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Galler-induced reduction of shoot growth and fruit production in the shrub *Colliguaja integerrima* (Euphorbiaceae)

Insectos cecidómidos reducen el crecimiento de brotes y la producción de frutos en el arbusto *Colliguaja integerrima* (Euphorbiaceae)

WILFREDO L. GONZÁLES[1]*, PAULA P. CABALLERO[2] & RODRIGO MEDEL[2]

[1]ECOBIOSIS, Departamento de Botánica, Universidad de Concepción,
Casilla 160-C, Concepción, Chile
[2]Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile,
Casilla 653, Santiago, Chile
*Corresponding author: e-mail: wgonzales@udec.cl

ABSTRACT

We evaluated experimentally the effect of a gall-maker insect on vegetative and reproductive traits of the shrub *Colliguaja integerrima* (Euphorbiaceae). We performed two experiments: (1) a chemical (insecticide) exclusion to prevent gall formation, and (2) a mechanical removal of new galls at the early stage to prevent gall growth. In the study area, galled shrubs were common (77 %). Because the pattern of insect attack may influence plant fitness, the distribution of egg clusters deposited by the galler and the number of galls among shrubs were also evaluated. Fruit production was inversely associated with the number of galls, but did not correlate with shrub height, shrub cover, and number of shoots. Ungalled shoots were longer than galled shoots after 12 months initiated the experiment. Chemical exclusion produced a delayed positive effect on plant reproduction. Fruit production was higher in experimental than control branches after 24 months. Mechanical removal of galls increased fruit production in comparison to control branches in the next reproductive season. These results indicate that the galler reduces shoot growth, and has a delayed detrimental impact on fruit production of *C. integerrima*. Because the chance of finding new galls was higher on the previously infected shrubs, it is possible that reinfection processes account for the cumulative negative effects of the bud-galling insect on plant fitness.

Key words: bud-galling insect, central Chile, Mediterranean ecosystem.

RESUMEN

Evaluamos experimentalmente el efecto de un insecto cecidómido sobre rasgos vegetativos y reproductivos del arbusto *Colliguaja integerrima* (Euphorbiaceae). Efectuamos dos experimentos: (1) una exclusión química (insecticida) para impedir la formación de cecidias, y (2) una remoción mecánica de cecidias recién formadas para evitar su crecimiento. En el sitio de estudio, los arbustos con cecidias fueron comunes (77 %). Como el patrón de ataque del insecto puede influir en el desempeño de la planta, evaluamos también la distribución de huevos depositados por el cecidómido y el número de cecidias entre arbustos. La producción de frutos se relacionó inversamente con el número de cecidias, pero no presentó asociación significativa con la altura del arbusto, su cobertura ni con el número de brotes. Brotes sin cecidias fueron más largos que los con cecidias. El tratamiento químico produjo un efecto positivo retrasado sobre la reproducción de la planta. Una vez transcurridos 24 meses de iniciado el experimento químico, el número de frutos fue mayor en las ramas experimentales que en las ramas control (con cecidias). De igual manera, la remoción mecánica de cecidias aumentó la producción de frutos en comparación a las ramas control en la siguiente estación reproductiva del arbusto. Estos resultados indican que el cecidómido reduce el crecimiento de los brotes y tiene un efecto negativo retardado sobre la producción de frutos de *C. integerrima*. Como la probabilidad de detectar cecidias nuevas fue mayor en los arbustos previamente infectados, es posible que el proceso de reinfección de cuenta de los efectos negativos acumulativos del insecto sobre el desempeño de la planta.

Palabras clave: cecidómidos de brotes, Chile central, ecosistema mediterráneo.

INTRODUCTION

Most studies on plant - herbivore relationships have focused on the fitness-impact of herbivores on annual plant species, where reduction in plant fecundity translates into a direct fitness loss across the individual lifetime (Crawley 1989, Marquis 1992a). In perennial plants, however, the impact of herbivory on plant growth and reproduction may be expressed in the same year in which damage actually occurs (Whitham & Mopper 1985, Weis & Sacchi 1996), in the following years (Primack & Hall 1990, Whigham 1990), or in both (Myers 1981), depending on the amount of resources acquired by the plant during the current and previous years (Obeso 1993). Because of the inherent difficulty to separate short- from long-term effects of herbivory on plant reproduction, most studies performed on perennial plants circumscribe to a short segment of the plant's life history (e.g., Marquis 1984, 1992b, Whitham & Mopper 1985, Paige & Whitham 1987, Crawley 1989, Weis & Sacchi 1996). This practice is unfortunate because plants may compensate or even overcompensate the immediate detrimental effect of herbivory when observed over a long period across reproductive seasons (e.g., Solomon 1983, Sacchi et al. 1988, Hendrix 1988, Messina et al. 2002).

