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Life cycle of *Rhachiptera limbata* (Diptera, Tephritidae) and its relationship with *Baccharis linearis* (Compositae)

Ciclo de vida de *Rhachiptera limbata* (Diptera, Tephritidae) y su relación con *Baccharis linearis* (Compositae)

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ABSTRACT

Baccharis linearis (R. et Pav.) Pers. "romerillo" is a shrub species abounding in degraded soils. The Tephritidae *Rhachiptera limbata* Bigot developsin association with this species. A study site comprising 8 stands was established in San Carlos de Apoquindo on the eastern part of Santiago. The number of individuals of *B. linearis* was counted, and the sex and absolute cover was determined in each of them. Periodical observations were carried out on the shrub phenology and the number of larval chambers was counted in each plant. Results show the presence of larval chambers throughout the year. In some periods this number increases. The adults of *R. limbata* emerge at the onset of spring, when maximum temperatures reach to averages of 10ºC and precipitation has ceased. Female lay their eggs in the middle of October, in the apical meristems of branches formed during the previous growth season. The larva actively feeds on the inner tissues of the stem. The outer tissues suberify and one thin layer of tissue forms the walls of the chamber that shelters the larva and later the pupa. The larvae secrete a liquid into the cavity of the bored stem, and expell the surplus to the exterior by means of synchronic movements. This secretion, when in contact with the air, solidifies and forms a white, globular structure which protects the larval chamber. The second period of larval chamber production occurs between December and March, when it reaches the highest values. Part of the insects emerge at the end of summer, while pupae in diapause remain inside the chambers until next spring. The number of larval chambers is neither related to sex nor to the shrub cover. Infection in juvenile plants suggests that availability of meristems would be an important factor. The damage produced by the insect is limited to the tip of the branch, where it provokes the death of this tissue and of the leaves involved in the formation of the chamber. This fact inhibits apical dominance and stimulates the development of lateral branches, thus modifying the branching system of the shrub.

Key words: Larval chamber, life cycle, phenology, *Baccharis linearis, Rhachiptera limbata.*

RESUMEN

Baccharis linearis (R. et Pav.) Pers. romerillo, es una especie arbustiva, que crece en lugares abiertos y erosionados. Asociado a esta especie se desarrolla el Tephritidae *Rhachiptera limbata* Bigot. Para conocer las relaciones que existen entre el arbusto y el insecto se estableció en San Carlos de Apoquindo, sector Oriente de Santiago, un área de estudio que comprendió 8 parcelas. Se contó el número de individuos de *B. linearis,* estableciendo el sexo y la cobertura absoluta en cada uno de ellos. Periódicamente se observó la fenología del arbusto, y se contó el número de cámaras larvales en cada planta. Los resultados muestran presencia de cámaras larvales durante todo el año, existiendo períodos en los que su número aumenta. Los adultos de *R. limbata* emergen al comenzar la primavera, cuando las temperaturas alcanzan valores promedios sobre 10ºC y las precipitaciones cesan. Las hembras ponen sus huevos a mediados de octubre, en los meristemas apicales de las ramas formadas durante la estación de crecimiento anterior. La larva se alimenta activamente de los tejidos internos del tallo. Los tejidos externos se suberifican y una delgada capa de ellos forma las paredes de la cámara que aloja a la larva y más tarde a la pupa. Un líquido secretado por la larva ocupa la cavidad del tallo horadado y el excedente es expulsado al exterior por movimientos sincrónicos de la larva. Esta secreción en contacto con el aire se solidifica y forma una estructura globosa, esponjosa y de color blanco que protege la cámara larval. El segundo período de producción de cámaras larvales ocurre entre diciembre y marzo, alcanzando en este último mes los valores más altos. Parte de los insectos emerge al finalizar el verano, quedando en el interior de las cámaras, pupas en diapausa hasta la primavera siguiente. El número de cámaras larvales no está relacionado con el sexo ni con la cobertura del arbusto. La presencia de infectación en plantas juveniles pareciera indicar que la disponibilidad de meristemas fuese un factor importante. El daño que el insecto provoca sólo se circunscribe al ápice de las ramas causando la muerte de este tejido y de las hojas involucradas en la formación de la cámara. Este hecho inhibe la dominancia apical y estimula el desarrollo de ramas laterales modificando el sistema de ramificación del arbusto.

