

The gall inducing insect community on *Baccharis concinna* (Asteraceae): the role of shoot growth rates and seasonal variations

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Abstract

Resource allocation patterns have been extensively studied on the dioecious shrub *Baccharis concinna* Barroso (Asteraceae) in rupestrian grasslands in Brazil. Female plants have longer apical shoots, more flowers per shoot, and greater leaf, flower and stem biomass on apical shoots while male plants have longer lateral shoots. Otherwise, no differences were observed in total biomass of vegetative parts between male and female plants. We further investigated the relationship between lateral shoot growth rates and the richness and abundance of galling-insect species on this host plant. Male plants had longer lateral shoots due to greater growth rates throughout the year. On the other hand, galling-insect richness and abundance did not differ between male and female plants throughout the year. Gall-inducing insects showed greater richness and abundance in the drier months of the year while lateral shoot growth rates were greater during the rainy season. In conclusion, male plants allocated more resources to the growth of lateral shoots when compared to female plants, but this differential growth did not reflect on male plants being more attacked by galling-insects.

Keywords: insect galls, insect herbivory, growth rates, plant dioecy, resource allocation, rupestrian grasslands, Serra do Cipó.

Introduction

The occurrence of dioecy in plants suggests the existence of differential patterns of resource allocation between the sexes (Bawa 1980). Differential habitat utilization has been documented in numerous species where female plants occurred more frequently in more humid and mesic sites while male plants were more abundant in drier and more xeric sites (Freeman et al. 1976). This distribution pattern has been interpreted as a strategy to maximize seed production by female plants and pollen dispersal by male plants, and therefore, reduce

intraspecific competition and resulting in biased population sex ratios (Freeman et al. 1976). Whether male plants are more tolerant to water stress or female plants compete with male plants under moister soil conditions or if sex is determined by environmental conditions remain as possible mechanisms resulting in biased population sex ratios (e.g., Freeman et al. 1976; Herms & Mattson 1992; Cornelissen & Stiling 2005).

Resource allocation in plants has been commonly studied by several measures such as

dry weight of leaves, flowers, stems and roots; number of individual leaves and flowers, plant size, and shoot length (e.g., Lloyd & Webb 1977; Lovett-Doust et al. 1987; Delph 1990; Delph et al. 1993; Marques et al. 2002; Espírito-Santo et al. 2003). Resource allocation has been extensively studied on the dioecious shrub *Baccharis concinna* Barroso (Asteraceae) and has been measured for apical shoots (Marques et al. 2015), for lateral shoots (Madeira et al. 1997; Marques et al. 2002; Carneiro et al. 2005, 2006; Marques et al. 2015) and for the entire plant (Marques 1997; Marques et al. 2002; Espírito-Santo et al. 2007, 2012). Female plants have longer apical shoots when compared to male plants, more flowers per shoot, and greater leaf, flower and stem biomass on apical shoots. Male plants, on the other hand, have longer lateral shoots when compared to female plants (Madeira et al. 1997; Marques et al. 2002; Carneiro et al. 2005, 2006). Although, female and male plants differ on the length and biomass of lateral and apical shoots no differences were encountered between male and female plants when total biomass of vegetative parts was measured (Marques et al. 2002).

The resource allocation patterns in *B. concinna* vary according to the resource studied. At the plant scale no differential resource allocation was found when total plant biomass was studied (Marques et al. 2015). Otherwise, differential resource allocation between male and female plants was observed when the scale was reduced from the whole plant to shoots. Female plants had longer apical shoots while male plants had longer lateral shoots indicating differential resource allocation between plant sexes for these resources. Therefore, resource allocation by this plant species is a phenomenon resulting from the combination of different resource allocation patterns.

The sex-biased herbivory hypothesis proposes that male plants frequently allocate more resources into growth and less into reproduction and chemical defenses when compared with female plants, and therefore, male plants should be more attacked by insect herbivores (e.g., Wallace & Rundel 1979; Gehring & Whitham 1982; Ågren 1988; Popp

& Reinartz 1988; Boecklen et al. 1990, 1994; Jing & Coley 1990; Pearson et al. 1990; Herms & Mattson 1992; Boecklen & Hoffman 1993; Cornelissen & Stiling 2005). Nevertheless, exceptions to this pattern exist where insect herbivores preferentially attack female plants or do not show attack preferences for plant sex (e.g., Krischik & Denno 1990; Ahman 1997; Madeira et al. 1997; Espírito-Santo & Fernandes 1998; Espírito-Santo et al. 1999, 2012; Faria & Fernandes 2001; Araújo et al. 2006).