In this report, we document the results of a three-year field study designed to evaluate the effect of a bud-galling insect on vegetative and reproductive traits of the native shrub *Colliguaja integerrima* Gill. et Hook. (Euphorbiaceae). *Colliguaja integerrima* is a native monoecious evergreen shrub that inhabits the Chilean Andean Range (Hoffmann 1998). Previous reports indicate that *Colliguaja* species suffer a low defoliation by chewing insects in comparison to other shrub species in central Chile (Montenegro et al. 1980), albeit they are commonly attacked by diverse native phloem-feeders and gall-makers insects (Martínez et al. 1992, Núñez & Sáiz 1994, Fuentes-Contreras et al. 1999, Gonzáles & Fernández 2000). Even though galling insects infect intensively *C. integerrima* (Martínez et al. 1992, Núñez & Sáiz 1994, Fuentes-Contreras et al. 1999), the extent to which insect damage translates into a lower reproductive success remains largely unknown. We investigated the impact of a bud-galling insect on vegetative growth (shoot growth) and reproduction (fruit set) of *C. integerrima* by using chemical and mechanical gall-exclusion experiments.

MATERIAL AND METHODS

Study site and natural history

The fieldwork was carried out at Cerro El Roble, located in the Region Metropolitana, Santiago, Chile (32°58' S, 71°00' W, 1.600-1700 m elevation) from summer 2000 to summer 2002. *Colliguaja integerrima* reaches 1-2 m height and its flowering season occurs from September to November (Navas 1976). The vegetative growth occurs from September to February. Male flowers are terminal spikes and one or two female flowers are at the base of the male-spikes. The fruiting season occurs during March-April, and fruits are 3-seeded dry capsules (Navas 1976, Ravetta et al. 1991, Hoffmann 1998). In the study area, we did not record floral galls but spherical green galls within vegetative buds were common. Other herbivore insects (chewing and sucking) were relatively scarce in the study site. Even though the specific taxonomic description of this bud-galling insect has to be done, it corresponds to a gall midge because the last instar larva has a sternal spatula (a dermal structure on the venter of the prothorax), which is exclusive of Cecidomyiidae (Gagné 1994). Its overall life cycle is similar to that described by Sáiz et al. (1999) in *C. odorifera* ("cecidia de copa"). The bud-galling insect is a univoltine species whose hatching occurs approximately one week after oviposition. After that, the small neonate larvae move deeply into crevices of the vegetative bud to initiate gall formation. The gall grows from September to February. Each gall contains 1 to 30 separated chambers, with one larva per chamber. Pupation occurs within the galls at the end of the autumn. During the next spring, an adult emerges through one circular hole at the apical zone of each gall chamber.

Impact of galls on plant growth and reproduction

We estimated gall prevalence from the percentage of infected shrubs using eight 50-

meter linear and parallel transects in January 2000 (n = 102 shrubs). In the same area, we chose randomly 55 shrubs (at least 5 m apart), and recorded shrub height (m) and cover (length x width, m^2), and the number of galls and vegetative buds in four branches per shrub. In addition, we recorded fruit production in the same branches. We regressed all the descriptive variables on fruit production in a multiple regression analysis. To determine how gall formation affected shoot growth, in November 2000 we tagged galled and ungalled apical vegetative buds on randomly chosen shrubs. A t-test for independent samples was performed to compare the shoot growth after 12 months (n = 50 shoots) (Sokal & Rohlf 1995).