Palabras claves: Cámara larval, ciclo de vida, fenología, *Baccharis linearis, Rhachiptera limbata.*

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INTRODUCTION

Baccharis linearis (R. et Pav.) Pers. is a dioecious, small to medium-sized evergreen shrub (0.5 – 2m height). It is found on the foothills and lower mountain slopes of the Coastal and Andes Mountains in Central Chile. It forms an open matorral, either as pure stands or associated with other evergreen or deciduous shrubs, such as *Lithraea caustica, Muehlenbeckia hastulata* and *Trevoa trinervis. Baccharis linearis* does not suffer damage from phytophagous insects as do many other matorral species (Montenegro *et al.* 1980, Etchegaray & Fuentes 1980, Fuentes *et al.* 1981). However, it is the specific host of the gall-inducing Tephritid fly, *Rhachiptera limbata* Bigot, an endemic species (Frías 1981). The gall appears as a white globular mass (Philippi 1873, cited Porter 1929, Kieffer & Herbst 1905, Stuardo 1929, Acuña & Morris 1973), and is produced by the developing larva in the tips of the branches. Most gall-inducing Tephritids are associated with Compositae (Shorthouse 1978, Frías 1982).

This paper describes the life cycle and feeding specialization of *R. limbata* and its relationship with the growth and phenology of *B. linearis.*

MATERIAL AND METHODS

Observations were made from August 1981 through October 1982 at San Carlos de Apoquindo, on the foothills of the Andes Mountains in Central Chile (33°27'S, 70°42'W), at an elevation of about 800m. The climate of this area is typical mediterranean and has been described in detail by di Castri & Hajek (1976) and Thrower & Bradbury (1977). Table 1 shows the air temperatures and precipitation for the period August 1981 to October 1982 in San Carlos de Apoquindo (Hajek, unpublished data).

A study site of 1500 m^2 was established to quantify the distribution and cover of both female and male shrubs of *B. linearis.* All individuals of *B. linearis* were labeled for observation. To follow the phenology and growth dynamics, branches of individual shrubs were tagged and measurements were made with the method described by Montenegro *et al.* (1979). The life cycle of *R. limbata* was followed *in situ* in the field site. Larval chambers were dissected throughout the season and their contents recorded.

Shoots for histological studies were fixed in formalin-acetic acid-alcohol (FAA). Free-hand and microtome sections from Paraplast-embedded material were stained with safranin and fast green (Johansen 1940). For SEM, the material was fixed for 30 min at 20°C in 1% glutaraldehyde, buffered to pH 7.0 with 0.25M Na-cacodylate. Then it was postfixed in 1% osmium tetroxide in 0.25M Na-cacodylate for 1h at 20°C, transferred to a graded acetone series dried from 100% acetone via CO_2 in a Polaron E 3000 critical-point drying apparatus, and finally coated with a layer of approximately 100 Å of gold.

RESULTS AND DISCUSSION

In early spring, vegetative buds (Fig. 1B) develop in the upper part of the canopy, and give rise to dolichoblasts (Fig. 1C). The elongation of dolichoblasts and of their new leaves takes place in November and is followed by the development of numerous brachiblasts. This increases significantly the leaf area of the branch (Fig. 1D).

Vegetative growth lasts until January. Flower buds appear, located at the branch tips, giving rise to female and male plants. Seed dispersal occurs at the beginning of autumn (Fig. 1E), marking the end of the shrub growth period.

The females of *R. limbata* lay eggs in the middle of the spring (October). The eggs are about 0.8mm in length. These eggs are deposited in the apical meristems of branches formed during the previous growing season (Fig. 1A). The larvae, about 3.0 mm in length, feed by chewing the inner tissues of the stem, leaving a protected chamber surrounded by a white material. This structure is formed by the activity of the larva, which secretes a liquid. This secretion surrounds the larva, and as a result of larval movements part of it is expelled through the damaged areas of the stem. This secretion is transparent, but in contact with the air forms a spongy material with a great capacity for water absorption. The larval chambers have a constant external shape and size. In other words, the white secretion comes from the insect as it feeds on the plant tissues in a typical phytophagous manner.