We were prompted to investigate how the most common herbivores, gall inducing insects, on *B. concinna* would respond to these complex resource allocation patterns. Gall inducing insects did not show differential attack rates on male and female plants of *B. concinna* when the entire plant was studied (Madeira et al. 1997; Marques et al. 2002). On the other hand, a study on the gall-inducing-insect community on lateral shoots of *B. concinna* did detect greater attack rates on male plants (Carneiro et al. 2005), while other studies conducted in the same system did not detect differential attack rates on male and female plants of *B. concinna* (Madeira et al. 1997; Marques et al. 2002; Araújo et al. 2006; Espírito-Santo et al. 2012) or on *B. dracunculifolia* (De Candolle) (Espírito-Santo & Fernandes 1998).

The objective of the present study was to further investigate the sex ratio for the host-plant population within the different habitats studied as well as resource allocation on lateral shoots and rates of herbivore attack on male and female plants of *B. concinna*. We tested three hypotheses: i) the differential distribution of plant sex between habitat hypothesis, which predicts that male plants are more abundant in xeric habitats, while female plants predominate in mesic habitats; ii) the differential resource allocation hypothesis which predicts that male plants would allocate more resources into growth and consequently have larger size and have greater lateral shoot growth rates; and iii) the sex-biased herbivory hypothesis which predicts that male plants support greater species richness or abundance of galling species. To

adequately address the differential resource allocation (ii) and the sex-biased herbivory hypotheses (iii) we chose to study lateral shoots, due to our previous knowledge that male plants had on average longer lateral shoots when compared to female plants (Marques 1997).

Materials and Methods

Study Site

This study was conducted along the highway MG-010 (km 110) in rupestrian grassland vegetation (high altitude fields) at the Reserva Natural Vellozia (19°16'54" S, 43°35'45" W), in the southern portion of Espinhaço Mountains, Minas Gerais, southeastern Brazil. *Baccharis concinna* Barroso (Asteraceae) is a dioecious woody shrub occurring along the altitudinal gradient (900m to 1400m) and endemic to the Espinhaço Mountains (Barroso 1976). It shows continuous production of flowers and growth meristems throughout the year enabling this species to support one of the richest insect galling communities in the tropics, totaling 15 morphospecies (Fernandes et al. 1996; Madeira et al. 1997, Santos et al. 2012).

Sampling

One population occurring along the Geraldinho stream at 1150m in elevation was studied for 12 months (description of the habitat can be found in Alvim et al. 2015). Sex ratio estimates of the population were obtained by counting all mature individuals within 10 transects, which laid parallel to the creek bed along a humidity gradient going from the stream up into the rocky fields. Forty individuals of each sex were haphazardly chosen and marked. Plant size was estimated by measuring plant height and two measures of crown width. Plants were easily sexed in the field for they produce flowers continuously throughout the year.

We measured the growth of lateral shoots as they became available for colonization by gall-inducing-insect species throughout 12 months. Lateral shoots are here defined as shoots growing along a main stem and with determinate growth. To assess the lateral shoot growth rates of the 40 previously

marked plants, 10 haphazardly chosen lateral shoots were marked with bird tags and labeled 1 through 10. These shoots were measured every month from February of 1998 to January of 1999, excepting July of 1998. Gall-inducing insect species were censused every month for 12 months, except for the months of July and October of 1998. Only galling species that had initiated a gall in that month (new green galls) were counted.

Statistical Analyses

To address the hypothesis on the differential distribution of plant sex between habitats we compared the sex ratios of *B. concinna* on 10 transects along the humidity gradient within the population by G tests (Sokal & Rolf 1984). To test the differential resource allocation hypothesis two analysis were performed: a) initial plant crown diameter and length of both sexes were transformed by natural logarithm to meet the assumption of normality and analyzed by Student t-test. The Levene's test was used to assess the equality of variances ($p > 0.05$); b) lateral shoot growth rates were measured on a monthly basis for 12 months on male and female plants, transformed by natural logarithm (+ 1), and analyzed by Two-Factor Repeated Measures Anova, after the Levene's test on the homogeneity of variance ($P > 0.05$) (Wilkinson et al. 1997).

