Gall midge attack intensity and host-plant response in a Neotropical coastal ecosystem

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ABSTRACT. Gall midge attack intensity and host-plant response in a Neotropical coastal ecosystem. The gall inducer *Clusiamyia nitida* Maia, 1996 (Diptera, Cecidomyiidae) often infests the shrub *Clusia lanceolata* (Camb.) (Clusiaceae) in the Neotropical vegetation of *restinga* of Rio de Janeiro State, Brazil. Leaves of *Clusia lanceolata* host up to 20 spheroid galls and show variation in their shape. We aimed to evaluate the effect of gall's intensity on leaves of *Clusia lanceolata*, and the extension of gall's impact on adjacent non-galled leaves. We analyzed the effect of the number of galls on leaf area, biomass, specific area and leaf appearance from 509 leaves of 14 individual plants. The results showed that differences of individual plants, pairs of leaves, and gall presence were responsible for more then 90% of variation on infested leaves. Variation on parasitic intensity level created differences in leaf response. Under moderate gall attack characterized by scattered galls on a leaf, the increase of the number of galls caused an increase of leaf biomass and area, and a decrease of specific area. The specific area was smaller also under high attack intensity, characterized by coalescent galls on a leaf. In those cases of extremely high parasitic intensity, galled leaves became deformed and the surface area was severely reduced. Leaf deformation due to gall attack led to early leaf abscission, indicated by the 90% of deformed leaves found in the youngest leaf pair of the branch. There was insufficient evidence that the impact of galls on leaf morpho-physiological parameters extended beyond the attacked leaves, because ungalled leaves did not change significantly when their opposite leaf had been galled.

KEYWORDS. Cecidomyiidae; *Clusia lanceolata*; *Clusiamyia nitida*; compensatory response; insect-plant interaction.

RESUMO. Intensidade do parasitismo de inseto galhador e resposta da planta hospedeira em um ecossistema neotropical costeiro. O inseto galhador *Clusiamyia nitida*, 1996 (Diptera, Cecidomyiidae) freqüentemente infesta o arbusto *Clusia lanceolata* (Camb.) (Clusiaceae) na vegetação Neotropical de restinga do Estado do Rio de Janeiro. As folhas de *Clusia lanceolata* hospedam até 20 galhas esferóides e apresentam variações em sua forma. Buscamos avaliar o efeito da intensidade de galhas nas folhas de *Clusia lanceolata*, e a extensão do impacto de galhas em folhas adjacentes não-galhadas. Analisamos o efeito do número de galhas sobre a área foliar, biomassa, área específica e aparência foliar de 509 folhas de 14 indivíduos. Os resultados indicaram que diferenças individuais entre plantas, nos pares de folhas e na presença de galhas, foram responsáveis por mais de 90% de variação entre folhas infestadas. A variação na intensidade de parasitismo criou diferenças de resposta foliar. Sob ataque moderado, caracterizado pela presença de galhas esparsas nas folhas, o aumento do número de galhas provocou o aumento de biomassa e área foliar e a diminuição da área específica. A área específica também foi menor sob ataque de alta intensidade, caracterizado por galhas unidas. Nos casos de parasitismo extremo, as folhas galhadas tornaram-se deformadas, apresentando a superfície foliar severamente reduzida. A deformação das folhas geradas pela presença de galhas provocou abscisão precoce, indicada pelos 90% de folhas deformadas encontradas apenas nos pares mais jovens de folhas. Não houve evidencias suficientes que indicassem o impacto das galhas em parâmetros morfo-fisiológicos além das folhas atacadas, já que folhas não galhadas não sofreram alterações quando opostas a folhas galhadas.

PALAVRAS-CHAVE. Cecidomyiidae; *Clusia lanceolata*; *Clusiamyia nitida*; interação inseto planta; resposta compensatória.