Pupation occurs within the larval chamber approximately 20 days after ovopo-

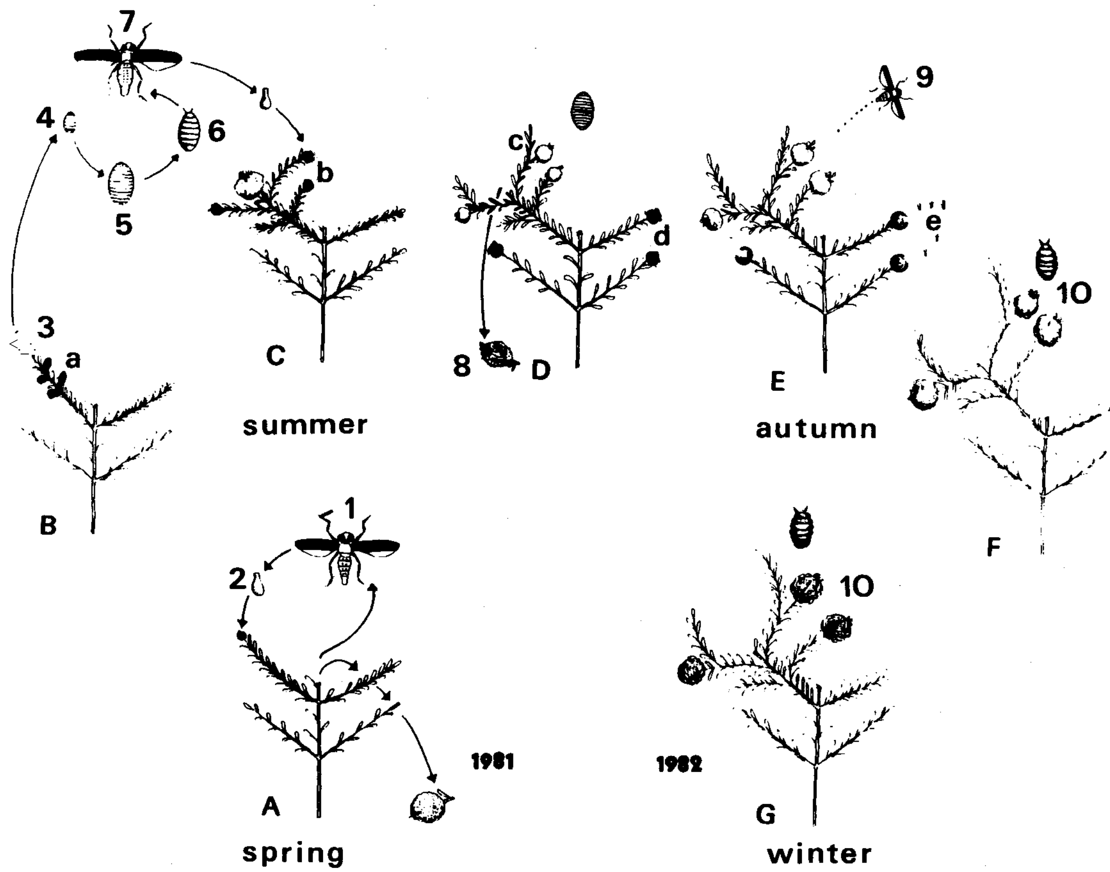

Fig. 1: Scheme of the biological cycle of the insect in relation to the plant phenology, in a representative branch of the shrub (From A to G). The numbers refer to the insect; small letters to the plant. Axillary bud *a*, dolichoblasts *b*, brachyblasts *c*, inflorescences *d*, seed dispersion *e*, adult emerging in spring 1, egg laid on apex of old branch 2, larval chamber 3, larva 4 and 5, pupa 6, adult emerging at the onset of summer 7, empty larval chamber, detached from the shrub 8, adult emerging at the end of summer 9, larval chambers with pupae that complete their development after the winter 10.

Ciclo biológico del insecto en relación a la fenología de la planta, esquematizados en una rama representativa del arbusto (De A a G). Los números se refieren al insecto, las letras minúsculas a la planta. Yemas axilares *a*, dolicoblastos *b*, braquiblastos *c*, inflorescencias *d*, dispersión de semillas *e*, adulto emergiendo en primavera 1, huevo ovopositado en ápice de rama vieja 2, cámara larval 3, larva 4 y 5, pupa 6, adulto emergiendo a inicios de verano 7, cámara larval vacía desprendida del arbusto 8, adulto emergiendo al finalizar el verano 9, cámaras larvales con pupas que terminan su desarrollo después del invierno 10.

sition. The pupa is about 3.8mm in length. At the beginning of the summer the emergence of adults takes place. The chamber is nondehiscent, and the adults must use an escape route formed by the larva. In December the new population of adults lays its eggs within the apical meristems of the new branches.

