistletoes were more frequent at the tree crowns, were intermediate branches are soft enough to allow the insertion of the haustorium and at the same time support mistletoe establishment. Branches with large diameters can hinder the penetration of the haustorium (Press & Phoenix 2005; Arruda *et al.* 2006). Another factor that interferes on mistletoe success is the size of the host plant. Our results are consistent with recent studies that demonstrated that larger hosts are more frequently attacked by mistletoes (Mourão *et al.* 2009; White *et al.* 2011). Thies *et al.* (2003) also reported that the effects of parasitism depend on the size, intensity, growth, metabolism and photosynthetic capacity of mistletoe, as well as the host development. Moreover, crown deformation and/or host mortality may affect the community structure due to a floristic composition loss (Cuevas-Reyes *et al.* 2011). In this manner, mistletoe infestation can be harmful to the host and, subsequently, to the community level. Increased dispersion of the seed disperser bird (*Elaenia cristata*) combined with the wide spreading occurrence of the host plant *B. dracunculifolia* in the mountain range has facilitated the parasitism by the once stabilized population of the mistletoe.

As mistletoes obtain nutrients and water from their host plants, we expected reductions in stomatal conductance, transpiration rate, $CO_2$ absorption, photosynthetic rate and water potential of parasitized hosts. Similarly, other authors that have studied the interference of *S. flexicaulis* on their hosts have not recorded changes in physiological parameters due to the interference caused by the mistletoe. It is possible that *S. flexicaulis* makes their host plants continue with a normal physiological metabolism but at the same time, the mistletoe drains the resources of their host acting as a sink in a source-sink relationship. Watling & Press (2001) report the effects of the parasitic angiosperms in the host in a number of ways, ranging from direct effects on photosynthetic metabolism or in more indirect effects.

Mistletoe parasitism interfered with the vigor and performance of infected *B. dracunculifolia* individuals by reducing the number of leaves on attacked branches, and partial or total replacement of the shrub crown. Reduced performance could lead to a decrease in fruit and seed production as well as a reduction of new individual recruitment (Mourão *et al.* 2009). Crown shadowing can cause reduced competitive efficiency of the host (Westwood *et al.* 2012) or even mediate interaction with natural enemies (Schwartz *et al.* 2003), which could lead to the death of the heavily parasitized hosts in the community.

The presence of mistletoes facilitated the occurrence of the major galling insect of the host plant which may ultimately led to a higher mortality of the attacked branches. These could potentially generate changes in competitive interactions and community dynamics (Pennings & Callaway 2002; Press & Phoenix 2005). A single parasitic plant may form connections among host species resulting in strong impacts on the plant community, despite representing less than 5% of vegetation biomass (Press & Phoenix 2005). Hosts exposed to high infestation degrees are also more susceptible of the attack by insect herbivores and to environmental stress than healthy individuals of the same species (Norton & Carpenter 1998). In this study, we demonstrated high infestation of *Struthanthus flexicaulis* in *Baccharis dracunculifolia* and a relationship between size, architecture, and performance-related factors of the host. We also showed a top-down control from *S. flexicaulis* over *B. dracunculifolia* due to the increase of galls incidence and a reduction of the number of leaves. Furthermore, the results showed that the occurrence of major parasites increases the mortality rate of the host branches.

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