

FREQUENCY OF GALLS IN THE ROOTS OF TILLANDSIA IONANTHA (BROMELIACEAE) IN A TROPICAL DRY FOREST IN THE STATE OF VERACRUZ, MEXICO

JOSÉ G. GARCÍA-FRANCO AND VICTOR RICO-GRAY

Instituto de Ecología, A.C., Apdo. Postal 63,
Xalapa, Veracruz 91000 México

ABSTRACT. We studied the association between root gall-forming insects and the epiphytic bromeliad *Tillandsia ionantha* Planchon in the lowland tropical dry forest of the coast of the state of Veracruz, Mexico. Galls are formed by the fly *Neolasioptera* sp. (Diptera: Cecydomyiidae). The fly has a parasitoid, *Aprostocetus* sp. (Hymenoptera: Eulophidae). Gall formation takes place during the rainy season, which is the period of root growth in *T. ionantha*. We collected 4,031 plant individuals in six 5 m × 5 m study plots. Average plant diameter was 4.88 ± 2.8 cm. Average number of galls per plant was 1.03 ± 2.1 ($N = 4,160$). Plants from diameter classes 4.5 to 9.5 cm had the greatest number of galls. There was a positive significant correlation between bromeliad size and number of galls per plant. Gall diameter was 0.48 ± 0.1 cm ($N = 582$). Number of adult insect emergence holes per gall was 5.95 ± 3.4 . Most holes were found in gall diameter classes 0.3 to 0.7 cm. There was a positive significant correlation between gall size and number of emergence holes. Our results suggest that parasitism by gall-forming flies is low; nevertheless, galls can be present at any stage in the life of the bromeliad. The presence of galls in the roots of *T. ionantha* does not prevent roots from accomplishing their role in plant attachment to substrate; plant individuals were always well-secured to the support tree. Nonetheless, the activity of the parasite, which diverts plant nutritive substances with the use of chemical stimuli, undoubtedly causes deficiencies during development that may decrease plant reproductive fitness.

Frecuencia de agallas en las raíces de *Tillandsia ionantha* (Bromeliaceae) en un bosque tropical seco del estado de Veracruz, México.

RESUMEN. Estudiamos la asociación entre insectos formadores de agallas y la bromelia epífita *Tillandsia ionantha* Planchon en un bosque tropical seco de la costa del estado de Veracruz, México. Las agallas son formadas por la mosca *Neolasioptera* sp. (Diptera: Cecydomyiidae). La mosca tiene un parasitoide, *Aprostocetus* sp. (Hymenoptera: Eulophidae). La formación de las agallas se realiza durante la época de lluvias, que es también el periodo de crecimiento radicular de *T. ionantha*. Colectamos 4,031 individuos de la planta en seis cuadros de muestreo de 5 m × 5 m. El diámetro promedio de las plantas fue 4.88 ± 2.8 cm. El número promedio de agallas por planta fue 1.03 ± 2.1 ($N = 4,160$). Las plantas con diámetros entre 4.5 y 9.5 cm tuvieron más agallas. Se encontró una correlación positiva significativa entre el tamaño de la bromelia y el número de agallas por planta. El diámetro de las agallas fue 0.48 ± 0.1 cm ($N = 582$). El número de perforaciones para la salida de insectos adultos fue 5.95 ± 3.4 por agalla. Se encontraron más perforaciones en agallas con diámetros entre 0.3 y 0.7 cm. Se encontró una correlación positiva significativa entre el tamaño de la agalla y el número de perforaciones. Nuestros resultados sugieren que es bajo el parasitismo por insectos formadores de agallas; sin embargo, pueden existir agallas en cualquier etapa de la vida de la bromelia. La presencia de agallas en las raíces de *T. ionantha* no impide que éstas cumplan su papel de fijación al sustrato; las plantas siempre estaban bien aseguradas al árbol soporte. Sin embargo, la actividad del parásito, quien desvía por medio de estímulos químicos las sustancias nutritivas de las plantas, indudablemente causa deficiencias durante el desarrollo que pueden disminuir el éxito reproductivo de la planta.

