

# Shrub defoliation in the Chilean matorral: what is its significance?

Defoliación de arbustos en el matorral chileno: ¿cuál es su significado?

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## ABSTRACT

This paper reviews the available information on shrub defoliation in the Chilean matorral. The phenomenon and its patterns in space and time are described. The roles of climate, predators, plant defenses and competition are analyzed within a comprehensive model.

Key words: Defoliation, climatic constraint, predation, competition, plant defenses.

## RESUMEN

Este artículo recopila la información disponible acerca del papel de la defoliación en el matorral chileno. Se describe el fenómeno y sus manifestaciones en el tiempo y en el espacio. Luego se discute un modelo en que se destacan la importancia del clima, depredadores, defensas de las plantas, y de la competición.

Palabras claves: Defoliación, restricciones climáticas, depredación, competición, defensas de las plantas.

## INTRODUCTION

This contribution is a complement to E. Bucher's presentation (in this volume) on the role of native grazers and browsers in South America. Similarly to what seems to be the Argentinian case, in the Chilean temperate areas there are still not many studies of this type. Most studies of interactions between terrestrial native herbivores and plants have been done rather recently and mostly by people associated to our research group. For that reason citations made will look somewhat restricted, but they only reflect the youth of the field in Chile.

Rather than attempting to recapitulate all that has been done, we will focus only on one question and will attempt to explain its ecological significance. Notwithstanding, we must mention the other papers concerning the relationships between herbivores and plants in Chile. For example, there is experimental evidence that browsers can have an important role as killers of shrub seedlings (Fuentes & Simonetti 1982, Fuentes *et al.* 1983, 1986) and that grazers can be effective removers of herbaceous plants (Fuentes & Le Boulenge 1977, Jaksic & Fuentes 1980, Espinoza & Fuentes 1983, Simonetti & Fuentes 1983). These and other studies (Fuentes & Hajek

1979, Fuentes & Etchégaray 1981) have shown that herbivores can greatly modify the physiognomy of the landscapes of central Chile. We do not intend to further discuss these phenomena.

Instead we will identify potentially interesting questions in relation with a still little understood phenomenon: the defoliation of large woody plants in the mediterranean-type shrublands. Our intention is to provide a general scheme where present observations and future experiments could fit, rather than a well proven model with "definite answers". As it will be seen, we are still far from those answers.

Although physiognomically similar formations exist in California and the Mediterranean Basin, as well as in South Africa and Southwestern Australia, there is very little information that allows between-continents comparisons. Perhaps one of the reasons that defoliation of evergreen and drought-deciduous shrubs has not attracted much attention up to now, is that in general the amounts of leaf tissue lost to chewing animals are small. In the Chilean matorral the average percentage lost is in the order of 8 to 10% (Fuentes & Etchégaray 1983), whereas comparable data for the fynbos (South Africa) are only 2% (F. Kruger, personal communication 1980). Only in

Australia, Morrow (1983) found levels of defoliation in the order of 20-30%, but these values seem to show high between-years fluctuations (EF, personal observation).

It is reasonable then to ask whether this defoliation has any biological significance at all. At this point we should clarify that our focus is only on the defoliation of large (reproductive) shrubs and small trees. In our presentation we will: 1) describe the shrub defoliation phenomenon, 2) show some of its patterns in space and time, and 3) present the results of tests designed to evaluate the significance of the phenomenon in a community context.

#### THE PHENOMENON

Shrubs in the Chilean region with winter rains and summer droughts exhibit their vegetative growth from September through October (spring) if they are drought-deciduous, or from November through January, that is from late spring to early summer, if they are evergreen plants (Montenegro *et al.* 1982). (See Mooney

1977, Thrower & Bradbury 1977, Rundel 1981 for descriptions of the Chilean matorral). Defoliating insects, the most important leaf-eating animals, have their peak abundances in spring (Atkins 1977) and show only partial overlap with the growing season of shrubs (Fuentes *et al.* 1981). Leaf chewing insects are mostly lepidopterans and coleopterans (Etchégaray & Fuentes 1980). There are no leaf-cutting ants in Chile.

