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LEAF PALATABILITY AND FOLIVORY IN A FRAGMENTED TEMPERATE FOREST

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Till mig

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ÍNDICE

ÍNDICE DE FIGURAS

RESUMEN

En el bosque maulino, la folivoría es menor en los fragmentos remanentes que en el bosque continuo original. Pusimos a prueba la hipótesis de que la depresión en los niveles de folivoría se debía a una disminución en la palatabilidad foliar causada por el microclima más xérico de los fragmentos. Para ello, comparamos la anatomía foliar en fragmentos y bosque continuo de las especies arbóreas *Aristotelia chilensis*, *Cryptocarya alba*, *Nothofagus glauca* y *Gevuina avellana* y evaluamos el consumo de hojas de ambos tipos de hábitat por las especies de insectos *Sericoides viridis* y *Ormiscodes rufosignata*.

La anatomía foliar de fragmentos difiere de las de bosque continuo en al menos uno de los caracteres evaluados para todas las especies vegetales, sin embargo, no todas las especies presentan caracteres más esclerófilos en fragmentos. *Aristotelia chilensis* es la especie que muestra el mayor número de cambios en su anatomía foliar, siendo más esclerófila en fragmentos. En los experimentos de palatabilidad, no hubo diferencias en el consumo de hojas de fragmentos versus hojas de bosque continuo, no habiendo, por lo tanto, evidencia de una alteración de la palatabilidad foliar en fragmentos.

Esta es la primera aproximación experimental de cambios en la palatabilidad foliar asociados a la fragmentación, por lo que la generalidad de nuestros resultados es incierta, sin embargo, por lo menos para el bosque Maulino costero, la depresión en los niveles de folivoría no puede atribuirse a una reducción en la palatabilidad de las hojas, apoyando la idea de que la menor abundancia y riqueza de especies son los factores que están afectando directamente la folivoría.

Palabras clave: Herbivoría, anatomía foliar, insectos, fragmentación, Chile.

ABSTRACT

In the Maulino forest, folivory is reduced in forest fragments compared to the original large and continuous forest. We experimentally assessed whether depressed folivory levels are related to a reduction in foliar palatability caused by the more xeric microclimate of fragments. For this objective, we compared foliar anatomy in fragments and continuous forest for the tree species *Aristotelia chilensis*, *Cryptocarya alba*, *Nothofagus glauca* and *Gevuina avellana*, and evaluated consumption of leaves of the two different habitats by the insect species *Sericoides viridis* y *Ormiscodes rufosignata*.

Anatomy of leaves of fragments differs from that of leaves of continuous forest in at least one of the traits considered, for all the plant species, however, not all species exhibit more sclerophyllous traits in fragments. *Aristotelia chilensis* is the species that exhibits the greatest number of changes in its anatomy, it being more sclerophyllous in fragments. In palatability trials, there were no differences in the consumption of leaves of fragments versus leaves of continuous forest, thus, there is no evidence of an alteration in foliar palatability in forest fragments.

This is the first experimental assessment of changes in foliar palatability associated to forest fragmentation, so the generality of our result is unknown, however, at least for the coastal Maulino forest, depressed folivory levels in forest remnants cannot be attributed to reduced foliar palatability, offering further support to the idea that decreased abundance and specific richness of folivorous insect are the facts directly impinging upon folivory.

Key words: Herbivory, leaf anatomy, insects, fragmentation, Chile.

