

## DIFFERENCES IN VEGETATIVE MORPHOLOGICAL TRAITS CAUSED BY HABITAT MEDIATES HERBIVORY RATES IN A PERENNIAL HERB

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### ABSTRACT

Distinct environmental conditions caused by different habitats may promote the development of different plant morphological traits. These different morphologies may alter a plant's relationships with other organisms in the community (e.g. through herbivory or trophic cascades). We studied plant traits and herbivory rates in *Ruellia brevifolia* specimens in different habitats, and hypothesized that plant vegetative morphological traits are linked to the habitat, and herbivory rates will be higher in habitats with bigger plants. We measured the morphological traits of plants in 10 'Cerrado' areas and 10 'Mata Seca' areas and surveyed the herbivory levels in each area. We tested the influence of the habitat on the plants' traits using generalized linear models (GLM's). We used GLM's to compare herbivory rates between habitats and analysis of covariance in order to compare the relative impacts of herbivory on both populations of *R. brevifolia*. Habitat strongly influenced plant morphology, and all the measured plant traits were higher in the 'Mata Seca' habitat. The relationship between herbivory levels and plant morphology was straightforward and depended on plant size. We suggest that future studies may focus on chewing insect communities and light variation in different habitats to verify their relationship with the observed herbivory levels.

**Keywords:** Cerrado; dry forests; life-history traits; morphological plasticity; plant architecture.

### INTRODUCTION

One of the most fundamental questions in ecology is how organisms are adapted to their habitats (MacArthur & Wilson 1967, Southwood 1977). Because an individual plant's habitat influences its life history strategy (Grime 1977) and its resource allocation patterns (Stearns 1992), the environmental conditions in the particular habitat play a crucial role on its biology. Habitat is a key feature to a plant's reproductive success (Kaiser *et al.* 2008), survival, genetic variability (Mataruga *et al.* 2012), morphology and anatomy (Lakušić *et al.* 2010), fruit and seed morphology (Goulart *et al.* 2006), phenotypic plasticity (Greulich *et al.* 2001), and growth allometry (Yu & Gao 2011). Habitats also influence large-scale processes, such as the structure of communities (Monção *et al.* 2012). The adaptation of plant

morphology to habitat conditions influences the plant's relationships with other organisms in the community. Plant morphological traits may affect the plant's competitive abilities (Yu & Gao 2011), allow it to escape herbivory (Allcock & Hik 2004), and allow it to reduce the rate of herbivory (Mazía *et al.* 2012, Schuldt *et al.* 2012). It is also interesting to note that differences in plant traits may influence higher trophic levels in natural communities. Furthermore, trait-mediated indirect effects are common and are often as strong as or stronger than density effects (Werner & Peacor 2003, Schmitz *et al.* 2004).

At least two hypotheses attempt to explain why different plant traits can generate different herbivory patterns (Endara & Coley 2010). The resource availability hypothesis assumes that plants that have established in more nutritive habitats support greater herbivory rates than plants in poor soils (Coley *et al.*

1985). The Appearance Hypothesis assumes that the plant growth is adapted to the seasonal presence of herbivores and so natural selection favours plants that grow and bloom in periods with less herbivore activity (Feeny 1976). The impact of herbivory might be different for a particular plant species that is found in different habitats, depending on the strategies the plants use to avoid loss of photosynthetically active area (Coelho *et al.* 2012, Mazia *et al.* 2012). Presumably, different habitats directly modulate plant traits and this indirectly affects the impact that other trophic levels, such as chewing herbivores, have on the plants. Specifically, the plant's phenotypic plasticity mediates an indirect interaction between the habitats and the herbivores. This holds true for individual plant species located in different habitats of the Cerrado domain, as *Qualea parviflora* which shows differences in leaf chemical composition and morphological studies that influences herbivory rates (Gonçalves-Alvim *et al.* 2010, 2011), and *Tabebuia ochracea*, which presents higher herbivory rates in late successional stages of dry forests (Moreira *et al.* 2013).

Our objective in the present study was to evaluate how habitat determines the morphology of *Ruellia brevifolia* (Pohl.) C. Ezcurra and to understand how these different morphologies are linked to herbivory rates in the Cerrado, a savanna-like biome in central Brazil. We hypothesized that plant vegetative morphological traits are linked to the habitat, and herbivory rates will be higher in habitats with bigger plants. Specifically, we addressed the following questions: (1) Are the morphological traits of *R. brevifolia* related to the habitat in which it grows? (2) Is there a difference in relative loss of leaf area due to the activity levels of chewing insects in different habitats?