Neither presently nor in the recent historical past there have been native browsing mammals that forage on large shrubs or trees (Simonetti & Fuentes 1983). However, there is a list (Tamayo & Frassinetti 1980) of such large Pleistocene herbivores, some of which might have had a role as defoliators of matorral shrubs (Table 1). Notwithstanding their possible past importance, because of the recent patterns of landscape modification (Fuentes & Hajek 1979) and the relative short turnover time of matorral ecosystems, their visible effects nowadays are most likely to be in some of the phenotypic attributes of the individual plants, rather than in their abundance patterns. One of these attributes could be the presence of

TABLE 1

Large herbivorous mammals in central Chile. Pleistocene (left column) and recent (right column) large mammals are indicated. The diversity in the past was higher than in historical times, but neither mammal abundances nor their importances as herbivores are known.

Grandes mamíferos herbívoros en Chile central. Se indican los animales del pleistoceno (columna izquierda) y de tiempos históricos recientes (columna derecha). La diversidad fue mayor que en el pasado reciente, pero no se conocen ni las abundancias ni su importancia en cuanto herbívoros de estos animales.

PLEISTOCENE	HISTORICAL TIMES
	Order Edentata
<i>Megatherium medinae</i> . . . . .	No analog
<i>Scelidodon chilense</i> . . . . .	No analog
	Order Litopterna
<i>Macrauchenia</i> sp. . . . .	No analog
	Order Proboscidea
<i>Cuvieronius humboldti</i> . . . . .	No analog
	Order Perissodactyla
<i>Equus curvidens</i> . . . . .	No analog
<i>Equus</i> sp. . . . .	<i>Equus caballus</i>
<i>Onohippidium</i> sp. . . . .	No analog
	Order Artiodactyla
<i>Lama weddelli</i> . . . . .	<i>Lama guanicoe</i>
<i>Lama</i> sp. . . . .	No analog
<i>Antifer</i> sp. . . . .	<i>Hippocamelus bisulcus</i>
No analog . . . . .	<i>Capra hircus</i>

lignotubers in most matorral shrubs (Montenegro *et al.* 1983). Although these subterranean burls have other explanations (Montenegro *et al.* 1983, Fuentes & Espinoza 1986), it may well be possible that defoliation of seedlings and saplings by some of the large Pleistocenic herbivores could have been an additional selective factor for their evolution. Experimental defoliation of *Quillaja saponaria* seedlings shows that they do recover even if this treatment is repeatedly applied. Due to lack of enough appropriate data regarding other such attributes we will not discuss these issues further.

The other currently important browsers in the matorral are goats (*Capra hircus*), which since their introduction have shown to be capable of devastating some central Chilean shrublands (Fuentes & Hajek 1978). Again, we will not discuss them here and interested readers are referred to Fuentes & Etchégaray (1983). We will thus concentrate all our attention on the relation between defoliating insect and large shrubs.

Studies using tagged branches of shrubs have shown that: a) insects forage only on newly produced leaves and frequently eat only a fraction of them (Fuentes *et al.* 1981), b) the probability of insect-attacked and non-attacked leaves of being dropped is about the same (Fuentes & Etchégaray 1983). Therefore, where there are no goats, the total damage caused to the photosynthetic apparatus of shrubs in any given year, can be evaluated by measuring damage to current year leaves in late summer or early fall.

Damage here includes not only what insects actually eat, but also the potential leaf area lost, given that parts of young and still growing leaves are eaten. The proportion of the photosynthetic surface lost by a particular shrub species at any one locality can be estimated by  $E(P) = P(L) \times L$ , where  $E(P)$  is the expected proportion of the average leaf area of a particular shrub species lost to herbivorous insects,  $P(L)$  is the probability of a randomly picked leaf of that shrub species exhibiting any sign of herbivore attack, and  $L$  is the average proportion of an attacked leaf that was actually eaten. We estimated  $L$  in the field by weighing large samples of oven-dried attacked and non-attacked leaves, and  $P(L)$  by randomly sampling between 500 and 900 leaves of 5 to 10 different individual plants of each species at each site.