INTRODUCTION

Forest fragmentation affects population abundance and species richness as well as biotic interactions (Fahrig 2003). Among the altered interactions is insect folivory, which is usually lower in forest fragments compared to the original large and continuous forest. Reduced population abundance and species richness of folivorous insects is presumed to account for this phenomenon (Arnold & Asquith 2002; Valladares, Salvo & Cagnolo 2006; Wesołowsi & Roviński 2006). However, decreased foliar palatability, an alternative, non-exclusive hypothesis, has not been tested. Fragmentation affects the abiotic conditions of the remaining habitat; forest fragments are more xeric, with decreased soil and air humidity and increased light penetration compared to the original continuous forest (Saunders, Hobbs & Margules 1991; Laurance, Lovejoy, Vasconcelos, Bruna, Didham et al. 2001). Foliage grown under these conditions ought to be thicker and tougher than the foliage grown in the more shaded continuous forest (Lambers, Chapin & Pons 1998; Henriksson, Haukioja, Ossipov, Ossipova, Sillanpää et al. 2003). Increased sun exposure might also induce chemical changes. Sun leaves usually exhibit increased phenolic content as well as lower water content (e.g. Dudt & Shure 1994; Arturi, Relva & Brown 1999; Henriksson et al. 2003). Altogether, these changes alter the digestibility, nutritional value and toxicity of leaves, rendering them less palatable to herbivorous insects (Coley & Barone 1996).

In the coastal Maulino forest, a highly fragmented forest of central Chile (Echeverría, Coomes, Salas, Rey-Benayas, Lara et al. 2006), folivory is, on average, 4.9 times lower in forest remnants compared to continuous forest (Simonetti, Grez, Celis-Diez & Bustamante 2007). Lower abundance of folivorous insects is argued to account for the reduced levels of folivory (Simonetti, Grez, Celis-Diez & Bustamante 2006; Simonetti et al. 2007). At the same time, leaves of *Aristotelia chilensis,* a common tree, exhibit thicker epidermis and spongy parenchyma in forest fragments (Repetto, Cavieres & Simonetti in press), indicating that leaves are responding to fragmentation and giving way to the possibility that reduced leaf palatability could also be accounting for depressed folivory levels in fragments.

Here, we experimentally assessed this hypothesis. First, we evaluated if foliage is responding to the more xeric habitat conditions, comparing leaf anatomy in fragments and continuous forest. Second, we determined if leaf palatability is lower in forest remnants compared to continuous forest, by simultaneously offering leaves of both habitats to folivorous insects in cafeteria tests. If foliar palatability in fragments is reduced, insects should consume less foliar tissue of leaves of fragments than of leaves of continuous forest.

METHODS

Study site:

The coastal Maulino forest is located in central Chile, between 35°20' and 37°20' S. It is dominated by caducifolious tree species such as *Nothofagus obliqua* and the endemic *Nothofagus glauca* (San Martin & Donoso 1996). The Los Queules National Reserve protects 145 ha of this forest, but is part of a larger patch of approximately 600 ha, being considered as a continuous forest. Several Maulino forest fragments occur nearby this continuous forest, surrounded by a matrix of *Pinus radiata* (Donoso, Grez & Simonetti 2003). Two of these fragments (measuring 2.3 and 3.0 ha respectively) and the Reserve were used in this study to obtain foliage and insects.

Foliar anatomy:

We studied four tree species: *Aristotelia chilensis*, *Cryptocarya alba*, *Nothofagus glauca* and *Gevuina avellana*. As a measure of anatomical differences between leaves of tress growing in continuous forest and forest remnants, we compared the thickness of the leaf lamina as well as the thickness of the adaxial and abaxial epidermis, and the palisade and spongy parenchymas. We collected two mature, non-senescent leaves from five tree individuals per habitat and species. Leaves were fixed in a mixture of formaldehyde (5%), alcohol (90%) and acetic acid (5%) during a week, dehydrated in a battery of ascending alcohol concentration (50%, 75%, 95% and 100%) and included in Paraplast. Histological sections were taken with a microtome and dyed with 'fast green' and safranin. Digital photographs were taken from the histological sections with a microscope camera (MiniVID MV110-U) and the image analysis software UTHSCSA ImageTool 3.0 was used to estimate thickness of the anatomical traits. Statistical differences between habitats were evaluated using a two tailed Mann-Whitney U test.

Palatability trials:

We assessed differences in palatability of leaves of trees growing in forest fragments and continuous forest by evaluating consumption by two common insect species: *Ormiscodes rufosignata* (Lepidoptera: Saturniidae) and *Sericoides viridis* (Coleoptera: Scarabeidae) (De la Vega 2007). Larvae of *O. rufosignata* were collected at fragments and continuous forest and tested with leaves of *A. chilensis*, *C. alba*, *G. avellana* and *N. glauca*. Adults of *S. viridis* were collected at fragments and tested with leaves of *A. chilensis*.

