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Landscape change under indirect effects of human use: the Savanna of Central Chile

Eduardo R. Fuentes, Reinaldo Avilés and Alejandro Segura
Facultad de Ciencias Biologicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

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Abstract

The Chilean Intermediate Depression to the north of Santiago has experienced a physiognomical transformation from a *Prosopis chilensis* woodland to an *Acacia caven* savanna. Today *P. chilensis* trees are scarce and belong mostly to the larger size classes. By contrast *A. caven* seems to reproduce frequently and its populations consist of individuals of all size classes. In this paper we document these changes and report the results of tests aimed at determining the causes of these physiognomical changes. We found that livestock, leporids, introduced Mediterranean forbs and agriculture account for differences in seed dispersal and survival of *A. caven* and *P. chilensis,* which can explain the documented changes in the Chilean landscape.

Introduction

In central Chile there are three main geomorphological elements: the Andes ranges to the east, the coastal ranges to the west and the Central Valley between them (Weischet 1970). The Central Valley is a tertiary graben (a lowered fault block) that, in its northern half, between Chillán (36" 34'S) and Cuesta de Chacabuco (33" S), is intermittently covered with savanna-type vegetation (Eiten 1986), locally known as 'espinal' (Rundel 1981; Ovalle and Avendaño 1988). Espinal refers to the fact that espino *(Acacia caven)* is the predominant woody element both in the flat non irrigated lands and on the emerging inselbergs (residual hills). Irrigated flat lands are now used for agricultural purposes and nothing of the original plant cover remains there. Climate is of the mediterranean type (Aschmann 1977) and consequently the herb cover of this savanna is seasonally green. Herbaceous cover is predominantly introduced Mediterranean region genera such a *Bromus*, *Vulpia*, *Erodium* and *Medicago* (see Gulmon 1977).

In addition to espino, there is a second woody element, *Prosopis chilensis,* in the northern sector of the graben (ca 34.5" 33"). *Prosopis chilensis,* locally known as 'algarrobo', is found only at some sites and in very low densities of less than one individual/ha. But, during Spanish colonial times and until recently, the areas to the north of Santiago were not known as espinales but rather as 'algarrobales', or algarrobo woodlands (review in Looser 1962). As recent as 1958, Looser (1962) saw remnants of these dense forests in the area just north of Santiago. Today such forests do not exist, and where algarrobo trees are present, they are sparsely distributed in the landscape.

The aim of this contribution is threefold: (1) to document current densities and size-classes of *Prosopis chilensis* and *Acacia caven* in the Central Valley north of Santiago, (2) to provide evidence indicating that the contemporary demographic pat-