#### PATTERNS

a) *Species.* Measurements taken in 1977, 1978 and 1980 at Santa Laura on the coastal ranges near Santiago (Thrower & Bradbury 1977), have shown that  $E(P)$  is generally lower than 0.20 and that within a given year between-species differences are significant (Fuentes & Etchégaray 1983). Some species, such as *Lithraea caustica* or *Quillaja saponaria*, consistently showed the higher  $E(P)$  values, whereas shrub species such as *Baccharis* spp., *Muehlenbeckia hastulata* and *Colliguaya odorifera* always exhibited  $E(P)$  values in the order of 0.01 to 0.02 (see also Fuentes *et al.* 1981). Other species, such as *Kageneckia oblonga*, had values that varied in the range between 0.06 and 0.14.

b) *Geographical variation.* Within the area with a mediterranean-type climate there is species—as well as community—wide geographical variation in average  $E(P)$  values. For example, *Colliguaya odorifera* and *Lithraea caustica* show statistically significant positive correlations ( $P$ 's < 0.05) in their  $E(P)$  values with either altitude or latitude of the collecting site (Fuentes & Etchégaray 1983). *Kageneckia oblonga* has been shown to exhibit an  $E(P)$  of 0.07 at a dry site on the Andean ranges, 0.11 at the more mesic Santa Laura site, and even 0.70 along very wet ravines (Fuentes & Etchégaray 1983).

At the community level, at a dry lowland site in Salamanca (about 100 km northeast from Santa Laura), the average community value of  $E(P)$  in 1980 was only 0.02 (SE = 0.01) whereas for that same year at the more mesic Santa Laura site it was 0.07 (SE = 0.02) (Fuentes & Etchégaray 1983). These tendencies point in the same direction, namely, that at wetter sites  $E(P)$  is frequently higher than at drier localities.

c) *Time variation.* Although rainfall occurs in winter and defoliation somewhat later, the high between-year variability in total amount of rainfall (Van Husen 1967) affects  $E(P)$  values. Table 2 (left column) shows the results of measuring  $E(P)$  in the fall of the years 1981 to 1985 on the same eight *L. caustica* shrubs at the Santa Laura site. There is a three-fold difference in the  $E(P)$  values measured. These  $E(P)$  values are significantly correlated ( $r = + 0.91$ ,  $P < 0.01$ ) with the total amount of rainfall during the preceding year, that is, with

the time when growth and defoliation occurred. This finding is in agreement with the above mentioned tendency for wetter conditions to be associated with higher defoliation levels. Both the geographical and between-year patterns, can be associated with the positive correlations between annual rainfall and insect abundances (Fuentes & Campusano 1985), and also with the high correlation ( $r = 0.79$ ,  $P < 0.05$ ) between E(P) values and the relative number of defoliating insects in a given year (Fuentes & Etchégaray 1983). Consequently the net effect of higher rainfall, plant growth, and insect abundances is a higher E(P). That is, the relative importance (cost) of defoliation increases with moisture availability.

In addition to the above mentioned patterns, there is evidence that defoliation is associated with the position of the leaf (sun versus shade) and with their chemistry (R. Cisternas, personal communication 1987).