INTRODUCTION

Epiphytic bromeliads exhibit different types of interactions with various organisms which have been documented for various species of myrmecophytic and tank bromeliads, and insects (Benzing, 1970; Beutelspacher, 1971, 1972), vertebrate fauna (fish, frogs, snakes, mice, and lizards) (e.g., Neil, 1951; Beutelspacher, 1971), and floral visitors (bats, hummingbirds, butterflies, bees) (e.g., Salas, 1973; Utley, 1983; Ackerman, 1986; Gardner, 1986; García-Franco & Rico-Gray, in press). Although bromeliads usually have

sturdy, highly sclerified leaves, which presumably reduces their palatability and nutritive value (Janzen, 1974) as well as adapting them for a potentially xeric environment, they are not immune from attacks by herbivores. Reports include Orthoptera eating the young shoots of *Guzmania monostachia* (L.) Rusby ex Mez, DC. (Benzing, 1990), squirrels eating the inflorescence spikes of *Tillandsia deppeana* Steudel (García-Franco & Rico-Gray, in press), and monkeys eating the young individuals of *Guzmania* sp. (L. Moreno, pers. comm.). The ter-

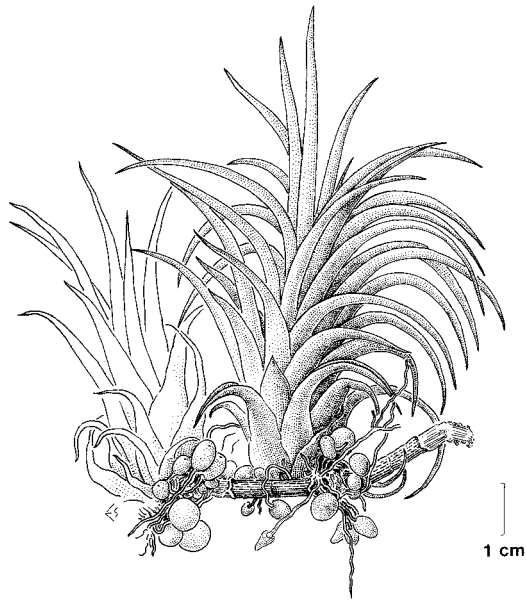


FIGURE 1. *Tillandsia ionantha* with root galls.

restrial bromeliad *Bromelia pinquin* L., has robust, highly sclerified leaves, whose surfaces are covered by a thick cuticle, and whose margins are armed with hard thorns, but it is attacked by land crabs (García-Franco *et al.*, 1991) and by at least four insect species (García-Franco & Rico-Gray, unpubl. data). Leaf-miners attack epiphytic bromeliads in Costa Rican forests (García-Franco, pers. obs.).

The presence of tender meristematic tissues in young vegetative bromeliad shoots, inflorescences, floral bracts, and roots, make them susceptible to insect attack, but parasitic interactions with gall-forming insects have not been reported for epiphytic bromeliads. Moreover, the association between gall-forming insects and roots has not been reported. Parasitism by gall-forming insects involves the parasite living inside its host during its larval stages, and emerging as adults. Galls are formed by certain species of Coleoptera, Diptera, Homoptera, Hymenoptera, and Lepidoptera (Borrer *et al.*, 1981). These insects induce deformations in highly vascularized plant tissues (e.g., leaf veins, young vegetative growth), and thus obtain protection and food from the host plant. Larval nutrition is obtained via chemical stimuli that modify plant metabolism and growth (Lalonde & Shorthouse, 1985). The presence of galls in epiphytic bromeliads has been noted in cultured bromeliads, particularly *Tillandsia* species that inhabit xeric environments (G. Brown, pers. comm.). Galls have also been observed in leaves of an unidentified species of

epiphytic bromeliad inhabiting the tropical wet forest at La Selva Biological Field Station, Costa Rica (E. Stur, pers. comm.). We have observed galls in roots of other epiphytic bromeliads living in the same environment as *T. ionantha*.