Trials were performed in form of cafeteria-tests (Fig. 1). Each test consisted in offering, to one insect individual, similarly-sized portions (2.5 x 2.5 cm) of a fresh leaf collected at a fragment and of one collected at continuous forest. Leaf portions were randomly placed equidistant from each other in a Petri dish and the insect was set in between them. Dishes were covered with a net to allow air flow and trials carried on for 24 hours. Foliar area eaten from each square was measured with help of a millimeter grid. Trials were performed on late spring of the Southern hemisphere, on 2006 for *O. rufosignata,* and on 2005 and 2006 for *S. viridis*. See Appendix 2 for number of replicates performed. Statistical differences were evaluated using a two tailed Wilcoxon matched pairs test.

Figure 1. Cafeteria test with a larva of *O. rufosignata* and leaf sections of *A. chilensis* of a fragment (right) and of the continuous forest (left).

RESULTS

Foliar anatomy:

Leaves of trees growing in forest fragments differed from those of trees growing in continuous forest in at least one of the anatomical traits considered, in all species. In *A. chilensis,* leaves of fragments exhibited a thicker lamina, abaxial epidermis and palisade and spongy parenchyma, while thickness of the adaxial epidermis did not differ significantly between fragments and continuous forest (Figs. 2 and 3). In *C. alba,* only palisade parenchyma differed significantly between habitats, and was narrower in fragments. In *G. avellana,* adaxial epidermis and palisade parenchyma were both thicker in fragments, while spongy parenchyma was thicker in continuous forest, and neither the lamina nor the abaxial epidermis differed significantly between habitats. Finally, in *N. glauca*, only the adaxial epidermis and the spongy parenchyma differed between habitats and both were narrower in fragments (Fig. 3).

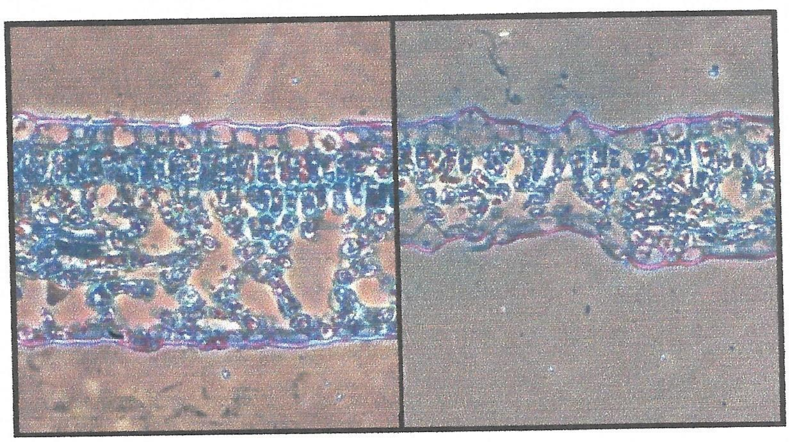

Figure 2. Histological sections of leaves of *Aristotelia chilensis* of a forest fragment (left) and of the continuous forest (right) (200x). Leaf lamina, abaxial epidermis and palisade and spongy parenchymas were thicker in fragments, indicating more sclerophylly.

In brief, palisade and spongy parenchymas differed between habitats in three species each, followed by adaxial epidermis, which differed in two. Thickness of leaf lamina and abaxial epidermis only differed between habitats in a single species each (Fig. 3, Appendix 1).