Plant responses to insect herbivory may vary depending on type of herbivore (Hartnett & Abrahamson 1979; Larson 1998; Nykänen & Koricheva 2004), intensity of parasitism (Craig *et al.* 1986; Fay & Hartnett 1991; Karban & Baldwin 1997) and distribution patterns of herbivory (Marquis 1992; Zangerl *et al.* 2002). The response can be chemical (*e.g.*, synthesis of defense compounds – Abrahamson & Weis 1987; Hartley 1998), physiological (*e.g.*, changes in photosynthetic rate - Andersen & Mizell 1987; Larson 1998) or morphological (*e.g.*, architectural changes – Whitham & Mopper 1985; Nakamura *et al.* 2003). The plant response can be associated with either negative (Belsky 1986; Belsky *et al.* 1993), neutral (Maschinski & Whitham 1989) or positive effects (Larson & Whitham 1991; Nakamura *et al.* 2003) on plants.

Gall-forming insects may affect host plant photosynthetic rates in a more complex way than leaf-chewing insects (Fay *et al.* 1993; Crawley 1997; Larson 1998; Fay & Throop 2005), since gall-makers do not remove photosynthetic tissue. Galling insects produce galls by inducing cellular hypertrophy and hyperplasia on plant meristematic tissues (Mani 1961). Because a galling insect's development depends entirely on the gall's tissues, a gall's effect on host plants possibly continues during the gall's metabolic activity (Fay *et al.* 1996). According to the nutritional hypothesis, gall inducers manipulate the host plant's physiology so that nutrients are channeled into gall tissues (Price *et al.* 1987; Hartley & Lawton 1992; Tscharntke 1999). As a consequence, galled leaves, even when reaching maturity, may behave as a sink organ rather than as a source of nutrients for the plant. Once galled organs become consumer structures, they may even compete against each other (Larson & Whitham 1997) redirecting resources from other organs (Larson & Whitham 1991). Leaf abscission or premature death of galled organs can protect a plant against high intensity parasitism by cutting the sink pathway and the energetic costs of non-productive structures (Condrashoff 1962; Craig *et al.* 1986). Hypersensitive reactions and gall abortion have been regarded as frequent host plant responses (bottom-up forces) during early gall development (Weis *et al.* 1988; Fernandes 1990; De Souza *et al.* 2001; Espirito-Santo & Fernandes 2002).

The parasite's effect, however, can be spread throughout the host plant and might not be restricted to attacked organs (Larson & Whitham 1991, 1997). Ungalled plant organs can potentially respond to galling parasitic effect (Larson 1998). Due to the sink characteristics of galled organs, the gall's effect is expected to affect ungalled organs located closer to the galled organ than those more distant, either negatively or positively.

In the *restingas* of Rio de Janeiro State, in southeastern Brazil, several species of *Clusia* L. (Clusiaceae) play important roles in vegetation structure and succession (Araújo *et al.* 2004; Scarano *et al.* 2004; Pereira *et al.* 2001). These species are often attacked by gall inducer (Monteiro *et al.* 2004). *Clusia lanceolata* (Camb.), a 3–4 m tall evergreen shrub, with opposite distichous leaves, is attacked by the gall inducer *Clusiamyia nitida*, 1996 (Diptera, Cecidomyiidae) (Maia 1996). This insect induces spherical galls that protrude from both sides of the leaf, which is sometimes densely infested. However, there have been no studies yet about the impact of this herbivory or about any other insect interactions involving *Clusia lanceolata*.

The present study aimed to evaluate the effect of galls induced by *Clusiamyia nitida* on *Clusia lanceolata* response. Four questions were addressed here: 1) What is the impact of *Clusiamyia nitida* galls on galled leaves? 2) Does the intensity of parasitism create differences in *Clusia lanceolata* responses? 3) Is the effect of *Clusiamyia nitida* galls locally restricted to galled leaves? 4) Does *Clusia lanceolata* compensate for *Clusiamyia nitida* Maia herbivory?