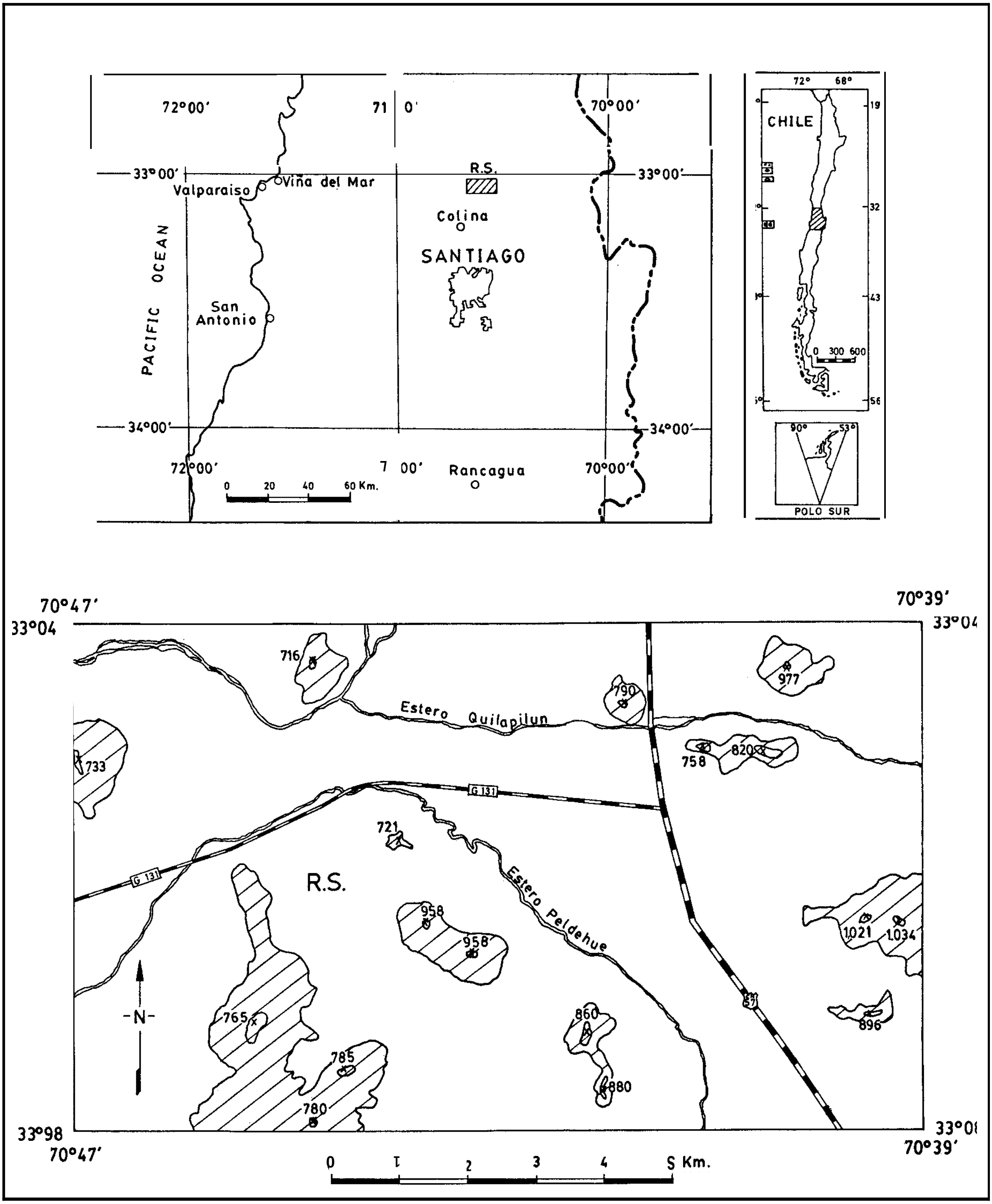

Fig. 1. The location of the Huechún study area. Inselbergs are indicated by dashed lines. RS is the site where the transect was done and experiments with seedlings were installed.

Table 1. Prosopis densities (individuals per ha) evaluated through linear transects in the areas shown in Fig. 1 using aerial photographs taken in 1954 and 1980. Means, standard errors (in parentheses) and sample sizes (n) are shown.

	Density of *Prosopis*	
	1954	1980
Flat land	$\bar{X}$ ± SD (n) 1.66 ± 0.36 (28)	$\bar{X}$ ± SD (n) 0.88 ± 0.29 (18)
Inselbergs	1.73 ± 0.84 (6)	0.75 ± 0.36 (6)

tern reflects a change in physiognomy, from a *Prosopis chilensis* woodland to a savanna landscape dominated by *Acacia caven*, and (3) to show that these changes can be related to the biology of these two species and to the patterns of land use in the area.

The methods used to examine these questions were as follows:

- Temporal changes in vegetation were determined by comparison of aerial photographs.
- Present size class analysis was used as a measure of age distribution of the woody species.
- Land use by humans and animals was evaluated by field surveys.

Some of these controlled observations were made in fields undergoing a conversion to vineyards.

- Seed germination trials were used to evaluate species responses to perturbations induced by different land use patterns.

Sites

All surveys were made in the area locally known as Huechun (33° 05' S), just north of Santiago (Fig. 1). This area is representative of the landscapes of the northern sector of the Central Valley, both by its physiognomy and by land use. This is the same general area where the algarrobo forests were found in the past.

