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Allelopathic effects of the Chilean matorral shrub *Flourensia thurifera*

Efectos alelopáticos del arbusto de matorral *Flourensia thurifera*

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ABSTRACT

This paper reports 4 types of evidence of the allelopathic effect of the drought-deciduous shrub *Flourensia thurifera* (Compositae) on forbs and shrubs. Field evidences include: (1) observed differences in grass abundances at neighboring sites with and without (removed) *F. thurifera;* (2) measured grass abundances at various distances and directions from isolated *F. thurifera* shrubs; and (3) the results of experiments in which *F. thurifera* was cut and the ensuing increment in the relative grass densities monitored. Laboratory evidences pertain to relative germination rates of rye and shrub seeds when irrigated with water in which shrub leaves had been soaked. All four evidences point in the same direction, namely, that *F. thurifera* produces water-soluble chemical substances capable of inhibiting the germination of other plant species. In addition, the paper supports previous results regarding the lack of demonstrable allelopathic effects in some evergreen species of shrubs. Finally, the ecological significance of these results is discussed.

Key words: Allelopathy, Forb densities, forb supression, germination rates.

RESUMEN

Este artículo informa sobre 4 tipos de evidencias que sugieren que el arbusto deciduo de verano *Flourensia thurifera* (Compositae) tiene efectos alelopáticos sobre hierbas y arbustos. Las evidencias de campo incluyen: (1) Observaciones de abundancia de hierbas en sitios vecinos con y sin *F. thurifera;* (2) mediciones de abundancia de pastos a distintas distancias y en varias direcciones a partir del centro de arbustos aislados de *F. thurifera,* y (3) resultados de experimentos donde se extrajo las plantas de *F. thurifera* y se midió el incremento posterior de la cobertura de hierbas. Las evidencias de laboratorio se relacionan con las tasas relativas de germinación de centeno y semillas de arbustos. Ambos grupos fueron regados con agua en la cual se remojaron previamente hojas de distintas plantas leñosas. Las evidencias sugieren que *F. thurifera* produce sustancias capaces de inhibir la germinación de algunas especies. Adicionalmente, este trabajo apoya resultados previos relativos a la carencia de efectos alelopáticos demostrables en algunas especies de arbustos siempreverdes. Al final se discute el significado ecológico de estos resultados.

Palabras claves: Alelopatía, densidad de hierbas, supresión de hierbas, tasas de germinación, plántulas.

INTRODUCTION

Allelopathy, the chemical inhibition of seed germination and plant growth, can produce important community patterns. Allelopathy has been reported to occur and produce such patterns in three out of the five world areas with a mediterranean-type of climate. In California (Müller 1966), the Mediterranean Basin (Delenil 1951, Guyot 1951, Ballester & Visitez 1979) and in Australia (del Moral *et al.* 1978) there have been reports of spatial segregation due to the inhibition produced by metabolites of one plant on another. But surprisingly, neither for the rich flora of the Southern Cape area (South Africa), nor for central Chile, the other two areas with wet winters and dry summers, there have been yet any claims of this type of interference. The only published work (Montenegro *et al.* 1978) testing for allelopathy in the Chilean matorral, reports that aqueous leaf extracts of five common species of shrub failed to produce measurable effects on the germination or growth

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of *Avena sativa*. These laboratory experiments were confirmed by experiences in the field in which shrub litter added to various plots also failed in generating distinct effects on the herbaceous cover.

The aim of this contribution is to document our field observations and laboratory experiments suggesting that the native shrub *Flourensia thurifera* (Compositae) is capable of producing allelopathic effects, not only on common field forbs, but even on other native shrubs. *F. thurifera* is a drought-deciduous, wind-dispersed shrub that is infrequently found in the area where Montenegro *et al.* (1978) worked (coastal ranges at 33° S.), but further north and on some of the drier interior slopes further east, it dominates the landscape (Etienne *et al.* 1982, and E.F. personal observations). In addition our paper will confirm the previous results by Montenegro *et al.* (1978) regarding the absence of demonstrable allelopathic effects in some of the evergreen shrubs they used.