MATERIAL AND METHODS

In October 2001, 509 leaves were randomly collected from the first, second and third pairs of branches of 14 individuals (35–40 leaves per plant) of *C. lanceolata* located at Restinga de Barra de Maricá, Rio de Janeiro (22°53'S; 42°50'W). Each leaf received an identification number indicating its plant, branch and leaf-pair position on the branch. The number of *C. nitida* galls on leaves and the leaf category were recorded. Paper models of each leaf were scanned and leaf area measured using the Scion Image program (Scion Corporation). Then leaves were dried at 50ºC for three days and their biomasses were recorded. The specific area was calculated as the leaf area/biomass ratio. This variable is directly related to growth and inversely related to the leaf cost for the plant defense (Lambers & Porter 1992; Westoby 1998; Fonseca *et al.* 2006).

Galling intensity and its impact on leaves

The 509 *C. lanceolata* sampled leaves were grouped into seven classes, as follow: ungalled leaves, with one gall, two galls, three galls, four or more scattered galls, coalescent galls (which are difficult to count) and deformed leaves, thick leaves with little horizontal surface expansion (Fig. 1). We used the GLM Procedure in SAS to fit a nested model of the effect of gall presence in leaves from different trees, considering leaf pairs nested within tree and leaf within pair as a random effect. Seven levels of the categorical predictor for galling intensity (ungalled leaves and the six galled leaves categories) were used in the Mixed ANOVA Procedure in order to identify the gall effect and the intensity of parasitism in galled leaves. We also tested for interaction effects for each tree with gall category. The percentage of deformed leaves was analyzed according to their pair position on the branch.

Gall effect extent

The 108 heterogeneous pairs (with one galled leaf and one ungalled leaf) were used to test the effect of gall on ungalled leaves opposite to galled leaves. The 77 pairs with both leaves ungalled and 39 pairs with both leaves galled were used as controls. The effect of galls in those leaves were tested by fitting an ANOVA using the Mixed Procedure with the class variable grouping leaves into 4 categories: ungalled leaves from heterogeneous pairs, galled leaves from heterogeneous

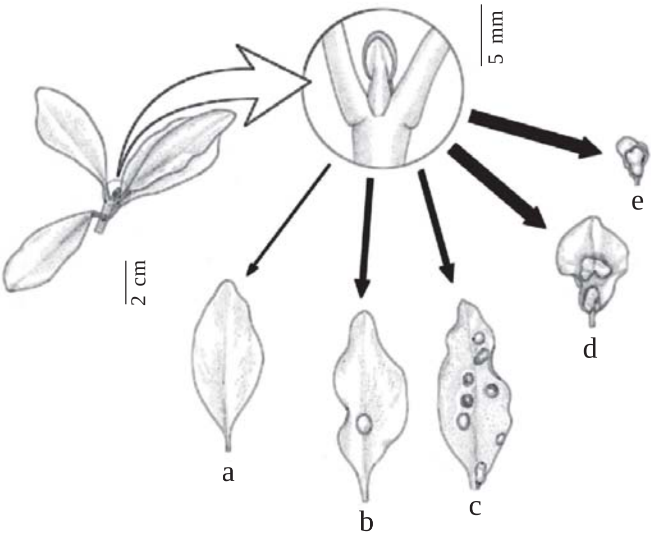

Fig. 1. *C. lanceolata* leaves under different parasitism intensity by the gall former *C. nitida* (Cecidomyiidae). a) ungalled leaf, b) leaf with just one gall, c) leaf with several galls (two, three, four or more scattered galls), d) coalescent galls, and e) deformed leaf.

Table I. Nested Mixed Effect ANOVA Model describing the sources of variation detected in *C. lanceolata* leaves' parameters. The † symbol indicates the interaction term.