Prosopis densities

Using aerial photographs (flight HYCON 1954 and SAF 1980), and based on the fact that we could recognize individual trees in these photographs, we surveyed the same part of the Huechun area (Fig. 1) in 1954 and 1980. Densities of *Prosopis chilensis* were low and did not differ between inselbergs and flat lands in either 1954 or 1980 (t-test, $P < 0.05$) (Table 1). Nevertheless, in both land units there was a parallel decrease (t-test, P's < 0.05) in the densities of *Prosopis* trees between 1954 and 1980. *Prosopis* density in 1980 was about 50% of the density in 1954. On the inselbergs there was a significant difference between the density of *Prosopis* on the equator-facing and polar-facing slopes (t-test, $P < 0.001$). On average, the density on polar-facing slopes was four times higher than on equator-facing slopes. Transects starting in the flat land and direct-

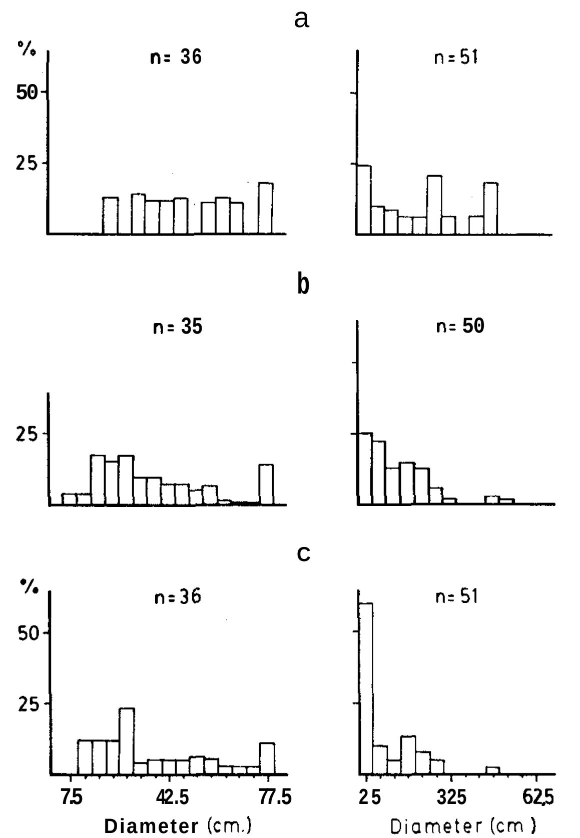

Fig. 2. Size distribution of algarrobo and espino. The left column shows the frequency distribution of *P. chilensis* diameters in cm. The right column shows the values for *A. caven.* The letters (a) indicate flat land sites, (b) inselbergs and (c) road sides. Sample sizes are indicated by (n).

ed towards an inselberg show that *Prosopis* exhibit relatively low frequencies on the flat lands and similar or somewhat higher densities on the inselbergs.

Tree size classes

The size classes of trees found in field surveys carried out in Huechun in 1985 are shown in Fig. 2. Diameters were used to indicate approximate age of the trees since neither *Prosopis* (V. Lamarche, personal communication) nor *Acacia* (M.E. Aljaro, personal communication) form reliable annual rings. From our experience in the field and consultations with locals, it is clear the *Prosopis* of 10 cm diameter at breast height are more than 10 years old. We found that on both flatlands and inselbergs the younger size classes of *Prosopis* are absent, indicating no recruitment in recent years. By contrast, the size classes of *Acacia caven* suggest a more regular recruitment.

Along roadsides, where the soil was removed, recent recruitment of both tree species was more vigorous (G-tests, P's $< .05$). Inselbergs have intermediate size distributions for both species, although *Prosopis* have significantly (G-test, $P < .03$) more juveniles here than on the neighboring flat land.

Seed dispersal and germination

The native dispersers of *Prosopis* and *Acacia* in Chile before the Spanish invasion are unknown. Today *Acacia caven* pods are eaten and dispersed by goats, cows and horses and even by guanaco (*Lama guanicoe*) in semicaptivity (Fuentes *et al.* 1984). It is likely that guanacos also dispersed espino in pre-Columbian times when they were numerous in the area. However, the possible role of large Pleistocene mammals (Fuentes *et al.* 1988) as dispersers of *A. caven* cannot be ruled out. No data are available as to the present or past dispersal agents of *Prosopis* in Chile, but it seems likely that the situation is similar to that of *A. caven*. Cows were common in our study area, and goats are numerous on the Andean foothills nearby. We measured pod densities under three *Prosopis* trees, each surrounded by an experimental fence preventing access to livestock and determined it to be about five times higher than under unfenced controls (Mann-Whitney U-test $P < .05$), indicating that these domestic herbivores removed a substantial part of the total seed crop. Thus, they could have a potentially large role as seed dispersers or as seed predators.

