Influence of altitude and host-plant species on gall distribution in *Colliguaja* spp. (Euphorbiaceae) in central Chile

Influencia de la altitud y la especie de planta hospedadora sobre la distribución de cecidias en *Colliguaja* spp. (Euphorbiaceae) en Chile central

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ABSTRACT

The shrub genus *Colliguaja* (Euphorbiaceae) shows a characteristic pattern of altitudinal distribution in central Chile. At lower altitudes it is represented by *C. odorifera*, at middle elevation by the putative hybrid *C. salicifolia* and at upper altitudes by *C. integerrima*. Flower buds of *Colliguaja* spp. are galled by gall-midges and also show the presence of associated parasitoids and hyperparasitoids. In this study we evaluated the effect of altitude and *Colliguaja* species on the distribution and abundance of flower galls resulting from parasitoid attack. Analysis of leaf morphology was used to represent either putative hybridisation or a host-plant species transition at different altitudes, while gall prevalence and relative abundance were measured as dependent variables. Gall prevalence and relative abundance decreased significantly as altitude increased, and leaf morphology indicated a host-plant transition from *C. odorifera* through *C. salicifolia* to *C. integerrima*. Path analysis revealed that altitude had a stronger direct effect on relative abundance of galls than host-plant, while the influence of host-plant hybridisation or species transition was mainly mediated by changes in elevation.

Key-words: Mediterranean matorral, elevation, flower galls, *Colliguaja*.

RESUMEN

El género *Colliguaja* (Euphorbiaceae) presenta un patrón de distribución altitudinal característico en Chile central. A altitudes bajas está representado por *C. odorifera*, a altitudes intermedias por el híbrido putativo *C. salicifolia* y a altitudes mayores por *C. integerrima*. Los brotes florales de *C. odorifera* son atacados por moscas formadoras de cecidias, encontrándose también parasitoides e hiperparasitoides asociados. En este estudio evaluamos el efecto de la altitud y la especie de *Colliguaja* sobre la distribución y abundancia de cecidias florales, producto de la acción de parasitoides. Se realizaron análisis de morfología foliar para representar ya sea la hibridación putativa o la transición entre especies de plantas hospedadoras, y se midió como variables dependientes la prevalencia y la abundancia relativa de cecidias. La prevalencia y abundancia relativa de cecidias disminuyeron significativamente a medida que incrementó la altitud y la morfología foliar representó una transición en la planta hospepadora desde *C. odorifera* pasando por *C. salicifolia* hasta *C. integerrima*. Un análisis de vías reveló que la altitud tuvo un efecto directo más fuerte que la planta hospedera sobre la abundancia relativa de cecidias, y que la influencia de la hibridación o transición en las plantas hospedadoras fue mediado principalmente por cambios en la altitud.

Palabras clave: matorral mediterráneo, altitud, cecidias, *Colliguaja*.

INTRODUCTION

Most gall-maker insects are highly organ and host-plant specific. Hence, they have attracted special attention for the evaluation of variables affecting host-plant range (Dreger-Jauffret & Shorthouse 1992). Elevation gradients normally produce transitions between closely related host-plant species, frequently regarded as putative hybrids, which show differences in their susceptibility to gall makers (Whitham

1989, Boecklen & Spellenberg 1990, Aguilar & Boecklen 1992, Moorehead et al. 1993).

Influences of the host-plant on gall-maker susceptibility to parasitoid attack (Price & Clancy 1986, Clancy & Price 1986) and subsequent survival and abundance of parasitoids (Fritz 1995, Roininen et al. 1996) have been previously shown. Furthermore, elevation gradients can influence "tritrophic" interactions when closely related host-plant species change their distribution with changes in altitude (Preszler & Boecklen 1996)

The shrub genus *Colliguaja* Mol. (Euphorbiaceae) is represented in Santiago valley (central Chile) by three species with a characteristic pattern of altitudinal distribution. In this area, from 600 to 1200 meters above sea level (hereafter masl) *Colliguaja odorifera* Mol. is a major component of the Mediterranean matorral landscape. It is gradually substituted by *Colliguaja salicifolia* Gill. et Hook. at mid elevations (1200-1500 masl), while at upper altitudes (1600-2000 masl) *Colliguaja integerrima* Gill. et Hook. becomes the

dominant representative of this genus. The hybrid status of *C. salicifolia* has been postulated in the botanical literature (Navas 1976). However, in the absence of experimental crosses or suitable molecular markers to recognise hybridisation is not possible to discern the actual status of the intermediate phenotypes (Paige & Capman 1993). Thus, it is possible that the altitudinal distribution already described for *Colliguaja* spp. represents just a transition between closely related species showing variation in leaf morphology associated with environmental heterogeneity caused by elevation.

