Revista Chilena de Historia Natural
69: 171-181, 1996

On the structural organization of the renewal buds and their implication for the survival of embryonic structures in central Chilean matorral shrubs

Organización estructural de las yemas de renuevo y su implicancia en la sobrevivencia de estructuras embrionarias en arbustos del matorral de Chile central

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ABSTRACT

In the matorral shrubs of the central zone in Chile, the renewal buds reinitiate vegetative growth after the recess imposed by drought during the summer and fall. The meristems of these buds are responsible for generating new shoots, thus directing continuity of growth of the shrub in time. In the majority of the woody species of the matorral the renewal buds are preformed, and contain morphological structures and chemical compounds that are developed in order to avoid water loss and to protect against the effects of high temperatures and solar radiation which occur during the period of vegetative rest, thus assuring the survival of the shrub. In this paper, the relative importance of the morphological structures and chemical compounds found in the renewal buds of the dominant species of the matorral was quantified. The aim was to test the importance of foliage and bud scales as structures that may reduce the effects of abiotic factors such as the high solar radiation and water stress, thus assuring the survival of the embryonic shoots contained in the renewal buds. The χ^2 index with Yates correction, indicated that the morphological structures have a greater relative presence than the chemical compounds. As for the response variables related to the percentage of resprouting and total biomass generated by the renewal buds, no significant differences were found between maintaining and eliminating the bud scales in the distinct life forms. However, differences were found when the foliage was eliminated in evergreen shrubs. Results are discussed in terms of the importance of abiotic and biotic (herbivores) factors as evolutionary pressures for the vegetation in central Chile.

Key words: matorral, plant growth, plant protection, abiotic stress, renewal buds.

RESUMEN

Las yemas de renuevo de los arbustos del matorral central de Chile reinician el crecimiento vegetativo después del receso vegetativo impuesto por la sequía estival. Los meristemas de estas yemas son los responsables de generar las nuevas ramas, siendo así fundamentales para mantener la continuidad del crecimiento de los arbustos de un año a otro. En la mayoría de los arbustos del matorral las yemas de renuevo están preformadas y presentan estructuras morfológicas y compuestos químicos que evitan la pérdida de agua y disminuyen el efecto de las altas temperaturas y de la radiación solar durante el período de receso vegetativo, asegurando la sobrevivencia de los arbustos. En este trabajo se cuantificó la importancia relativa de las estructuras morfológicas y de los compuestos químicos en yemas de renuevo de especies dominantes del matorral. El objetivo fue probar la importancia del follaje y de las escamas presentes en las yemas como estructuras que reducirían los efectos de los factores abióticos, tales como la alta radiación solar y el estrés hídrico, asegurando así la sobrevivencia de los vástagos embrionarios contenidos en las yemas de renuevo. El índice χ^2 con corrección de Yates indicó que las estructuras morfológicas y los compuestos químicos tendrían una presencia relativa similar. No se encontraron diferencias significativas para las variables respuesta porcentaje de brotación y biomasa generada a partir de las yemas de renuevo, al mantener o remover las escamas en las distintas formas de vida analizadas, pero sí se encontró diferencias significativas cuando se eliminó el follaje en las especies siempreverdes. Los resultados se discuten en términos de la importancia de los factores abióticos y bióticos (herbívoros) como presiones evolutivas para la vegetación de Chile central.

Palabras clave: matorral, crecimiento vegetal, protección en plantas, estrés abiótico, yemas de renuevo.

INTRODUCTION

In regions with mediterranean type climate, such as the central zone in Chile, growth and the production of biomass are limited by the availability of water (Kozlowski 1972, Mooney et al. 1977, Miller 1981, Montenegro et al. 1989), temperature (Mooney et al. 1977,

(Received 5 June 1995; accepted 13 November 1995; managed by Mary T. Kalin-Arroyo)

Aljaro & Montenegro 1981, Miller 1981, Di Castri 1981) and soil nutrients (Beadle 1966, Specht 1979, Mooney 1981, Lamont & Kelly 1988). Water availability and temperature show seasonal variation, limiting plant activity in certain periods of the year (Mooney et al. 1974) with consequent seasonal patterns of growth (Montenegro 1987, Montenegro et al. 1989).

In the semi-arid mediterranean zone in central Chile the majority of the dominant shrubby species show decreasing values of water potential from the middle of the summer onward, indicating increasing water stress (Montenegro & Riveros 1977, Giliberto & Estay 1978, Montenegro et al. 1980a), eventually resulting in the ceasation of the majority of the growth processes. Growth in woody plants is reinitiated in summer deciduous species after the first winter rains, and in evergreen species in the spring, when temperatures reach adequate values for plant development (Montenegro et al. 1989).

The renewal buds are the structures from which vegetative growth is reinitiated after dormancy imposed by seasonal drought. The meristems of these buds generate the structures of the plant, being therefore responsible for the continuity of growth in time. For matorral shrubs five distinct types of modules (defined as shoot units resulting from the development of an axillary or terminal bud during one growth season (Hallé & Oldeman 1970)) have been described: vegetative long shoots, absolute short shoots, temporal short shoots, spiny short shoots, and inflorescences (Ginocchio & Montenegro 1992, 1993, Montenegro & Ginocchio 1993). Plant growth is described as the production of these basic units, or modules, which are generated from the buds in a species-specific sequence.

