

Plant organ abscission and the green island effect caused by gallmidges (Cecidomyiidae) on tropical trees

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Received: 11 July 2007 / Accepted: 8 February 2008 / Published online: 28 March 2008
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Abstract Plants exhibit a wide array of inert and induced responses in defense against herbivore attack. Among these the abscission of organs has been argued to be a highly effective mechanism, depending, however, on the herbivore's feeding mode. While consisting of plant tissues, insect induced galls are seen as the extended phenotype of the gall inducer which might circumvent many or most of the plant defenses. There is very little information whether and how far beyond the gall tissue gall inducers might affect plant tissues. A localized impact is likely to leave the abscission of galled organs as a viable defense although at a cost. Here, we report on an instance where the host plant, *Neea madeirana* (Nyctaginaceae) abscises leaves galled by two species of *Bruggmannia* (Diptera: Cecidomyiidae), more frequently than ungalled leaves in a rain forest in Amazonia, Brazil. Once on the forest floor the leaves decay quickly, while both gall types show signs of localized maintenance of healthy tissues for a while (the green island effect). However, on the forest floor galls are exposed to a new set of potential natural enemies. Both gall types show

a minimum of a five-fold increase in mortality due to pathogens (fungi and bacteria) compared to galls that were retained on the host tree. We discuss the adaptive nature of plant organ abscission as a plant defense against gallers and as a gall inducer adaptive trait.

Keywords Amazonia · Insect galls · Insect herbivory · Leaf abscission · Plant-induced defense · Gall mortality

Introduction

Plants have evolved a wide variety of inert (stings, spines, thorns, lignified tissues) and induced defenses against herbivore attack. Induced defenses include the increase in secondary metabolites, such as tannins and phenolics, toxins, latex production (Azarkan et al. 2004; van Zandt and Agrawal 2004; Agrawal and Fishbein 2006), but also developmental responses at the cellular level, e.g. hypersensitive responses and apoptosis, i.e. localized cell death to isolate the herbivore (Fernandes 1990), and at the level of plant organs, abscission (Fernandes and Witham 1989; Fernandes et al. 1999; Arnold and Schultz 2002; Egan and Ott 2007). Among herbivorous insects, gall inducing species have arguably the most intimate physiological interaction with their host plants. While the mechanism of gall formation has not been determined for any of the galling groups, which include among others aphids, thrips, coleopterans, lepidopterans, gall midges, gall wasps and gall inducing flies, a wide variety of symptoms of the developmental and physiological changes in gall tissue have been described (Rohfritsch and Shorthouse 1982 and therein; Hartley 1998; Schönrogge et al. 2000; Harper et al. 2004; Allison and Schultz 2005; Shorthouse et al. 2005). Because gall morphologies are gall inducer species specific

Handling editor: Graham Stone.

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and since their physiology appears to solely benefit the insect, galls are often referred to as the extended phenotype of the inducing larva (Stone and Schönrogge 2003; Carneiro et al. 2008).

Consequently plant defense mechanisms are disabled in the tissues the gall inducer feeds on, while for instance tannin and phenolic concentrations in the outer gall tissues can be extremely high (Berland and Bernard 1951). However, it is well documented that galls are physiological sinks for nutrients within a plant and do for instance compete with each other normally on the scale of the affected plant organ (Whitham 1978, 1979; Sitch et al. 1988; Larson and Whitham 1991, see also Fernandes 1987; Raman et al. 2006). The sessile habit of gall induction may provide the opportunity for the host plant to respond more efficiently to galling by developing alternative defense mechanisms, such as the induced hypersensitive response (Fernandes 1990, 1998; Abrahamson et al. 1991; Fernandes et al. 2000; Fernandes and Negreiros 2001). Although plant chemical resistance mechanisms that reduce the probability of successful gall induction have received some attention, the impact of other mechanisms such as the ability to prematurely abscise galled leaves are less well studied. Gallers are sessile and shedding of galled organs by the host plant could represent a key adaptation leading to greater larval mortality. However, in some galling species abscission from the host plant appears to be adaptive and part of the annual life-cycle, e.g. *Andricus foecundatrix* where the larval chamber is ejected from the gall before the end of the season, or non-adaptive, e.g. *A. quercuscalicis* (both Cynipoidea, Cynipidae) where the sheer weight of the galled acorn causes them to shed about 2 weeks before the ungalled acorns. Thus where abscission occurs, the fate of the galler needs to be established to assess the value of such events as a plant defense.