While *C. odorifera* suffers low defoliation in relation to other shrub species of the Chilean mediterranean matorral (Montenegro et al. 1980), it is strongly attacked by gall-makers (Martínez et al. 1992). From the beginning of this century the identity of gall inducer species has been under debate (Porter 1928, Martínez et al. 1992), having been solved only recently (Núñez & Sáiz 1994, Sáiz et al. in press). These latter studies definitively showed, as initially stated, that the insects *Riveraella*

TABLE 1

Means and standard deviations (SD) of morphological variables of populations of *C. odorifera*, *C. salicifolia* and *C. integerrima* utilised in the discriminant analysis. Sample size = 10

Medias y desviaciones estándar (SD) de las variables morfológicas utilizadas en el análisis discriminante de poblaciones de *C. odorifera*, *C. salicifolia* y *C. integerrima*. Tamaño muestral = 10

Variable	C.odorifera 1150 masl		C.odorifera 1300 masl		C. salicifolia 1450 masl		C. salicifolia 1600 masl		C. integerrima 1650 masl	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Leaf length (l) (cm)	2.99	0.47	2.98	0.27	3.59	0.50	5.03	0.76	8.44	0.51
Leaf width (w) (cm)	1.27	0.32	1.30	0.16	0.69	0.08	0.86	0.17	0.47	0.06
l w⁻¹	2.42	0.26	2.33	0.18	5.31	0.96	6.05	0.92	18.82	2.36
Leaf perimeter (p) (cm)	8.72	1.67	8.64	0.95	9.18	1.72	14.13	3.61	21.57	5.20
Leaf area (a) (cm²)	2.80	1.21	2.77	0.57	1.76	0.29	3.13	0.25	3.20	0.42
Leaf shape (4π a p⁻²)	0.46	0.04	0.48	0.05	0.29	0.06	0.21	0.06	0.10	0.03
Glands per leaf (g)	37.06	5.11	38.14	6.00	18.73	3.71	32.1	13.41	0	0
g p⁻¹	4.37	0.43	4.50	0.66	2.11	0.44	2.30	0.76	0	0

colliguayae Kieffer & Herbst and *Promikiola rubra* Kieffer & Herbst (Diptera: Cecidomiiydae) are the inducers of the ament (male flower) gall in *C. odorifera*. Both gall-midges can be attacked by the ectoparasitoid *Exurus colliguayae* Philippi (Hymenoptera: Eulophidae) which kills the gall-midge larvae after the gall has been induced (Sáiz et al. in press). This parasitoid wasp species remains in the gall while it shows lignification until the typical floral galls are formed, as described by Núñez & Sáiz (1994) and Sáiz et al. (in press). Furthermore, an ectohyperparasitoid wasp, *Torymus laetus* Philippi (Hymenoptera: Torymidae), may attack and consume the eulophid larvae (Sáiz et al. in press). Those gall-midges not attacked by *E. colliguayae* leave the gall while the gall tissues are still soft, in early spring (August-September) (Sáiz et al. in press). Therefore, typical lignified galls observed on *C. odorifera* during the late summer season are the result of a tritrophic interaction, since they would not be formed without the action of *E. colliguayae*.

We studied *Colliguaja* spp. (Euphorbiaceae) along an elevation gradient to evaluate whether "tritrophic" effects, related with either putative hybridisation or an altitudinal transition between host-plant species, and environmental heterogeneity associated with elevation, affect the distribution and relative abundance of floral galls.

MATERIALS AND METHODS

Morphological analysis of the leaves of Colliguaja *species*

The study site was Quebrada de Lo Cañas (33° 31' S, 70° 29' W), a ravine running in E-W direction at the foothills of the Andes range facing Santiago. Sampling sites were selected in an altitudinal transect along the sunny (northfacing) slope every 150 meters in altitude from 1150 to 1600 masl. Additionally, a fifth site at 1650 masl was chosen since it contained an extensive population of *C. integerrima* which marked the upper limit of shrub vegetation.