The renewal buds are preformed in the majority of the native matorral species, and consist of a bud in an embryonic state formed by an apical meristem. The apical meristem is surrounded by almost all of the leaf primordia differentiating into the leaves in the next growing season (Ginocchio & Montenegro 1989, 1992). The advanced state of development of these buds represents an investment by the plant to generate vegetative structures rapidly, only by elongation and cellular differentiation, so as to take advantage of the short favorable growth period characteristic of Mediterranean climate regions.

The soil conditions, atmospheric drought, and intense solar radiation which prevail during the period of vegetative recess can be expected to produce morphological and chemical adaptations in the renewal buds of the woody species. These adaptations should aid in limiting water loss and the effects of high temperature and incident solar radiation (Wiebe 1980, Ginocchio & Montenegro 1989). The structural adaptations that assure the survival of these buds during the period of dormancy in the dominant shrubs of the matorral would correspond to: trichomes (Agarwal 1969, Feeny 1970, Levin 1973, Johnson 1975, Esau 1977, Silva & Acevedo 1984), bud scales and bracts (Mauseth 1988), tannins (Johnson 1975) and laticifers (Montenegro & Riveros 1977). Foliage may also constitute additional protection in those species which maintain their leaves during the whole year (evergreens) (Ginocchio & Montenegro 1989).

Although the protective role of these structures in mature leaves against abiotic factors has been speculated (see references in Ginocchio & Montenegro 1989), their relative importance in renewal buds of matorral shrubs has not been studied. Nor has the effectiveness of the structures been experimentally demonstrated; that is, it has not been proven that such structures successfully increase the probability of survival of the embryonic shoots contained in the renewal buds and thus assure the continuity of growth of the plant in time.

The objectives of this paper were: 1) to demonstrate the presence and determine the relative importance of morphological structures (bud scales, bracts, trichomes) and chemical compounds (secretory glands, oil cavities, crystals, tannins, laticifers) in protecting the renewal buds between dominant woody species of the matorral, and 2) to demonstrate experimentally using two distinct life forms, *Lithrea caustica* (an evergreen shrub) and *Trevoa trinervis* (a summer deciduous shrub), if the presence of bud scales and/or of foliage increases the survival rate of the embryonic shoots contained in the renewal buds during the period of vegetative rest. We chose to test bud scales and foliage because they are the most common structures among the woody matorral species and they are easy to remove *in situ,* thus facilitating experimental manipulation.

MATERIAL AND METHODS

Study site

The area of the study, Los Dominicos (33°25' S 70°32' W) is located at approximately 900 m.a.s.l. in the foothills of the Andes outside of Santiago. Yearly average precipitation at the site totals 400 mm. Depending on the exposure, the vegetation type is either matorral or a sclerophyllous forest, in which the typical shrub species are *Quillaja saponaria, Lithrea caustica, Trevoa trinervis* and *Colliguaja odorifera.* The specific study site was an alluvial cone, where the native vegetation experiences little disturbance.

Determination of the relative abundance of morphological structures and chemical compounds in renewal buds of matorral shrub species

Dormant terminal and axilar buds were collected from *Cestrum palqui, Kageneckia oblonga, Maytenus boaria, Muehlenbeckia hastulata* and *Talguenea quinquinervia* between January and May of 1989, when the species were vegetatively inactive. Samples were fixed in FAA (formalin-alcohol-acetic acid), observed and dissected under microscope, and processed for analysis under light microscope and scanning electron microscope (SEM) to determine presence or absence of different morphological and chemical compounds described as protective elements for plant tissues in literature (eg, trichomes, phenols, crystals, etc).

Material for analysis under the light microscope was dehydrated in an increasing series of alcohols, imbedded in paraplast, cut in thin slices (18 μm) and stained with safranina-fast green. Material for SEM was dehydrated in a gradual series of acetones, dried to critical point (CO_2) and covered with a layer of approximately 100Å of gold-palladium for observation with SEM. Using the χ^2 Similitud Index with Yates correction (Saiz 1980) we determined if shrub species protected their renewal buds with the same or different morphological structures and chemical compounds. This index was calculated as:

$$\chi^2 = \frac{(n\,(|\,cd-ab\,| - n/2)^2}{(a+c)(b+c)(a+d)(b+d)}$$

where,

a = characters shown only by species A
b = characters shown only by species B
c = characters shared by presence between species A and B
d = characters shared by absence between species A and B
n = total characters considered for species A and B (= a+b+c+d)

If χ^2 probe to be significative, then if cd-ab is greater than 0, there is significative similitud between characters present in renewal buds of species A and B, but if cd-ab is lower than 0 there is not simmilitud between characters, predominating exclusive presence of characters in each species (Saiz 1980).

Experimental demonstration of the protective role of the bud scale and/or the foliage in the renewal buds

The species under study

Lithrea caustica is the most common and widely distributed shrub in the matorral of central Chile. It occurs along a North-South aridity gradient, being found equally on slopes with northern and southern exposure, as well as in valley bottoms. It is characterized by maintainance of crown foliage throughout the year; it is also one of the last species to initiate vegetative growth (Montenegro 1987, Montenegro et al 1989). The renewal buds begin to grow in December, originating new shoots until the