Empty larval chambers remain attached to the shrub until late in the summer, when the shrub water stress increases, and they usually fall on the ground. At the end of summer the new adults emerge (Fig. 1E). However, the pupae in about 40% of the larval chamber entered diapause, finishing their development during the following autumn and winter (Fig. 1F, 1G). It seems that only the insect benefits from this association with *B. linearis*, gaining food, shelter and a moist, warm environment. In this area of mediterranean climate, the winter is cold and the temperatures can drop below 0°C (Miller & Hajek 1981). The fact that the flower buds in *B. linearis* are formed in the tips of the new branches means that the infected meristem will not develop flowers, and reproductive output should be considerably diminished. However, since the apical dominance is inhibited, the axillary buds develop into new branches.

In spite of the fact that the second emergence of adults occurs in the period of flowering, it was not clear whether *R. limbata* pollinated the shrub. No pollen grains were found on the flies. The percentage of female shrubs attacked is not significantly larger than that of males by Student's "t" test ($t = 1.38$; $P > 0.1$) (Table 2). The survey of *B. linearis* plants showed remarkable number of juvenile shrubs, in which the sexes were indistinguishable. Juvenile shrubs were also infected by *R. limbata* (Table 2). This suggests that the insect does not choose shrubs on the basis of sex, but selects only meristematic tissue. No correlation was found between the sizes of individual shrubs (canopy projection) and the number of larval chambers present ($r = 0.002$; $P > 0.90$).

Rhachiptera limbata appears to be a bivoltine species with adult populations emerging in spring and summer when mean temperatures are above 10°C. The maximum percentages of infected shrubs, about 80% at the end of the summer, correspond with the period where the highest number of larval chambers were counted (Fig. 3). The percentage of infected shrubs remained constant from May to August, but during this period the number of larval chambers diminished no-

TABLE 1

Air temperature and precipitation in San Carlos de Apoquindo* between August 1981 and October 1982

Temperatura del aire y precipitaciones en San Carlos de Apoquindo* desde agosto de 1981 a octubre de 1982

	Aug. 1981	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sept.	Oct. 1982
Mean maximum °C	15.2	17.1	17.9	23.2	26.5	26.8	25.9	24.7	20.4	15.9	11.9	12.5	14.7	13.6	17.3
Mean temperature °C	9.6	10.1	10.7	14.7	17.3	18.4	17.6	16.7	13.3	10.5	7.7	8.2	9.1	9.1	11.0
Mean minimum °C	4.5	4.6	4.9	7.9	8.9	11.2	10.6	10.6	8.2	6.9	4.7	5.2	5.4	5.8	5.8
Precipitation mm	46.7	23.0	1.0	–	1.0	–	–	2.0	0.5	103.5	334.6	115.7	100.7	69.2	46.5

* Data from meteorological station of Departamento de Biología Ambiental y de Poblaciones, Pontificia Universidad Católica de Chile.

TABLE 2

Total number of shrubs of *B. linearis:* females, males, and juveniles present in the study site in December 1981. Percentage of each group that showed larval chambers. Values of absolute cover and mean values of chambers per shrub for each group are given

Número total de arbustos de *B. linearis:* femeninos, masculinos y juveniles presentes en el sitio de estudio en diciembre 1981. Porcentaje de individuos infectados, de cobertura absoluta y valores promedios de cámaras larvales por arbustos en cada grupo.