At each altitude, ten mature shrubs were randomly selected regardless of the presence of galls. On each individual shrub sampled, two branches were chosen at random and the largest ten fully expanded leaves on them were collected for morphometric studies. At the laboratory, the leaves were placed within glass plates and scanned in a Scanjet 3p® for further analysis with the SigmaScan® software. Finally, the shrubs were identified to the species level following the key of Navas (1976).

The morphological measures of the leaves (Table 1) were subjected to a canonical discriminant function analysis to evaluate if the a priori classification by altitude or by *Colliguaja* species reflected any morphological change. Furthermore, following the approach proposed by Moorehead et al. (1993) to order hybrids and parental host-plant species, the canonical scores from the first discriminant function were re-scaled to obtain a modified leaf morphology index (LMI). This measure, which varies between 0 and 1, represents a morphological continuum, with values near 1 for *C. odorifera*, close to 0 for *C. integerrima* and intermediates for *C. salicifolia*.

Gall prevalence and relative abundance in the field

The same shrubs selected for morphometric analysis were used to estimate the prevalence and relative abundance of flower galls. Sampling was performed during February-March of 1996, the end of the summer season, when all the flower galls attacked by parasitoids-hyperparasitoids are fully developed (Martínez et al. 1992). Four shoots were randomly selected and the number of apical buds and flower galls per shoot recorded. We considered only apical buds because these meristems contain the preformed reproductive structures (Hoffmann & Hoffmann 1976) which are galled by *R. colliguayae* and *P. rubra*, the gall-midges used as host by the parasitoid-hyperparasitoid wasps. Although other gall types are produced by the same insect species (e.g., galls in vegetative buds of *C. odorifera*; Martínez et al. 1992), they were not re-

corded due to their low abundance in the study sites. Gall relative abundance was expressed as the proportion of flower galls relative to total apical buds (galls plus non-attacked apical meristems).

Prevalence was expressed as the proportion of galled shrubs relative to total shrubs sampled. These data were analysed with the G heterogeneity test, using the STP procedure for a posteriori multiple comparisons (Sokal & Rohlf 1995). Significant differences in relative abundance between sampling sites were evaluated with Kruskal-Wallis analysis of variance (Siegel & Castellan 1988).

Influence of altitude and LMI on gall relative abundance

Elevation and LMI, this last variable representing either the transition between host-plants or a putative hybridisation phenomenon, were used as predictor variables in a multiple regression on gall relative abundance as response variable. LMI values were subjected to the Arcsin $\sqrt{x}$ transformation prior to multiple regression. Although a correlation between altitude and

LMI was found ($R^2 = 0.68$), the tolerance was good enough to allow multiple regression analysis. Therefore, ridge regression was not necessary and path analysis (Kingsolver & Schemske 1991, Mitchell 1992) was performed to discern the direct and indirect effects of the predictor variables on gall relative abundance. Standardised partial regression coefficients and correlation coefficients for elevation and LMI were used to calculate path coefficients of the path diagram as described in Sokal & Rohlf (1995).