Source	D.F.	Type I SS	Mean Square	F	P
Leaf biomass					
Tree	13	0.99	0.08	19.65	0.001
Pair within tree	268	3.73	0.01	3.59	0.001
Categories	2	0.15	0.07	18.82	0.001
Tree†categories	19	0.41	0.02	5.59	0.001
Leaf area					
Tree	13	965.32	75.56	41.37	0.001
Pair within tree	268	5,175.79	19.31	10.86	0.001
Categories	2	87.13	43.57	24.50	0.001
Tree†categories	19	221.04	11.63	6.54	0.001
Specific area					
Tree	13	11,498.73	884.52	15.77	0.001
Pair within tree	268	37,734.69	140.80	2.51	0.001
Categories	2	8,856.47	4,428.24	78.93	0.001
Tree†categories	19	3,128.05	164.63	2.93	0.001

pairs, ungalled pairs and galled pairs. Therefore, 446 leaves were used in the analyses. Leaves from pairs missing a leaf were not considered.

RESULTS

Galling intensity and its impact on leaves

There was significant variation of leaf biomass, leaf area, and specific area of *C. lanceolata* explained by the presence of *C. nitida* galls. There was also a significant difference due to individual trees and pairs of leaves in leaf morpho-physiological characteristics (Table I). The statistical model composed by the variables "tree", "pair of leaves", and "presence of gall" described more than 90% of the variation of *C. lanceolata* leaf parameters (Table II). Regarding the importance these factors have on leaves, from here our analysis deals only with the impact *C. nitida* galls have on *C. lanceolata* leaves.

All parameters analyzed were significantly influenced by the attack intensity (Table III). Gall effect on *C. lanceolata*, however, was different according to variation in the intensity of parasitism (Table IV). The biomass of leaves attacked by *C. nitida* galls significantly increased according to the number of galls per leaf. Leaves with few galls (ranging from 1 to 4 galls) were significantly different from ungalled leaves. Leaves with lots of scattered galls, leaves with coalescent galls and deformed leaves were significantly heavier than leaves with few galls and ungalled leaves (Fig. 2A). The area of leaves with few galls did not increase compared to ungalled leaves. Only leaves with more than four galls had their surface significantly increased by the presence of galls. However, leaf area significantly decreased into very small values in leaves with coalescent galls and deformed leaves (Fig. 2B). The specific area of *C. lanceolata* leaves with few galls significantly decreased as the number of galls increased. Leaves with two or three scattered galls were not significantly different from leaves with more than four galls. However, specific area significantly decreased in leaves with coalescent galls and, then, deformed leaves (Fig. 2C). Besides, 90% ($n = 30$) of the total deformed leaves collected in this study were located in the youngest pair of leaves in *C. lanceolata* branch. The other 10% of deformed leaves were found in older (second and third) pairs of leaves.

Gall effect on opposite leaves

Ungalled leaves in the same pair of galled leaves were not affected by the presence of galls, since ungalled leaves of heterogeneous pairs behaved like the typical ungalled leaves (represented by the class of leaves of ungalled pairs). The three parameters analyzed were not significantly different between these two classes of ungalled leaves (Fig. 3). As a control, galled leaves of heterogeneous pairs were compared to leaves of galled pairs. All parameters were not significantly different between classes of galled leaves (Fig. 3).

DISCUSSION

Our statistical model detected *C. nitida* interaction with plant individuals and branches explaining more then 90% of variation in morpho-physiological leaf characteristics, although there is possibly variation on *C. lanceolata* leaf characteristics due to resource variation.

The variation of *C. nitida* herbivory intensity level determined changes in *C. lanceolata* leaf characteristics. As the herbivory intensity increases until moderate intensity attack, the plant increases galled leaf biomass and does not lose leaf surface area, however, the specific area decreases. This intensity level response is typified by leaves with scattered galls. Under high herbivory intensity, galled leaves have reduced surface area and the biomass is kept high. It causes extremely low values of specific area. This intensity level response is typified by deformed leaves. The specific area decreasing gradient indicates that the more intense is the gall midge parasitism, the more it costs the plant to maintain its leaf structure. Therefore, morpho-physiological plant traits changes depending on the levels of parasitism intensity.