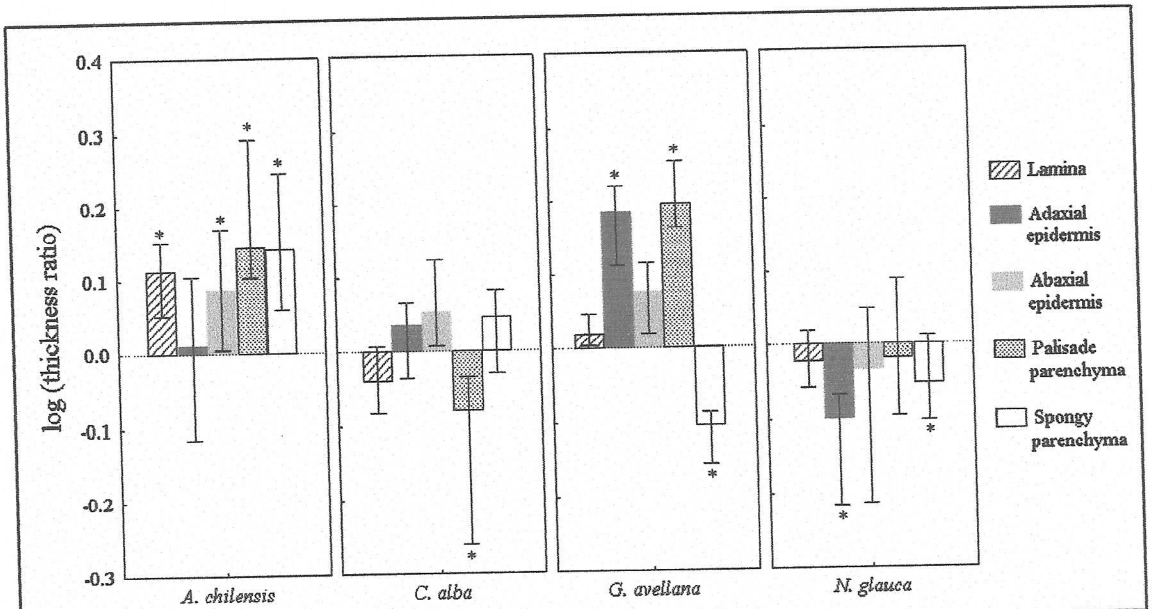

Figure 3. Compared foliar anatomy, presented as the logarithm of the ratio between thickness of a given anatomical trait in fragments and in the continuous forest. Median, first and third quartiles are depicted. * = Significant differences between habitats ($p \leq 0.05$, $n = 10$).

Palatability trials:

Regardless of the plant species tested, foliar area consumed by *O. rufosignata* of leaves of forest fragments compared to that consumed of leaves of continuous forest did not differ significantly (Fig. 4). Similarly, foliar area consumed by *S. viridis* of leaves of *A. chilensis* growing on the two different habitats did not differ significantly, both in the trials performed in 2006 as well as those performed in 2005 (Fig. 4, Appendix 2).