METHODS

a) Field: Casual observations suggested a negative correlation between cover by *F. thurifera* and common naturalized forbs *(Tricetobromus* sp., *Chaetanthera moechioides, Bromus* spp., *Vulpia dertoenis, Carthamus lanatus;* see also Keeley & Johnson 1977). We quantified these observations by measuring relative abundance of these forbs in: (1) areas with *F. thurifera* and in neighbouring areas (30 m) where *F. thurifera* had been completely removed at least 10 years before; and (2) along radial transects out of isolated *F. thurifera* shrubs. Relative grass abundances were measured by the number of contacts along linear transects or by throwing a 30 x 30 cm metalic grid. This grid was thrown 30 times on each experimental plot as well as on each one of the controls.

We also made experiments in which the *F. thurifera* canopy was cut 5 cm above ground level and grass relative abundances were monitored throughout the season. We made two types of removal experiments. In the first *F. thurifera* was cut in the spring of 1982 and again in winter 1983, but the measurements were done only in the second year (1983). In the second type of experiment the shrubs were cut at the end of June of 1983 (winter), before the grasses started their annual growing season (see Montenegro *et al.* 1978) and final measurements were taken in November of the same year, after annual plant growth was completed.

The first type of removal experiment was done on two 50 x 30 m plots, one of which was on an equator-facing slope and had an almost complete cover by *F. thurifera*. There were also a few cacti *(Trichocereus chilensis)* present. The second plot, on a northwest-facing slope was covered by a mixture of *F. thurifera* and *Colliguaya odorifera*. For each plot we had a neighbouring control site of the same size.

The other removal experiments were done on 50 x 10 m plots located on a north-facing slope covered by *F. thurifera* and some sparse *T. chilensis* individuals. Here we made an additional type of control which consisted of eliminating only *T. chilensis* cover from one plot.

All these experiments and field observations were carried out approximately 60 km north of Santiago at a site (32° 53' LS, 70° 43' W) located at about 750 m above sea level.

b) Laboratory. Our experimental design followed the classical lines of our predecessors (Mc Pherson and Muller 1969) and basically consisted of irrigating seeds of various species with solutions obtained from soaking leaves of several shrub species. By following the time course of such a series and by comparing the germination rate with that of controls (distilled water), the evidence for allelopathy is obtained. Fresh leaves (150 g) collected by stripping them from the stems, and distilled water (2 l) were used to prepare the various solutions. The leaves were left in the water for 36 hours before the solutions were sieved and used on the seeds. To prepare the four experimental solutions, we used leaves of *Quillaja saponaria, Lithraea caustica, Colliguaya odorifera* and *F. thurifera*. Of these, the first three species were also used by Montenegro *et al.* (1978). The experimental solutions were used to irrigate Petri dishes with 40 seeds each. These seeds belonged to each of the following four species: *Q. saponaria, L. caustica, Acacia caven* (Leguminosae) or common rye. Seeds of *L. caustica* and *A. caven* were scarified with a concentrated sulfuric acid solution before the experiment. Rye was used as it was the most similar seed to grasses available at the time, and because it allowed comparison with the previous results by Montenegro *et al.* (1978). All experiments were carried out under laboratory conditions (18^{o}C room temperature and 8 - 10 h fluorescent light).

RESULTS

a) Field. Relative forb densities with shrubs and where shrubs had been removed at least 10 years before our experiment, are shown in Table 1a. It can be seen that forb density where *F. thurifera* had been removed was several times higher than with the shrubs, notwithstanding the seasonal increment in the shrub covered plot.