RESULTS

Morphometric analyses of Colliguaja *spp.*

Descriptive statistics of the leaf variables measured in the populations of *Colliguaja* spp. studied are given in Table 1. The discriminant analysis showed highly significant differences between groups (Wilk's Lambda = 0.00104, $F_{(32, 141)}$ = 24.084, $P < 0.0001$), four groups being distinguishable based on squared Mahalanobis distances (Fig. 1). Leaf mor-
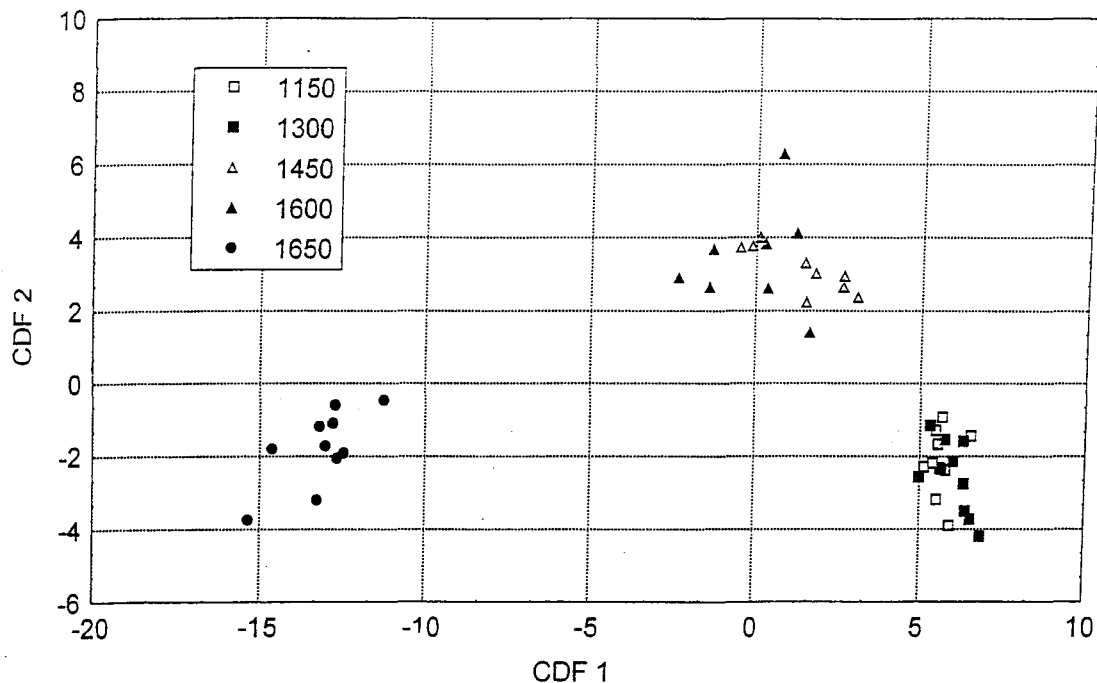

Fig. 1: Scatter-plot of the first two canonical discriminant functions (CDF) obtained from the analysis of leaf morphology in the genus *Colliguaja*. Symbols represent different altitudes of the sampling sites.

Gráfico de las dos primeras funciones canónicas discriminantes (CDF) obtenidas del análisis de la morfología de hojas en el género *Colliguaja*. Los símbolos representan las diferentes altitudes de los sitios de muestreo.
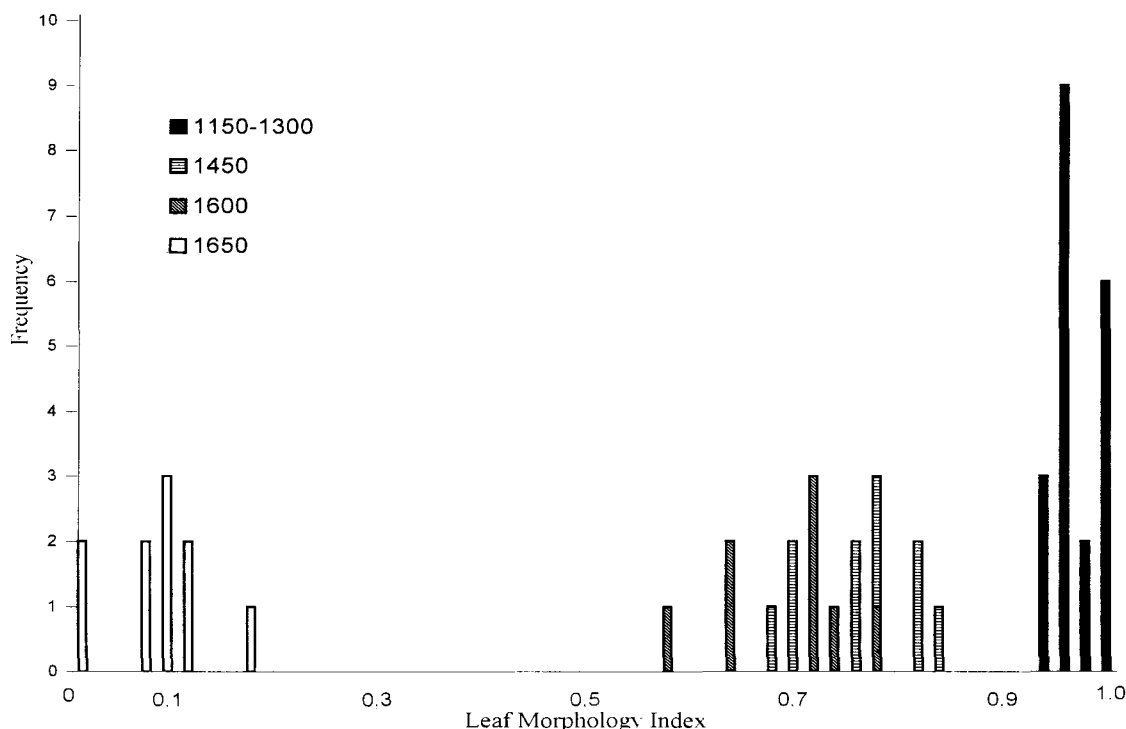
Fig. 2: Frequency of leaf morphology indexes observed in *Colliguaja* spp. sampled at different altitudes. Bars with different backgrounds represent different altitudes of the sampling sites.