The sex-biased herbivory hypothesis has been commonly tested by analyzing the abundance of individuals of any given insect species between male and female plants. We chose to approach this hypothesis in two steps. First we compared the mean number of gall inducing insect morphospecies associated with male and female plants during 10 months by Two-Factor Repeated Measures ANOVA (Levene's homogeneity of variance test, $p > 0.05$). A species accumulation curve illustrated the rate at which new species were added throughout the year. Secondly, we compared the abundances of all gall inducing insect species associated with male and female plants during 10 months by Two-Factor Repeated Measures ANOVA. Mean and cumulative galling abundance were transformed by natural logarithm to meet the assumption of normality

of the tests used (Levene's homogeneity of variance test, $p > 0.05$). The composition of the component galling insect community on male and female individuals of *B. concinna* was compared by descriptive statistical analyses.

Results

Differential distribution of plant sex between habitat hypothesis

The population studied was female biased (M/F = 0.722) and distributed within an area of 4359 m². Female plants were significantly more abundant at the wetter sites and no difference in sex ratio was found at the drier sites except for one site where females were more abundant (Tab. 1).

Differential resource allocation hypothesis

Male and female plants did not differ in plant height and were on average 1,15m tall (mean female height = 115.25 ± 4.05 cm; mean male height = 114.9 ± 3.89 cm; $t = 0.062$, $N = 80$, $P > 0.95$). Nevertheless, when total crown area was considered (crown width x crown length) male plants had on average twice the crown area of female plants (mean male area = 6726.37 ± 628.4 cm²; mean female area = 3220.25 ± 335.13 cm²; $t = 5.331$, $N = 80$, $P < 0.01$). Male plants had a wider crown while female plants had narrower crowns.

Table 1. Distribution of male and female plants of *Baccharis concinna* (Asteraceae) along humidity gradients in a population at 1150m in elevation in Serra do Cipó, Brazil.

Humidity Gradient	M/F	Sex Ratio	G	P
High Humid	30/90	0.33	16.42	<0.05
Humid	40/94	0.42	16.32	<0.05
Humid	15/34	0.44	15.4	<0.05
Xeric	43/43	1.0	0	ns
Xeric	4/8	0.5	16.45	<0.05
Xeric	42/60	0.7	3.14	ns
Xeric	51/31	1.64	5.99	ns
Xeric	82/61	1.34	2.14	ns
Xeric	28/37	0.75	1.9	ns
Xeric	24/39	0.61	5.7	ns

Mean lateral shoot growth rates over 11 months varied between plant sexes and month with a significant interaction term between sex and month (natural logarithm) (sex: $F = 59.9$, $df = 1$, $P < 0.001$; months: $F = 892.4$, $df = 10$, $P < 0.001$; sex*month: $F = 9.86$, $df = 10$, $N = 5740$, $P < 0.001$, $N = 5740$). Overall, monthly growth rates of lateral shoots were greater on male plants with a slow but steady increase from March (the end of the rainy season) throughout May and September (dry season), and showing a greater increase in November, December and January (rainy season) (Fig. 1a).

As a result of the general pattern of greater growth rates of lateral shoots on male

plants, their cumulative growth rates were greater than those of female plants (Fig. 1b). Cumulative growth rates of lateral shoots varied between sex and months with a non-significant interaction term - plant sex and months - (Natural Logarithm)(sex: $F = 4.16$, $df = 1$, $P < 0.042$; months: $F = 498.12$, $df = 9$, $P < 0.01$; sex*month: $F = 2.82$, $df = 9$, $P < 0.01$, $N = 5175$) (Fig. 1). When the shoots were initially marked they were one year old and were on average 0.6cm longer on male plants. By the end of the second growth season lateral shoots on male plants were on average almost 2cm longer than those on female plants (Fig. 1). The resource allocation hypothesis was corroborated in this study suggesting that male

plants actually show greater lateral shoot growth rates throughout the year when compared to female plants.