## MATERIAL AND METHODS

### Study area

Sumidouro State Park is a protected area in the centre of Minas Gerais State, Southeast Brazil (7,838,805.96 Easting; 609,213.25 Northing, datum – WGS84) (IEF 2010). It is composed by a mosaic of habitats within the Cerrado domain. Cerrado vegetation

is highly diverse and includes numerous types of sub-vegetation types (Ribeiro & Walter 2008). For example, in the study area, it is common to find tropical dry forest patches established over limestone outcrops, merged with forested areas located in valleys (IEF 2010).

Our sampling period matched the dry season (September 2011), when the loss of leaves is common in dry forests (Ribeiro & Walter 2008), and may reach 90% of the canopy leaves (Scariot & Sevilha 2005). In typical Cerrado areas, however, the leaf loss is asynchronous among species. These main differences allowed us to visually distinguish between two main kinds of physiognomies that were sampled and are described below. Besides, these differences are probably linked to abiotic conditions variation among areas, what may influence herbivores behavior.

Our study plots were located in two types of habitat, the 'Cerrado' and the 'Mata Seca'. The study species, *R. brevifolia*, was dispersed extensively over both areas, mainly on shaded paths, near trees. The 'Cerrado' area is composed of tall trees with a relatively closed canopy and a small understory composed by grasses and shrubs. These features determine a vegetation type called 'Cerradão' (Ribeiro & Walter 2008), hereafter called 'Cerrado'. The 'Mata Seca' area is a tropical dry forest established over limestone outcrops (Ribeiro & Walter 2008), having smaller trees than in the 'Cerrado' and with a less pronounced canopy. The soil is shallow but it was possible to find places where soil and organic matter had accumulated, due to the action of rainfall. We sampled these areas because they were adjacent, allowing us to diminish landscape effects and also to stress the importance of ecotypic variation in relation to ecological interactions, as herbivory.

### Study species

*Ruellia brevifolia* is a bushy perennial forest plant (Wasshausen & Wood 2003), typically measuring 1 m in height (Lima *et al.* 2005), but sometimes reaching 2 m (Sigrist & Sazima 2002). It is widely distributed in South America, ranging from Colombia to Northern Argentina, and occurs in habitats that vary from the understory in open areas to shaded areas (Ezcurra 1993). *Ruellia brevifolia* is dispersed worldwide because of

its ornamental potential and has the potential to be invasive (Meyer & Lavergne 2004) because of its continuous seed production by alternation of chasmogamy and cleistogamy. It is considered native from Brazil (Fernandes 2016), and is widespread in the Cerrado domain occurring in many different habitats.

*Ruellia brevifolia* was selected for this study as a model organism due to its great range of distribution in both sampled habitats, with large population sizes, what allowed us to sample a high number of plants, covering homogeneous areas inside each habitat. *Ruellia brevifolia* ability of retaining its leaves during dry season was also an important feature, because it enabled us to measure accumulated herbivory rates even when most plants were without leaves due to the effects of low water availability in the soil.

#### *Plant traits sampling*

We established 10 circular sampling plots (Felfili *et al.* 2011) of 28.26 m<sup>2</sup> (r=3m) in each area: 'Cerrado' and 'Mata Seca'. The plots were marked departing from a central point from where we extended a rope of 3 m length, that had one end attached to the soil, and was used to draw a circle, by circulating the central point. The plots were randomly distributed in the study area accounting for a minimum distance of 50 m from each other. In each plot, we measured 10 individual plants, totaling 100 plants per area. We measured the height and counted the number of leaves of each plant in the field. Samples were measured in September 2011, during the dry season. The height was measured from the soil to the last leaf placed in the longitudinal plant axis.

We randomly collected four healthy mature leaves (fully expanded and without signs of herbivory or damage from sickness) from each plant, totaling 40 leaves per plot, in order to determine mean leaf area, mean leaf mass, and leaf specific mass (leaf mass divided by leaf area) per plot. The mean leaf area was determined using a photograph of the leaves and posterior analysis using the demo version of Image J software. To determine the leaf dry mass, we dried them at 60°C for at least 3 days and weighed them with a precision balance.

#### *Herbivory survey*

We considered herbivory as the leaf-area loss caused by chewing insects. To determine the mean area consumed, we randomly collected four mature (fully expanded) leaves showing signs of chewing insects herbivory from each plant per plot in each area, totaling 800 leaves. In order to determine the proportion of leaf area loss per habitat, we photographed the leaves inside the plot and used the demo version of Image J software to calculate the leaf total area and the area that was damaged by chewing insects.