Table 2. Germination of seeds of ***Prosopis*** and ***Acacia*** after being consumed and defecated by different animals. Mean and standard error (in parenthesis) are shown.

	cows	Goats	Controls
P. chilensis	6.6(1.2)	8.6(1.2)	41.0(3.1)
A. caven	6.3(1.0)	6.3(1.8)	1.3(.7)

Since linear transects of contiguous 20 m^2 plots on the flat lands ($n = 24$) and on inselbergs ($n = 18$) showed that cow feces were four times more numerous on the flatlands (t-test, $P < 0.01$), we decided to test the effect of large domestic mammal consumption of seeds from the two legume trees on their germination. Seeds were removed from dung found in the field and planted on sand in the laboratory. **As** controls, seeds were removed directly from pods or collected free on the ground. These were also planted on sand. All of the treatments consisted of three dishes, each with 60 seeds. Germination was monitored until no more emergence was seen for 10 consecutive days.

Results obtained in these germination experiments are shown in Table 2. We found that in comparison with the controls, cows and goats had a significant effect (ANOVA, $P < 0.05$) on increasing the germination of ***A.*** *caven* seeds. In fact, on the average, after the gut treatment, espino seeds germinated at a rate about five times higher than the controls. However, *Prosopis* germination was significantly lower (ANOVA, $P < 0.01$) for seeds passing through cows or goats than for the controls. On the average, seeds that had passed through the gut of these herbivores germinated only about 20% as well as undigested seeds. Thus, large domestic herbivores tended to favor germination of *A. caven* and

Table 3. **Mean seedling densities per hectare on sites with different treatments. Number of 3 x 3 m plots sampled is indicated** by (n).

	P. chilensis	A. caven
'Control' (n = 85)	0	60
'Intermediate' (n = 51)	10.000	230
'Vineyard' (n = 43)	90	4.290

reduce the germination rate of *Prosopis chilensis.*

Seedling survival

The transformation of some parts of Huechun area into vineyards gave us the opportunity in January **1987** to compare the effects of three types of neighboring 'experimental' situations on seedling survival.

The first situation was a savanna plot like the one we described earlier. This was our 'control'. The second site was a large plot thh had been completely cleared in April **1986** (that is, in the fall). Planting and irrigation of the vines was started in August **1986,** when seeds usually germinate, and five full months before our sampling. This 'treatment' included complete removal of the tree and herb cover and elimination of the leporids. The third site, within two kilometers of the other two, was intermediate in disturbance. This 'treatment' included the removal of all trees, cattle and leporids in July **1986.** The soil at this site had not been plowed yet, and it was, therefore, hard and covered with exotic annuals. We were told that after the initial activities ending in July **1986** no further work had been done, and none was intended until the onset of the next rainy season (ca. April–May **1987).**

In sum, the conversion of parts of a large homogeneous area into vineyards gave the seeds that were in the soil in April **1986** the possibility of germinating and establishing under three different conditions. The normal months for the emergence of *Prosopis* seedlings are March and April (Balboa *et* ***al.*** **1988)** and for *Acacia,* February to May (P. Arce, personal communication). Essentially, we had a design with cattle, exotic forbs, leporids and trees (controls), and sites in which none of these factors were operating (vineyard). The third situation (intermediate) had no mammalian herbivores or trees, but still had the original exotic herbaceous cover. Since the initial situation in March **1986** was the same, this fortuitous situation allowed us to study the impact of herbivores and the Mediterranean herbaceous cover on seed germination of espino and algarrobo.

Sampling was done along N-S transects using **3** x **3** m plots in the grid already established for the vineyard. At the control and intermediate sites we measured abundances in similar **3** x **3** m plots along comparable transects.