Results of the radial transects out of *F. thurifera* shrubs (Fig. 1) show that forb density is non-increasing ($r = .20$, $P > .05$) and low under the canopy, but increasing ($r = .90$, $P < .01$) and higher at greater distances, particularly beyond the canopy projection. Moreover, the number of contacts at the first meter away from the trunk (Fig. 1b) was higher on the uphill than on the downhill side of shrubs (t-test, $P < .01$), suggesting that inhibition is not a product of competition but of water-soluble compounds leaching from the shrubs.

Summarizing, in closed stands of *F. thurifera,* there are clearly fewer forbs than in open spaces, and where isolated *F. thurifera* individuals occur, they tend to have fewer forbs under them, than similar places somewhat more distant from the canopy projection.

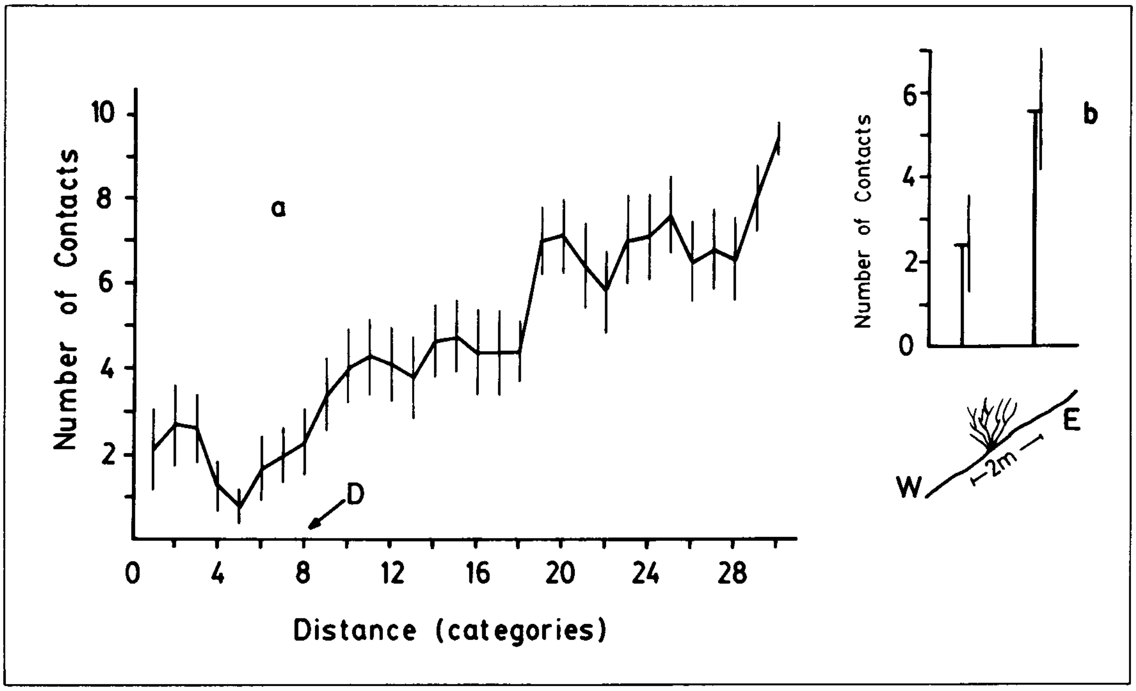

Fig. 1: Forb density and distance to isolated shrubs. a) North facing slope. Ordinate is number of forb contacts within every 10 cm category and abscissa is increasing distance (in 10 cm categories) from an isolated shrub. D is the average *F. thurifera* radius. b) West facing slope. Ordinate is number of forb contacts at 1 m downhill (left) and uphill (right) from the center of the shrub. The mean and standard errors are shown in each case.

Densidad de hierbas y distancias a arbustos aislados. a) Ladera de exposición norte. La ordenada muestra el número total de contactos cada 10 cm y la abscisa muestra distancias crecientes (en categorías de 10 cm) a un arbusto aislado. D es el radio promedio de *F. thurifera.* b) Ladera de exposición oeste. La ordenada muestra el número de contactos a 1 m de distancia del tronco. El lado izquierdo muestra el resultado pendiente abajo, mientras el lado derecho lo muestra arriba del arbusto. Se muestran el promedio y el error estándar en cada caso.