Many of the measured plant traits are size-dependent, and therefore we used generalized linear models to determine whether the habitat was responsible for difference in plant height. After this analysis, we used plant height as a proxy for habitat, not with the same ecological meaning, but with the same statistical effect, since both variables presented the same behavior and plant height is a continuous variable that was easier to relate to the other measured traits than the categorical division of habitats. To assess the effects of habitat on other traits, we used GLMs with plant height as the predictor variable to assess differences in plant morphology between habitat types. We used GLMs because they were better suited to our data, as they did not meet the Gaussian distribution assumptions and allowed us to fit another error distribution to the data set (Crawley 2007).

Herbivory was compared between areas using a GLM with quasi-binomial distribution, using the percentage of leaf area lost as the response variable, and habitat as the categorical factor. We also performed analysis of covariance using the percentage of leaf area lost as the response variable, habitat as the categorical factor, and plant morphological traits as predictor variables, in order to assess if the plant traits were good predictors of herbivory rates between habitats. These analyses were performed using R Statistical Environment (R Core Team 2015).

## **RESULTS**

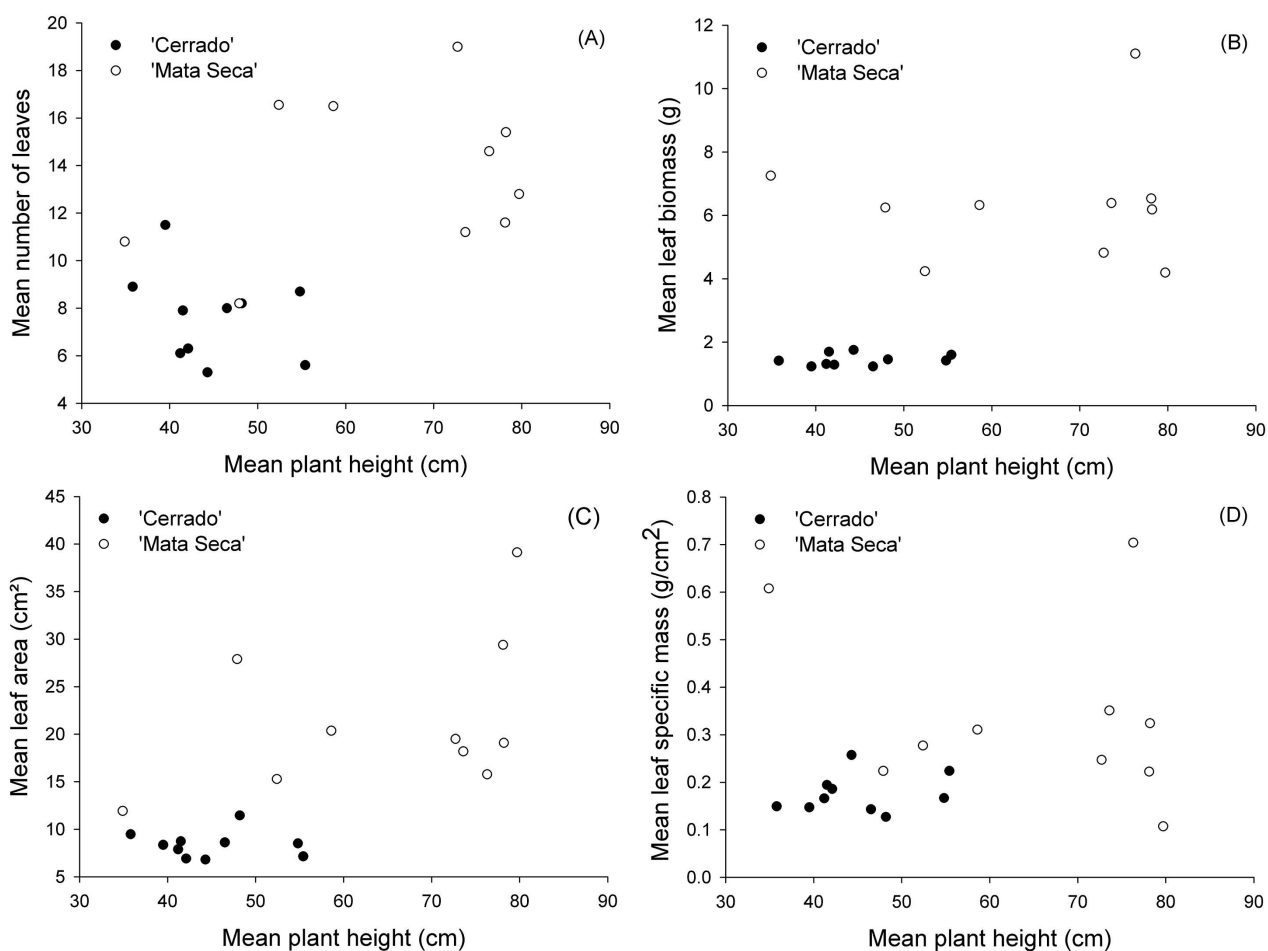
Plant traits were significantly affected by habitat. Specifically, plants from the 'Mata Seca' area were significantly taller than those from the 'Cerrado'