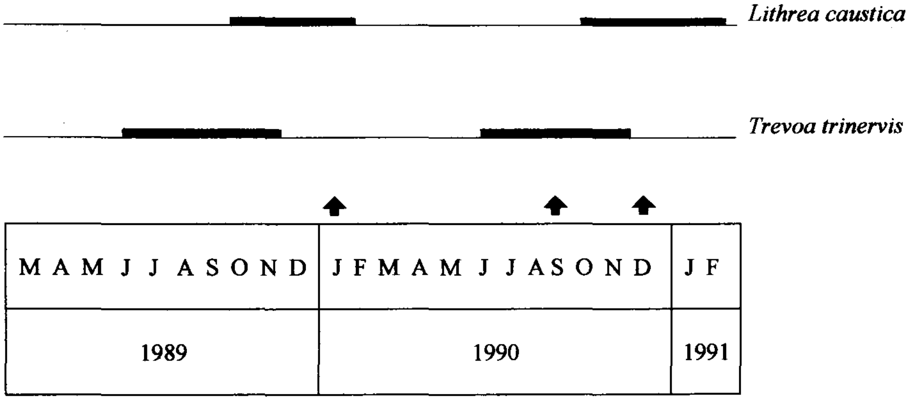

Fig. 1: Periods of dormancy (–) and growth (■) in *Lithrea caustica* and *Trevoa trinervis* from 1989 to 1991. The first arrow indicates the moment in which the treatments for both species started. The second and third arrows indicate the time of harvest of branches of *T. trinervis* and *L. caustica* respectively.

Períodos de dormancia (–) y crecimiento (■) de *Lithrea caustica* y *Trevoa trinervis* desde 1989 a 1991. La primera flecha indica el momento en que se iniciaron los experimentos. La segunda y tercera flechas indican la época de cosecha de las ramas de ambas especies, respectivamente.

end of January (Figure 1). The branches which are created during the short growth period in turn generate renewal buds which will remain dormant until the next growing season (Figure 1).

Trevoa trinervis is found on hillsides with northerly exposure and in valley bottoms in the more arid areas of the North-South gradient. It is a summer deciduous species, which begins vegetative growth after the first rains of the season, from June (winter) until the end of November (Figure 1). Depending on their spatial location the renewal buds in this species originate vegetative spiny long shoots or absolute short shoots (Montenegro et al. 1989, Ginocchio & Montenegro 1992). The vegetative spiny long shoots are the structures that sustain the renewal buds which reinitiate growth in the next growing season (Montenegro et al. 1989, Montenegro & Ginocchio 1993).

The renewal buds of both species have large bud scales (Figure 2), making them appropiate for on-site manipulation.

Field experiments

To evaluate the importance of foliage and the bud scales in the survival of embryonic shoots contained in the renewal buds, three study sites were chosen in a North-South aridity transect. The study area contained one site on a hillside with northerly exposure, one in a valley bottom and the third on a hillside with southerly exposure. The two hillside sites were located at the same altitude (1040-1060 masl), while the valley bottom site was at approximately 880 m.a.s.l.

In each of the study sites, one individual of *Lithrea caustica* and of *Trevoa trinervis* was chosen. From these shrubs, three nearby co-specific individuals were chosen in order to assure similar microclimatic conditions for the manipulative experiments. At the end of January 1989, when the species were dormant (Figure 1), the following procedures were carried out with one replication. The experiments were carried out on the ten first renewal buds located in branches of the shrub which had been formed in the 1988 growth season. For *L. caustica*, the treatments were: a) elimination of the bud scales maintaining the foliage intact, b) elimination of the leaves maintaining the bud scales, c) elimination of the bud scales and the leaves, and d) control branch (with bud scales and leaves intact). For *T. trinervis* the treatments were: a) elimination of the bud scales, and b) control branch, with bud scales intact.

Several studies have shown that herbivorous insects play an important role in the community under study (see Fuentes et al. 1981, 1987). For this reason, in order to ensure that the responses to the treatments have not due to herbivores, each of the branches was protected with a burlap bag. In order to determine if the burlap bag changed the microclimate around the branches, one control branch was marked without burlap bag, with one replication.

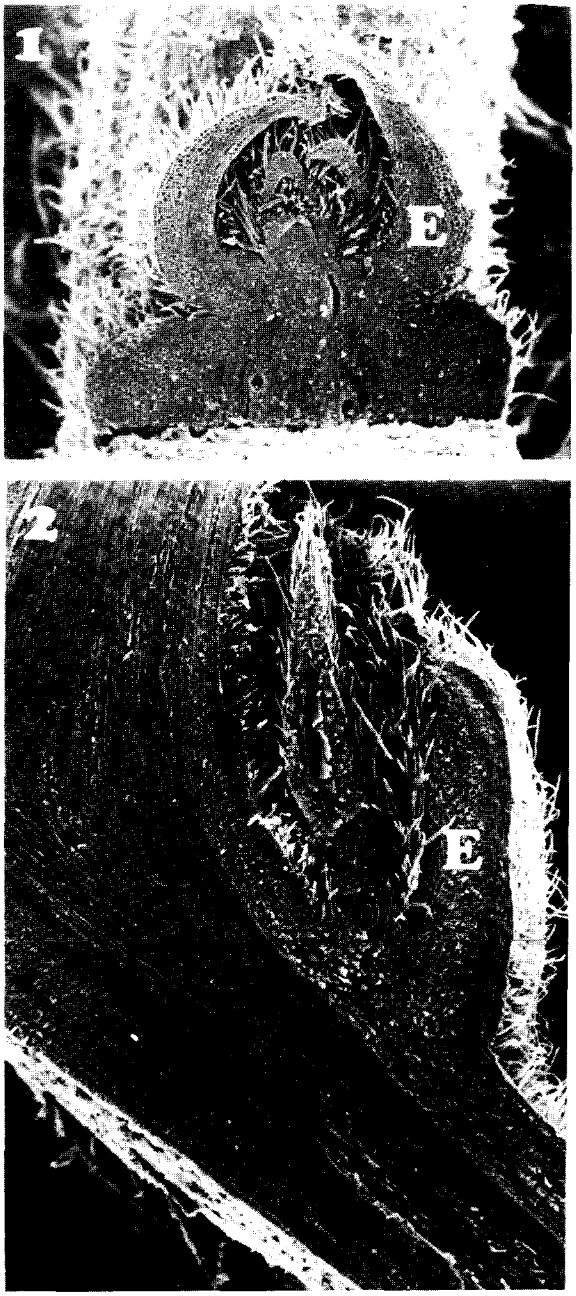

Fig. 2: SEM microphotographs of longitudinal cuts of the renewal buds of *L. caustica* (1) and *T. trinervis* (2) with magnification x 45. The presence of bud scales is indicated (E).