Contingency-table analysis using G-tests on the frequency distributions for the legume species in the three sites (Table **3)** showed that the two treatments had significant (P's $<$ 0.005) effects on both species. In other words, both herbivores (control versus intermediate) and the herbaceous cover (intermediate versus vineyard) act as factors influencing the densities of the two species.

The additional effect of irrigation can be obtained by densities within the vineyard plots. The density of ***A.*** *caven* along a leaking irrigation line was more than 200 times higher than where the soil was dry between irrigation lines. *Prosopis* density along these irrigation lines was more than **1000** times higher than between irrigation lines. This confirms the suggestion of our earlier finding that polar-facing (wet) slopes have denser *Prosopis* populations that equator facing slopes, *i.e.*, that water is probably a significant limiting factor for the local abundance of both of these species in the Huechun area.

The joint effect of cows and leporids on seedlings of both species was tested in a further experiment. Seedlings of **10** cm height of each of the two species were planted at about **15** m from each other on June **15, 1987** in the flatland and on a nearby inselberg, indicated as R.S. in Fig. 1. Survival was measured for **13** months, from before the beginning of one dry season and until the following rainy seasons

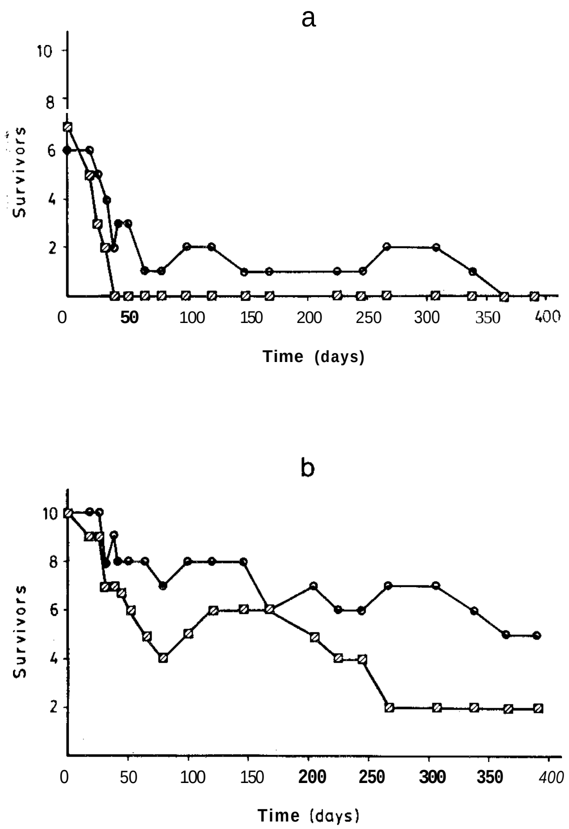

Fig. 3. Seedling survival of ***Prosopis*** and ***Acacia*** on flat land (a) and inselbergs (b). Squares are seedlings of ***P. chilensis*** and circles indicate seedlings of ***A. caven.*** These are survival curves of plants subject to herbivory by cows and leporids and desiccation. The year **1988** was unusually dry and the first winter storms occurred at the end of June, whereas in a normal year they are expected in March (approximately day ***266*** of our experiment).

(Fig. **3).** Contingency-table analysis, using Fisher's exact probability test at day 266 of our experiment (estimated to coincide with the usual beginning of the fall and winter showers) (di Castri and Hajek 1976), indicates that:

i. as a whole, and especially on inselbergs, ***Acacia*** survives better than ***Prosopis*** (*P*'s < 0.05).
ii. ***Prosopis*** and ***Acacia,*** as individual species, survive better on inselbergs.

Effect of agriculture

Sampling **3** x **3** m plots in one-year old abandoned agricultural fields with (n = 59) and without irrigation (n = 51), showed that no seedlings of either legume species were present. However, we found vigorous resprouts of ***A. caven*** in both types of fields. There were 60 individuals of ***Acacia*** per ha in the formerly irrigated wheat fields, and only 4.2 in the dry ones. We did not find a single ***Prosopis*** resprsut in our sampling.