At the Biological Reserve Km 41 in an Amazonian rain forest near Manaus (Brazil) we found large numbers of abscised galled leaves of *Neea madeirana* (Nyctaginaceae), a normally evergreen tree, on the forest floor. Two distinct insect galls induced by *Bruggmannia* (Diptera: Cecidomyiidae) occurred on the leaves of *N. madeirana*. One was a simple, discoid swelling on the lamina (Fig. 1a; from here on referred to as *Bruggmannia* sp. 1) whereas the other one appeared more elaborate with an oval shape (Fig. 1b; from here on referred to as *Bruggmannia* sp. 2). We hypothesize that once abscised, gall-inducers would suffer higher mortality on the forest floor compared to those retained in the tree canopy. Also, the enemy hypothesis on the adaptive nature of galls, which is subject to a lively debate, would predict that complex gall structures evolved in response to natural enemy pressure (Fernandes and Price 1992; Stone and Schönrogge 2003). We therefore predict that the more complex gall (more

layers of tissue), *Bruggmannia* sp. 2, will suffer less natural enemy induced mortality, including from pathogens on the forest floor, than the simpler, discoid gall. Finally, where the weight of the gall is a larger proportion relative to ungalled leaves, i.e. small leaves, one might expect through simple shedding (see above e.g. *A. quercuscalicis*) galled leaves on the ground to be smaller than those on the tree.

Here we investigate the effect of leaf abscission on the two types of galls and aim to answer four specific questions: (1) Is the proportion of galled leaves higher among the abscised leaves compared to those in the canopy? (2) Are abscised leaves smaller than those in the canopy? Although we expect variation in leaf size among trees, abscission or retention of galled leaves may be influenced by leaf size (\approx biomass). (3) What sources of mortality (parasitoid- and predator attack, pathogen contamination) affect the two gall types and are they more severe for abscised galls? (4) Would gall complexity result in higher protection in the forest floor against pathogens?

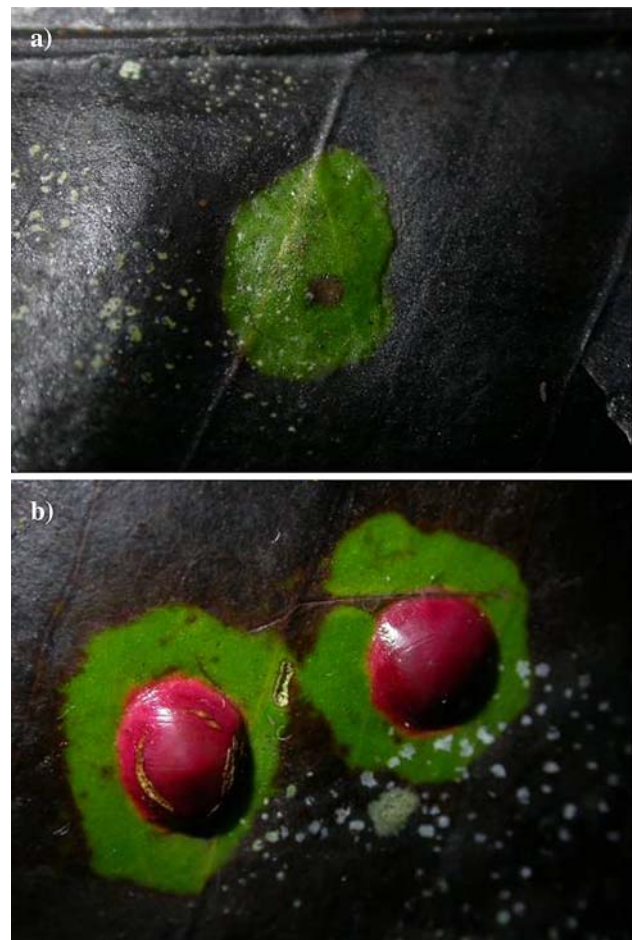


Fig. 1 *Bruggmannia* galls on *Neea madeirana* (Nyctaginaceae) in an Amazonian rain forest. *Bruggmannia* sp. 1 induces flat discoid leaf galls (a) while *Bruggmannia* sp. 2 induces ovoid leaf galls (b). Notice the black leaf coloration and fungi growth on the leaf lamina

