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THE EPIPHYTIC FILMY FERNS OF A TROPICAL LOWLAND FOREST – SPECIES OCCURRENCE AND HABITAT PREFERENCES

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INTRODUCTION

The family Hymenophyllaceae comprises some 630 mostly tropical species of small to middle-sized ferns (Lellinger 1994). For the Neotropics alone we know of more than 200, mostly epiphytic species. Leaves with one-cell-thick laminas and lack of a cuticle restrict most species to very humid environments, although at least some filmy ferns are known to withstand repeated desiccation. Apart from this basic characterization of the family very little quantitative information is available about virtually any aspect of their ecology. For example, while there are at least some quantitative studies on the vertical distribution of filmy ferns within forests from montane regions (Van Leerdam *et al.* 1990, Hietz & Hietz-Seifert 1995), information on filmy ferns in lowland forests rarely exceeds the level of annotated species lists for particular areas (e.g., De la Sota 1971, De la Sota 1972, Croat 1978, Grayum & Churchill 1989). Although these publications often contain at least some ecological information, the need for more quantitative ecological baseline data is obvious. This was the starting point for the present study, which took advantage of a tower crane set up in a lowland rain forest in Panama. Although filmy ferns as a group are known to inhabit primarily the lower strata even in humid cloud forests (Kelly 1985, Hietz & Hietz-Seifert 1995), access to all strata of the forest was important to guarantee that no canopy-dwelling taxa were missed.

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MATERIALS AND METHODS

This study was carried out in late 1999 at the Fort Sherman Canopy Crane site, which is located within the former Fort Sherman area near the Atlantic coast of the Republic of Panama (Fig. 1). The average annual rainfall is estimated to be around 3500 mm (Lerdau & Throop 1999). Canopy height of this primary rain forest is quite variable and reaches a maximum of *c.* 40 m. Although most filmy ferns were

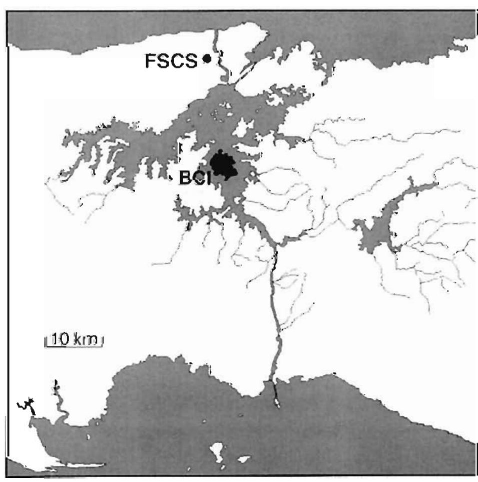

FIG. 1. Geographical location of the study area. The map shows the Canal Area in Central Panama with the Ft. Sherman Crane site (FSCS, black dot). The well known Barro Colorado Island (BCI) is also shown as a point of reference (shaded area).

expected to be found at the stem bases, we did not confine our study to the understory: the use of a small gondola allowed access to all strata of the forest, which ensured that the possible presence of filmy ferns in higher strata would not be missed (the larger study covering all epiphytes of this forest is in progress and will be published later).

Each tree in an area of c. 2100 m^2 was inspected for the occurrence of Hymenophyllaceae. The following data were collected: diameter at breast height (dbh) of the host tree, species name, height on tree (minimum and maximum), azimuth, and frond number. Species names follow Lellinger (1989), with the exception of *Trichomanes anadromum* Rosenst., which is a Brazilian species probably related to *T. polypodioides* and known from several recent collections from Costa Rica and Panama (Lellinger, pers. comm.). The delimitation of individuals was impossible in these fern species with very thin, long-creeping rhizomes. Therefore we use "individual" *sensu* Sanford (1968), i.e., a group of rhizomes and fronds belonging to one species, which forms a clearly delimited patch. Frond numbers were estimated in steps of ten in smaller individuals (= patches), and in steps of 100 in large individuals. Voucher specimens are deposited in the herbarium of the Smithsonian Tropical Research Institute, Panama (Tupper Center).

Statistical analysis was carried out with STATISTICA software (STATISTICA 5.1, StatSoft Inc., Tulsa, OK, USA). Few variables were normally distributed. To allow the employment of parametric statistics, data were log-transformed before analysis (Sokal & Rohlf 1995).

RESULTS AND DISCUSSION

We found 234 individual filmy ferns on 104 of the 716 trees with a dbh > 10 mm in our 2100 m^2 study plot, i.e., 14% of all trees were used as substrate by epiphytic Hymenophyllaceae. Eight different species were identified (Table 1), all of which are characterized by small (< 3 cm long, e.g., *T. ekmanii*) or even tiny fronds (< 1 cm long, e.g., *T. angustifrons*). The lack of species with larger laminae could be interpreted as a consequence of the relative dryness of lowland forests compared with cloud forests. However, our findings contrast with those from wet lowland rain forest in Costa Rica, where *T. collariatum*, with up to 50-cm-long fronds, is the most abundant species in the genus (Grayum & Churchill 1989).

The most common taxon, *T. angustifrons*, which is widespread in the New World (Wessels Boer 1962), occurred on 84 trees with 147 individuals, while half of all species can be considered to be rare in our study area, i.e. were observed on just one or two trees with a correspondingly low number of individuals (Table 1). All species were confined to the lower strata of the forest, with the exception of *Hymenophyllum brevifrons*. This canopy species (Grayum & Churchill 1989) was found once, high on a branch of a large *Poulsenia armata* at almost 25 m above the ground. There were only four more observations of filmy fern individuals at heights above 5m, i.e., at 6–9.5m, which clearly highlights the exceptional growing site of *H. brevifrons*.