We studied the association between root gall-forming insects and the epiphytic bromeliad *Tillandsia ionantha* Planchon (FIGURE 1) in a tropical dry forest on the coast of the state of Veracruz, Mexico. We addressed the following questions: What is the frequency of galls in the roots of *T. ionantha* individuals? Is there a relationship between the frequency of galls and plant size? How many adult parasites emerge from the galls? Is there a relationship between gall size and the number of emerging adult insects? Can roots be parasitized throughout the year?

STUDY SITE

Field work was conducted in a lowland tropical dry forest located at the highest elevations of the field station "Estación Biológica El Morro de la Mancha," located on the coast of the state of Veracruz, Mexico (19°36'N, 96°22'W; elevation <100 m). The climate is warm and subhumid, with the rainy season occurring between June and September. Total annual precipitation is 1,100–1,300 mm, and mean annual temperature is 22°–26°C (minimum 10°C–maximum 38°C). Several types of vegetation are present at the station, including tropical deciduous forest, tropical dry forest, sand dune matorral, and mangrove forest (Novelo, 1978; Moreno *et al.*, 1982; Rico-Gray & Lot-Helgueras, 1983).

METHODS

We collected all *Tillandsia ionantha* individuals (single and multiple shoots) in six 5 m × 5 m study plots. Plots were arranged in two parallel rows of three plots each; distance between rows and between plots in a row was 5 m. The location of the first plot was selected haphazardly. We measured plant diameter as the distance between the longest leaves of the rosette.

The number of galls present in the roots of each plant was counted. *Tillandsia ionantha* usually grows in clumps and all rosettes were carefully separated to measure diameters and count galls on roots. All galls were cut off at the roots, kept in separate plastic containers (one for each study plot), and covered with fine mesh. Galls were maintained in the containers at ambient temperature and humidity conditions (laboratory at the Instituto de Ecología, A.C. in Xalapa, Veracruz) for four months to allow insect maturation and emergence. At the end of this time,

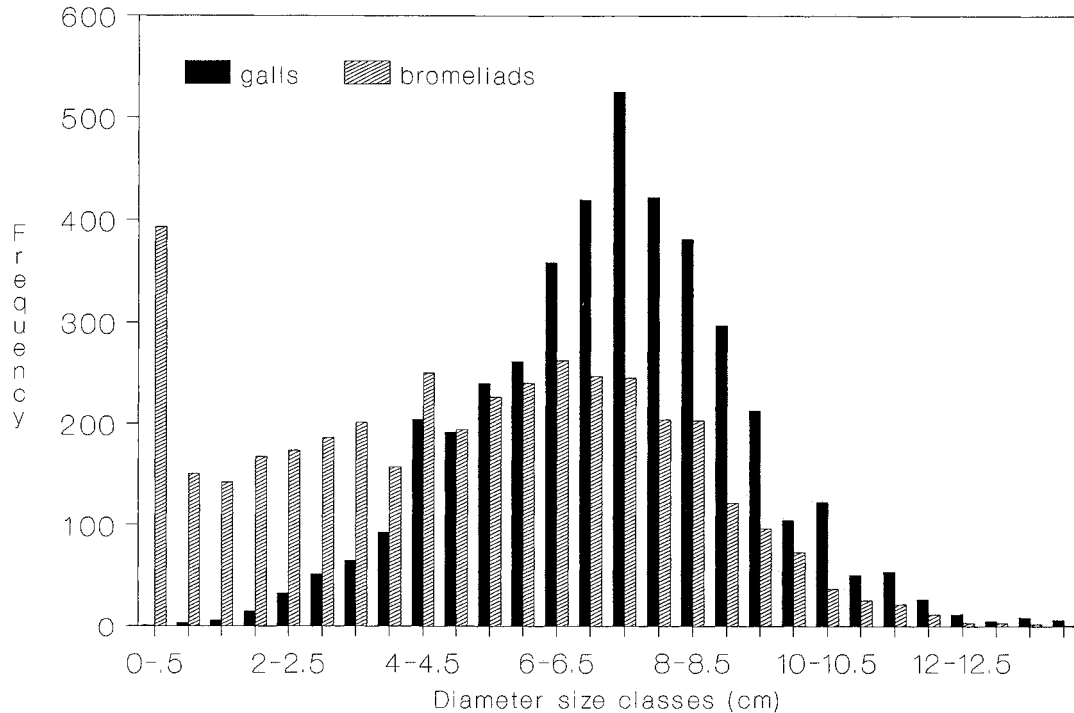


FIGURE 2. Frequency distribution of *Tillandsia ionantha* individuals for different plant diameter size classes, and number of galls found per plant diameter size class in a tropical dry forest of the coast of the state of Veracruz, Mexico.