Materials and methods

Study area

The study was carried out at the Reserva Florestal do Km 41 (approx. 90 km NNE of Manaus—AM, Brazil between the coordinates 2°24'26"–2°25'31" S, 59°43'40"–59°45'50" W; 50–125 m a.s.l.) (Oliveira 1997). The climate is humid tropical with monsoons with excessive precipitation and occurrence of 1–2 months of low precipitation ('Am' in Köppen's system), average temperature of $26.7 \pm 2^\circ\text{C}$ (see Lovejoy and Bierregaard 1990), average precipitation is 2.200 mm/year with rainy months being December–May and dry months being June–November (Fisch et al. 1998). The dominant vegetation is the "Floresta de Terra Firme" (see Oliveira 1997).

Two types of insect galls are induced on the leaves of *Neea madeirana*. The host species is a common tree of the forest canopy and occurs in northern Brazil and Bolivia (Ribeiro et al. 1999). Two new, undescribed species of *Bruggmannia* (Diptera: Cecidomyiidae) (VC Maia, pers. comm.) induce the galls. Gall one, induced by *Bruggmannia* sp. 1, is a simple discoid, green, glabrous swelling that occurs singly, and has one single larval chamber (0.3–0.4 mm in diameter). It is inhabited by a single larva and is visible on both sides of the lamina (Fig. 1a). Gall 2 induced by *Bruggmannia* sp. 2, also occurs on the leaves of the host plant. It is ovoid, glabrous, reddish along the adaxial lamina but bright green at the abaxial side. This gall also occurs singly and has one larval chamber inhabited by a single larva (Fig. 1b). The walls of the ovoid gall turn hard and brown as galls age. When the study was conducted the vast majority of both galls (approx. 90%) contained mature larval instars, pupae, or showed signs of insect emergence. Galls were parasitized by species of the parasitoid families Platygasteridae and Encyrtidae (Hymenoptera).

Sampling and gall dissection

In July 2005, 50 leaves were randomly collected from the floor beneath the canopy (approximately 5 m radius from the tree trunk) of the only five host plants found in a 20 ha area. Wherever possible, 50 leaves were haphazardly collected around the canopy of *N. madeirana* (Table 1) at the height of 15–25 m of each tree. Trees were climbed by a trained field assistant and branches cut with the help of a pole of 10 m length. The galls of both *Bruggmannia* species were of a similar mature developmental stage and the leaves on the forest floor were abscised within 15–30 days prior to collection (A. Oliveira, pers. comm.). Leaves found on the forest floor were mostly black, although both gall types still presented their natural coloration (Fig. 1). Sampled leaves were placed into plastic

bags, numbered, and taken to the laboratory for further investigation. Galls were dissected to determine the following sources of mortality: (a) predation: when the gall walls were opened by predators (i.e. signs of chewing marks), (b) parasitoid attack: when parasitoids were found in the larval chamber, (c) pathogen infestation: when fungus hyphae were found on dead larva inside the gall chamber. Some Cecidomyiidae, for instance members of the Asphondyliini, have mutualistic relationships with fungi (Rohfritsch 1997). However, none of the species in the genus *Bruggmannia* are known to have such mutualistic partners and no hyphae were detected with surviving larvae (Fernandes, pers. obs.). We therefore regard the fungi detected in the galls as entomopathogens, yet their virulence remains to be demonstrated, (d) unknown death: when the cause of death could not be identified. The final category (e) was survival: when we found healthy larva, pupae or emergence hole of the galling insect (see Fernandes and Price 1992 for details).

Statistical analysis

To answer the question whether *N. madeirana* leaves with galls were more likely to be abscised we performed log-linear analyses for each galling species separately, including individual host plant as a variable to control for heterogeneity of responses.

To analyze whether abscised leaves with galls differ in size (estimated by width*length) compared to those retained on the parent tree, we performed an ANOVA nested by host tree to control for differences among tree individuals (Zar 1996).