Microfotografías al MEB de cortes transversales de yemas de renuevo de *L. caustica* (1) y *T. trinervis* (2); aumento x 45. Se indica la presencia de escamas (E).

The treatments were performed on the same day in each one of the sites of the study. In September 1990, 9 months after manipulation, all the branches of *T. trinervis* were collected; those of *L. caustica* were collected at the end of December of 1990 (Figure 1). For each branch, the percentage of resprouting of the renewal buds and the total dry weight (total biomass) of the new structures formed by the branches were measured. Percentage dates were arc-sine transformed before statistical analysis were performed.

Nested experimental designs were used with mixed ANOVA models for each one of the treatment variables measured (Figure 3). These models included variables of exposure (fixed factor of two or three levels, depending on the species), shrub (random factor, with four levels), branch (random factor with two levels), bud scales (fixed factor with two levels), foliage (fixed factor with two levels) and burlap bag (fixed factor with two levels). The Tukey test was used as *a posteriori* test. Models were statistically analyzed using software from Systems of Statistical Analysis (SAS Institute, Inc. 1991).

RESULTS

Determination of the relative abundance of morphological structures and chemical compounds in renewal buds of matorral shrub species

Structures present in renewal buds of each species are indicated in Table 1. The quantification of the relative presence of these structures in the woody species of the matorral, using the X^2 Similitud Index with Yates correction ($p < 0.05$) (Saiz 1980), suggests that the bud scales, trichomes, and bracts have a greater relative abundance in comparison to the crystals and tannins. Oil cavities, secretory glands and laticifers have a lesser relative abundance, according to the lower frequency of their occurance in the renewal buds.

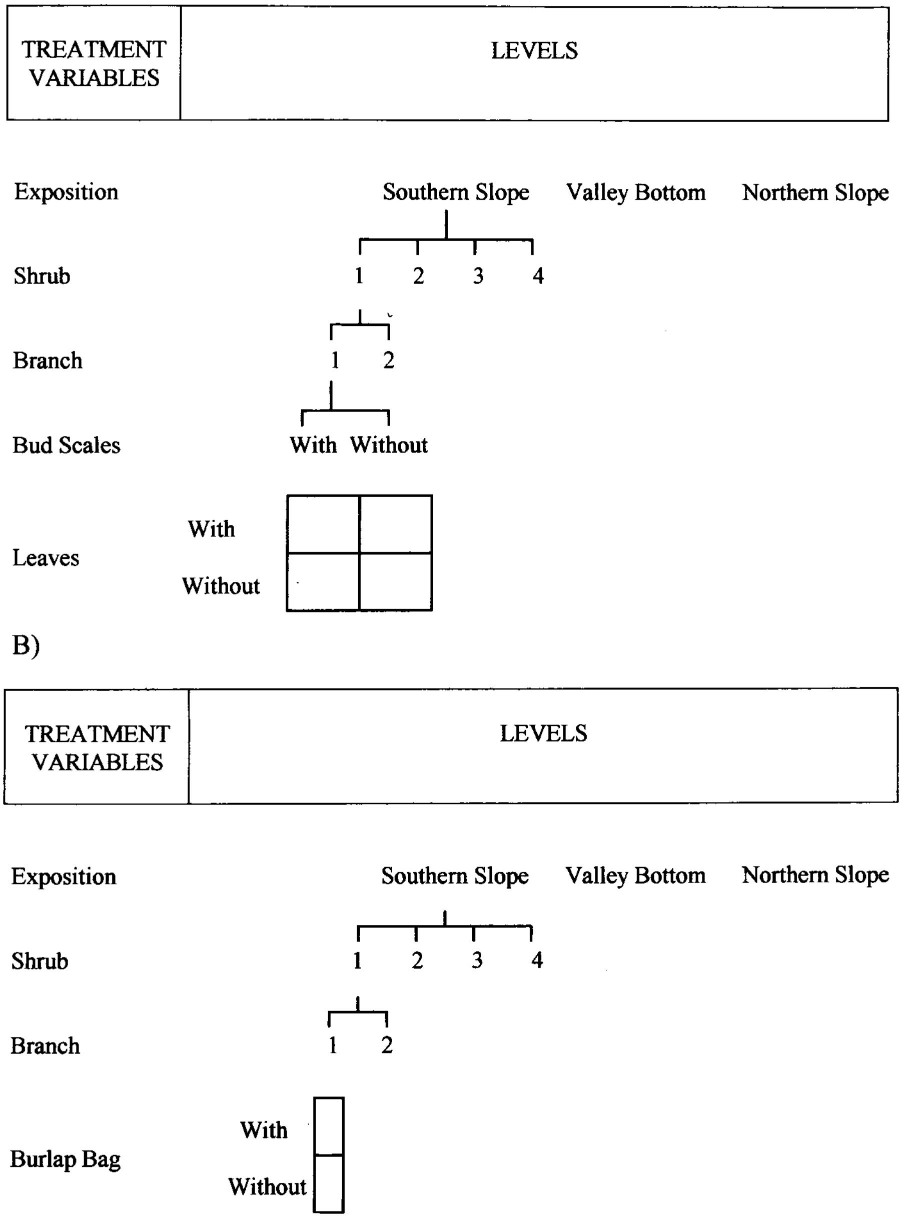

Fig. 3: Nested experimental designs utilized for the treatment variables related with: A) the protective role of the renewal buds of the bud scales in *L. caustica* and *T. trinervis*, and foliage in *L. caustica*, and B) the effect of a burlap bag surrounding the treatment branches in both plant species. The response variables measured in each experimental design were total biomass (dry weight) and percentage of resprouting.