we assumed that the majority of the insects had emerged. We selected 97 galls per plot (minimum number of galls found) to measure diameter, and count emergence holes; these galls were in good condition and holes used by adult insects to emerge were easily seen.

We used Spearman's rank correlation coefficient (r_s) to test for a significant association between plant diameter and number of galls per plant, and between gall diameter and the number of emergence holes. Plants (and galls) were collected in August–September 1990. Insects were identified by members of the United States Department of Agriculture (R. Gagné and M. Schauff). Plant voucher specimens were deposited at XAL herbarium (V. Rico-Gray 21).

RESULTS

We collected 4,031 individuals of *T. ionantha* in the six study plots. Mean plant diameter was 4.9 ± 2.9 cm. Mean number of galls per bromeliad was 1.0 ± 2.1 ($N = 4,160$ galls), suggesting that parasitism on *T. ionantha* individuals is low. Nevertheless, gall-forming flies can be present at any stage in the life of the bromeliad. More galls occurred on plants in diam-

eter size classes 4.5 cm to 9.5 cm, which were also the most common size classes (FIGURE 2). Moreover, we obtained a positive significant correlation between plant size and number of galls per plant ($r_s = 0.481$, $P < 0.01$, $N = 4,031$). Mean gall diameter was 0.48 ± 0.11 cm ($N = 582$). Mean number of adult insect emergence holes per gall was 5.95 ± 3.45 . Most holes were found in the 0.3 cm to 0.7 cm gall size classes (FIGURE 3). There was a positive significant correlation between gall size and the number of insect emergence holes ($r_s = 0.543$, $P < 0.01$, $N = 582$).

Galls are usually round in shape and light-brown in color. Galls are formed by the fly *Neolasioptera* sp. (Diptera: Cecydomyiidae). Females of *Neolasioptera* sp. oviposit at the tip of the developing roots of *T. ionantha*. After the larvae develop, large numbers of adult flies emerge. Gall formation takes place during the rainy season, which is also the period of root growth in *T. ionantha* (pers. obs.). We also found individuals of the wasp *Aprostocetus* sp. (Hymenoptera: Eulophidae), which is a parasitoid of *Neolasioptera* sp. The life cycles of *Neolasioptera* sp. and *Aprostocetus* sp. are synchronized with the development of tender meristematic root tissues.