We carried out two experiments to evaluate the effect of bud galling insects on plant reproduction. First, a non-systemic pesticide was applied to prevent new gall formation. We sprayed a solution of Malathion (171 $\mu g/L^{-1}$ of active ingredient) on one branch of *C. integerrima* shrubs on a weekly basis, leaving a second branch of the same plant as control (n = 30 plants). Experimental and control branches were isolated and covered with plastic bags during pesticide application. The chemical was applied throughout the galling insect emergence season (which occurred from October 15 to November 30, 2000). We recorded the number of fruits and new gall formation in experimental and control branches during two consecutive reproductive seasons of *C. integerrima* (summer 2001 and summer 2002). A t-test for dependent samples was performed to compare the paired branches during the two years (Sokal & Rohlf 1995). Second, in order to assess the consequences of mechanical gall abortion on the future reproductive success of the host plant, two branches per shrub were randomly chosen in December 2000 (n = 37 galled shrubs). On one branch, all the recently developed galls were mechanically damaged with entomological pins and the second branch was left intact. A t-test for dependent samples was performed to compare the number of fruits/branch on each shrub during the summer 2002.

We assessed whether previous gall attack influenced subsequent oviposition and gall pattern distribution among host shrubs. First, we looked for egg clusters deposited by the galler and recorded the number of vegetative buds and galls from the previous year on randomly chosen shrubs (n = 48 plants) during the maximal activity date of adult emergence (last week of October 2000). We run a logistic regression to estimate the chance of finding at least one egg cluster, using the number of vegetative buds and galls from the previous year as predictor variables. Second, to determine whether the amount of previous galls influenced the occurrence of new galls, we randomly chose 49 shrubs in January 2001, and evaluated the relationship between the number of galls formed in the previous year and the presence of new galls.

RESULTS

The prevalence of galled shrubs was 77 %. A multiple regression analysis showed that while fruit production decreased with the number of galls, the height and cover of shrubs as well as the number of shoots had no influence on shrub fecundity (Table 1). Regarding vegetative growth, shoots were longer in ungalled than

TABLE 1

Multiple regression analysis to estimate the mean fruit production per branch of *Colliguaja integerrima* using as predictor variables plant traits and the number of galls from vegetative buds (summer 2000). R^2 model = 18.9 %, $F_{5,50} = 2.93$, $P < 0.029$

Análisis de regresión múltiple para estimar la producción promedio de frutos por rama de *Colliguaja integerrima* usando como variables independientes rasgos de la planta y el número de agallas de yemas vegetativas (verano del 2000). R^2 modelo = 18.9 %, $F_{5,50} = 2.93$, $P < 0.029$

Variable	B ± SE	P
Gall number/branch/plant	- 0.414 ± 0.129	0.002
Plant height	0.117 ± 0.147	0.427
Cover	0.217 ± 0.159	0.179
Shoot number	- 0.041 ± 0.137	0.768

galled shoots (ungalled = 64.04 ± 5.68 mm, galled = 21.48 ± 1.63 mm, t_{48} = 9.41, P < 0.001). The leaves of the galled shoots were reduced to packed small scales because of the short internodes resulting from gall infection.

Experimental branches had a lower number of galls than control branches in the summer 2001 (experimental = 0.98 ± 0.23, control = 9.65 ± 1.03, t_{29} = 8.93, P < 0.001). In spite of that, fruit production did not vary significantly between treatments in 2001 (t_{29} = 0.544, P = 0.589, Fig. 1). In the summer 2002, the number of galls was also lower in experimental than control branches (experimental = 0.33 ± 0.21, control = 19.07 ± 3.07, t_{29} = 6.19, P < 0.001). Unlike the situation observed in 2001, however, in the summer 2002 experimental branches had a higher fruit production than control branches (t_{29} = 3.158, P < 0.01, Fig. 1). The mechanical damage applied to new galls resulted in an increased fruit production in experimental branches in the next reproductive season as compared to control branches (experimental = 5.95 ± 0.98, control = 3.49 ± 0.90, t_{36} = 2.20, P < 0.034).

Gall infection correlated to past gall infection on shrubs (r = 0.74, t_{47} = 7.59, P < 0.001), and the probability of finding an egg cluster increased significantly with the number of galls present in the previous year (logistic regression analysis, Wald = 15.5, P < 0.001). The number of vegetative buds had no effect on the chance of finding egg clusters (logistic regression analysis, Wald = 0.23, P = 0.63).