Diseños experimentales anidados utilizados para los tratamientos relacionados con: A) el rol de protección de las escamas en las yemas de renuevo de *L. caustica* y *T. trinervis* y del follaje en *L. caustica* y B) el efecto de una bolsa de tul alrededor de las ramas en ambas especies vegetales. Las variables respuesta medidas en cada diseño experimental fueron la biomasa total (peso seco) y el porcentaje de brotación.

Experimental demonstration of the protective role of the bud scales and/or foliage

In *L. caustica,* although variability in shrub response was found, (ANOVA, $p<0.05$), no significant difference was found in both response variables for the factors exposure, branch, and bud scales (Table 2 A and Table

TABLE 1

Morphological structures and chemical compounds found in renewal buds of representative matorral woody species. 1: presence of the character 0: absence of the character. Percentage of analized species that shown each character in their renewal buds is shown in the lower part of the table. (*: data from Ginocchio & Montenegro 1989)

Estructuras morfológicas y compuestos químicos presentes en yemas de renuevo de especies arbustivas representativas del matorral. 1: presencia del carácter; 0: ausencia del carácter. En la parte inferior de la tabla se indica el porcentaje de las especies analizadas que presenta cada una de los caracteres en sus yemas de renuevo. (*: dato tomado de Ginocchio & Montenegro 1989)

Species	Scales	Trichomes	Secretory Glands	Oil Cavities	Crystals	Tannins	Laticifers	Bracts
*Baccharis linearis**	0	0	1	1	0	0	0	0
Cestrum parqui	1	1	0	0	0	0	0	1
*Colliguaja odorifera**	0	0	0	0	0	0	1	1
*Cryptocarya alba**	1	0	0	1	0	0	0	1
Kageneckia oblonga	1	1	0	0	1	1	0	1
*Lithrea caustica**	1	1	0	0	0	0	0	1
Maytenus boaria	1	0	0	0	1	1	0	1
Muehlenbeckia hastulata	1	0	0	0	1	1	0	0
*Peumus boldus**	1	1	0	1	0	0	0	1
*Quillaja saponaria**	1	1	0	0	1	1	0	1
Talguenea quinquinervia	1	1	0	0	0	0	0	0
*Trevoa trinervis**	1	1	0	0	1	0	0	0
Percentage	83.3	58.3	8.3	25	41.6	33.3	8.3	66.6

3 A). Both the percentage of resprouting and the biomass generated per branch were significantly reduced when leaves were removed compared with when they were maintained (Table 2 A and Table 3 A). None of the interactions between the factors was significant, which indicates that the effects would be independent of each other.

For *T. trinervis* significant differences were found for exposure, branch, and bud scales but significance was not found in the interaction between the factors exposure and buds (Table 2 B and Table 3 B). Variability in the response of this species was also found. (ANOVA, $p < 0.05$).

Burlap bag did not produce significant effect in either species (Tables 4 and 5), although varibility was found in the response of the individuals of each species (ANOVA, $p < 0.05$). These results suggest that the burlap bag did not generate a microclimate around the branches that favor the development of the renewal buds, indicating that the results are attributable to the treatments.

For *L. caustica* a significant difference was found in the percentage of resprouting due to the factor of exposure (ANOVA, $p < 0.05$), but not in biomass generated by each branch (Table 5 A and Table 4 A, respectively). The *a posterior* test indicates that the percentage of resprouting is significantly greater in the valley bottom than in the hillsides. This could be due to more soil water availability in the valley bottom.

TABLE 2

ANOVA table for response variable total biomass (dry weight) in *L. caustica* (A) and *T. trinervis* (B) for the treatment variables under study and their interactions

Tabla de ANDEVA para la variable respuesta biomasa total (peso seco) en *L. caustica* (A) y *T. trinervis* (B) para los tratamientos en estudio y sus interacciones.

A) Sources of Variability	d.f.	F	P>F
Exposition	2	1.33	0.3124
Shrub	9	3.49	0.0075
Branch	12	1.49	0.0830
Leaves	1	443.20	0.0022
Bud Scales	1	0.65	0.4411
Exposition * Leaves	2	0.06	0.9441
Shrub * Leaves	9	3.19	0.0119
Shoot * Leaves	12	0.64	0.7901
Exposition * Bud Scales	2	0.30	0.7452
Shrub * Bud Scales	9	1.05	0.4308
Branch * Bud Scales	12	0.93	0.5328
Leaves * Bud Scales	1	0.01	0.9136
Error	23		

B) Sources of Variability	d.f.	F	P>F
Exposition	1	2.01	0.2064
Shrub	6	121.13	0.0001
Branch	8	0.68	0.7021
Bud Scales	1	2.40	0.1722
Exposition * Bud Scales	1	0.05	0.8327
Shrub * Bud Scales	6	11.44	0.0015
Error	8		

TABLE 3

ANOVA table for response variable percentage of resprouting in *L. caustica* (A) and *T. trinervis* (B) for the treatment variables under study and their interactions.