Statistical analysis of vertical distribution patterns was only possible for species that were found on a larger number of host trees (Table 2): differences in maximum height on tree trunks were significant (ANOVA, $F_{(3,142)} = 7.64$, $P < 0.001$), with *T. ekmanii* being confined to the very base of the trunks and both *T. ovale* and *T. punctatum* ssp. *sphenoides* reaching average heights of *c.* 1.4 m.

Differences in azimuth of the substrate were only analyzed for the two most common species, *T. angustifrons* and *T. ekmanii*, with frond numbers as the dependent variable. As shown in Table 3, considerably more fronds than expected of these species were found on the south-facing sides of tree trunks, while rather few were observed on the west-facing sides. Differences in spatial distributions in respect to cardinal directions have been observed before in tropical epiphytes (e.g., Bennett 1984, Frahm 1987), but the reasons remained obscure. Large-scale climatic factors, like strong north-easterly trade winds during the drier period from January through April, can hardly explain the more than expected abundance of filmy ferns on east-facing sides. Differences in light availability offer another possible explanation. For example, west-facing ferns may dry out somewhat during the day, limiting net photosynthesis when light levels are highest during the afternoon. However, no data are available to test this notion. As pointed out by Frahm (1987), local explanations are more likely in the tropics. The possible influence on local distributions of filmy ferns of a small creek adjacent to our plot in the south-east was analyzed by comparing the distance from the creek of all trees with and without Hymenophyllaceae. Lack of significance for all species (t-test, $t = 0.3$, $P = 0.76$), or for the two most common species alone (t-test, *T. angustifrons*: $t = 0.03$, $P = 0.53$;

TABLE 1. List of species of Hymenophyllaceae found in the 2100 m² plot at the Ft. Sherman Crane Site. Given are total number of colonized trees (phorophytes), number of individuals, and number of fronds.

Species	Phorophytes (n)	Individuals (n)	Fronds (n)
Trichomanes angustifrons (Fée) W. Boer	84	147	46000
T. ekmanii W. Boer	41	51	7515
T. ovale (Fourn.) W. Boer	13	17	11085
T. punctatum ssp. *sphenoides* (Kunze) W. Boer	8	11	4130
T. anadromum Rosenstock	2	2	30
T. nummularium (v. d. Bosch) C. Chr.	1	1	1500
T. godmanii Hook	1	1	330
Hymenophyllum brevifrons Kunze	1	1	100

T. ekmanii, $t = 1.0$, $P = 0.31$) does not suggest any effect of this creek. Consequently, we cannot offer a satisfying hypothesis for the differences in respect to compass orientation.

As in most studies on epiphyte distributions (e.g., Went 1940, Johansson 1974, Hietz & Hietz-Seifert 1995, Zotz *et al.* 1999), our study species preferred larger and presumably older host trees. The average host tree had a significantly greater dbh (mean: 10.0 cm) compared to trees without Hymenophyllaceae (mean: 2.8 cm, t-test with log-transformed data, $t = 15$, $P < 0.001$). Differences between the three commonest filmy ferns (i.e., *T. angustifrons*, *T. ekmanii*, *T. ovale*) in respect of the dbh of their host trees were not detectable (ANOVA with log transformed data, $F_{(2,131)} = 0.53$, $P = 0.59$). To determine whether the increased occurrence on larger trees was simply a consequence of differences in total substrate area, we compared observed vs. expected (= evenly distributed) numbers of fern fronds on the lower 5 m of tree trunks ($\chi^2 = 37947$, $P < 0.001$). The largest discrepancy between expected and observed numbers of fronds was noted in the host trees of the largest size class (> 50cm dbh), where almost twice the expected number of fronds were found. Two explanations seem possible: either larger trees are intrinsically better places to establish and grow, e.g., due to thicker bark with higher water holding capacities or, alternatively, the pattern is simply the consequence of the longer time period available for colonization on larger and presumably older host trees. Transplant experiments would allow us to distinguish between these two possibilities.

In summary, we report the first *quantitative* study of the occurrence of filmy ferns in a tropical lowland forest. While the majority of species were restricted to the lowest strata of the forest, one exceptional species, *Hymenophyllum brevifrons*, was found high in the canopy. Much more subtle differences were observed among the remaining species, with *Trichomanes ekmanii* being the one closest to the forest floor of the four more common species. Future studies should now analyze the underlying mechanisms behind the observed differences, e.g., search for possible correlations with interspecific differences in ecophysiological characteristics such as drought tolerance.

TABLE 2. Comparison of the vertical distribution of filmy ferns (ANOVA on log-transformed data, $P < 0.001$). Different letters indicate significant interspecific differences (Newman-Keuls post-hoc test, $P < 0.05$).

Species	Maximum height (m) (means)	Range (m)
T. angustifrons	0.77	0 – 6.0
T. ekmanii	0.40	0 – 3.0
T. ovale	1.40	0 – 7.0
T. punctatum ssp. *sphenoides*	1.42	0.1 – 9.5

TABLE 3. Observed vs. expected number of fronds with respect to compass orientation ($\chi^2 = 1246$, $P < 0.001$ and $\chi^2 = 2148$, $P < 0.001$).

Compass orientation	*T. angustifrons*		*T. ekmanii*	
	observed	expected	observed	expected
W	9012	11501	518	1879
N	10332	11501	1318	1879
E	13130	11501	2738	1879
S	13530	11501	2943	1879

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