area (d.f.=19,  $F=16.60$ ,  $p<0.001$ , Table 1). Therefore, for the other analyses, we considered plant height to be a representative proxy for habitat and assumed it to be a unique source of variation for the plants'

morphological traits. For all analyses, taller plants also had a greater number of leaves, greater amount of leaf biomass, greater leaf area, and greater leaf specific mass (Figure 1a–d, Table 1).

**Table 1.** Generalized linear models used to assess the effect of habitat on plant mean height and the relationship between plant mean height and other morphological traits measured.

Dependent Variable	Predictor	F	df	Deviance	Residual df	Residual deviance	p
Mean height	Habitat	16.06	1	37.657	19	82.625	<0.001
Mean leaf area	Mean height	17.23	18	46.039	19	88.346	<0.001
Mean leaf mass	Mean height	8.361	18	13.901	19	38.476	<0.01
Mean number of leaves	Mean height	9.582	18	10.155	19	28.596	<0.01
Mean leaf specific mass	Mean height	9.576	18	0.515	19	1.416	<0.01



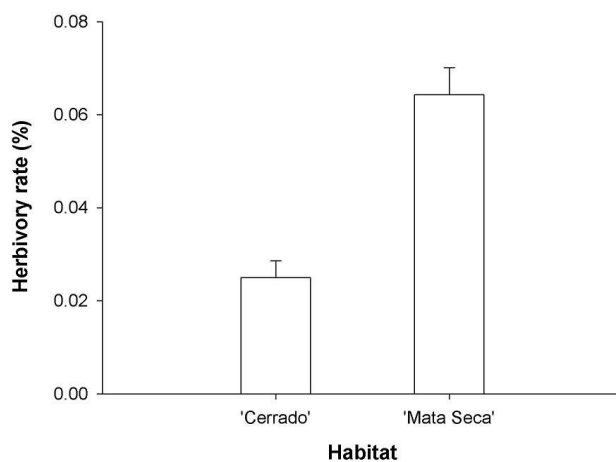
**Figure 1.** Relationships between plant mean height (cm) and morphological traits of *Ruellia brevifolia* in the Sumidouro State Park, Minas Gerais, Southeast Brazil. (a) Mean plant height  $\times$  mean number of leaves; (b) Mean plant height  $\times$  mean leaf biomass (g); (c) Mean plant height  $\times$  leaf mean area (cm<sup>2</sup>); (d) Mean plant height  $\times$  mean leaf specific mass (g/cm<sup>2</sup>).

Herbivory rates were significantly different between habitats, with higher values in the 'Mata Seca' area ( $t=-5.54$ ,  $p<0.001$ ; Figure 2, Table 2). In addition, analysis of covariance showed that the morphological traits had a significant positive influence on the amount of leaf consumed by herbivores. More leaf area was consumed in larger

plants than from smaller plants, and this pattern seems to be linked to the habitat because the larger plants were all located in the 'Mata Seca' area. However, leaf biomass presented a different pattern. Although it was significantly associated with leaf area loss, it was not associated with habitat as the other variables (Table 2).

**Table 2.** Analysis of covariance for leaf area loss (herbivory) and plant morphological traits.

Dependent variable	Predictor	df	SS	MS	F	p
Height	Mean height	1	0.0028	0.0028	11.4500	<0.01
	Habitat	1	0.0050	0.0050	20.0480	<0.001
	Mean height $\times$ Habitat	1	0.0002	0.0002	0.7150	0.4100
	Residuals	16	0.0040	0.0002		
Leaf area	Mean leaf area	1	0.0049	0.0049	19.5980	<0.001
	Habitat	1	0.0029	0.0029	11.6250	<0.01
	Mean leaf area $\times$ Habitat	1	0.0002	0.0002	0.8090	0.3810
	Residuals	16	0.0040	0.0002		
Leaf mass	Mean leaf mass	1	0.0071	0.0071	28.9880	<0.001
	Habitat	1	0.0008	0.0008	3.3850	0.0840
	Mean leaf mass $\times$ Habitat	1	0.0000	0.0000	0.1090	0.7450
	Residuals	16	0.0039	0.0002		
Number of leaves	Mean number of leaves	1	0.0028	0.0028	12.5110	<0.01
	Habitat	1	0.0054	0.0054	24.2170	<0.001
	Mean number of leaves $\times$ Habitat	1	0.0001	0.0001	0.5420	0.4720
	Residuals	16	0.0036	0.0002		
Leaf specific mass	Mean leaf specific mass	1	0.0023	0.0023	8.9860	<0.01
	Habitat	1	0.0054	0.0054	20.8530	<0.001
	Mean leaf specific mass $\times$ Habitat	1	0.0000	0.0000	0.1360	0.7160
	Residuals	16	0.0042	0.0003	11.4500	<0.01