Frecuencia de los índices de morfología foliar observados en *Colliguaja* spp. muestreadas a diferentes altitudes. Las barras con distintos fondos representan las diferentes altitudes de los sitios de muestreo.

phology was not significantly different at sites at 1150 and 1300 masl (F $_{(8,38)}$ = 0.44, P = 0.89), sites at 1450 and 1600 masl differing significantly between them (F $_{(8,38)}$ = 5.10, P = 0.0002). The site at 1650 masl was clearly separated from all the other groups (for all multiple comparisons P < 0.00001).

The frequency distribution of LMI (rescaled canonical scores) from different sites along the *Colliguaja* spp. morphological continuum is shown in Fig. 2. Group 1 according to the discriminant analysis, composed by sites at 1150 and 1300 masl, represent *C. odorifera*, while groups 2 (site at 1450 masl) and 3 (site at 1600 masl) according to the discriminant analysis, represent *C. salicifolia*. Finally group 4, according to the discriminant analysis, at 1650 masl is composed only by *C. integerrima*.

Gall prevalence and relative abundance

The prevalence of floral galls across the altitudinal sites and LMI gradient is shown

in Table 2. In general, the G test agrees with the groups obtained from the morphological canonical discriminant analysis. The STP procedure for multiple comparisons showed that the following three groups are significantly homogeneous: i) sites at 1150 and 1300 masl, ii) sites at 1450 and 1600 masl, and iii) site at 1650 masl. Table 2 also presents the mean floral gall relative abundance. Kruskal Wallis ANOVA showed significant differences in floral gall relative abundance between sites (H = 41.06, d.f.= 4, N = 10, P < 0.0001). As previously observed with prevalence data, a decrease in relative abundance with LMI and altitude was shown by multiple comparison procedures (Table 2).

Influence of altitude and LMI on gall relative abundance

Multiple regression with elevation and LMI as predictor variables of gall relative abundance was significant (F $_{(2,47)}$ = 53.26, P < 0.001, R^2 = 0.694). Path coefficients were

calculated for the path diagram shown in Figure 3. Direct and indirect effects of elevation and LMI were calculated and showed a strong direct negative effect of altitude on gall relative abundance (-1.1), while the indirect effect of altitude through changes in LMI was positive but of smaller magnitude (-0.83 x -0.30 = 0.25). On the contrary, the effect of LMI was mainly positive and indirect through changes in altitude (-0.83 x - 1.1 = 0.91) in comparison with a less important negative direct effect (-0.3) of LMI on gall relative abundance.

DISCUSSION

The canonical discriminant analysis of LMI of *Colliguaja* spp. showed significant differences between the populations studied. Also a good correspondence with the a priori classification by altitude of the populations, with the only exception of 1150 and 1300 masl, was found (Fig. 1). The frequency distribution of LMI by altitude (Table 2, Fig. 2) suggested that attributes of the leaf morphology of *C. odorifera* were present in 1150-1300 masl, then a transition to *C. salicifolia* occurred at 1450

and 1600 masl, and a sharp change to *C. integerrima* occurred at 1650 masl.

The rather gradual transition from *C. odorifera* to *C. salicifolia* along the elevation gradient with an abrupt change to *C. integerrima* in a small elevation range may be interpreted as: i) a hybrid status of *C. salicifolia* with an unidirectional introgression toward *C. odorifera* and not toward *C. integerrima*, ii) a proper species status for *C. odorifera* and *C. salicifolia* with hybridisation between them and not with *C. integerrima*, and iii) a strong phenotypical variation in leaf morphology of *C. odorifera* caused by altitude with a sharp transition to *C. integerrima*, i.e. *C. salicifolia* would not be a "good" species. Our data on leaf morphology can not discriminate between these hypotheses, but other sources of information such as the overlapping flowering phenology and the parapatric geographical distribution of *C. odorifera* with *C. salicifolia* and *C.salicifolia* with *C. integerrima* support a putative hybrid status for *C. salicifolia* (Navas 1976).