TABLE 1

Number of forb contacts. a) In a normal (control) stand with *F. thurifera* and in a nearby site where it had been removed 10 years before; b) in three experimental situations.

Número de contactos de hierbas. a) En un sitio control con cubierta normal de *F. thurifera* y en un sitio en que ésta había sido removida al menos 10 años antes del muestreo; b) en tres situaciones experimentales.

a)

	Mean no. of forb contacts ± SE	
	with *F. thurifera*	10 years without *F. thurifera*
Winter (7/2/83)	1.0 ± 0.2	20.7 ± 0.5
Spring (11/9/83)	5.2 ± 0.6	21.0 ± 0.6

b)

	Mean no. of forb contacts ± SE		
	cacti removed	*F. thurifera* removed	both cacti and *F. thurifera* removed
Winter (7/2/83)	0.9 ± 0.2	1.1 ± 0.3	1.3 ± 0.3
Spring (11/9/83)	4.8 ± 0.8	10.0 ± 1.1	11.8 ± 0.8

The removal of the *F. thurifera* cover always produced increases in forb density relative to the controls. Table 1b shows the results of removing the cactus *T. chilensis,* of removing *F. thurifera,* and of removing both. The control for this series is the "with *F. thurifera*" column in Table 1a. A one-way ANOVA on the spring data shows that there was no overall difference (P > .10) regarding the initial forb densities in these four situations. There were also no differences (t-tests, P's > .20) between the control and no-cacti situation. But in both situations in which *F. thurifera* was cut (alone or with the cacti), significantly higher increments than in the controls occurred (one-way ANOVA, and Scheffé tests, P's < .01). Thus, although removal of the crown of *F. thurifera* has an effect on forb density, a similar treatment with *T. chilensis* does not, or at least has a negligible effect.

A similar result holds when the remaining two crown removal experiments are examined (Table 2). The forb increment was greater, relative to the controls, when *F. thurifera* was removed. Both differences to the controls are statistically significant (t-tests, P's < .01).

In sum, when *F. thurifera* was already absent there were more forbs than when it was present, and when this shrub was experimentally removed an increase in forb density follows. By comparing Table 1b and 2 it can be seen that winter densities of forbs were higher where the shrubs had been cut the year before. From the spring data in these same tables, it seems likely that densities comparable to the ones measured in the plot without *F. thurifera* for at least 10 years (Table 1a), would be reached within few years after cutting the shrubs.

TABLE 2

Effect of removal of *F. thurifera* after one year. a) Northwest-facing slope. b) North-facing-slope.

Efecto de remoción de *F. thurifera* después de un año. a) Ladera de exposición noroeste. b) Ladera de exposición norte.

a)

	Mean no. of forb contacts ± SE	
	Control	Shrubs cut
Winter (7/2/83)	10.7 ± 1.3	13.3 ± 1.2
Spring (7/2/83)	7.4 ± 1.0	18.7 ± 0.9

b)

	Mean no. of forb contacts ± SE	
	Control	Shrubs cut
Winter (7/2/83)	10.7 ± 1.0	5.3 ± 0.8
Spring (7/2/83)	11.7 ± 1.1	17.9 ± 0.9

b) Laboratory: Germination results are shown in Table 3. An overall two-ways ANOVA showed that there are seed effects (P < .01), solutions effects (P < .01) and interaction effects (P < .01). A chi-square analysis showed that the overall effect on germination of the solutions of *Q. saponaria, L. caustica* and *C. odorifera* did not differ from the control neither on rye (P > .50), nor on shrubs seeds (P > .05), thus confirming previous results by

Montenegro *et al.* (1978). However, the *F. thurifera* control solutions differed in their effect on rye ($P < .01$) and on shrub seeds ($P < .01$). In both of these latter cases fewer seeds germinated with the *F. thurifera* solution, just as expected from the allelopathy hypothesis and in support of the previously documented results on the abundance patterns of forbs in the field.