Table 1 Proportion survival and mortality rates ($\bar{x} \pm \text{SD}$) caused by predators, parasites, pathogens, and unknown factors on galls induced by *Bruggmannia* sp. 1 (discoid gall) and *Bruggmannia* sp. 2 (ovoid gall) on retained and abscised leaves of *Neea madeirana*

	Abscised		Retained		Wald χ^2	P
	\bar{x}	SD	\bar{x}	SD		
<i>Bruggmannia</i> sp 1						
Predated	0.279	0.408	0.149	0.332	3.156	0.076
Parasitized	0.121	0.276	0.116	0.271	0.009	0.926
Pathogen	0.124	0.293	0.000	0.000	59.497	<0.001
Unknown	0.211	0.384	0.093	0.294	3.854	0.049
Survived	0.265	0.373	0.643	0.436	8.511	0.004
<i>Bruggmannia</i> sp 2						
Predated	0.035	0.138	0.046	0.171	0.088	0.767
Parasitized	0.134	0.263	0.094	0.240	0.479	0.489
Pathogen	0.123	0.237	0.009	0.043	8.325	0.004
Unknown	0.094	0.247	0.094	0.245	0.000	0.998
Survived	0.614	0.386	0.758	0.333	0.912	0.340

Finally, differences in mortality rates in galls on abscised and retained leaves were tested separately for each *Bruggmannia* species using generalized linear models with Poisson errors and an identity link function according to Crawley (1993). All the models were inspected for the absence of heteroscedasticity and the normality of errors.

Results

The proportion of leaves with galls induced by *Bruggmannia* sp. 1 varied considerably among individual trees ($\chi^2 = 43.2$, $df = 8$, $P < 0.001$). However, the proportion of leaves with galls was consistently higher on abscised leaves on the forest floor than on leaves retained in the canopy ($\chi^2 = 95.7$, $df = 5$, $P < 0.001$). Within all trees the proportion of leaves with *Bruggmannia* sp. 1 galls was at least two fold higher on the abscised leaves (Fig. 2). The same pattern was observed for *Bruggmannia* sp. 2, which occurred at least 10% more often on abscised leaves ($\chi^2 = 39.3$, $df = 5$, $P < 0.001$), while galling rates varied significantly between trees ($\chi^2 = 52.5$, $df = 8$, $P < 0.001$).

No statistical difference was found between the sizes of leaves with galls collected on the ground or from the trees, although leaf size varied among individual trees (controlled by plant differences in a nested ANOVA). The average length of abscised leaves with galls was 15.208 ± 0.241 cm, while the average length of retained leaves with galls was 15.395 ± 0.241 cm ($F_{1, 440} = 0.030$; $P = 0.862$). The average width of abscised leaves with galls was 6.840 ± 0.090 cm while the average width of retained leaves with galls was 6.726 ± 0.088 cm ($F_{1, 440} = 0.001$; $P = 0.973$). This suggests that despite the variation in leaf

size among trees, the abscission or retention of galled leaves was not influenced by leaf size.

Abscission by *N. madeirana* strongly affected the survival of the galls induced by the simpler galler, *Bruggmannia* sp. 1 (Table 1). Survival rates in galls by *Bruggmannia* sp.1 retained on the tree were more than twice ($\sim 65\%$) that recorded from abscised leaves ($\sim 25\%$; $P < 0.01$; Table 1).

While mortality caused by predators, which would eat the gall wall tissue, and by larval parasitoids did not differ between galls on retained and abscised leaves, the rates of mortality caused by pathogens were clearly higher in galls on abscised leaves ($P < 0.001$; Table 1). In fact no pathogen affected gall was recorded from *Bruggmannia* sp.1 galls on retained leaves, while pathogen infestation was common (12.4%) in galls on abscised leaves (Table 1). Mortality induced by unknown factors was also significantly higher in abscised leaves compared to retained leaves (Table 1).

Abscission of galled leaves by *Neea madeirana* also affected the survival of the more complex galls induced by *Bruggmannia* sp.2 (oval shaped gall). Otherwise, the difference in the proportion of gallers that survived on abscised ($\sim 61\%$) and retained leaves ($\sim 76\%$; Table 1) was approximately 15%. With *Bruggmannia* sp.2 we found no statistical difference in the rates of mortality caused by predators, parasitoids or unknown factors between galls on abscised or retained leaves. However, similar to *Bruggmannia* sp.1 galls, mortality induced by pathogens was about ten times more common in galls on abscised leaves (ca. 12%) than on retained leaves (1%; $P = 0.004$). Interestingly, both gall types suffered similar mortality from fungal attack in the leaf litter (Table 1). Also, green island effects were only observed on leaves where galls contained a living gall former.