Tabla de ANDEVA para la variable respuesta porcentaje de brotación en *L. caustica* (A) y *T. trinervis* (B) para los tratamientos en estudio y sus interacciones

A) Sources of Variability	d.f.	F	P>F
Exposition	2	2.12	0.1758
Shrub	9	5.93	0.0003
Branch	12	1.10	0.4048
Leaves	1	44.33	0.0218
Bud Scales	1	3.82	0.0823
Exposition * Leaves	2	1.35	0.3080
Shrub * Leaves	9	2.19	0.0622
Branch * Leaves	12	0.98	0.4967
Exposition * Bud Scales	2	0.14	0.8742
Shrub * Bud Scales	9	1.24	0.3202
Branch * Bud Scales	12	0.87	0.5901
Leaves * Bud Scales	1	0.01	0.9153
Error	23		

B) Sources of Variability	d.f.	F	P>F
Exposition	1	2.01	02064
Shrub	6	121.13	0.0001
Branch	8	0.68	0.7021
Bud Scales	1	2.40	0.1722
Exposition * Bud Scales	1	0.05	0.8327
Shrub * Bud Scales	6	11.44	0.0015
Error	8		

TABLE 4

ANOVA table for response variable total biomass (dry weight) in *L. caustica* (A) and *T. trinervis* (B) for the burlap bag treatment

Tabla de ANDEVA para la variable respuesta biomasa total (peso seco) en *L. caustica* (A) y *T. trinervis* (B) para el tratamiento con bolsa de tul.

A) Sources of Variability	d.f.	F	P>F
Exposition	2	1.44	0.2867
Shrub	9	4.80	0.0070
Branch	12	2.42	0.0697
Burlap Bag	1	2.62	0.1397
Exposition * Burlap Bag	2	0.53	0.6053
Shrub * Burlap Bag	9	1.12	0.4197
Error	12		

B) Sources of Variability	d.f.	F	P>F
Exposition	1	4.55	0.0770
Shrub	6	176.43	0.0001
Branch	8	1.46	0.3039
Burlap Bag	1	0.20	0.6721
Exposition * Burlap Bag	1	0.72	0.4286
Shrub * Burlap Bag	6	42.74	0.0001
Error	8		

TABLE 5

ANOVA table for response variable percentage of resprouting in *L. caustica* (A) and *T. trinervis* (B) for the burlap bag treatment

Tabla de ANDEVA para la variable respuesta porcentaje de brotación en *L. caustica* (A) y *T. trinervis* (B) para el tratamiento con bolsa de tul

A) Sources of Variability	d.f.	F	P>F
Exposition	2	5.53	0.0271
Shrub	9	1.98	0.1347
Branch	12	0.95	0.5351
Burlap Bag	1	1.36	0.2730
Exposition * Burlap Bag	2	0.03	0.9712
Shrub * Burlap Bag	9	1.43	0.2751
Error	12		

B) Sources of Variability	d.f.	F	P>F
Exposition	1	1.55	0.2600
Shrub	6	5.68	0.0141
Branch	8	3.44	0.0500
Burlap Bag	1	0.01	0.9178
Exposition * Burlap Bag	1	1.08	0.3385
Shrub * Burlap Bag	6	2.84	0.0868
Error	8		

DISCUSSION

The low occurence of oil cavities, secretory glands and laticifers in the renewal buds of the shrubby species analyzed does not mean that these structures are less protective against high solar radiation and water stress. Their decreased relative abundance could be due to that fact that their formation and maintainance is too costly for the plant in comparison to the other structures mentioned (Merion et al. 1982). This high cost for the plant would be a disadvantage in an environment where soil nutrients are limited (Specht 1979, Mooney 1982, Lamont & Kelly 1988) and the period available for photosynthesis is very short (Montenegro et al. 1989).

It is important to note that the secondary phenolic metabolites (tannins) function as filters against the ultraviolet radiation by absorbing it selectively (Caldwell 1968, 1971, Robberect & Caldwell 1978). The effective attenuation of ultraviolet radiation by these compounds represents an important mechanism to protect against damages such as degradation of nucleic acids, proteins and other components (Van et al. 1976, Mulroy 1979), especially in the embryonic shoots of woody plants that possess these compounds in their renewal buds. Reduction of the ozone layer results in increasing ultraviolet radiation, with serious biological consequences (Robberect & Caldwell 1978). The capacity of the phenols to attenuate ultraviolet radiation coupled with the capacity of some plants to synthesize greater quantites of these compounds in the presence of greater ultraviolet radiation intensity could be important for the survival of embryonic shoots contained in the renewal buds in the case of an significant increase in this radiation.

Although a high percentage of the analyzed species demonstrated the presence of bud scales (83.3%), the results of the field experiments indicate that the presence or absence of these structures does not effect the survival of the embryonic shoots contained in the renewal buds. This result is independent of the growth form of the species and holds true for both species along the length of the North-South aridity gradient. This result does not support the hypothesis that the bud scales have been selected as protective structures against abiotic factors that ensure the survival of the embryonic shoots during the dormant period of the matorral in central Chile.

Morphological structures and chemical compounds found in the renewal buds have been also interpreted as protective mechanisms against herbivory (eg., trichomes, bud scales -Feeny 1970, Levin 1973, Johnson 1975, Mabry & Gill 1979; secretory glands -Levin 1975; tannins -Feeny 1979, Johnson 1975; and laticifers -Cates & Orians 1975, Levin 1976). Atsatt and O'Dowd (1976) suggested that the leaves act as a distractive factor, helping to avoid the loss of the elements that have the greatest value for the plant, such as leaf primordia, apical meristems and axilar renewal buds.