A likely explanation to the response gradient is given by the nature of the insect-plant parasitic interaction. Galling insects induce their galls in the first stages of leaf development (Mani 1961), when leaves still behave as consumer organs (Taiz & Zeiger 2002). Thus, the presence of gall inducer should enhance the sink characteristics of leaves. In the case of *C.*

Table II. Model Summaries for nested mixed effects ANOVAs for variation detected in the three morpho-physiological characteristics of *C. lanceolata* leaves.

Leaf parameters	R^2	Coefficient of variation	Root MSE	Mean
Biomass	0.92	32.88	0.06	0.19
Area	0.96	15.26	1.33	9.74
Specific area	0.94	13.48	7.49	55.56

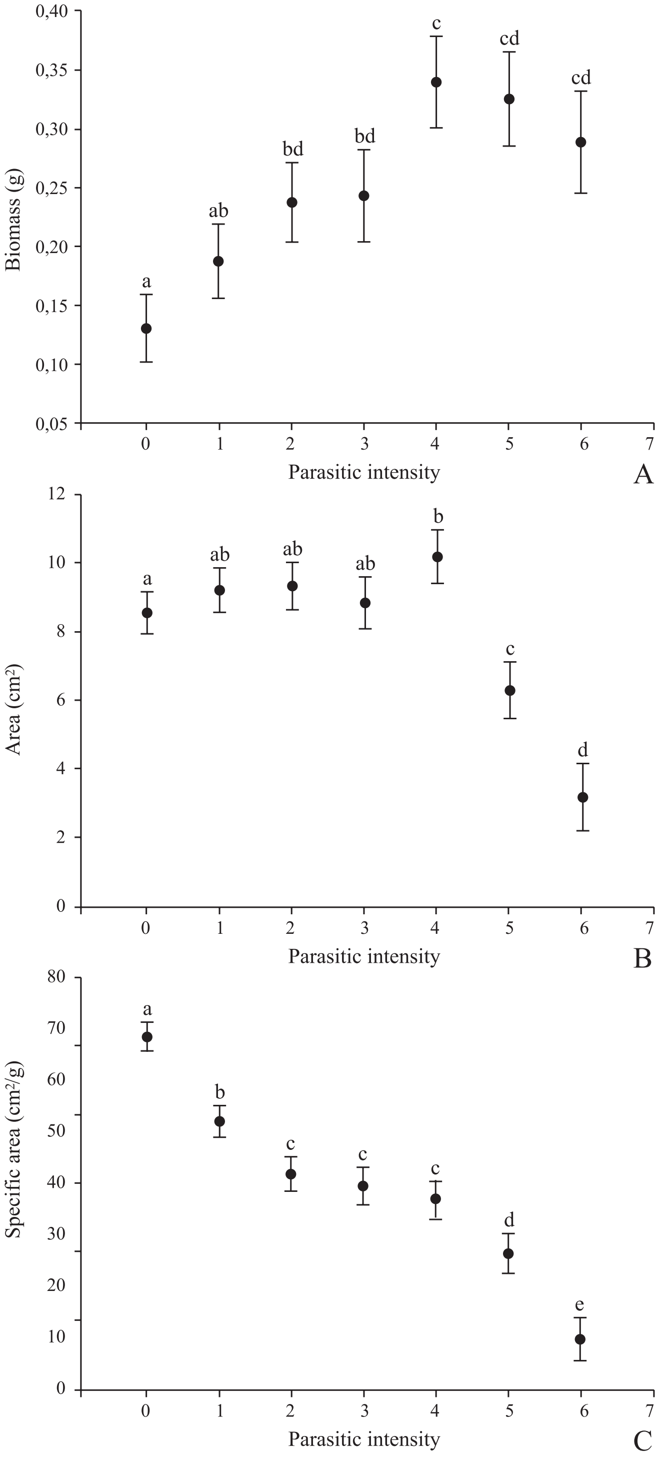

Fig. 2. Response of *C. lanceolata* leaves' morphological parameters to variation on *C. nitida* parasitic intensity level. A) Biomass; B) Area; and C) Specific area. Intensity levels are represented