Prevalence and relative abundance of floral galls on *Colliguaja* spp., decreased with altitude up to vanish at 1650 masl corresponding to *C. integerrima* (Table 2). Since

TABLE 2

Means and standard deviations of gall prevalence (proportion of galled shrubs in relation to total shrubs sampled) and relative abundance (proportion of floral galls in relation to total apical buds, i.e. galls plus non-attacked apical meristems) along elevation and leaf morphology index (LMI) of *Colliguaja* spp. Means showing the same letter within a column are not significantly different. Sample size = 10

Medias y desviaciones estándar de la prevalencia (proporción de arbustos con cecidias en relación al total de arbustos muestreados) y la abundancia relativa de cecidias (proporción de cecidias florales en relación al total de meristemas apicales, i.e. cecidias más meristemas apicales no atacados), a lo largo del gradiente de altitud y de índice de morfología foliar (LMI) de *Colliguaja* spp. Las medias de la misma columna que presentan la misma letra no son diferentes significativamente. Tamaño muestral = 10

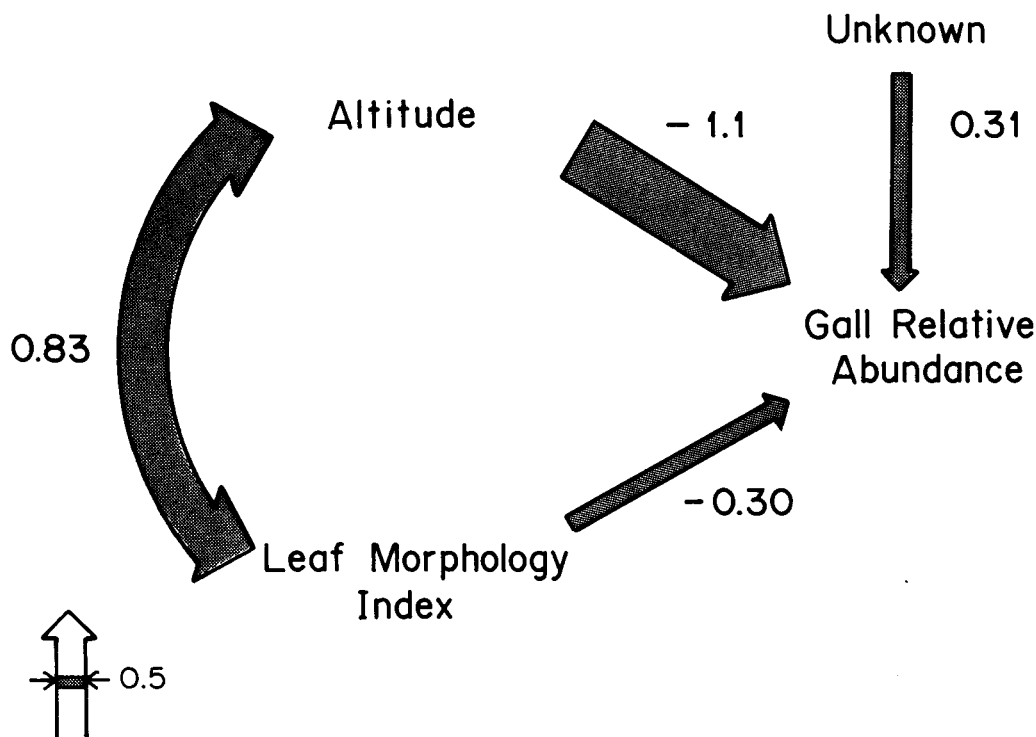| Altitude (masl)	Leaf Morphology Index (LMI)		Gall prevalence	Gall relative abundance	
	mean	SD		mean	SD
1150	0.95 a	0.02	1 a	0.153 a	0.099
1300	0.97 a	0.03	1 a	0.037 ab	0.032
1450	0.76 b	0.06	0.5 b	0.002 bc	0.003
1600	0.69 c	0.06	0.1 b	0.0002 c	0.0005
1650	0.08 d	0.00	0 c	0 c	0

Fig. 3: Path diagram showing the predictor variables affecting gall relative abundance. Figures near arrows connecting altitude and LMI with gall relative abundance are standardised partial regression coefficients, while the figure near the curve arrow connecting altitude with LMI is the Pearson's correlation coefficient between these variables. Unexplained variation by altitude and LMI is represented by the coefficient of multiple nondetermination (figure near the arrow connecting unknown with gall relative abundance).