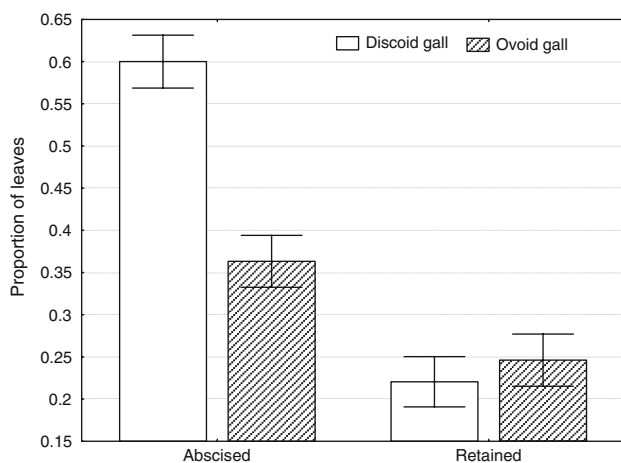


Fig. 2 Proportion of leaves with galls induced by *Bruggmannia* sp.1 (discoid) and *Bruggmannia* sp. 2 (ovoid) on *Neea madeirana* leaves on the tree and abscised leaves in the forest floor

Discussion

In both *Bruggmannia* species we found a higher proportion of galled leaves on the ground than in the canopy. These differences could result if galled leaves decayed more slowly than ungalled ones or by active abscission of galled leaves by *N. madeirana*. While we cannot discount differential rates of decay entirely, we consider it unlikely because any preserving effect by the gallers should have ceased in galls where the gall former was killed on the tree (parasitized or predated). If so, the proportion of leaves with galls that were predated or parasitized found on the ground would be expected to be lower than in the canopy, while we found them to be similar or higher suggesting galled leaves were abscised. Galls on the ground showed increased gall inducer mortality mainly due to pathogen/

fungal infestation. Fungal attack is a known source of gall former mortality and for some cynipid gallers it has been suggested that the location on the host plant of the galls and their phenology have evolved to avoid the attack by endophytic fungi (Wilson 1995; Wilson and Carroll 1997). It is also possible that fungi invaded after the gall structure was compromised by parasitoid or predator attack (Stone et al. 1995), however, no indication of either was detected in fungus infested galls during the dissections.

In one species, *Bruggmannia* sp.1, mortality on the ground affects the overall survival rate. In *Bruggmannia* sp.2 mortality suffered on the ground was still 15% higher than in the canopy. However differences are less pronounced than in *Bruggmannia* sp.1, because mortality from pathogens suffered on the ground is compensated by higher predation rates in the canopy. That leaf abscission was independent of leaf size suggests that neither did the galls affect the leaves to a degree that it would deform and become less functional, nor that the tree was shedding the least productive leaves, which for an unknown reason would be attractive for gall induction.

Previous studies have reported that plants may defend themselves against herbivore attack by abscising damaged leaves (Faeth et al. 1981; Fernandes and Whitham 1989; Preslzer and Price 1993; Karban and Thaler 1998; Chapman et al. 2003; Stiling et al. 2002), although the mechanism has been more widely reported as a defense against other localized damage, e.g. by fungal or virus pathogens (Hull 2002). The sessile life style of gallers appears to make abscission a likely mechanism of defense and has also been reported from a number of galling insects including aphids, psyllids and now cecidomyiids (Williams and Whitham 1986; Yukawa and Tsuda 1986; Fernandes et al. 1999; Wool and Bogen 1999; Stromgren and Lanciani 2001; Espírito Santo and Fernandes 2002). The consequences for the gallers, however, are not always the same. Aphids for instance can migrate off the abscised leaf (Williams and Whitham 1986), while with *Bruggmannia* spp. we found abscission to be the indirect cause of increased mortality mainly due to pathogens.

