American Fern Journal 94(2):70–76 (2004)

The Occurrence of *Trichomanes godmanii* (Hymenophyllaceae) on *Welfia georgii* (Arecaceae) at the La Selva Biological Station, Costa Rica

ROBBIN C. MORAN
The New York Botanical Garden, Bronx, New York 10458-5126, USA
ROMINA VIDAL RUSSELL
Department of Plant Biology, Southern Illinois University at Carbondale, Carbondale, Illinois 62901-6509, USA

ABSTRACT.—Field observations suggested that the epiphytic fern *Trichomanes godmanii* occurred more frequently and abundantly on the trunks of the palm *Welfia georgii* than on the trunks of dicotyledonous trees. We tested this observation statistically by randomly selecting 25 individuals of *W. georgii* and the nearest dicotyledonous tree of similar dbh, for a total of 50 trunks. For each trunk up to a height of three meters, we recorded the presence or absence of *T. godmanii* and, if present, we visually estimated percent cover using a ranked scale. We found that the fern occurred more frequently and abundantly on the palm than on dicotylendonous trees. No relationship was found between the diameter of the trunks and vegetative cover. This is one of the few host-specific preferences recorded among epiphytic ferns. We cannot fully explain why the fern occurs more frequently and abundantly on the trunks of *Welfia georgii* instead of dicot trees, but the fern's adhesive hairs on its rhizomes and petioles probably help attachment to the smooth trunk of the palm.

The epiphytic habit is prominent in pteridophytes. Of the approximately 9,000 species of pteridophytes considered by Kress (1986, 1990) worldwide, about one-third were epiphytes. In Mesoamerica about 36% of the pteridophyte species are epiphytic (compiled from Moran and Riba, 1995), and in Costa Rica at the Monteverde Cloud Forest Reserve and the La Selva Biological Station, epiphytic species compose 49% and 42% of the pteridoflora, respectively (Grayum and Churchill, 1987; Nadkarni and Wheelwright, 2000). Despite the prominence of epiphytism in pteridophytes, little work has been done on documenting species-specific host associations. Most reports of associations consist of casual observations, such as those reported for fern epiphytes largely or entirely restricted to the root mantles of tree ferns—epiphytes such as *Tmesipteris* in Australasia (Brownsey and Smith-Dodsworth, 1989), and *Blechnum fragile* (Liebm.) C. V. Morton & Lellinger, *Costaricia werckleana* H. Christ, *Terpsichore lehmanniana* (Hieron.) A. R. Sm., *T. semihirsuta* (Klotzsch) A. R. Sm., and *Trichomanes capillaceum* L. in Mesoamerica (Moran and Riba, 1995, p. 399). The only statistical demonstration of species-specific host relationships in ferns was by Moran *et al.* (2003). They studied low-trunk epiphytic ferns on tree fern root mantles versus angiosperms at four sites in Costa Rica. They found that of the 31 species that occurred frequently enough in their samples to be tested statistically, 11 (35%) occurred more frequently on tree fern root mantles.

The present study was prompted by an observation made by Grayum and Churchill (1989) at the La Salva Biological Station in Costa Rica about the frequency of occurrence of *Trichomanes godmanii* Hook. on the trunks of the palm *Welfia georgii* H. A. Wendl. *ex* Burret. They observed that *T. godmanii* was frequently found as a low-trunk epiphyte on the palm—a palm ubiquitous at the La Selva—and that it is one of the few epiphytes seen on the palm (Fig. 1). This observation was subsequently confirmed by the senior author at the La Selva Biological Station and at other nearby lowland forests in Costa Rica. We decided to test these observations by sampling and analyzing the results statistically. We tested the following two null hypotheses: first, that there is no difference in the frequency of occurrence of *T. godmanii* on *Welfia georgii* vs. dicotyledonous trees; second, that there is no difference in the abundance, expressed as percent vegetative cover, of *T. godmanii* on *Welfia georgii* versus dicotyledonous trees.

Besides these two hypotheses about host preference, we examined the possible influence of the palm's dbh on the percent cover of *Trichomanes godmanii.* We expected no influence because the age of the palm is not correlated with the diameter of its trunk (Rich, 1986). Therefore, larger diameter trunks would not necessarily be available for a longer time for the fern to colonize and form a greater percent cover. The null hypothesis we tested was that of no correlation between percent vegetative cover of the fern and the trunk diameter of the palm.