by numbers: 0 – ungalled leaves; 1 – leaves with one scattered gall; 2 – leaves with two scattered galls; 3 – leaves with three scattered galls; 4 – leaves with four or more scattered galls; 5 – leaves with coalescent galls; 6 – deformed leaves. Plots indicate least square means and bars indicate standard error. Letters indicate significant differences between means.

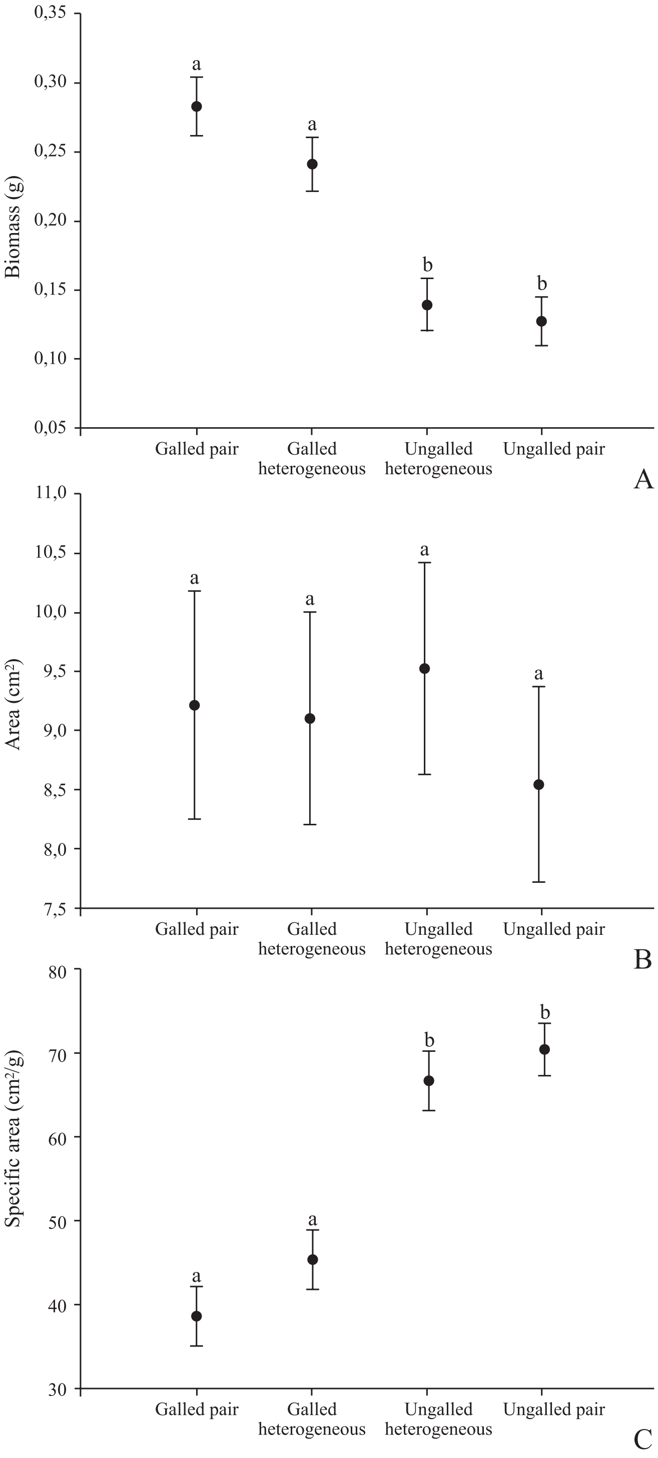

Fig. 3. *C. nitida* gall's effect on pairs of *C. lanceolata* leaves. A) Biomass; B) Area; and C) Specific area. Leaves are organized in natural pairs of two ungalled leaves (ungalled pair), two galled leaves (galled pair), and one galled and one ungalled leaf (heterogeneous pair). Leaves of heterogeneous pair are separated as ungalled heterogeneous and galled heterogeneous. Plots indicate least square means and bars indicate standard error. Letters indicate significant differences between means.