#### THE COMMUNITY CONTEXT

Why is E(P) so low? We will attempt to answer this question by examining the role of climate and meteorological conditions in restricting insect activity, and in thus reducing the chances of higher defoliation. Then, we will discuss what is known about the role of insect predators in reducing defoliation damage, and, finally, we will analyze the answer resulting from focusing on the potential impact of defoliation on individual shrubs.

a) *Climatic constraints.* Because defoliating insects are active only in spring and shrubs grow only from spring to early summer, it is conceivable that meteorological constraints (e.g., low humidity and high temperature) and not food supply, set the limit to insect activity. Under these circumstances there may be a "climatic window" that, depending on the current year's meteorological conditions, would determine a more or less protracted season during which insects can be active. Thus, in years with a broad window, allowing a longer defoliation season, E(P) could be higher than when the predation window is narrow, but there would always be a climatic imposed limit on how much defoliation can occur. A related explanation also connected to climate, would be that

with the onset of summer, leaves become sclerified (evergreen shrubs) or are dropped (drought-deciduous shrubs), and thus they "escape" herbivory. The main difference between these two hypotheses is that under the first one, young leaves produced late in the "wrong" season would not be eaten, whereas under the second hypothesis they would be attacked as long as they are not sclerified.

Testing of these explanations requires decoupling the role of meteorological conditions in their effect on defoliating insects and on leaf maturation. Matorral shrubs have different root depths and root/shoot ratios (Hoffman & Kummerow 1978 and have access to ground water at different times during the season. *Lithraea caustica* is a species with a deep root system that in addition shows a high within-site variability in its phenology (Hoffmann & Alliende 1984). These characteristics and a specially protracted leaf growing season, allowed us to compare the E(P) values of *L. caustica* plants completing leaf development in late spring (November of 1981), with the E(P) values of plants with late leaf maturation (February 1982). Insects had a "normal" spring season during 1981-1982. It was found that defoliation was on the average 0.26 for the spring growers and only 0.06, significantly lower (Student's t-test,  $P < 0.001$ ), for the summer growing plants. This comparison supports the hypothesis that leaf-eating insects cannot track plant growth into the summer and suggests the importance of climatic constraints in keeping insect herbivory low.

From an evolutionary standpoint, however, the answer is more complex, given that in the mediterranean-type ecosystems of Australia defoliating insects are active during the summer (Edmonds & Specht 1981). But here the growing season of shrubs is also shifted towards the summer! The suggestion arising from comparing these two patterns is that insects accommodate their development to the climatic conditions prevailing when their food is available. For the Chilean matorral this finding implies that climatic conditions are only a proximal constraint for insect phenology, but that in the long-term it is the modal season of leaf growth and maturation (spring-summer), that plays the key role in determining insect activity.

At this point, our question becomes: What prevents insects from attaining higher

densities and thus increasing defoliation during spring? We will attempt to answer this question in the next sections.

b) *Predation of defoliating insects.* A possible explanation for the low values of E(P) is that predation on herbivores is so high that defoliating insects are not food-limited but predator-limited.

Field observations have shown that the main defoliators of *L. caustica* shrubs in central Chile are two relatively specialized (Jerez 1985) chrysomelid beetles: *Procalus viridis* and *P. malaisei* (A. Poiani, in preparation). These two species of beetles are food specialists and tend to be quite sedentary once they land on *L. caustica*, but they leave soon after landing on other plants. It is reasonable therefore to assume that, because *L. caustica* is one of the two or three dominant matorral shrubs (see Mooney 1977, and references therein), the two *Procalus* species spend most of their time on *Lithraea* shrubs and that the predation risks they face are highest during the time they spend on these shrubs.

At Santa Laura there are several species of predators that could potentially reduce *Procalus* densities on the shrubs. Among the larger sized potential predators are some birds (*Falco sparverius*, *Leptasthemura aegithaloides*, *Agriornis livida*, *Asthenes humicola*, *Mimus thenca*, *Pyrope pyrope*, *Anaeretes parulus*, *Sturnella loyca*), lizards (*Callopistes maculatus*, *Liolaemus* spp.), foxes (*Dusicyon* spp.), and small mammals (*Akodon olivaceus*, *Marmosa elegans*).