DISCUSSION

Bud-galling insect attack was common in *C. integerrima* and fruit production decreased with the number of galls formed. Several studies have shown that fitness components of perennial plants are often reduced in the presence of insect attack (Crawley 1989, Strauss 1991, Marquis 1992a, Karban & Strauss 1993, Root 1996, Maron 1998, Sacchi

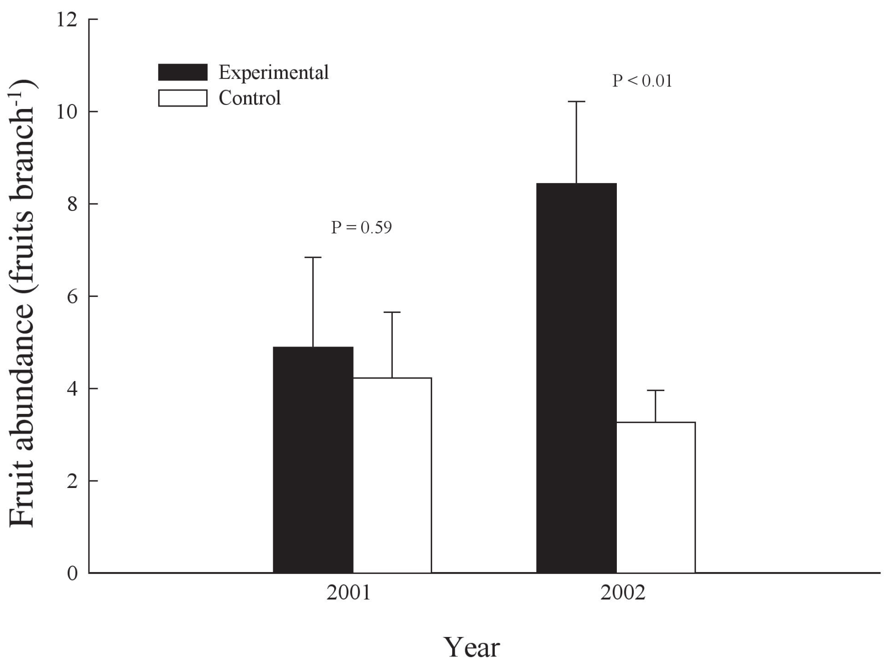

Fig.1: Mean fruits/branch of *C. integerrima* for experimental (▬) and control (▭) branches after chemical treatment in the summer of 2001 and 2002 (n = 30 branches). Bars represent one standard error.

Producción de frutos de *C. integerrima* de ramas experimentales (▬) y controles (▭) después del tratamiento con insecticida durante el verano del 2001 y el verano del 2002 (n = 30 ramas). Las barras representan un error estándar.

& Connor 1999). Our results provide additional evidence that insect attack has dramatic consequences for fruit production, and stress that detrimental effects on plant fecundity may occur over long periods across reproductive seasons in perennial plants. Even though the chemical treatment reduced gall infection in the summer 2001, fruit production did not differ significantly between experimental and control branches. However, this result does not rule out that short-term effects may occur on other fitness related traits, such as seed size or seed viability, which were not evaluated in this study. Interestingly, experimental branches produced a higher number of fruits than control branches in the summer 2002. Mechanical abortion of new galls at an early stage increased fruit production in the next reproductive season. Both plant phenology and the pattern of plant resource allocation may explain the delayed negative effect of the gall infection on plant reproduction. Flowering and fruiting of *C. integerrima* occurred at the beginning of the growing season, previous to vegetative growth. Arroyo et al. (1981) showed that high mountain plants present different flowering strategies. In the high Andean Cordillera of central Chile (2300-3500 masl), the flowering and fruiting season of most shrubs are often preceded by a long period of shoot and leaf growth. However, it is well known that the flowering of some shrub species occurs before leaf emergence in early spring (Arroyo et al. 1981, Rathcke & Lacey 1985) such as in *C. integerrima* (Navas 1976). *Colliguaja integerrima* leaves pre-formed floral buds for the next reproductive season at the end of summer. In alpine areas, most early and mid season flowering plants present flower-preformation, indicating that flower initiation occurs in the previous season (Körner 1999). Thus, the delayed impact of gall attack on plant reproduction could be explained if the current plant reproductive outcome is a consequence of nutrient production, storage and allocation to reproductive structure during the previous growing season (Obeso 1993, Ehrlen & Groenendael 2001).