Diverse studies have shown that herbivores play an important role in ecosystems with mediterranean climate, changing the abundance, specific composition (Christensen & Muller 1975, Mills 1983, Quinn 1986, Fuentes et al. 1987, Frazer & Davis 1988) and vegetation architecture (Ginocchio & Montenegro 1993). In particular, in the matorral, the gall-forming and defoliating insects are important components of the system (Ginocchio & Montenegro 1994), and in addition to abiotic factors, have constituted another important evolutionary pressure for the vegetation in Central Chile (Mooney et al. 1977, Etchegaray & Fuentes 1980, Montenegro et al 1980b, Fuentes et al. 1981, Fuentes et al. 1987). The results obtained in this study leave open the possibility that bud scales might have been selected for to as protective structures against herbivores, rather than against abiotic influences. Nevertheless, this hypothesis must be tested.

Walkowiak et al. (1984) found that matorral species without significant foliar insect herbivory, do not have characteristics in common that could be interpreted as strategies against herbivores. This situation might indicate that each species has its own coevolution history with certain groups of insects (Etchegaray & Fuentes 1980). For example, it is possible that the high concentration of phenols (Montenegro et al. 1980b) and presence of laticifers (Montenegro & Riveros 1977) found in *Colliguaja odorifera* serve as effective barriers against herbivors. The large number of trichomes in *Talguenea quinquinervia* act as a physical barrier against herbivorous insects (Walkowiak et al. 1984). Nevertheless, in *L. caustica* the apical meristem suffers damage from insects in spite of the abundant presence of trichomes (Montenegro et al. 1980b).

The relative presence of each of the structures related in protection against abiotic factors versus herbivory apparently varies from species to species, preventing generalizations about the specific roles of individual morphological structures and chemical compounds.

ACKNOWLEDGMENTS

The authors thank the Fondo Nacional de Desarrollo Científico y Tecnológico (Chile) (Project FONDECYT 1940655 to G. Montenegro and FONDECYT 2950085 to R. Ginocchio), Andrew W. Mellon Foundation, P. Universidad Católica de Chile, and Project CEE N° 918049. R. Ginocchio was supported by a Fundación Andes doctoral fellowship. Appreciation is expressed to Catherine Copass for helping with the English presentation of the manuscript.

LITERATURE CITED

AGARWAL RA (1969) Morphological characteristics of sugar cane and insect resistence. Entomología Experimental Applied 12: 767-776.

ALJARO ME & G MONTENEGRO (1981) Growth of dominant Chilean shrubs in the Andean Cordillera. Mountain Research and Development 1: 287-291.

ATSATT PR & DJ O'DOWD (1976) Plant defence guilds. Science 193: 24-29.

BEADLE NC (1966) Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47: 992-1007.

CALDWELL MM (1968) Solar ultraviolet radiation as an ecological factor for alpine plants. Ecological Monographs 38: 243-268.

CALDWELL MM (1971) Solar UV irradiation and the growth and development of higher plants. In: Giese AC (ed) Photophysiology: 131-177. Academic Press, New York.

CATES RG & GG ORIANS GG (1975) Successional status and the palatability of plants to generalized herbivores. Ecology 56: 410-418.

CHRISTENSEN NL & CH MULLER (1975) Relative importance of factors controlling germination and seedling survival in *Adenostoma* chaparral. American Midland Naturalist 93: 71-78.

DI CASTRI F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, DW Goodall & RL Specht (eds) Mediterranean-type shrublands: 1-52. Elsevier Scientific Publications, New York.

ESAU K (1977) Anatomy of seed plants. John Wiley & Sons Inc., New York. 376 pp.

ETCHEGARAY J & ER FUENTES (1980) Insectos defoliadores asociados a siete especies arbustivas del matorral. Anales del Museso de Historia Natural (Valparaíso) 13: 159-166.

FEENY PP (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51: 565-581.

FRAZER JM & SD DAVIS (1988) Differential survival of chaparral seedlings during the first summer drought after wild fire. Oecologia 76: 215-221.

FUENTES ER, J ETCHEGARAY, ME ALJARO & G MONTENEGRO (1981) Shrub defoliation by matorral insects. In: Di Castri F, DW Goodall & RL Specht (eds) Mediterranean-type shrublands: 345-359. Elsevier Scientific Publishing Co., Amsterdam.

FUENTES ER, A POIANI & JD MOLINA (1987) Shrub defoliation in the Chilean matorral: what is its significance?. Revista Chilena de Historia Natural 60: 276-283.

GILIBERTO J & H ESTAY (1978) Seasonal water stress in some Chilean matorral shrubs. Botanical Gazete 139: 236-240.

GINOCCHIO R & G MONTENEGRO (1989) Organización estructural de yemas vegetativas de especies arbustivas dominantes del matorral. Medio Ambiente (Chile) 10: 51-56.

GINOCCHIO R & G MONTENEGRO (1992) Interpretation of metameric architecture in dominants shrubs of the Chilean matorral. Oecologia 90: 451-456.

GINOCCHIO R & G MONTENEGRO (1994) Effects of insect herbivory on plant architecture. In: Ariatnoutsou M & RL Specht (eds) Plant-animal interactions in mediterranean type ecosystems: 115-122. Kluwer Academic Publishers, Dordrecht.