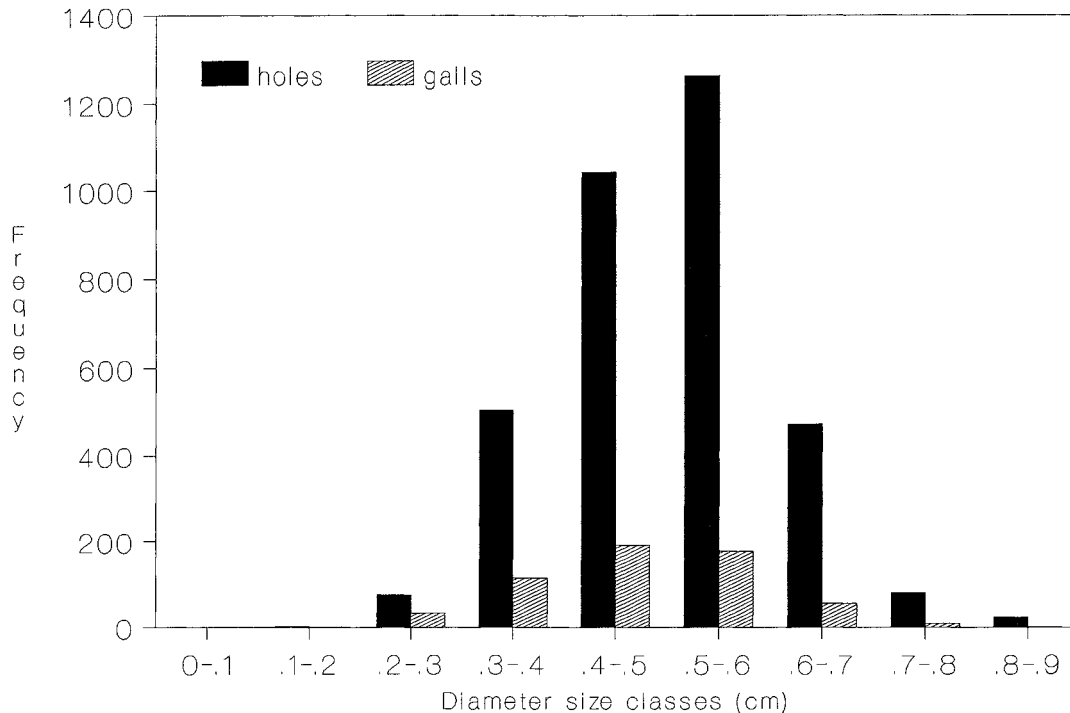


FIGURE 3. Frequency distribution of galls for different gall diameter size classes, and total number of emergence holes per gall size class made by the adults of *Neolasioptera* sp. and *Aprostocetus* sp., in a tropical dry forest of the coast of the state of Veracruz, Mexico.

DISCUSSION

Tillandsia ionantha is an atmospheric bromeliad, whose roots function primarily as attachment to the host (but see Burt-Utley & Utley, 1975). The presence of galls in the roots of this species apparently does not prevent roots from anchoring the plants to the substrate. Regardless of the number of galls per bromeliad sampled with galls (1 minimum–14 maximum), *T. ionantha* individuals were well secured to the tree, which suggests that the parasite does not cause direct damage to the plant. We speculate that although gall formation has no apparent effect on the attachment function of these roots, parasitism may decrease plant reproductive fitness. Further research on resource allocation of plants with and without galls is necessary.

The number of galls present in the different diameter size classes of *T. ionantha* may be related to the age of the plant and to the rate of root production. Larger and presumably older individuals have been exposed to attacks by the parasite for a longer period of time than smaller, younger plants. If an individual produces more than one root per growing season, the chances of being attacked by individuals of *Neolasioptera*

sp. would increase. Individuals of *T. ionantha* in the larger diameter size classes had more galls, suggesting that age is a determining factor; the older the bromeliad, the greater the number of galls present. It also is possible that more eggs are laid on certain individuals. Larger galls produced more insects (based on number of emergence holes per gall).

Unfortunately, we could not distinguish how many holes were made by the parasite (*Neolasioptera* sp.), and how many by the parasitoid (*Aprostocetus* sp.). *Aprostocetus* sp. takes advantage of the conditions offered by the gall (protection, food), attacking and killing the larvae of *Neolasioptera* sp. before they reach their full development. Parasite-parasitoid associations are quite common in nature and more than one parasitoid per parasite can be found (Borror *et al.*, 1981). Associations are determined by gall appearance, plant architecture, the part of the plant where the gall is formed, and the biogeographic region (Hawkins & Gagné, 1989). The characteristics favoring the presence of the parasitoid *Aprostocetus* sp. in the association between *T. ionantha* and *Neolasioptera* sp. are unknown.

Epiphytic bromeliads are important in the life cycle of a great number of insects and vertebrates

(Laessle, 1961; Benzing, 1990). It is likely that the association between epiphytic bromeliads, gall-forming insects, and parasitoids are far more common than previously documented, and that the small number of reports reflects only that the association has passed unnoticed in most habitats.

ACKNOWLEDGMENTS

We acknowledge V. Hernández (Instituto de Ecología), R. J. Gagné (USDA) and M. E. Schauff (USDA) for their help in insect determination, and E. Saavedra for the illustration of *T. ionantha*. Field work was partially supported by CONACYT grant No. 903579 to VRG.