**Figure 2.** Herbivory rates (% of accumulated relative leaf loss) of *Ruellia brevifolia* between habitats in the Sumidouro State Park, Minas Gerais, Southeast Brazil. The impact of herbivory was higher in 'Mata Seca' area than in the 'Cerrado' area.

## DISCUSSION

We found evidence for the role of habitat in determining the morphology of *R. brevifolia*. In our study, plants from the 'Mata Seca' area were more robust than those from the 'Cerrado' area, possibly indicating differences between the nutrient content of soil in these areas. Not only the body size of plants but also other traits, such as leaf specific mass (the amount of leaf mass per leaf area), were higher in the 'Mata Seca'. The 'Cerrado' area is known to present stressful conditions, mainly because of its low soil nutrient content (Skorupa *et al.* 2012). In contrast, the 'Mata Seca' area is more related to tropical dry forest soils over limestone outcrops and has better levels of soil nutrients (Neves *et al.* 2010). As resources are limited,

plants partition them in order to survive, grow, and reproduce (Stearns 1992). In more limiting habitats, plants are expected to exhibit lower growth rates and smaller body sizes (Wijesinghe & Hutchings 1997).

Our results do not support the prediction that leaves with a short life span, growing in nutrient-rich habitats, will have a lower leaf specific mass than leaves with long life spans, growing in nutrient-poor habitats (Turner 1994). These unexpected results may have occurred because *R. brevifolia* does not lose their leaves during the dry period, as arboreal species from dry forests. Instead, *R. brevifolia* is an understory shrub that usually retains its leaves throughout the year. The richer soil in the 'Mata Seca' area may allow the plants to form more robust leaves than the plants in the 'Cerrado' area, which has nutrient-limited soil.

The different habitats promoted the development of different plant morphological traits that mediated different herbivory levels. Higher absolute leaf area loss was observed in the 'Mata Seca' plants than in the 'Cerrado' plants. All morphological traits were positively related to leaf area loss, suggesting that larger plants support higher rates of herbivory. This finding holds true for both habitats, providing an argument against the resource availability hypothesis for plant resistance to herbivory. This hypothesis predicts that plants in richer habitats will be more resistant to herbivory than those in habitats with lower resource availability. In this study, plants showed a similar pattern of consumption by chewing insects in both areas, and leaf area loss increased with greater plant size, number of leaves, leaves mass, leaf area, and leaf specific mass. Neves *et al.* (2010) found higher levels of herbivory in dry forests, which are corroborated by our results. However, they attributed this result to a lower specific leaf mass in dry forest plants, and assumed that this lower specific leaf mass may have facilitated consumption by herbivores in general.

When we consider the analysis of covariance, it is reasonable to conclude that the leaf area loss differed between habitats and that herbivory was higher in the 'Mata Seca' area, what may be linked to the larger plant size in this habitat. Greater availability of plant resources for herbivores naturally generates higher consumption rates, as stated by Moreira *et al.* (2015), which showed that in a latitudinal gradient,

higher levels of leaf herbivory are found near the equator, where leaves availability is higher than in higher latitudes. Moreover, the fact that *R. brevifolia* retains its leaves during the dry season makes it a good food alternative for herbivores and may cause higher herbivory in this species during the dry periods, when most canopy leaves usually fall, since the resource accessibility is also a great predictor of herbivory levels (Wahungu *et al.* 1999).

The ability of *R. brevifolia* to resist herbivory, even under nutrient-limited conditions, and its conspicuous seed production during the year, may contribute to its invasive potential in other areas of the world. Future studies may focus on the herbivore community itself in order to understand how differences in abundance and composition of the chewing insect assemblage affect herbivory in contrasting habitats, and how light may mediate this differences, since light availability may differ between 'Cerrado' and 'Mata Seca' areas.

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