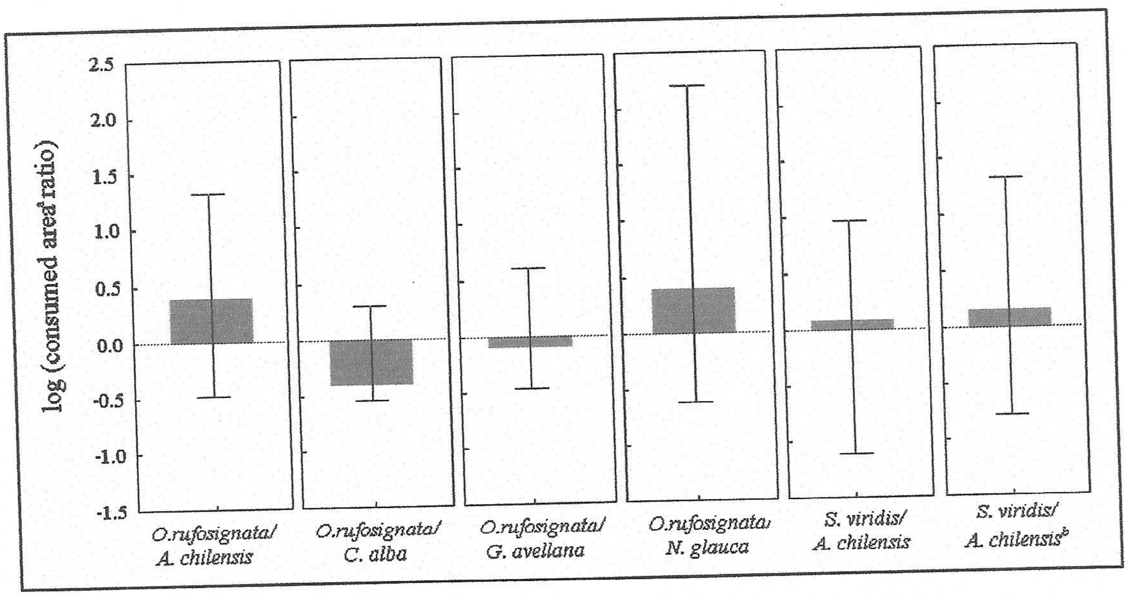

Figure 4. Compared foliar area consumed in cafeteria tests, presented as the logarithm of the ratio between foliar area[a] consumed of leaves of fragments and of leaves of continuous forest. Median, first and third quartiles are given. There were none significant differences between consumption ($p \geq 0.05$, n = see appendix 2). [a] = Area consumed was added 1, to allow ratio calculation in cases where area consumed from continuous forest was zero. [b] = Trials performed on 2005.

DISCUSSION

In tropical and temperate forests, folivory decreases when habitat is fragmented (Arnold et al. 2002; Valladares et al. 2006; Wesołowsi et al. 2006). Similarly, at the Maulino forest, folivory of *A. chilensis*, *C. alba* and *Persea lingue* is reduced in forest fragments (Vásquez, Grez, Bustamante & Simonetti 2007; Simonetti et al. 2007). Forest remnants are more xeric, which could cause leaves to alter their morpho-chemical characteristics (Lambers et al. 1998; Henriksson et al. 2003), thus possibly lowering their palatability and contributing to reduce folivory.

Our results indicate that, in fact, foliar anatomy differs in individuals of the same species grown in the continuous forest as compared to individuals grown in forest fragments. However, the response is variable between species and traits and no general trend is observed in the magnitude or the direction of the change in thickness of the different anatomical traits. Consistent with the results of Reppeto et al. (in press), *A. chilensis* exhibited thicker and thus more sclerophyllous leaf traits in forest fragments, and we expected the other species to respond in a similar way to fragmentation, however, some anatomical traits of *C. alba*, *G. avellana* and *N. glauca* were narrower in forest remnants, and several did not differ between the two habitats. The observed variability may be related to the specific light demands and successional status of each species. Generalist species (in terms of their shade tolerance) are expected to be more plastic than shade-tolerant species. At the same time, pioneer species are expected to be more plastic than late successional ones (Jackson 1967, Bazzaz 1970, Ashton & Berlyn 1992, Hunter 1996). Thus, higher plasticity of leaves of *A. chilensis* is not surprising, as this species is the only of the four analyzed that is both a generalist and pioneer species, and can grow in sunny, dry habitats as well as in shaded ones maintaining a similar photosynthetic capacity (Lusk & del Pozo 2002; Repetto et al. in press).

We found no differences in palatability of leaves of fragments as compared to leaves of continuous forest. Neither *O. rufosignata* nor *S. viridis* discriminated between leaves according to their

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origin. Since *C. alba* and *N. glauca* exhibited few anatomical modifications in response to fragmentation, it was expectable that foliar palatability remained unchanged, as for *G. avellana*, in which the response did not follow a clear trend towards sclerophylly. The absence of a change in foliar palatability is more unexpected in the case of *A. chilensis*, the only species that exhibited an increase in thickness of the leaf lamina in forest fragments. Thus, the effect of fragmentation on leaves is not significant enough to alter their acceptance by folivores, not even in the species that exhibited the strongest response.

There are no other experimental assessments of changes in foliar palatability associated to forest fragmentation, so the generality of our results is unknown, however, at least at the coastal Maulino forest, depressed folivory levels in forest remnants cannot be attributed to reduced foliar palatability, offering further support to the idea that decreased abundance and specific richness of folivorous insects are the facts directly impinging upon folivory.