JOHNSON HB (1975) Plant pubescence: an ecological perspective. The Botanical Review 41: 233-257.

HALLE F & RAA OLDEMAN (1970) Essai sur l'architecture et la dynamique de croissance des abres tropicaux. Masson, Paris. 178 pp.

KOZLOWSKI TT (1972) Water deficits and plant growth. Academic Press, New York, London.

LAMONT BB & W KELLY (1988) The relationship between sclerophylly, nutrition and water use in two species from contrasting soils. In: Di Castri F, Ch Floret, S Rambal & J Roy (eds) Time scales and water stress: 617-621. Proceeding 5th International Conference on Mediterranean Ecosystems, I.U.B.S., Paris.

LEVIN DA (1973) The role of trichomes in plant defense. The Quarterly Review of Biology 48: 3-15.

LEVIN DA (1976) Alkaloid-bearing plants: an ecogeographic perspective. American Naturalist 110: 261-284.

MAUSETH JD (1988) Plant Anatomy. The Benjamin Cummings Publishing Company, Inc. 560 pp.

MERINO J, C FIELD & HA MOONEY (1982) Construction and maintenence costs of mediterranean-climate evergreen and deciduous leaves. I. Growth and CO2 exchange analysis. Oecologia 53: 208-213.

MILLER PC (1981) Resource use by chaparral and matorral. A comparison of vegetation function in two mediterranean-type ecosystems. Springer, Berlin, Heidelberg, New York. 455 pp.

MILLS JN (1983) Herbivory and seedling establishment in post-fire southern California chaparral. Oecologia 60: 267-270.

MONTENEGRO G (1987) Quantification of mediterranean plant phenology and growth. In: Tenhunen JD, O Catarino, L Lange & WC Oechel (eds) Plant response to stress. Functional analysis in mediterranean ecosystems: 470-488. Springer-Verlag, Berlin, Heidelberg. NATO ASI Series Vol. G15.

MONTENEGRO G & F RIVEROS DE LA PUENTE (1977) Comparison of differential environmental responses of *Colliguaja odorifera*. Flora 166: 125-135.

MONTENEGRO G, F RIVEROS & C ALCALDE (1980a) Morphological structure and water balance of four Chilean shrub species. Flora 170: 554-564.

MONTENEGRO G, M JORDAN & ME ALJARO (1980b) Interactions between Chilean matorral shrubs and phytophagous insects. Oecologia 45: 346-349.

MONTENEGRO G, G AVILA, ME ALJARO, R OSORIO & M GOMEZ (1989) Chile. In: Orshan G (ed) Plant pheno-morphological studies in mediterranean type ecosystems: 347-389. Kluwer Academic Publishers, The Netherlands.

MONTENEGRO G & R GINOCCHIO (1993) Modular interpretation of architecture in shrub species. Anais da Academia Brasileira de Ciencias 65: 189-202.

MOONEY HA (1981) Primary production in mediterranean-climatic regions. In: Di Castri F, DW Goodall & RL Specht (eds) Ecosystems of the world: 149-255. Elsevier, New York.

MOONEY HA, DJ PARSONS & J KUMMEROW (1974) Plant development in mediterranean climates. In: Lieth H (ed) Phenology and seasonality modeling: 255-267. Springer Verlag, New York.

MOONEY HA, A JOHNSON, D PARSONS, S KEELEY, A HOFFMANN, A HAYS, J GILIBERTO & C CHU (1977) The producers, their resources and adaptative response. In: Mooney HA (ed) Convergent evolution in Chile and California mediterranean climate ecosystems : 224. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

MULROY TW (1979) Spectral properties of heavily glaucous and non-glaucous leaves of a succulent rosette-plant. Oecologia 38: 349-357.

QUINN R (1986) Mammalian herbivory and resilence in mediterranean-type ecosystems. In: Dell B, AJ Hopkins & BB Lamont (eds) Resilience in mediterranean ecosystems: 113-128. Dr. Junk Publ., Dordrecht, The Netherlands.

ROBBERECHT R & MM CALDWELL (1978) Leaf epidermal transmittance of ultraviolet radiation and its implications for plant sensitivity to ultraviolet-radiation induced injury. Oecologia 32: 277-287.

ROBBERECHT R, MM CALDWELL & WD BILLINGS (1980) Leaf ultraviolet optical properties along a latitudinal gradient in the artic-alpine life zone. Ecology 61: 612-619.

SAIZ F (1980) Experiencias en el uso de criterios de similitud en el estudio de comunidades. Archivos de Biología y Medicina Experimentales (Chile) 13: 387-402.

SILVA H & E ACEVEDO (1984) Adaptaciones anatomorfológicas foliares al déficit hídrico en *Atriplex repanda*. Phil. Revista Chilena de Historia Natural 57: 69-78.

SPECHT RL (1979) Heathlands and related shrublands. Elsevier, Amsterdam.

VAN TK, LA GARRARS & SH WEST (1976) Effects of UV-B radiation on net photosynthesis of some crop plants. Crop Science 16: 715-718.

WALKOWIAK AM, JA SIMONETTI, I SEREY, M JORDAN, R ARRANZ & G MONTENEGRO (1984) Defensive patterns in shrubs of central Chile; a common strategy? Acta Oecologica 15: 191-199.

WARDLAW IF (1990) The control of carbon partitioning in plants. New Phytologist 116: 341-381.

WIEBE HH (1980) Morphological adaptations to water stress. In: Turner NC & PJ Kramer (eds) Adaptation of plant to water and high temperature stress: 439-443. Wiley and Sons, New York.