In this study, gall infection reduced the length of vegetative shoots. The leaves of galled shoots were small and crowded due to the highly reduced internodes that resulted from gall infection as compared to unaffected vegetative shoots. In addition, galled shoots inhibited the production of new shoots in the following years. This effect on plant architecture may affect plant reproduction. Since reproductive buds are located in the apical portion of shoots (Navas 1976, Hoffmann 1998), it is quite possible that flower production decrease in the following years. A similar result has been reported for *C. odorífera*, where gall infection on vegetative buds inhibits shoot development and future production of new shoots and fruits (Martínez et al. 1992). However, unlike *C. integerrima* (which is galled mainly on vegetative buds), gall infection in *C. odorífera* frequently occurs in both male flowers and vegetative buds (Martínez et al. 1992, Fuentes-Contreras et al. 1999, Sáiz et al 1999) and dissect the impact of each gall type is more complex in the absence of an experimental approach. Other studies have documented a decreased ramet production, and biomass allocation to leaves, rhizomes, and inflorescences in attacked ramets (e.g., Hartnett & Abrahamson 1979, Abrahamson & Weis 1997, but see Craig et al. 1990). It is possible that gall makers modify plant tissues that would otherwise serve to other function, therefore competing for assimilates with plant tissues (Larson & Whitham 1991, Stinner & Abrahamson 1979, 1997, Fay et al. 1996).

The negative association between the number of galls and fruit production in the summer 2000 was not in agreement with the absence of short-term effect of gall attack on fruit production observed in the summer 2001. This situation may be explained, at least partially, by the reinfection pattern of the galling insect. Even though the mechanistic explanation for reinfection is beyond the scope of this paper, it is possible that gallers require maximizing the availability of plant reactive tissue to get a successful gall establishment (see also Weis *et al.* 1988, Gagné 1994), and consecutive gall attacks on the previously galled hosts may contribute to cumulative negative effects on plant reproduction. In conclusion, the bud galler insect caused a direct reduction on shoot length and a delayed negative effect on the fruit production of *C. integerrima*. Cumulative negative effects probably result from the reinfection pattern of *C. integerrima*. These results represent the first step to a fully understanding of the relevance of an herbivorous insect on the ecology of *C. integerrima*. Future work must take into account the role of defensive plant traits against insect attack and the factors that influence the observed reinfection pattern.

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LITERATURE CITED

ABRAHAMSON WG & AE WEIS (1997) Evolutionary ecology across three trophic levels. Goldenrods, gallmakers, and natural enemies. Princeton University Press, Princeton, New Jersey, USA. 456 pp.

ARROYO MTK, JJ ARMESTO & C VILLAGRÁN (1981) Plant phenological patterns in the high Andean Cordillera of central Chile. Journal of Ecology 69: 205-223.

CRAIG TP, JK ITAMI & PW PRICE (1990) Intraspecific competition and facilitation by a shoot-galling sawfly. Journal of Animal Ecology 59: 147-159.

CRAWLEY MJ (1989) Insect herbivores and plant population dynamics. Annual Review of Entomology 34: 531-564.

EHRLEN J & JV GROENENDAEL (2001) Storage and the delayed costs of reproduction in the understorey perennial *Lathyrus vernus*. Journal of Ecology 89: 237-246.

FAY PA, RW PRESZLER & TG WHITHAM (1996) The functional resource of a gall-forming adelgid. Oecologia 105: 199-204.

FUENTES-CONTRERAS E, E GIANOLI, PP CABALLERO & HM NIEMEYER (1999) Influence of altitude and host-plant species on gall distribution in *Colliguaja* spp. (Euphorbiaceae) in central Chile. Revista Chilena de Historia Natural 72: 305-313.

GAGNÉ RJ (1994) The gall midges of the Neotropical Region. Cornell University Press, New York, USA. 352 pp.

GONZÁLES WL & R FERNÁNDEZ (2000) Do host plant traits and galling insects affect the abundance of *Issus* sp. on *Colliguaja odorifera* Mol. along an altitudinal gradient? Revista Chilena de Entomología 26: 93-95.

HARTNETT DC & WG ABRAHAMSON (1979) The effects of stem gall insects on life history patterns in *Solidago canadensis*. Ecology 60: 910-917.

HENDRIX SD (1988) Herbivory and its impact on plant reproduction. In: Lovett Doust J & L Lovett Doust (eds) Plant reproductive ecology: 246-263. Oxford University Press, Oxford, United Kingdom.

HOFFMAN AJ (1998) Flora silvestre de Chile. Cuarta edición. Ediciones Fundación Claudio Gay, Santiago, Chile. 142 pp.

KARBAN R & SY STRAUSS (1993) Effect of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. Ecology 74: 39-46.