Appendix 1. Thickness of anatomical traits of leaves of four Maulino forest tree species of forest fragments and continuous forest. The U stadigraph and the probability (p) of type I error of the Mann-Whitney U test are shown. When U value is zero the alternative Z value is given (values marked with *).

		Continuous forest		Fragments			
Species	Trait	Median (µm)	1st - 3rd quartile (µm)	Median (µm)	1st-3rd quartile (µm)	U	p
A. chilensis	Lamina	115.8	108.9 - 118.4	152.2	130.4 – 169.1	7	≤ 0.01
	Adaxial epidermis	15.5	14.3 – 17.6	16.8	15.0 - 18.1	40	0.45
	Abaxial epidermis	8.2	6.8 – 9.3	9.4	8.5 - 10.8	23	≤ 0.05
	Palisade parenchyma	33.3	25.1 – 40.3	49.8	45.2 - 52.5	-3.78*	≤ 0.01
	Spongy parenchyma	47.1	42.6 – 49.6	65.2	51.7 - 85.6	12	≤ 0.01
C. alba	Lamina	249.7	242.0 - 260.2	239.6	204.9 - 251.8	31	0.15
	Adaxial epidermis	32.7	28.8 – 35.6	34.5	33.3 – 37.2	36	0.29
	Abaxial epidermis	8.7	8.3 - 9.7	10.0	8.9 - 11.4	27.5	0.29
	Palisade parenchyma	73.3	59.4 – 82.3	51.9	43.4 - 61.8	17	≤ 0.05
	Spongy parenchyma	124.2	118.7 - 132.9	136.4	112.2 - 145.4	40	0.45
G. avellana	Lamina	378.8	362.3 - 402.8	386.9	370.7 – 440.6	33	0.19
	Adaxial epidermis	11.0	9.4 - 12.7	16.3	14.6 - 19.1	-3.78*	≤ 0.01
	Abaxial epidermis	8.6	7.8 - 9.4	10.4	8.4 - 12.0	25.5	0.06
	Palisade parenchyma	80.0	73.0 – 86.0	128.5	118.4 - 140.0	3	≤ 0.01
	Spongy parenchyma	274.3	254.9 - 294.0	214.3	198.6 - 221.7	4	≤ 0.01
N. glauca	Lamina	158.5	150.1 - 168.0	144.2	137.8 - 156.5	31	0.15
	Adaxial epidermis	17.8	13.7 – 18.5	14.2	10.9 – 15.0	24	≤ 0.05
	Abaxial epidermis	12.3	11.3 – 17.5	11.4	10.2 - 14.2	35.5	0.27
	Palisade parenchyma	53.1	49.6 – 55.2	51.0	46.0 - 54.0	39	0.41
	Spongy parenchyma	72.3	67.7 – 77.5	62.4	59.7 - 69.6	24	≤ 0.05

Appendix 2. Area consumed of leaves from continuous forest and from fragments by *O. rufosignata* larvae and *S. viridis* in palatability trails. The Z stadigraph and the probability (p) of type I error of the Wilcoxon rank-paired test are shown.

		Continuous forest		Fragments			
Insect / Plant species	n	Median (mm^2)	1^{st}-3^{rd} quartile (mm^2)	Median (mm^2)	1^{st}-3^{rd} quartile (mm^2)	Z	p
O. rufosignata / A. chilensis	18	0	0-26	6.5	1-23	0.35	0.73
O. rufosignata / C. alba	8	2.5	1-4.5	2	0-6.5	0.59	0.55
O. rufosignata / G. avellana	10	28	0-82	14.5	3-134	0.25	0.80
O. rufosignata / N. glauca	22	34	0-224	120.5	25-184	0.89	0.37
S. viridis / A. chilensis	62	7	1-25	9	1-19	0.49	0.62
S. viridis / A. chilensis^b	25	2.5	0-15	10	0-20	0.66	0.51

^{b} = *Trials performed in 2005. See Methods.*