In an attempt to evaluate the impact of these predators on the E(P) values of *L. caustica*, we started an exclusion experiment in early November 1980. Exclosures made of chicken wire mesh (2 cm in diameter), capable of excluding the above listed predators, were built around eight large (6 to 8 m<sup>3</sup>) shrubs. Within 5 to 15 m of each protected *Lithraea* shrub, a similarly sized individual was used as a control. The first E(P) evaluation was made in October 1980, just prior to building the exclosures, and the following ones in the next Fall (April 1981) and in April of 1982, 1983, 1984 and 1985. Initial E(P) values of protected and unprotected shrubs did not differ significantly (Student's t-test,  $P > 0.30$ ). However, in the 1981 through 1985 measurements there was significantly (ANOVA of ranked E(P)'s,  $P < 0.001$ ) more defoliation of the protected plants (Table 2). That is, the eight shrubs where large predators were excluded, showed more defoliation than unprotected shrubs, just as expected from the hypothesis that predation of herbivores by large animals has a significant role in reducing leaf losses.

Nevertheless, the actual impact of predators could be higher than measured for at least two reasons: First we did not evaluate the impact of predation on defoliators while they were outside *L. caustica* shrubs. Second, we did not evaluate the impact of small predators (other insects, spiders, etc.) that could

TABLE 2

E(P) in different years. Measurements of expected defoliation values (E(P)) of *Lithraea caustica* at Santa Laura for 1980 to 1985 are shown. Values are for shrubs unprotected and protected from large insectivorous animals. On the average (years 1981 through 1985) protected shrubs show an E(P) value of 0.18 and unprotected ones of 0.13, that is, 28% less. Measurements for year 1980 are initial controls.

E(P) en años diferentes. Se muestran los valores esperados de defoliación (E(P)) para *Lithraea caustica* en Santa Laura entre los años 1980 y 1985. Los E(P) corresponden a arbustos desprotegidos y protegidos de grandes animales insectívoros. En promedio (años 1981 a 1985) los arbustos protegidos muestran valores de 0.18 y los desprotegidos de 0.13, es decir, 28% menos. Las cifras indicadas para 1980 corresponden a la situación inicial de control.

Year	E(P) unprotected	E(P) protected	Notes
1980	0.05	0.06	Measurement in October before exclosures were built.
1981	0.13	0.14	Measurements in the fall of indicated year.
1982	0.10	0.16	Same as above.
1983	0.16	0.27	Same as above.
1984	0.13	0.18	Same as above.
1985	0.15	0.16	Same as above.

have a significant impact in reducing herbivore densities. (We verified that protected shrubs were actually pollinated during our experiments and therefore that other insects, besides *Procalus* had access to them). These are still untested considerations that require further work, perhaps with the aid of selective insecticides.

At any rate, predators of insect herbivores seem to have a statistically significant effect on  $E(P)$ , but provided that the difference of  $E(P)$  values between protected and unprotected plants is not different from the between-years difference of  $E(P)$  in one plant, the biological significance of these findings still remains unresolved. In the next section we will address this issue.

c) *What does  $E(P)$  mean to the plants?*

There are two main reasons why defoliation could be important for the shrubs: First, by reducing their seed output, and second, by changing their competitive performance and thus their status in the community.

Although Crawley (1983) shows evidence that the seed output of woody plants is sensitive to small-scale defoliation, experiments with matorral shrubs do not support this contention. Poiani & del Pozo (1986) experimented with shrubs of *Colliguaya odorifera* by removing 20% of their foliage in two consecutive years. They did not find any statistically significant effect on seed production neither on the first nor on the second year of the experiment. This, despite the fact that *C. odorifera* was expected to be relatively sensitive to defoliation owing to its generally low levels of  $E(P)$  and potentially low compensation capacity (Torres *et al.* 1980). It was only at very high hand-made defoliation level that *C. odorifera* reduced its seed output (Poiani & del Pozo 1986), in agreement with previous findings with the shrub *Baccharis rosmarinifolia* (Fuentes *et al.* 1981) under similar experimental conditions.