Diagrama de vías que muestra las variables predictoras que afectan la abundancia relativa de cecidias. Las cifras junto a las flechas que conectan altitud y LMI con la abundancia relativa de cecidias son los coeficientes estandarizados de regresión parcial, mientras que la cifra junto a la flecha curva que conecta altitud con LMI es el coeficiente de correlación de Pearson entre estas variables. La variación no explicada por la altitud y el LMI es representada por el coeficiente de indeterminación múltiple (cifra junto a la flecha que conecta el Desconocido con la abundancia relativa de las cecidias).

in our system LMI covaried with altitude, these variables might interact affecting directly and indirectly the observed distribution of galls. Path analysis revealed that the direct effect of altitude was negative (lower gall abundance at higher altitude) and stronger than the positive (higher gall abundance at higher LMI associated to *C. odorifera*) indirect effect of altitude through changes in LMI. On the other hand, the direct effect of LMI was negative and weaker than the positive indirect effect of LMI observed through changes in altitude. These results indicated that changes in elevation contributed directly and changes in LMI mostly indirectly to the observed pattern of gall relative abundance along the elevation gradient.

Several mechanisms have been proposed to explain reductions of parasitism with altitude, such as the progressive reduction in days-degree with altitude that may cause asynchrony of developmental time schedules of both the parasitoid and herbivore (Taylor 1981), or the hazardous nature of sites at high elevations related to unstable population dynamics of the herbivore (Randall 1982a, b). However, elevation can also influence several aspects of host-plant quality. For instance, Paige & Capman (1993) reported that the quality of *Populus* spp. as hosts for *Pemphigus* spp. aphids was affected by abiotic factors probably related with elevation. Furthermore, Preszler & Boecklen (1996) also postulated the influence of altitude on the third-

trophic level to occur via host-plant quality. Thus, altitude could influence natural enemies of herbivorous insects concomitantly with the change in host-plant quality.

Concerning probable mechanisms involved in host-plant susceptibility or resistance to gall-makers, secondary metabolites have been reported affecting galling sawflies on *Salix* (e.g., Kolehmainen et al. 1986). In *C. odorifera* the latex content of the leaves has been mentioned as a relevant mechanism of defence against chewing insects (Montenegro et al. 1980). This latex is composed of alkanes which show qualitative and quantitative differences between species of the genus *Colliguaja* (Gnecco et al. 1989), thus being a probable source of antiherbivore defence against gall-makers. Another mechanism that might be involved in the observed pattern of herbivory is host-plant phenology. Floate et al. (1993) proposed that early and staggered leaf flushing in hybrid zones contributed to explain the peak density of chrysomelids on *Populus fremontii* x *P. angustifolia*. In our case, preformed reproductive structures inside dormant apical buds of *C. odorifera*, necessary for gall-midges and their natural enemies, are present during the whole drought period (November-April) (Hoffmann & Hoffmann 1976, Martínez et al. 1992). Therefore, phenological variability is restricted and probably does not play a major role in the distribution of gall-midge and hence parasitoid attack.

In conclusion, abiotic heterogeneity associated with altitude seemed to be more relevant than host-plant transition or putative hybridisation to explain the observed pattern of gall distribution and abundance in *Colliguaja* spp.

ACKNOWLEDGMENTS

LITERATURE CITED

AGUILAR JM & WJ BOECKLEN (1992) Patterns of herbivory in the *Quercus grisea* x *Quercus gambelii* species complex. Oikos 64: 498-504.

BOECKLEN WJ & R SPELLENBERG (1990) Structure of herbivore communities in two oak (*Quercus* spp.) hybrid zones. Oecologia 85: 92-100.

CLANCY KM & PW PRICE (1986) Temporal variation in three-trophic-level interactions among willows, sawflies and parasites. Ecology 67: 1601-1607.