LITERATURE CITED

- ACKERMAN, J. D. 1986. Coping with the epiphytic existence: pollination strategies. *Selbyana* 9: 52-60.
- BENZING, D. H. 1970. An investigation of two bromeliad myrmecophytes: *Tillandsia butzii* Mez, *T. caput-medusae* E. Morren and their ants. *Bull. Torrey Bot. Club* 97: 109-115.
- . 1990. Vascular epiphytes. Cambridge University Press, Cambridge. 354 pp.
- BEUTELSPACHER, B. C. R. 1971. Una Bromeliaceae como un ecosistema. *Biología (México)* 2: 82-88.
- . 1972. Fauna de *Tillandsia caput-medusae* E. Morren, 1880 (Bromeliaceae). *An. Inst. Biol., U.N.A.M., Ser. Zool.* 43: 25-30.
- BORROR, D. J., D. M. DE LONG, AND C. A. TRIPLEHORN. 1981. An introduction to the study of insects, 5th ed. Saunders College Publishing, Philadelphia. 827 pp.
- BURT-UTLEY, K. AND J. F. UTLEY. 1975. Calcium⁴⁵ translocation in *Tillandsia balbisiana* Schult. (Bromeliaceae). *Brenesia* 5: 51-65.
- GARDNER, C. S. 1986. Inferences about pollination in *Tillandsia* (Bromeliaceae). *Selbyana* 9: 76-87.
- GARCÍA-FRANCO, J. G., V. RICO-GRAY, AND O. ZAYAS. 1991. Seed and seedling predation of *Bromelia pinquin* L. by the land crab *Gecarcinus lateralis* Frem. in Veracruz, Mexico. *Biotropica* 23: 96-97.
- AND ———. (in press) Biología reproductiva de *Tillandsia deppeana* Steudel (Bromeliaceae) en Veracruz, México. *Brenesia* 35.
- HAWKINS, B. A. AND R. J. GAGNÉ. 1989. Determinants of assemblage size for the parasitoids of Cecidomyiidae (Diptera). *Oecologia (Berlin)* 81: 75-88.
- JANZEN, D. H. 1974. Epiphytic myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. *Biotropica* 6: 237-259.
- LAESSLE, A. M. 1961. A micro-limnological study of Jamaican bromeliads. *Ecology* 42: 499-517.
- LALONDE, R. G. AND J. D. SHORTHOUSE. 1985. Growth and development of larvae and galls of *Urophora cardui* (Diptera, Tephritidae) on *Cirsium arvense* (Compositae). *Oecologia (Berlin)* 65: 161-165.
- MORENO, P., E. VAN DER MAAREL, S. CASTILLO, M. L. HUESCA, AND I. PISANTY. 1982. Ecología de la vegetación de dunas costeras: estructura y composición en el Morro de la Mancha, Ver. *Biotica (México)* 7: 491-526.
- NEIL, W. 1951. A bromeliad herpetofauna in Florida. *Ecology* 32: 140-143.
- NOVELO, A. 1978. La vegetación de la Estación Biológica El Morro de la Mancha, Veracruz, *Biotica (México)* 3: 9-23.
- RICO-GRAY, V. AND A. LOT-HELGUERAS. 1983. Producción de hojarasca del manglar de la Laguna de la Mancha, Veracruz, México. *Biotica (México)* 8: 295-301.
- SALAS, D. S. 1973. Una bromeliaceae costarricense polinizada por murciélagos. *Brenesia* 2: 5-10.
- UTLEY, J. F. 1983. A revision of the Middle American Thecophylloid Vrieseas (Bromeliaceae). *Tulane Stud. Zool. Bot.* 24: 1-81.

SPATIAL VARIABILITY IN THE INTERCEPTION OF INCLINED RAINFALL BY A TROPICAL RAINFOREST CANOPY

STANLEY R. HERWITZ

Graduate School of Geography, Clark University,
Worcester, Massachusetts 01610 U.S.A.

ROBERT E. SLYE

Ecosystem Science and Technology Branch, NASA/Ames Research Center,
Moffett Field, California 94035 U.S.A.