lanceolata under moderate attack, the leaf area expansion caused by gall presence may suggest that this parasitic interaction function as a mobilizing sink (McCrea *et al.* 1985) directing resources to the leaves, even when leaves are developed. Considering that changing levels of parasitism also cause variation in both biomass and specific area in the host

Table III. Overall F test of the three Mixed ANOVA models for the affects of *C. nitida* gall on *C. lanceolata* leaves.

Leaf parameters	Num DF	Den DF	F	P
Biomass	6	42	5.74	0.0002
Area	6	42	11.16	< 0.0001
Specific area	6	42	53.15	< 0.0001

plant, galls induced by *Clusiamyia nitida* can be considered as a very strong resource sink (Fay *et al.* 1993). Thus, in *C. lanceolata* more resources than would normally be diverted to leaves are directed to galled leaves under moderate gall midge parasitism, and the number of galls is correlated with the intensity of this resource allocation. Given that resources are mobilized by leaves in order to maintain the galled structures and insect growth (Larson & Whitham 1991), this structure can be compared to fruits, buds and new branches (Larson & Whitham 1997).

In cases of high parasitism intensity in *C. lanceolata*, leaves are deformed and represent very strong sinks with apparently low production capacity. This is the case even in adult leaves with very small surface area. Similarly, cottonwood's galled leaves lose their normal function; they act as consumers and may even compete with other organs for plant resources (Larson & Whitham 1997). According to Williams & Whitham (1986) these changes in function associated with the extremely high cost to maintain this type of leaf would explain the abscission of deformed leaves as *C. lanceolata* response to high intensity parasitism. Leaf abscission may be an adaptive response of plants to herbivory and an unfavorable energy balance (Faeth *et al.* 1981; Williams & Whitham 1986; Karban 2007; Fernandes *et al.* 2008). The sporadic presence of deformed leaves in older pairs of *C. lanceolata* supports the idea that they are readily abscised as already observed in *Pseudotsuga menziesii* (Pinaceae) leaves (Condrashoff 1962) and *Rhus glabra* (Anacardiaceae) (Fernandes *et al.* 1999) in response to their gall-midge.

Our results suggest that gall density is not the only factor responsible for the variation of aspects of galled leaves, given that leaves hosting similar numbers of galls can have very different shapes (i.e. some deformed leaves were found galled by a single midge larva). Other factors such as oviposition pattern and development or fluctuating asymmetry of leaves (Cornelissen & Stiling 2005; Dongen 2006) can also affect vegetative growth and leaf expansion, and consequently the outcome of interaction.

Compensatory Response

Moderate insect gall infestation of *C. lanceolata* leaves resulted in the redirection of plant resources, creating an effect inverse to that of leaf chewing insects that reduce the surface area while feeding (Hartnett & Abrahamson 1979; Larson 1998; Nykänen & Koricheva 2004; Zangerl *et al.* 2002). McNaugthon (1983) proposed that moderate herbivory may benefit plants by enhancing primary production. According to Larson (1998) there should be a compensatory response by the same leaves that are attacked by gall inducers, as a consequence of their role as sinks. The surface of *C. lanceolata* leaves increases under moderate attack intensity (leaves with more then four scattered galls), which could possibly enhance the photosynthetic potential. The specific area of leaves under moderate attack, however, is lower then those from ungalled leaves, indicating that galled leaves were costly. Thus, *C. lanceolata* does not compensate *C. nitida* herbivory under moderate attack intensity that damages the leaf. Additionally, records on leaf color support the negative effect of this intensity level: the gall induced by *C. nitida*, and the leaf as a whole, may become yellowish indicating a possible local decrease in photosynthetic ability differently from its adjacent, from the same cohort, leaf that developed completely and remained green. A similar effect has been noticed in galls induced by aphids in temperate regions (Andersen & Mizell 1987; Larson & Whitham 1991) and Cecidomyiidae in Neotropics (Fernandes *et al.* 2008).