Methods

The La Selva Biological Station is located in Heredia Province, at the confluence of the Puerto Viejo and Sarapiquí rivers, near Puerto Viejo de Sarapiquí, on the Caribbean side of Costa Rica, 10°26′N, 83°59′W. The elevation is about 50 m, and the vegetation is relatively aseasonal, tropical wet forest, with an average annual rainfall of 4,000 mm (McDade and Hartshorn, 1994).

We sampled along an established trail called the *Camino Experimental Sur* beginning at a point where it meets the *Sendero Tres Ríos* in front of the clearing that harbors the laboratory buildings. We sampled 25 pairs of trees, each pair consisting of one *Welfia georgii* and one angiosperm. We first sampled a palm and then selected the nearest dicotyledonous tree of similar (± 10 cm) dbh. We sampled pairs to control for microclimatic effects, and we sampled trunks of similar dbh to control for differences in presence or percent cover that might be associated with trunk width. Only the lower three meters of the trunks were sampled. When the fern was present, percent vegetative cover on each trunk was visually estimated and then scored using a ranked scale where 0 = absent, 1 = 1–10% cover, 2 = 11–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–100%.

To test the first hypothesis (no difference in the frequency of occurrence of *Trichomanes godmanii* on *Welfia georgii* versus dicot trunks), we used Fisher's Exact Test (Langley, 1971). This test is a 2×2 contingency table that should be used instead of a chi-square contingency table when N is between 8 and 50 (we had $N = 50$; i.e., the 25 pairs). The probabilities were calculated for a

FIG. 1. A. *Welfia georgii* without *Trichomanes godmanii*, showing smooth surface of trunk. B. Trunk of *Welfia georgii* covered with *T. godmanii*. C. Close up of *T. godmanii* colony. D. Fertile frond of *T. godmanii* (about 1 cm long). All photographs taken at the La Selva Biological Station, Costa Rica.

TABLE 1. Contingency table showing the occurrence of *Trichomanes godmanii* on the trunks of *Welfia georgii* and dicotyledonous trees at the La Selva Biological Field Station, Costa Rica. According to a Fisher's exact test, *T. godmanii* occurred more frequently on the trunks of *W. georgii* ($P = 0.0014$).

	Dicot	*W. georgii*	Total
Absent	20	8	28
Present	5	17	22
Total	25	25	50

two-tailed test because we were interested in whether *T. godmanii* occurred more frequently on either *Welfia georgii* or angiosperms trunks. To test the second hypothesis (no difference in the percent vegetative cover of *T. godmanii* on *Welfia georgii* versus dicot trunks), we used a Wilcoxon/ Kruskal-Wallis rank sum test. Included in this test were only those trunks where the fern was present (17 palms, 5 dicots). For the third hypothesis (no correlation between percent vegetative cover of *T. godmanii* with the dbh of the palm trunks), we included only those 17 trunks where the fern was present. We then tested for a correlation between dbh of the palm and percent cover of the fern using Spearman's rank coefficient. The significance level for all three hypotheses was set at $P < 0.05$. The statistical tests described in this paragraph were performed using the JMP statistical package, version 3.3.2 (Sall and Lehman, 1996).

Several species of *Trichomanes* with leaves less than 3 cm long occur at the La Selva Biological Station, and these can be easily confused with *T. godmanii* (Grayum, 1989). During sampling we examined suspected individuals of *T. godmanii* for the presence of cross-connections between the false veins. This characteristic distinguishes *T. godmanii* from all other similar small species of *Trichomanes* (Wessels Boer, 1962). Other characteristics helpful in identifying the species were glabrous lamina margins (i.e., without black paired or stellate hairs) and green-margined involucres (not black margined; Fig. 1D). At the La Selva Biological Station, none of the other small species of *Trichomanes* form large extensive mat-like colonies that *T. godmanii* does on the trunks of *Welfia georgii*.

RESULTS

In the 25 paired samples, *Trichomanes godmanii* was present on 17 palms and 5 dicot trees. The mean dbh of the palms sampled in this study was 17 cm (s.d. 2.2), with a range of 13–25 cm. The mean for the nearest dicot trees of similar dbh was 17.7 cm (s.d. 5.5), with range of 9–26 cm dbh.