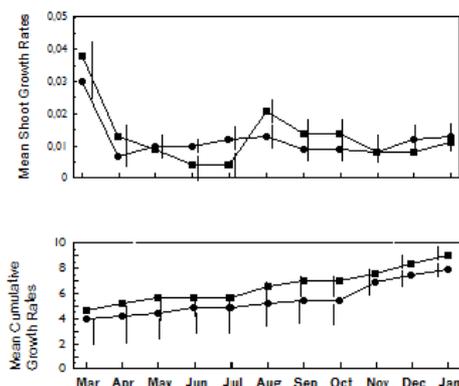


Figure 1 a) Mean lateral shoot growth rates of female (λ) and male (v) plants of *Baccharis concinna*; b) Mean cumulative lateral shoot growth rates for female (λ) and male (v) plants of *Baccharis concinna* for 1998 in Serra do Cipó, Brazil.

The sex-biased herbivory hypothesis

Mean gall-inducing-insect richness differed between months but not between plant sex, with a non-significant interaction term - plant sex and months - (natural logarithm + 1) (sex: $F = 0.153$, $df = 1$, $P > 0.47$; month: $F = 17.63$, $df = 8$, $P < 0.01$; sex*month: $F = 1.63$, $df = 8$, $P > 0.114$, $N = 355$). Gall-inducing-insect richness showed an initial peak in March (the end of the rainy season) through July (dry season), with a sharp decrease in November (beginning of the rainy season). A species accumulation curve showed that male plants had 11 gall-inducing-insect morphospecies, while female plants had 10 morphospecies accumulated over the 11 months of study. Otherwise, gall-inducing-insect morphospecies accumulated at a faster rate on male plants as opposed to female plants. Male plants had accumulated all 11 morphospecies by August (after 6 months of sampling), while female plants accumulated all 10 morphospecies by December (after 10 months). This difference may have been caused by rare morphospecies, which took longer to be detected on female plants.

Mean gall inducing insect abundance on male and female plants showed a very similar seasonal pattern to that of insect richness. Mean galling-insect abundance differed between months but not between plant sex (sex: $F = 0.057$, $df = 1$, $P > 0.813$; months: $F = 5.5$, $df = 8$, $P < 0.01$; sex*month: $F = 1.88$, $df = 8$, $P > 0.064$, $N = 355$). Similarly, cumulative galling insect abundance differed between months but not between plant sex (Natural Logarithm + 1) (sex: $F = 0.17$, $df = 1$, $N = 48$, $P > 0.17$; months: $F = 178.9$, $df = 8$, $N = 368$, $P < 0.01$; sex*month: $F = 0.83$, $df = 8$, $N = 368$, $P > 0.05$). In some months, male plants would have a greater abundance of galling insects associated, while the opposite pattern was seen in other months where female plants had greater abundance of galling insects. A few abundant species directed the patterns observed (Tab. 2).

The only clear pattern observed was the seasonal distribution of gall inducing insects on *B. concinna*. Gall inducing insect species richness and abundance were higher in the drier months decreasing towards the rainy season. This pattern becomes more evident through a stepwise backward linear regression analysis where 42 percent of the variation in insect species richness was accounted for by months (seasonal effects) and not by plant sex or lateral shoot growth rates (Tab. 3). Similarly, 29.4 percent of the variation in the abundance of gall-inducing-insects was accounted for by months (seasonal effect) and lateral shoot growth rates but not by plant sex (Tab. 3). This data indicates that the sex-biased herbivory hypothesis was not corroborated in this study.

The community of galling-insects in this population over 12 months consisted of 11 morphospecies out of the 15 known to be associated to *Baccharis concinna* (Fernandes et al. 1996). Only 5 of these morphospecies had abundances above the hundreds and only 4 species were common throughout the study period. The abundance of morphospecies “A” and “B” (stem) were below 100 individuals but were constant throughout the year while morphospecies “F” and “G” (apical bud) doubled or tripled their abundance reaching the

hundreds in the summer months (December to March). Morphospecies “E” (leaves) only occurred in the winter months from May to August. The six morphospecies remaining

occurred mainly in the summer months but were too rare to show any clear pattern (Tab. 2).

Table 2. Composition of the galling-insect community on male and female plants of *Baccharis concinna* (Asteraceae) in a population during a year in Serra do Cipó, Brazil. Coding for galling morphospecies according to Fernandes *et al.* 1996.