ABSTRACT. Many epiphytes in forest canopies are drought-adapted due to the limited water-holding capacity of the aboveground woody surfaces that support them. The objective of our study was to evaluate whether neighboring tropical rainforest canopy trees differentially intercept inclined rainfall, and discuss the possible effects on epiphyte distribution patterns. The study involved: (1) developing a computer model representing the 3-D geometry of a tropical rainforest canopy surface in northeast Queensland, Australia, using photogrammetric crown elevation data and a geographic information system; (2) generating a shaded canopy relief image to compute the effective rainfall-intercepting crown areas of 50 selected canopy trees during a single precipitation event; and (3) analyzing the relationships between the selected trees' effective crown areas and the net rainfall totals measured beneath their crowns. A significant correlation between the effective crown areas and net rainfall totals indicated that the inclined rainfall was differentially intercepted, with the more prominent canopy trees creating rainshadows on less prominent neighboring canopy trees. It has been generally assumed that the vertically projected crown areas of canopy trees intercept the same depth equivalent of precipitation. The results of our study suggest that rainforest canopy trees in the cyclone-prone tropics do not receive the same depth equivalents of mean annual rainfall. We conclude that the differential interception of rainfall may influence the spatial pattern of water availability and thus the distribution of epiphytes in a forest canopy.

La geometría tri-dimensional y microhabitats de las copas del bosque lluvioso tropical.

RESUMEN. Muchas epífitas que crecen en las bóvedas arbóreas de los bosques tropicales húmedos están adaptadas a la sequía debido a que las cortezas que las sostienen por encima del suelo ofrecen muy baja capacidad de retención de agua. La meta de nuestro estudio consistió en analizar si en estos bosques, las bóvedas de los árboles vecinos interceptaban en forma diferencial el agua de lluvia que cae en ángulo para, enseguida, evaluar los efectos que esto pudiese tener en las pautas de distribución de las epífitas. En el estudio se incluyó lo siguiente: (1) el desarrollo de un modelo informático en el que figura la representación tridimensional de la superficie de una bóveda arbórea en un bosque tropical húmedo del noreste de Queensland, Australia. Esto se hizo en base a datos sobre la elevación de la corona arbórea obtenidos mediante fotogrametría, junto con un sistema de información geográfica; (2) se generó la imagen del relieve de una bóveda ensombrecida a fin de calcular las áreas efectivas de intercepción de precipitación pluvial de las coronas de 50 árboles seleccionados en un evento de precipitación; y (3) se llevó a cabo el análisis de las relaciones existentes entre las superficies efectivas de las coronas de los árboles seleccionados y los totales netos de precipitación pluvial medidos bajo dichas coronas. Al establecerse la correlación entre las superficies efectivas de las coronas y los totales netos de precipitación pluvial se observó que la lluvia que caía en forma oblícua era interceptada en forma diferencial, dándose el caso que los árboles de bóvedas más prominentes obraban como cortinas, impidiendo así que la lluvia cayese sobre las cúpulas de árboles vecinos menos prominentes. Por cuanto hace a las bóvedas arbóreas, en general, se supone que las superficies de las coronas que se proyectan verticalmente, interceptan la misma profundidad de precipitación equivalente. Los resultados de nuestro estudio sugieren que las bóvedas arbóreas de los bosques tropicales húmedos expuestos a huracanes no reciben en promedio anual el mismo equivalente de profundidad de lluvia. Por lo tanto, llegamos a la conclusión de que la intercepción diferencial de precipitación pluvial puede influenciar las pautas espaciales del agua disponible y, con ello, la distribución de las epífitas en la bóveda del bosque.

INTRODUCTION

The substantial epiphyte loads that characterize many tropical rainforest canopies contribute significantly to the ecosystem's biotic diversity and many ecosystem-level processes (Richards,

1952; Madison, 1977; Nadkarni, 1984; Gentry & Dodson, 1987). Factors affecting the distribution and abundance of epiphytes in forest canopies include differences in canopy tree architecture, microclimate, bark structure, and the accumulation of humus on aboveground surfaces