DREGER-JAUFFRET F & JD SHORTHOUSE (1992) Diversity of gall-inducing insects and their galls. In: Shorthouse JD & O Rohfritsch (eds) Biology of insect-induced galls: 8-33. Oxford University Press, New York.

FLOATE KD, MJC KEARSLEY & TG WHITHAM (1993) Elevated herbivory in plant hybrid zones: *Chrysomela confluens*, *Populus* and phenological sinks. Ecology 74: 2056-2065.

FRITZ RS (1995) Direct and indirect effects of plant genetic variation on enemy impact. Ecological Entomology 20: 18-26.

GNECCO S, J BARTULIN, J BECERRA & C MARTICORENA (1989) n-Alkanes from Chilean Euphorbiaceae and Compositae species. Phytochemistry 28: 1254-1256.

HOFFMANN AJ & AE HOFFMANN (1974) Growth pattern and seasonal behaviour of buds of *Colliguaja odorifera*, a shrub from the Chilean mediterranean vegetation. Canadian Journal of Botany 54: 1767-1774.

KINGSOLVER JG & DW SCHEMSKE (1991) Path analysis of selection. Trends in Ecology and Evolution 6: 276-280.

KOLEHMAINEN J, H ROININEN, R JULKUNEN-TIITO & J TAHVANAINEN (1994) Importance of phenolic glucosides in host selection of shoot galling sawfly, *Euura amerinae*, on *Salix pentandra*. Journal of Chemical Ecology 20: 2455-2466.

MARTINEZ E, G MONTENEGRO & M ELGUETA (1992) Distribution and abundance of two gall-makers on the euphorbiaceous shrub *Colliguaja* odorifera. Revista Chilena de Historia Natural 65: 75-82.

MITCHELL RJ (1992) Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. Functional Ecology 6: 123-129.

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

MOOREHEAD JR, ML TAPER & TJ CASE (1993) Utilization of hybrid oak hosts by a monophagous gall wasp: how little host character is sufficient? Oecologia 95: 385-392.

NAVAS E (1976) Flora de la cuenca de Santiago de Chile. Tomo II: Dicotyledoneae - Archichlamydeae. Editorial Universidad de Chile, Santiago. 559 pp.

NUÑEZ C & F SAIZ (1994) Cecidios en vegetación autóctona de Chile de clima mediterráneo. Anales del Museo de Historia Natural de Valparaíso 22: 57-80.

PAIGE KN & WC CAPMAN (1993) The effect of host-plant genotype, hybridisation, and environment on gall-aphid attack and survival in cottonwood: the importance of genetic studies and the utility of RFLPs. Evolution 47: 36-45.

PORTER CE (1928) Cecidiología Chilena. Breve reseña histórica y bibliografía acerca de las agallas del colliguay (*Colliguaja odorifera* Mol.). Revista Chilena de Historia Natural 32: 73-80.

PRESZLER RW & WJ BOECKLEN (1996) The influence of elevation on tritrophic interactions: opposing gradients of top-down and bottom-up effects on a leaf mining moth. Ecoscience 3: 75-80.

PRICE PW & KM CLANCY (1986) Interactions among three trophic levels: gall size and parasitoid attack. Ecology 67: 1593-1600.

RANDALL MGM (1982a) The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in northern England. Journal of Animal Ecology 51: 993-1016.

RANDALL MGM (1982b) The ectoparasitization of *Coleophora alticolella* (Lepidoptera) in relation to its altitudinal distribution. Ecological Entomology 7: 117-185

ROININEN H, PW PRICE & J TAHVANAINEN (1996) Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly, parasitoids and inquilines. Oikos 77: 44-50.

SAIZ F, A MORALES & M OLIVARES (in press) Sobre el complejo de cecidios de *Colliguaja odorifera* Mol. (Euphorbiaceae). Anales del Museo de Historia Natural de Valparaíso.

SIEGEL S & NJ CASTELLAN (1988) Nonparametric statistics for the behavioral sciences. Second edition. Mc Graw Hill, New York. 399 pp.

SOKAL RR & FJ ROHLF (1995) Biometry. Third edition. W.H. Freeman, San Francisco. 887 pp.

TAYLOR F (1981) Ecology and evolution of physiological time in insects. American Naturalist 117: 1-23.

WHITHAM TG (1989) Plant hybrid zones as sinks for pests. Science 244: 1490-1493.