Species	Months								
	3/98	4/98	5/98	6/98	8/98	9/98	11/98	12/98	1/99
A	14/25	17/17	18/12	9/14	0/2	9/10	18/6	13/18	5/8
B	44/55	13/20	27/10	47/50	16/11	20/13	0/8	6/12	0/7
C	9/2	7/1	0/1	0/1	0/0	0/0	0/0	0/0	0/0
D	0/0	1/0	3/0	1/0	0/0	0/0	0/0	0/1	0/0
E	0/0	0/0	5/0	1/0	13/6	0/1	0/2	0/0	0/0
F	110/90	46/71	70/60	37/31	0/9	17/29	6/3	10/9	14/21
G	60/70	22/17	27/70	24/28	7/3	15/32	9/17	162/111	71/108
H	0/1	9/2	2/4	2/11	4/3	0/3	0/0	0/0	0/0
K	0/0	0/0	0/0	2/1	0/0	0/0	0/0	0/0	0/0
M	0/0	0/0	0/0	2/0	0/0	0/0	0/0	0/0	0/0
N	0/0	0/0	0/0	0/0	7/25	359/487	0/0	0/0	0/0

Table 3. Effects of plant sex, plant biomass and altitude of plant location on galling insect species richness and abundance attacking *Baccharis concinna*, in Serra do Cipó, M.G., Brazil. General minimum model for species richness is $gsp = alt + sex + intercept$, and for galling abundance is $gab = alt + sex + biom + intercept$ where gsp = number of galling species; gab = abundance of gallers; alt = altitude; sex = plant sex and $biom$ = plant biomass or dry weight.

Multiple Regression		df	F	P	
Galling Species Richness					
Months		1	77.97	<0.05	
Plant sex			0.26	0.61	
Mean Shoot Growth Rate			0.12	0.73	
Error		353			
Total		355			
Minimum Adequate Model		n	r²	F	P
$L_{nsp} = 1.397 - 0.06 \text{ month}$		355	0.406	69.63	<0.05
Galling Abundance					
Months		1	29.07	0.05	
Plant sex			0.119	<0.73	
Mean Shoot Growth Rate		1	4.7	<0.032	
Error		326			
Total		329			
Minimum Adequate Model		n	r²	F	P
$L_{nab} = 2.62 - 5.94 \text{ shoot} - 0.074 \text{ month}$		329	0.294	15.5	<0.05

Discussion

Female plants were more abundant in mesic habitats corroborating the differential distribution of plant sex between habitat hypothesis (Freeman *et al.* 1976). The predominance of female plants on the three

transects closest to the creek, and on a fourth transect on a dry site were responsible for shifting the population sex ratio towards females. No significant sex ratio differences were detected within the remaining 6 transects. This suggests differences in the energetic

requirements and survival rates of male and female plants in different environments. Although we detected differential allocation of resources in relationship to lateral shoots by male plants, which produced longer lateral shoots, male plants were not more attacked by gall-inducing-insects than were female plants. Therefore, the sex-biased herbivory hypothesis was not corroborated in this study suggesting that the female biased sex-ratio observed in this population of plants is not driven by herbivores but most likely by environmental factors.

Differential resource allocation in *Baccharis concinna* has been well studied by our research group. Previous studies have measured total plant dry biomass as well as the biomass of leaves, flowers and stems but failed to detect evidence of differential resource allocation in growth for *B. concinna* (Marques et al. 2002). Nevertheless, differential growth has been reported in *B. concinna* for apical and lateral shoots. Female plants had longer apical shoots, more flowers per shoot, greater leaf, flower and stem biomass of apical shoots when compared to the apical shoots on male plants (Marques 1997), while male plants had longer lateral shoots as suggested by other studies (Madeira et al. 1997; Marques et al. 2002; Carneiro et al. 2005). The existence of architectural differences between the sexes was corroborated in this study in which male plants had on average twice the crown area of female plants.

Male plants had longer lateral shoots due to greater growth rates during the months of April and August (Fig. 1a). In these months lateral shoot growth rate on male plants was greater than that of female plants. Although lateral shoot growth rates between male and female plants differed in only 3 out of 12 months it was enough to ensure greater lateral shoot growth rates on male plants throughout the season (Fig. 1b). Therefore, the differential resource allocation hypothesis was corroborated in this study when lateral shoots were considered.