Baccharis linearis	Number of individuals	Total infected individuals %	Absolute cover %	Larval chambers/shrub $\bar{X}$ ± s
Females	39	51	59	5.1 ± 4.4
Males	28	46	28	7.8 ± 9.6
Juveniles	13	53	13	9.7 ± 15.9

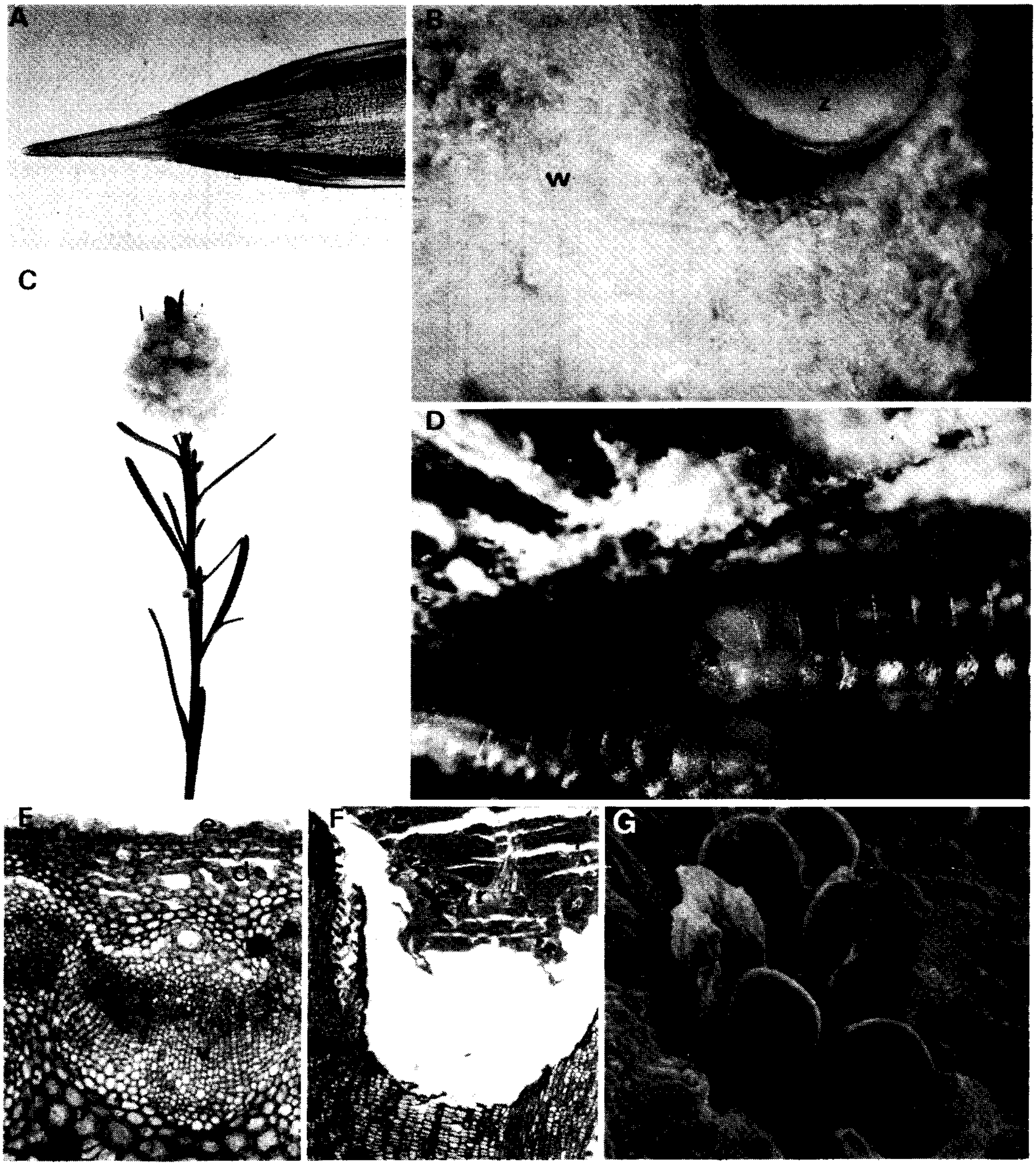

Fig. 2: A Ovopositor of *R. limbata,* x 30. *B* Cross section of larval chamber: chamber z, suberized tissues s, larval secretion w, x 22. *C* Aspect of a typical infected branch of *B. linearis,* x 1. *D* Two larvae in the same chamber, x 22. *E* Cross section of the stem showing: initial damage d, epidermis e, cortical zone c, vascular zone v, medular zone p, x 70. *F* Longitudinal section of stem showing: larva r, medular zone p, vascular zone v, cortical zone c, axillary bud y, trichomes t, x 25. *G* Glandular trichomes of *B. linearis* leaves, x 1000.