For plants to defend against gallers at the scale of a plant organ they have to be able to detect the parasite, yet galling insects are able to control the development and physiology of the gall tissues, including senescence and abscission (Mani 1964; Rohfritsch and Shorthouse 1982; Schönrogge et al. 2000; Harper et al. 2004). If some or all the plant defense mechanisms within the gall tissues are controlled by the inducer (Shorthouse and Rohfritsch 1992; Allison and Schultz 2005), the scale at which a gall inducer affects the plant beyond the gall tissues could determine what further defenses are available to the plant. Gall induction over a longer range has been reported for the adelgid *Adelges cooleyi* fecundatrix, which induces galls in buds on

shoots of *Picea glauca* × *engeimani* at more than 5 cm away from the point where the mouthparts are inserted (Sopow et al. 2003). It is thought that any, as yet unidentified, morphogenetic signal is injected directly into the phloem and moves with the flow. Another indicator might be the so called “Green Island Effect”, which are regions on leaves that remain apparently active and healthy and thus green (Fig. 1), while the remainder of the leaf senescences and decays. Green Island Effects can extend beyond the boundary of gall tissue and are also known to be caused i.a. by fungi and gallers, and are thought to indicate higher concentration of auxins and cytokinins (Mapes and Davies 2001; Abramovitsch and Martin 2004). In both *Bruggmannia* species the galls themselves maintained their coloration which for *Bruggmannia* sp. 2 extended for 1–2 mm into the leaf blade (Fig. 1a, b). The remainder of the leaf blade quickly turned black, suggesting that the galling effect extends only a very short distance beyond the gall tissues.

Galls in general are well known to be a ‘sink’ for plant resources (e.g. Kirst and Rapp 1974; Larson and Whitham 1991), which has been shown in some systems to be due to high concentrations of invertases in the gall tissues. The impact of galls as a sink for nutrients certainly reaches beyond the gall tissues as indicated by the competition for nutrients among gallers that share the same plant organs, e.g. *Pemphigus betae* on poplar trees and *Cynips divisa* on oaks (Whitham 1978; Sitch et al. 1988). Thus, while gall inducers might control the plant defense mechanisms inside the gall tissues and modify them for their purpose, the larger range of sink effects could act as a trigger for leaf or organ abscission as a plant defense, which at least in *Bruggmannia* sp.1. reduced overall survival.

It is worth noting that not every event of plant organ abscission in relation to galls is necessarily a symptom of induced plant defense. With some galling species, particularly in temperate regions and on deciduous plants, the galled organ will abscise earlier than ungalled organs. For instance in the cynipid *Andricus quercuscalicis* gall bearing acorns fall about 2 weeks before ungalled acorns (Schönrogge et al. 1994) and galls of *Neuroterus quercusbaccarum* control their abscission from the leaves before the leaves themselves start to fall (Hough 1953). *Andricus quercuscalicis* is a substantial gall equivalent in size and weight to the acorn itself and the early shedding of gall bearing acorns might be simply due to the additional weight on the acorn peduncle. *Neuroterus quercusbaccarum* might in fact benefit by coming to overwinter under the leaf litter where tannins and phenolic compounds that leach from the decaying leaves could act as fungicides (Taper and Case 1986). However, just weight appears not to be the reason for leaves with *Bruggmannia* galls to be shed or we would have expected a larger proportion of

small galled leaves on the ground relative to those in the canopy.

Finally, where mortality due to leaf abscission and subsequent exposure to fungal pathogens is severe, one might expect natural selection to promote gall structures that are more resistant to fungal invasion. Certainly galls of *A. quercuscalicis* can be covered in mould with no apparent effect on emergence success (KS, pers. obs.). In this study *Bruggmannia* sp.2, which induces the somewhat more complex ovoid gall, suffers very similar levels of mortality by fungal attack compared with *Bruggmannia* sp.1 and a similar increase from retained to abscised leaves. Overall survival, however, was higher in *Bruggmannia* sp.2 due to lower levels of predation and mortality by unknown causes. This illustrates that evolutionary consequences cannot be inferred from only one process. *Bruggmannia* sp.2 could potentially escape a late acting predator on the tree by being abscised to the ground earlier than *Bruggmannia* sp.1. However, the identity and thus life-history traits of a potential predator is unknown and at this point statements of evolutionary consequences would be mere speculation. Galler systems like the *Bruggmannia* species have been model systems in community and evolutionary ecology and provide an excellent opportunity to study evolutionary trade offs that shape the evolution of extended phenotypes (Schönrogge and Crawley 2000; Stone et al. 2002; Stone and Schönrogge 2003; Nyman et al. 2007).

Acknowledgments This manuscript was improved by the comments of A. Raman, M.A.C. Carneiro, G.N. Stone and an anonymous referee. We thank A. Oliveira for the species identification and field assistance. This research was supported by CNPq (472491/2003-2, 30 4851/2004-3).

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