KÖRNER C (1999) Alpine plant life. Functional plant ecology of high mountain ecosystems. Springer Verlag, Berline, Germany. 343 pp.

LARSON KC & TG WHITHAM (1991) Manipulation of food resources by a gall-forming aphid: the physiology of sink-sources interactions. Oecologia 88: 15-21.

LARSON KC & TG WHITHAM (1997) Competition between gall aphids and natural sinks: plant architecture affects resistance to galling. Oecologia 109: 575-582.

MARON JL (1998) Insect herbivory above- and belowground: individual and joint effects on plant fitness. Ecology 79: 1281-1293.

MARQUIS RJ (1984) Leaf herbivores decrease fitness of a tropical plant. Science 226: 537-539.

MARQUIS RJ (1992a) Selective impact of herbivores. In: Fritz RS & EL Simms (eds) Plant resistance to herbivores and pathogens: ecology, evolution, and genetics: 301-325. University of Chicago Press, Chicago, Illinois, USA.

MARQUIS RJ (1992b) A bite is a bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). Ecology 73: 143-152.

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

MESSINA, FJ, SL DURHAM, JH RICHARDS & ED MCARTHUR (2002) Trade-off between plant growth and defense? A comparison of sagebrush populations. Oecologia 131: 43-51.

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

MYERS JH (1981) Interaction between western tent caterpillars and wild rose: a test of some general plant herbivore hypothesis. Journal of Animal Ecology 50: 11-25.

NAVAS LE (1976) Flora de la cuenca de Santiago de Chile. Tomo II: Dicotiledoneae – Archichlamydeae. Editorial Universidad de Chile, Santiago, Chile. 559 pp.

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

OBESO JR (1993) Does defoliation affect reproductive output in herbaceous perennials and woody plants in different ways? Functional Ecology 7: 150-155.

PAIGE KN & TG WHITHAM (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. American Naturalist 129: 407-416.

PRIMACK RB & P HALL (1990) Cost of reproduction in the pink lady's slipper orchid: a four-year experimental study. American Naturalist 149: 955-974.

RATHCKE B & EP LACEY (1985) Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16: 197-214.

RAVETTA DA, A SORIANO & P CATTANEO (1991) *Colliguaya integerrima* (Euphorbiaceae): its seed oil residual meal and propagation. Economic Botany 45: 288-290.

ROOT RB (1996) Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. Ecology 77: 1074-1087.

SACCHI CF & EF CONNOR (1999) Changes in reproduction and architecture in flowering dogwood, *Cornus florida*, after attack by the dogwood club gall, *Resseliella clavula*. Oikos 86: 138-146.

SACCHI CF, PW PRICE, TP CRAIG & JK ITAMI (1988) Impact of shoot galler attack on sexual reproduction in the arroyo willow. Ecology 69: 2021-2030.

SÁIZ F, A MORALES & M OLIVARES (1999). Sobre el complejo de cecidios de *Colliguaja odorifera* MOL. (Euphorbiaceae). Anales del Museo de Historia Natural de Valparaíso (Chile) 24: 61-78.

SOKAL RR & FJ ROHLF (1995) Biometry. Third Edition. W. H. Freeman and Company. New York, New York, USA. 887pp.

SOLOMON BP (1983) Compensatory production on *Solanum carolinense* following attack by a host-specific herbivore. Journal of Ecology 71: 681-690.

STINNER BR & WG ABRAHAMSON (1979) Energetics of the *Solidago canadensis* stem gall insect-parasitoid guild interaction. Ecology 60: 918-926.

STRAUSS SY (1991) Direct, indirect and cumulative effects of the three native herbivores on a shared host plant. Ecology 72: 543-558.

WEIS EA, R WALTON & CL CREGO (1988) Reactive plant tissue sites and the population biology of gall makers. Annual Review of Entomology 33: 467-486.

WEIS MJ & CF SACCHI (1996) Impact of two specialist herbivores on reproduction of horse nettle, *Solanum carolinense*. Oecologia 108: 328-337.

WHIGHAM DF (1990) The effect of the experimental defoliation on the growth and reproduction of a woodland orchid, *Tipularia discolor*. Canadian Journal of Botany 68: 1812-1816.

WHITHAM TG & S MOPPER (1985) Chronic herbivory: Impacts on architecture and sex expression of Pinyon pine. Science 228: 1089-1091.

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