It seems, therefore, that as long as  $E(P)$  values are not very high and are held within the 10-20% level indicated earlier, defoliation does not reduce plant fitness. We will now explore its role in modifying the importance value of shrub species in the community.

Although the observed leaf losses to herbivorous insects do not kill the plant directly, it is conceivable that if shrubs compete with each other, even small can-

opy losses could have a relatively important effect on their intra- and interspecific competitive performance (Fuentes & Etchegaray 1983). The main reason for this claim is that photosynthetic losses related to  $E(P)$  can have high opportunity costs if they convey reductions of actual and future resource acquisition by non-realized shoot and root growth. Thus, even small annual losses could compound in time and account for major plant size differences. In the next paragraphs we will briefly recapitulate the main evidence supporting this hypothesis.

First, there is observational and experimental evidence that matorral shrubs compete intra as well as inter-specifically (Hoffmann & Kummerow 1978, Gutiérrez & Fuentes 1979, Fuentes & Gutiérrez 1981). It is reasonable therefore to expect that in evolutionary time, factors that reduce resource acquisition by the canopy or root systems, will be minimized as far as possible.

Second, within a site, if  $E(P)$  is unrelated to shrub species abundance, one would expect that  $E(P)$  is positively correlated with plant cover. That is, if other factors besides herbivory account fully for shrub species abundances, insects should be eating more of the most abundant resources if for no other reason that they are more frequently encountered. In favor of this expectation is the evidence that species such as *L. caustica* (Poiani & Fuentes 1985) and *Muehlenbeckia hastulata* (Fuentes *et al.* 1981) exhibit a significant resource concentration effect (Root 1973). That is, insect attack is plant density-dependent.

On the other hand, if  $E(P)$  is a main factor accounting for within-site abundances of shrub species, one would expect that the correlation between  $E(P)$  and shrub species abundance be negative. That is, species would be abundant because they have low values of  $E(P)$  and viceversa. In agreement with this idea is the fact that *Kageneckia oblonga*, for example, shows high  $E(P)$  values where it is scarce (moist sites), and shows lower  $E(P)$  values in more xeric habitats where it is in general more abundant (Fuentes & Etchegaray 1983). Along the same line are also the findings that in unstable successional phases, *M. hastulata* exhibits high defoliation levels, but in mature matorral, where this species

is infrequent, it experiences low herbivory (Fuentes *et al.* 1981).

A third possibility for the relationship between plant abundance and E(P), is that if defoliation is a factor that significantly modifies the competitive performance of shrubs, its impact should always be minimized. In other words, all species independently of their cover, should minimize leaf losses as well as all factors that affect negatively their competitive performance. That is, species or individuals with high values of E(P) should either not be part of the "stable" community at that site or should be frequent only during transient stages.

Results of actually measuring E(P) at Santa Laura in 1977, 1978 and 1980 over a hundred-fold shrub abundance range, showed that E(P) is not significantly correlated with plant species abundance ( $r = 0.06$ ,  $P > 0.86$ ) (Fuentes & Etchegaray 1983). This relationship, the low mean E(P) value (ca. 10%), and the very low variability of data points around the regression line, support the hypothesis that shrub species in a given stand tend to all have low values of E(P) and that all of them tend to minimize the negative effect of defoliation on competitive performance.

How can plants actually minimize E(P) values? As mentioned before, variations in the breadth of the predation window, that is, the time between leaf initiation and sclerification can have very important effects on total defoliation. The extent to which this variable has been important is not known yet. However, leaves of Chilean shrubs have been shown to have several morphological and chemical attributes usually associated (Rhoades & Cates 1976) with anti-herbivore defenses (Thrower & Bradbury 1977, Montenegro *et al.* 1980, Fuentes *et al.* 1981, Walkowiak *et al.* 1984) which presumably contribute to reducing herbivore damage to the leaves. There is also evidence (Sierralta & Fuentes, unpublished) that some species such as *L. caustica*, have herbivore-induced defenses, further suggesting the importance to the plants of preventing defoliation.