Hypothesis 1.—no difference in the frequency of occurrence of *Trichomanes godmanii* on *Welfia georgii* versus dicot trunks. The null hypothesis was rejected ($P = 0.0014$; Table 1). The fern occurs more frequently on the palm.

Hypothesis 2.—no difference in the percent vegetative cover of *T. godmanii* on *Welfia georgii* versus dicot trunks. The null hypothesis was rejected

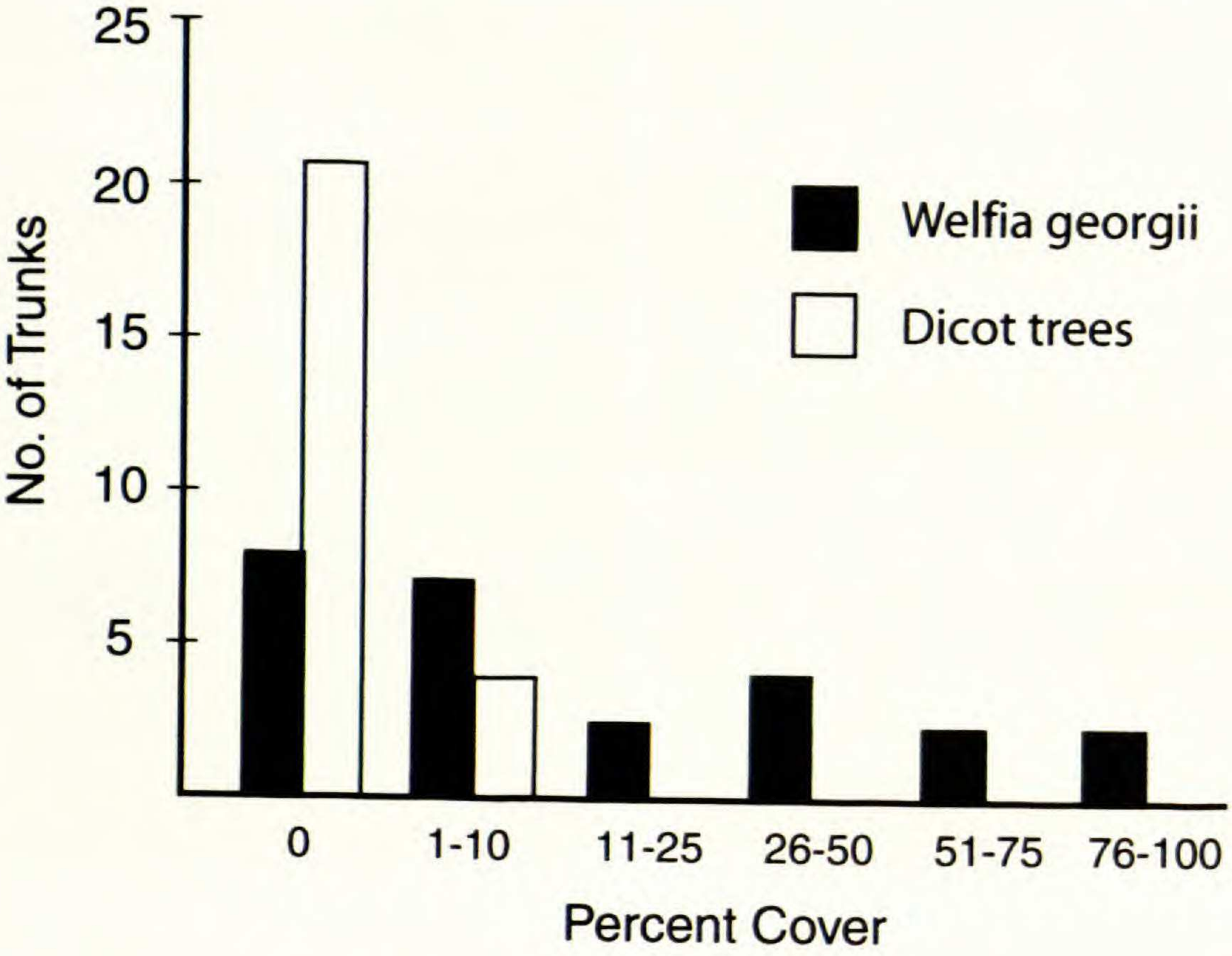

FIG. 2. Comparison of percent vegetative cover of *Trichomanes godmanii* on 25 trunks of *Welfia georgii* and 25 trunks of dicotyledonous trees at the La Selva Biological Station, Costa Rica. According to a Wilcoxon/Kruskal-Wallis rank sum test, *T. godmanii* had greater percent cover on *Welfia georgii* than on dicotyledonous trees ($P = 0.0186$).