A Ovopositor de *R. limbata,* x 30. *B* Sección transversal por la cámara larval: cámara z, tejidos suberificados s, secreción larval w, x 22. *C* Aspecto típico de una rama de *B. linearis* infectado, x 1. *D* Dos larvas en una cámara, x 22. *E* Sección transversal por tallo mostrando daño inicial d, epidermis e, zona cortical c, zona vascular v, zona medular p, x 70. *F* Corte longitudinal por tallo mostrando: larva r, zona medular p, zona vascular v, zona cortical c, yema axilar y, tricomas t, x 25. *G* Tricomas glandulares en hojas de *B. linearis,* x 1000.

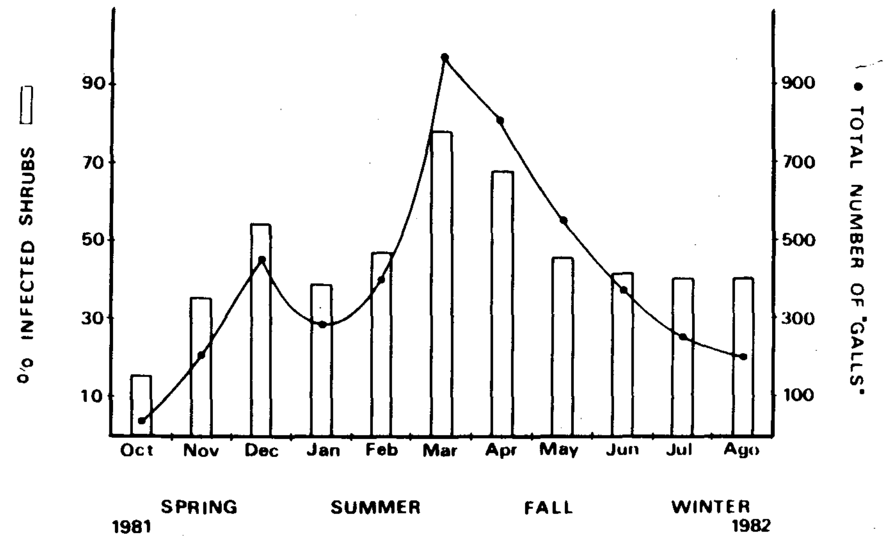

Fig. 3: Percentage of infected shrub and total number of larval chambers ("galls") from October 1981 to August 1982.

Porcentaje de arbustos infectados y número total de cámaras larvales ("agallas"), desde octubre de 1981 a agosto de 1982.

ticeably, probably due to climatic stress and/or herbivore pressure. Emergence of new adults in the field was not observed during this period. In its feeding, the larva acts through mechanical injury, but does not apply active cecidogenetic substances that may lead to abnormal patterns of tissue growth and differentiaton. The insect causes the dissolution of the cell walls of the cortical parenchymatic layers (Fig. 2E). The larva feeds upon the stem tissues (Fig. 2F) leaving a chamber formed by suberized tissues (Fig. 2B). The shrub does not develop differentiated tissues and nutritive cells. On *Baccharis pilularis,* Force (1974) described a multichambered gall, which is produced by the midges *Rophalomya californica* on the terminal growing stems. This gall may contain 50 or 60 larvae. On *B. linearis* one larva is usually found in each gall (Stuardo, 1929), *R. limbata* introduces only one egg with its ovipositor (Fig. 2A), but on occasion two larvae can be found (Fig. 2D). In our opinion the term gall (Rohfritsch & Shorthouse 1982) does not correspond to this specific type of structure formed by *R. limbata* (Fig. 2C), because rather than inducing the plant tissue to proliferate and differenciate the insect simply forms a protective chamber around its source of food.

The leaves of *B. linearis* have pluricellular glandular trichomes (Fig. 2G). It is now generally accepted that many natural products and secondary compounds serve as defense against insects (Feeny 1975, 1976, Schnoohoven 1972, Wallace & Mansell 1976; Harbone 1979). Mabry & Gill (1979) indicate that Compositae are often characterized by the presence of sesquiterpene lactones (bitter principals), which are known for their anti-herbivore properties. The presence of such compounds in the adult leaves of *B. linearis* may explain why the species is not defoliated by *R. limbata* or other phytophagous insects. It is also possible that *R. limbata* uses *B. linearis* as its exclusive host in order to avoid predation by other insects.

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