That some shrub species respond to the attack of herbivores is seen in the "leaf flushing" response of commonly attacked shrubs, such as *L. caustica*. This is a response at low E(P) levels (ca. 20%) and is not observed in species that are not heavily

attacked by insects, such as *Colliguaya odorifera* (Torres *et al.* 1980).

Another intriguing "defense strategy" concerns the reduction in apparency (Feeney 1976) that shrubs of the Chilean matorral exhibit when they associate with other species to form multispecific clumps (Fuentes *et al.* 1984). Up to now efforts to show that these associations are defense guilds (Atsatt & O'Dowd 1976) have failed (Poiani 1984a, Poiani & Fuentes 1985). Nevertheless, the interspersed nature that shrubs generate could increase local diversity (*sensu* Pimentel 1961, Tahvanainen & Root 1972) and thus reduce herbivory at large spatial scales by reducing potentially high resource concentration effects.

The evidence given about plant defenses also supports the hypothesis that defoliation can have an important effect on shrub community composition and that only plants with low E(P) can coexist at any one site. To the extent that shrubs do not compensate defoliation by increasing the photosynthetic rate of neighboring leaves (Oechel & Fuentes, unpublished), the removal of even a small amount of photosynthetic tissue can have an opportunity cost in terms of future photosynthesis and resource acquisition (see Fuentes & Etchegaray 1983, for a broader description). Through time, even small annual E(P)'s can thus compound and become very important for the total carbon economy and overall competitive abilities during the entire life of the shrubs. It is also quite possible that the E(P) levels we observe in the matorral are the result of a mini-max equilibrium process (Maki & Thompson 1973) and that they are nearly as low as they can be. In other words, lower E(P) might convey too high defense costs to the plants, and lower investments in defenses could have repercussions on plant abundance *via* competition (see Fuentes & Etchegaray 1983, for a model).

The scheme presented in this section has also been validated by observations of the effects of light grazing by goats on relatively undisturbed matorral stands. Let us recapitulate the relevant evidence: First, it is known that shrub species compete with each other and that *L. caustica* has relatively high interaction coefficients (Fuentes & Gutiérrez 1981). Second, it is also known that species such as *L. caustica*, that usually show the higher values of E(P), exhibit shoot compensation mech-

anisms that other species (e.g., *C. odorifera*) do not show (Torres *et al.*, 1980). Third, food preferences of goats and insects are not correlated, and species such as *L. caustica* are not as eagerly eaten as *C. odorifera* (Fuentes & Etchégaray 1983). From these three findings and the model already explained, it is reasonable to expect that even light goat grazing should "shift" the species balance towards an overdominance of species such as *L. caustica*. And this is exactly what has been found in areas where goats have been recently introduced, or where their loads have been relatively light!

#### PERSPECTIVE

The model presented to explain the observed defoliation levels in the matorral is based on our work with relatively few species. In future research with more shrub and herbivore species, the general pattern described will either be confirmed or, most likely, somewhat modified. Hopefully these investigations can be carried out soon given that some of its results could have important applications for the conservation of habitats in central Chile.

At a more speculative level, our results suggest that the defoliation cost to the plant (E(P)) increases with moisture availability, so that it would be interesting to test the general model in localities south of Santiago, where rainfall is higher. The test would have to include an independent verification of between-plants competition and, of the damage caused by defoliation, but also, perhaps, a detailed study of the situation that seedlings and saplings confront.

It would also be desirable to study the defoliation phenomenon in the other four areas in the world with the same type of climate. It is not immediately obvious that the same relationships should hold elsewhere, given that some of them are either fire-climaxes or dis-climaxes (California, Mediterranean Basin) and others have very low soil and plant nutrient levels (Australia and South Africa). In any one of these, the relationship between shrubs and herbivores are likely to be different from what we found in Chile.

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