Discussion

The survey area is the same general area as that where the algarrobo forests were found in the past. A common land use practice in this area has been to cut ***Prosopis*** and ***Acacia*** trees as a source of fuel, but both species resprout vigorously after coppicing (Looser 1962, and personal observations). Therefore, it is unlikely that wood-cutting alone can explain the change in the landscape.

A second common practice in the area has been to cut all ***A. caven,*** plow the field, sow wheat (with or without irrigation) for a year and then leave the fields for cattle pasture for the following eight to 10 years. Then the cycle is started again. During the cycle ***Prosopis*** trees are not cut, since their large size provides shade for cattle during the hotter part of the spring and summer of the fallow periods. In our study area this sowing-grazing rotation is found only on the flat lands and not on the inselbergs. Nevertheless, inselbergs are used by cattle as part of their grazing grounds. Where underground water is abundant, parts of this savanna have been converted into vineyards during the last five years. It is still unclear how far this latest landscape transformation will proceed.

Since we found the average density of trees on polar-facing slopes was four times greater than that on equator-facing slopes, humidity could be an important limiting factor for the distribution of ***Prosopis.*** Measurements of soil humidity indicated that the flat lands were 60% wetter than the inselbergs in April, the driest month of the year (t-test, $P < 0.01$). Accordingly, we would expect to find a greater density of ***Prosopis*** on flat lands than on inselbergs. Surprisingly, the densities are similar to those on the inselbergs.

In sum, although densities of ***Prosopis*** are relatively low, and their recent recruitment is not measurable, there are local differences that suggest this lack of recruitment is not due to overall climatic reasons but rather to local constraints.

Although both legume species resprout vigorously when coppiced, only espino regenerates from its roots after plowing. This capacity of *A. caven* to resprout from the roots is probably an additional cause for the transformation of the flat lands from *Prosopis* forests into *Acacia* dominated fields.

The net effect of the consumption of seeds by cows or goats is that the germination rate of *A. caven* is more than 25 times higher than the rate of *P. chilensis* in the presence of these herbivores. In contrast, comparison with the controls suggests that in the absence of domestic herbivores the germination rate of algarrobo is much higher than the rate in espino. The results tend to confirm that *Acacia* survives the attack of leporids and cattle better than *Prosopis.*

We have refered to effects produced by activities such as rotational agriculture and wood-cutting and also to the introduction of species, such as hares, rabbits (see Jaksic and Fuentes 1989) and cows. These activities were not explicitly planned to transform the *Prosopis* forest into an *Acacia* savanna, but the landscape changes are an inadvertent product of human practices. Because changes are the net result of 'triggering' responses in the system, we call these effects indirect.

Conclusions

The observed pattern of the lack of regeneration of *Prosopis chilensis* and of vigorous regeneration of *Acacia caven* can be related to the effects of introduced herbivores, forbs and of agriculture, all of which tend to affect *Prosopis* more than *Acacia*. Thus, *Prosopis chilensis* is more sensitive than *Acacia caven* to ingestion by herbivores, browsing, desiccation and plowing. This result is surprising in view of the reputation that mesquite has in North America as a tree very tolerant of disturbance and capable of colonizing areas perturbed by man.

The effects of disturbance on these two species were not desired. They are all by-products of the interaction between the biological potentialities of the species and human use. Moreover, until now these effects were unknown. Thus, little could be done to favor the conservation of *P. chilensis* in the Huechun area.

At this point it is important to make a cautionary remark. Here we have only described and explained a change from a *Prosopis chilensis* to an *Acacia caven* forest and how man could have been an important factor in this transformation. There are authors (Mann 1968; Rundel 1981) who think that these algarrobales and espinales are climax formations; there are other investigators (Schlegel 1966; Schmithiisen 1956; Oberdorfer 1960) who suggest that these formations are all degraded evergreen forests or shrublands. If the latter suggestion is correct, the *Prosopis* woodlands are a resistant remnant of more diverse stands in the past. There is also the question of what future transformations these landscapes will undergo in view of the fact that they are very close to Santiago, which is not only the largest city in the country but is expanding very fast.

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