

Vegetative Responses to Defoliation of Two Chilean Matorral Shrubs

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Summary. This paper reports the results of experimental defoliation of two common matorral species: *Lithraea caustica* and *Colliguaya odorifera*. *L. caustica* and *C. odorifera* are the matorral species previously shown to exhibit the highest and lowest levels of natural defoliation by browsing. Experimental defoliation was performed at four levels: 0% (controls), 25%, 66%, and 100%. *C. odorifera* exhibited vegetative responses stronger than controls only in the two highest levels of defoliation (66% and 100%), whereas *L. caustica* responded vigorously at the 25% and 100% levels. The results are related to the observed position of both species in the matorral community and their relative defoliation risks by natural and introduced herbivores.

Introduction

The dominant plant community in Central Chile is the matorral which consists mostly of evergreens with some deciduous and semi-deciduous trees and shrubs (Parsons 1976). Several studies on the physiognomy of the matorral have been conducted (Mooney 1977; Thrower and Bradbury 1977), but little information exists about the factors structuring the matorral communities. Defoliation has been postulated to be an important structuring factor of shrub communities in Central Chile, and evidence collected by Fuentes et al. (1978) suggests that even low defoliation leads, in an intensely competitive community, to shifts in the competitive equilibrium and thus leads to the exclusion of the most palatable species. Although average defoliation levels for various matorral species tend to be low (of the order of 10%), more heavily defoliated plants are not necessarily less abundant (Fuentes et al. 1978).

These observations suggested that shrub species might differ in their responses to defoliation and might perhaps even be able to compensate for moderate canopy losses. The aim of this work was therefore to quantify, during one complete growing season, the patterns of recovery from experimental defoliation in two contrasting matorral shrub species: *Colliguaya odorifera* which has an average natural defoliation of 2% and *Lithraea caustica* with an average of about 18%. These two species represent the extreme low and high plant defoliation types measured in the matorral community, and were therefore expected to exhibit the greatest differences in their responses.

The Species

Both shrubs are very common in the Chilean matorral community (Mooney 1977). *L. caustica* (Anacardiaceae) is an evergreen dense shrub that grows up to 5 m in height and 1–2 cm in diameter. It is frequently found on mesic slopes and forms dense mixed-species stands (Parsons 1976; Armesto and Martínez 1978). Its growing season starts late in October, extends through the summer, and ends in February (Montenegro et al. 1979). *L. caustica* is known to have a root system at least 1 m deep, (Hoffmann and Kummerow 1978), sclerified leaves (Mooney 1977), and is capable of photosynthesis all year round (Mooney and Dunn 1970; Martínez 1978). Phenological observations suggest that flowering and fruiting depend on the amount of accumulated photosynthate (Montenegro et al. 1979). *C. odorifera* (Euphorbiaceae) is a semi-deciduous shrub (Hoffman and Hoffmann 1976) that grows up to 1.5 m in height and which is approximately spherical in total shape. *C. odorifera* is often found on xeric equator-facing slopes where plants tend to be sparsely distributed and to have a low biomass per individual (Armesto and Gutiérrez 1978). It begins its vegetative growth late in September and ends it in December (Montenegro and Riveros 1976). It has a shallow root system extending about 30 cm in depth (Hoffmann and Kummerow 1978), exhibits stomatal closure during the dry summer period, and does not photosynthesize during that time (Gilberto and Estay 1978; Martínez 1978). Partial shedding of old leaves occurs simultaneously with the appearance of new leaves (Hoffmann and Hoffmann 1976). As has already been mentioned, its foliage infrequently presents evidence of defoliation.

Methods

The experiments were carried out between October 1977 and late February 1978 at Los Dominicos (33°27' S, 70°42' W), in the Andean foothills east of Santiago and at about 1000 m of altitude. A site of approximately 50 × 500 m was chosen where both shrub species were present. Inside this area individuals of each species were assigned to one of four preselected defoliation treatments. Each treatment had four randomly chosen individuals of each species.

0% Treatment. This was our control group in which no leaves were removed.

25% Treatment. One out of every four leaves was removed from each shoot.

66% Treatment. Two out of every three leaves in each shoot were removed.

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100% Treatment. All leaves were removed. Leaves were hand-picked and the counting started from the newest leaf in each shoot. The defoliation experiments were carried out during the last week in October 1977 which approximately coincides with the time of natural defoliation by insects in the matorral (Fuentes et al. 1978). Every week from then on the following data were monitored on a sample of 6 marked shoots randomly chosen on each one of the 16 plants:

- Shoot length in mm from the last node.
- Number of leaves per shoot (old and new ones).
- Length of each leaf in mm.
- Leaf length data were converted into leaf area with previously obtained regressions between the two variables.

Although we initially tagged a sample of six shoots per plant, some were lost during the study period. Therefore in the following report the number of shoots per treatment is not always the same.