($P = 0.0186$; Fig. 2). The fern is more abundant (higher percent cover) on the palm.

Hypothesis 3.—no correlation between percent vegetative cover of *T. godmanii* with the dbh of the palm trunks. The null hypothesis was retained ($r_s = 0.37$; $P = 0.149$). There was no correlation between the abundance of fern and the dbh of the palm.

DISCUSSION

The results support the observations of Grayum and Churchill (1989) that *Trichomanes godmanii* occurs more frequently on the trunks of *Welfia georgii* than on dicot trees (hypothesis 1). This is one of the few host-specific relationships that have been documented statistically in ferns (for others see Moran *et al.* 2003).

Trichomanes godmanii seems to be one of the few ferns capable of colonizing the trunks of *Welfia georgii*. Grayum and Churchill (1989) noted that an unnamed species of *Elaphoglossum* also occurred rarely on the trunks, but we did not find this species in or outside our samples. The only other fern we found on the palm was *Trichomanes* (sect. *Didymoglossum*) *angustifrons* (Fée) W. Boer. It occurred as isolated individuals near the base of three trunks.

The results also showed that *Trichomanes godmanii* was not only more frequent on the palm, but also more abundant (hypothesis 2). The colonies could be so dense that the surface of the trunk was obscured. When present, they always occurred around the base of the trunk (Fig. 1B) and diminished upward, but in some cases dense colonies extended five meters above the ground (at La Selva the palm can attain a height up to 23 meters; Rich, 1986). The large extensive colonies of the fern (Fig. 1B) are formed by the plants' long-creeping rhizomes that occasionally branch and run horizontally or upward around the trunk.

There was no correlation, however, between percent cover of the fern and dbh of the palm (hypothesis 3). Like many palms, *Welfia georgii* begins vertical growth with a stem girth that is sufficient to support its maximum height, and it maintains the same or nearly same width as it grows taller (Rich, 1986). Thus wider trunks do not necessarily represent older individuals that have been available for colonization for a longer time by epiphytes. Given this, one would expect an equal amount of the fern in terms of percent cover on both narrow and wide diameter trunks, and this is what we found.

Why is *Trichomanes godmanii* most frequent and abundant on *Welfia georgii*? Perhaps allelopathy plays a role, with the palm trunk presenting a chemical that inhibits epiphytes other than the fern. This idea, however, cannot be assessed because allelopathy has never been investigated in the trunks of *W. georgii* nor any other palm (Andrew Henderson, pers. com.). More likely in promoting growth of the fern is the smooth texture of the palm trunk. This might favor the fern two ways. First, it could hinder other epiphytes from establishing and attaching the trunk. This might be because of the smooth surface itself or because such surfaces retain less water or nutrients than rougher surfaces. In either case, fewer epiphytes would free the fern from competition, allowing it more space, light, and nutrients. Second, unlike other epiphytes, the smooth surface of the palm might be an easy substrate for *T. godmanii* to grasp. Like all members of *Trichomanes* sect. *Didymoglossum*, *T. godmanii* is rootless, but its rhizomes, petioles, and sometimes basal portions of the midrib, bear abundant specialized hairs called "adhesive hairs" (Schneider, 2000). These usually form a dense mat surrounding the rhizome and are dark, stiff, and several-celled. They have a cuticle (as do the rhizomes) and apparently do not absorb water or mineral nutrients, but they might hold water by capillary action and gradually release this water to the lamina as it dries. Many species of *Trichomanes* absorb water and mineral nutrients directly through their leaves, which are only one cell layer thick between the veins and lack a cuticle or nearly so (Haertel, 1940). The main function of the hairs, however, appears to be for attachment. The presence of these numerous hairs greatly increases the surface area for clinging to the substrate. In some species of *Trichomanes* sect. *Didymoglossum*, the adhesive hairs branch or enlarge at the tip when they touch the substrate (Duckett *et al.*, 1996), increasing adhesive ability. *Trichomanes godmanii* has such branched or swollen hairs (pers. obs.) that would facilitate its colonizing smooth surfaces. *Trichomanes angustifrons*, the only other fern we found on the trunks, is also