One assumption of the sex-biased herbivory hypothesis involves the existence of differential resource allocation between male

and female plants (Cornelissen & Fernandes 2001; Cornelissen & Stiling 2005; Imaji & Seiwa 2010). As we detected resource allocation between the sexes of *B. concinna* we expected that the gall inducing insects would show differential patterns of attack between male and female plants due to their responses to the differential growth rates of lateral shoots on male plants. Gall inducing insects utilize meristematic tissues that are still growing and differentiating (Mani 1964, Carneiro et al. 2009; Fernandes et al. 2012). The 11 morphospecies detected in this study utilized leaves, apical buds or stems of this host plant. All of these resources should be affected by the differential growth rates observed for lateral shoots between male and female plants and potentially should affect the herbivores. Nevertheless, the sex-biased herbivory hypothesis was not corroborated. Gall inducing insect richness between male and female plants differed only in three months but with no clear trends. Galling richness was greater on female plants in March but greater on male plants in May and August. Although male plants accumulated morphospecies at a faster rate when compared with female plants, the most abundant morphospecies were present on both plant sexes, and the rare species, with very few occurrences, were responsible for driving this pattern. Gall inducing insect abundance was greater on male plants only for the month of August with no difference was observed between sexes for the remaining 10 months.

The lack of relationship between lateral shoot growth rates and the gall inducing insect richness and abundance on this host plant may be attributed to seasonal differences in microhabitat and host plant quality for the insects. Seasonal differences (months) accounted for 42 percent of the variation observed in the richness and for 29 percent of the variation in the abundance of morphospecies associated with *B. concinna*. Shoot growth rates were greater in the rainy season while galling-insect richness and abundance were greater in the dry season. These results corroborate our previous findings suggesting that gall inducing insect species showed greater success when host plants are

growing in dry or xeric habitats (Fernandes & Price 1988, 1991, 1992). On the other hand, detailed studies are needed on the differential performance of gall inducing insects during the rainy and dry seasons to test the hypothesis that galling insects are constrained by greater mortality factors during the rainy season in spite of the greater growth rates present on lateral shoots of their host plants.

A detailed analysis of the composition of the galling insect community on *Baccharis concinna* also suggest that male and female plants have similar attack rates and share the same species of gall inducing insects. The galling insect community was represented by 11 morphospecies that galled leaves, buds and stems, where 10 morphospecies attacked both sexes and one morphospecies had only one occurrence on male plants.

Studies conducted on small windows of time or any one sampling event could yield any combination of results. For example, if these same plants were sampled in May or August there would have been greater richness of galling insects on male plants. Had these same plants been sampled in March or November greater galling insect richness would have been found on female plants. All other 9 months of sampling showed no patterns of richness or abundance mainly because the dominant galling species were present all year round and colonize both sexes having similar abundance (see also Fernandes et al. 2012). A real pattern in nature should remain strong and consistent throughout seasons and be general enough to be relevant to more than one insect species.

This study has shown that measures of resource allocation can yield conflicting results when different resources are measured or if the same resources are measured at different scales. Galling-insects often utilize growing meristems to oviposit on, and so one would imagine that meristems that grew more or faster would be a limiting resource for gallers. In this study galling insects did not respond to the faster growing lateral shoots on male plants but attacked both male and female plants. Great caution should be used when generalizing patterns observed in one or a few species. More studies are necessary

on entire gall inducing-insect communities to clarify the relationship between insect herbivore attack and biased sex ratios of host plant populations.

Further studies in this system should unveil the role of gall inducing insect attack on the sex ratios of populations of *Baccharis concinna*, and on the differential performance of gall-inducing-insects during the rainy and dry seasons.

Acknowledgements

We would like to thank V. Gomes, D. Negreiros and C. Jacobi for field assistance and P. De Marco and two anonymous reviewers for their comments on the manuscript. Field logistic support was provided by Vellozia private reserve. We thank Reserva Natural Vellozia, Lemman Foundation, Conselho Nacional de Desenvolvimento Científico e Tecnológico, and Fundação de Amparo à Pesquisa do Estado de Minas Gerais for support, and E.S.A. Marques acknowledges a Post-Doctoral fellowship by the CNPq.

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