We considered that a shoot had stopped growing, if during four consecutive weeks, no changes were detected in the three variables. This happened early in January for *C. odorifera* and late in February for *L. caustica*. Values obtained at these times are referred to as 'final' in this paper. Analogously, measurements taken in the first week of November 1977 are entitled 'initial'.

Because the patterns of response exhibited by the shrubs differ in a complex way and cannot be associated with just one number, we attempted to describe them by using the following five indices:

N = Final number of shoots branching out from each of the original shoots tagged.

S = Final total shoot length/length of the original shoot. Here final total shoot length is the sum of the lengths of all the shoots sprouted from the original one, plus the final length attained by the original shoot.

li = Initial number of leaves per shoot. li is not 0 for 100% defoliation because, when the first measures were made, the leaves had already appeared.

lf = Final number of leaves per shoot.

a = Leaf area per shoot. The value of a is obtained by adding the areas of all leaves in one shoot. The values of af and ai correspond respectively to the final and initial states.

L = Increment in the density of leaves. We define density of leaves as number of leaves per unit of shoot length. L was computed using the formula:

$$L = \frac{lf/Sf - li/Si}{li/Si}$$

where Sf and Si are the final and initial shoot lengths respectively. L is thus the fractional increment in the number of leaves per unit of shoot length. L , together with the ratio lf/li , is an estimator of the change in the capacity to intercept branches of competing neighbours.

Variables lf , li , af , and ai , on the other hand, relate to growth in number of leaves and leaf area respectively, and are proportional to total photosynthetic capacity.

Comparisons between control values and treatment effects at various defoliation levels within species were tested with a One-way Kurskall-Wallis Analysis of Variance and then with Multiple Comparison tests (Hollander and Wolfe 1973).

Results

Results are shown in Table 1. It can be seen that, when compared with their controls, the two shrub species differ from each other's responses at the 25% and 66% level but less at 100% defoliation.

Table 1. Growth responses by two species of matorral shrubs in Chile to experimental defoliation. For meaning of symbols, see text. Asterisk indicates significant differences ($P < 0.05$) from control group, using One-way Kurskall-Wallis Analysis of Variance and then a Multiple Comparisons test (see Hollander and Wolfe 1973)

Index	<i>Colliguaya odorifera</i>				<i>Lithraea caustica</i>			
	Defoliation				Defoliation			
	0%	25%	66%	100%	0%	25%	66%	100%
N	1.6	1.4	1.8*	2.8*	2.1	6.2*	3.7	9.5*
S	1.2	1.2	1.3*	1.6*	1.5	3.3*	3.3	5.6*
lf/li	1.2	1.2	2.9*	4.5*	1.5	7.1*	4.3*	1.2*
af/ai	1.2	1.3	2.1*	6.2*	4.8	5.7	5.8	7.7
L	0.1	-0.1	1.0*	1.4*	-0.2	1.7*	0.6	0.4
Sample size	21	23	16	16	16	16	11	14

Thus, whereas the responses in *C. odorifera* are restricted to the two highest defoliation treatments, *L. caustica* tends to exhibit strong responses at the 25% level, but not at the 66% level.

Discussion and Conclusions

Our results indicate that *L. caustica* differs more from *C. odorifera* at low defoliation levels which are comparable to levels that could be related to herbivores, than at high or complete defoliation levels, where other perhaps more general responses could prevail (Churchill et al. 1964; Rockwood 1973). The significance of these differences is apparent when their microdistribution and relations to herbivores are compared.

These responses of the two shrub species suggest that even though they differ in their amounts of natural defoliation, *L. caustica* is able to compensate for moderate leaf losses. Thus natural defoliation in this species would not diminish its photosynthetic capacity during the subsequent spring when peak vegetative growth occurs (Montenegro et al. 1979). This 'functional response' exhibited by *L. caustica* could thus be one of the mechanisms that prevents this relatively highly defoliated species from being excluded from the strongly competitive mesic slopes of the matorral community.

C. odorifera, on the other hand, is generally part of drier slopes, is known to have more toxic compounds in its leaves than *L. caustica* (Montenegro et al. in press), and therefore fits more into the stress-tolerant strategy (*sensu* Grime 1977). This latter species usually sheds parts of its canopy in late summer (Hoffmann and Hoffmann, 1976), greatly diminishes its photosynthesis during this season and seems to have an adaptive strategy where the renewal of parts of its leaves after moderate defoliation in late spring would have an insignificant fitness value.

A common observation around sites where introduced goats are kept seems to support our suggestions regarding the adaptive value of the functional response of *L. caustica*. Goats are known to eat most of the matorral shrub species indiscriminately and where these animals are fed, the relative abundance of *L. caustica* increases at the expense of other shrubs, particularly *C. odorifera*,

which does not exhibit a strong functional response at low defoliation levels.

As mentioned above *L. caustica* and *C. odorifera* are two extreme species in their naturally occurring defoliation levels, and future work will show if other intermediately defoliated species also exhibit intermediate responses to low level defoliation experiments.

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