TABLE 3

Number of germinated seeds out of 40 originally placed in each one of the 20 situation indicated.

Número de semillas germinadas de un total de 40 en cada una de las 20 situaciones indicadas.

	Solutions				
Seeds germinated	*Q. saponaria*	*L. caustica*	*F. thurifera*	*C. odorifera*	Control
Q. saponaria	13	16	0	9	11
L. caustica	1	2	0	3	2
A. caven	34	32	17	29	29
Rye	38	38	7	36	39

DISCUSSION

Our set of observational and experimental results are consistent with the hypothesis that the low forb density measured under *F. thurifera* stands is not produced by competition but by chemical inhibition through a relatively short-lived water-soluble substance. Through competition alone it would not be possible to explain our results on the selective inhibition of seed germination. The fact that inhibition of forbs is higher down the slope is also suggestive of the presence of water-soluble chemical substances. In this regard a prediction that could have been made from our results is that where rainfall is less, this inhibition effect should also be lower. Dr. J. Gutiérrez (personal communication 1985) observed that by La Serena where annual rainfall (approx. 130 mm) is less than one half of that recorded by Santiago, this inhibition is not at all obvious. Again, this contrast is not something to be expected from competition alone.

As an alternative for allelopathy, in the California chaparral Bartholomew (1970) showed that bare zones around shrublands can be explained by the greater activity of herbivores in those areas. We (Fuentes and Le Boulenge 1977) have shown that the Chilean caviomorph rodent *Octodon degus* can also produce these bare zones around patches of the Chilean evergreen shrub *Muehlenbeckia hastulata,* and recognize that this explanation would not be satisfactory in the case of the drought-deciduous species *Flourensia thurifera.* On the one hand, we did not find any evidence of *O. degus* in the stands where we worked. On the other, the pattern we report is of bare zones in extensive areas under *Flourensia* stands and of downhill oriented bare zones around isolated plants. From our experience there is no herbivore in Chile capable of producing such effects.

Thus, although we cannot exclude that there might be some competitive interference from *F. thurifera* shrubs on the forbs, the evidence as a whole, including all observations and the experiments, in particular the laboratory germination trials, point towards the allelopathy hypothesis as the best explanation available. There is no other single explanation that can account of all our results.

Harper (1977) predicted that allelopathy should be relatively uncommon for two reasons: i) plants would rapidly envolve tolerance to such substances, and ii) the toxic molecules would be quickly broken down in the soil. In the case of *Flourensia thurifera* the allelopathic effects seem to be short-lived (less than a year) just as expected from Harper's hypothesis. However, our finding that target species include both introduced European forbs and native shrubs, suggests that his prediction regarding fast adaptation to allelopathic compounds does not hold.

The presence of allelopathic substances in *F. thurifera* is important because they are capable of inhibiting forbs and shrubs. Our results regarding the inhibition of shrub seeds are in good agreement with the high frequency with which *F. thurifera* forms monospecific stands or is part of communities with very few other shrub species.

This allelopathic effect of *F. thurifera* is also important from an ecological-economical perspective. Our personal observations show that although goats can eat young leaves of *F. thurifera,* they clearly do not prefer them over forbs or other shrubs, if available. Since *F. thurifera* can exclude forbs and other more palatable shrubs, its invasion of man-cleared sites can become a constraint for the spontaneous development of a more diverse plant cover. This implies that *F. thurifera* could end up reducing the potential carrying capacity of some habitats, and thus conveying less economical well-being than the original and more diverse vegetation. Moreover, our evidence suggests that once a stand is invaded by *F. thurifera* it could be costly to manage the stand to its former composition.

F. thurifera is the first matorral shrub for which there is evidence of allelopathic inhibition. It would not be surprising, given the relatively rich flora of central Chile, that more such species will be found in future research.

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