a member of sect. *Didymoglossum* and has the adhesive hairs, suggesting the importance of this type of indument for growing on smooth surfaces. Nevertheless, adhesive hairs cannot be the only reason why *T. godmanii* flourishes on palm. Four other species of *Trichomanes* sect. *Didymoglossum* occur at the La Selva Biological Station (Grayum and Churchill, 1989), and although they have adhesive hairs, only one of them (*T. angustifrons*) was found on the palm. All of the other four grow primarily on dicots. Thus, although adhesive hairs probably play an important role, they are not the entire reason why *T. godmanii* prefers the trunks of *Welfia georgii*.

Acknowledgments

This study was done while the junior author was a student in *Sistemática de Plantas Tropicales*, a course sponsored by the Organization for Tropical Studies (OTS). This course was coordinated by the senior author, and funding for the course came primarily from the Andrew G. Mellon Foundation, who we thank for their outstanding generosity. We thank OTS Academic Advisor Barbara Lewis for her help with administering the course, and students Eduardo Mendoza and Alvaro Idárraga for their help with sampling. We also thank Andrew Henderson for generously sharing his extensive knowledge of palms, and Harald Schneider for his comments on adhesive hairs in *Trichomanes*.

Literature Cited

Brownsey, P. J., and J. C. Smith-Dodsworth. 1989. *New Zealand Ferns and Allied Plants*. David Bateman Ltd., Auckland.

Duckett, J. G., A. J. Russell and R. Ligrone. 1996. Trichomes in the Hymenophyllaceae. Pp 511–514. *In*: J. M. Camus, M. Gibby and R. J. Johns, eds. *Pteridology in Perspective*. Royal Botanic Gardens, Kew, UK.

Kress, W. J. 1986. The systematic distribution of vascular epiphytes: an update. Selbyana 9:2–22.

Kress, W. J. 1990. The systematic distribution of vascular epiphytes. Pp. 234–261. *In:* U. Lüttge, ed. *Vascular Plants as Epiphytes, Evolution and Ecophysiology*. Ecological Studies 76. Springer-Verlag, New York, New York.

Grayum, M. H. and H. W. Churchill. 1987. An introduction to the pteridophyte flora of Finca La Selva. Amer. Fern J. 77:73–89.

Grayum, M. H. and H. W. Churchill. 1989. The vascular flora of the La Selva Biological Station, Costa Rica. Polypodiophyta. Selbyana 11:66–118.

Haertel, O. 1940. Physiologische studien an Hymenophyllaceae. II. Wasserhaushalt und resistenz. Protoplasma 4:489–514.

Langley, R. 1971. *Practical Statistics Simply Explained*. Dover Publications, New York.

McDade, L. A. and G. S. Hartshorn. 1994. La Selva Biological Station. Pp. 6–18. *In*: L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn, eds. *La Selva Ecology and Natural History of a Neotropical Rain Forest*. The University of Chicago, Illinois, USA.

Moran, R. C., S. Klimas and M. Carlsen. 2003. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. Biotropica 35:48–56.

Rich, P. M. 1986. Mechanical architecture of arborescent rain forest palms. Principes 30:117–131.

Sall, J. and A. Lehman. 1996. *JMP Start Statistics, A Guide to Statistical and Data Analysis using JMP and JMP IN Software*. SAS Institute, Cary, North Carolina. USA.

Schneider, H. 2000. Morphology and anatomy of roots in the filmy fern tribe *Trichomaneae* H. Schneider (Hymenophyllaceae, Filicatae) and the evolution of rootless taxa. Bot. J. Linn. Soc. 132:29–46.

Wessels Boer, J. G. 1962. The New World species of *Trichomanes* sect. *Didymoglossum* and *Microgonium*. Acta Bot. Neerl. 11:277–330.