Impact Severity

Herbivore response in non-attacked adjacent organs reported in the literature is contradictory. Kirst & Rapp (1974) identified that *Mikiola fagi* (Cecidomyiidae) galls on *Fagus sylvatica* (Fagaceae) derive nutrients from opposite ungalled

Table IV. Mixed ANOVA Model results for *C. lanceolata* leaf characteristics response to six levels of parasitic intensity plus ungalled leaves. Intensity levels are represented by numbers: 0 – ungalled leaves; 1 – leaves with one scattered gall; 2 – leaves with two scattered galls; 3 – leaves with three scattered galls; 4 – leaves with four or more scattered galls; 5 – leaves with coalescent galls; 6 – deformed leaves. SE represents standard error.

	Biomass				Area				Specific area					
Intensity	Least square means (g)	SE	T	P	Least square means (cm^2)	SE	t	P	Least square means (cm^2/g)	SE	t	P	DF	N
0	0.131	0.028	4.60	<.0001	8.538	0.591	14.46	<.0001	68.801	2.824	24.36	<.0001	42	298
1	0.188	0.031	6.06	<.0001	9.194	0.643	14.29	<.0001	52.316	3.077	17.00	<.0001	42	74
2	0.238	0.332	7.16	<.0001	9.314	0.697	13.37	<.0001	42.115	3.280	12.84	<.0001	42	40
3	0.243	0.039	6.29	<.0001	8.818	0.764	11.54	<.0001	39.756	3.679	10.81	<.0001	42	26
4	0.340	0.039	8.80	<.0001	10.163	0.774	13.14	<.0001	36.971	3.665	10.09	<.0001	42	27
5	0.326	0.040	8.15	<.0001	6.276	0.829	7.57	<.0001	26.595	3.838	6.93	<.0001	42	24
6	0.289	0.043	6.68	<.0001	3.172	0.979	3.24	0.002	9.907	4.124	2.4	0.021	42	20

leaves. Larson (1998) detected a decrease in photosynthetic rates at ungalled leaves neighboring galled leaves. Silva *et al.* (1996) found no change in branches that were neighbors of galled branches of *Vernonia polyanthes* (Asteraceae) while Fay *et al.* (1993) recognized that *Silphium integrifolium* (Asteraceae) galled leaves induce an increase in photosynthesis at adjacent leaves.

Concerning the interaction between *C. lanceolata* and its parasite *C. nitida*, even the plant diverting more resources to galled leaves then usually is directed to ungalled leaves, these resources are restricted to galled leaves. Given that galls creating processes like galls induced by *C. nitida* act as a strong resource sink (Fay *et al.* 1993), one possibility is that this strength would direct resources to the pair of leaves because both leaves are in the same developing cohort. Therefore, the effect of *C. nitida* galls would be detected in ungalled leaves opposing galled leaves. However, ungalled leaves seemed not to be affected by the effect of gall's presence on their opposite paired galled leaves, since the biomass, leaf area, and specific area of ungalled leaves in heterogeneous pairs were similar to those found in leaves of ungalled pairs. Additionally, if there was an effect on adjacent leaf, leaves in pairs of galled leaves would reinforce each other and expand their resource manipulation, extending leaf surface. However, the area of leaves in galled pairs is similar to those in heterogeneous pairs.

Although this study suggests that the effect of galling on morpho-physiological leaf traits is locally restricted in galled leaves, further research would be necessary to investigate the extent of gall's effect other physiological processes and plant characteristics, such as reproductive traits and fitness.

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