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THE RELATIONSHIP OF EPIPHYLLOUS LIVERWORTS WITH LEAF CHARACTERISTICS AND LIGHT IN MONTE VERDE, COSTA RICA

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ABSTRACT - In a study of the ecology of epiphyllous liverworts in a Tropical lower montane et forest, it was found that the degree of epiphyllic cover and herbivory are generally higher in larger leaves, vhich indicates that both behave as functions of area. The epiphyllic growth and area consumed by herbivores increase more rapidly than leaf area, and there is no statistical relationship between epiphyllv, and herbivory and leaf shape. Absolute and relative epiphyllic cover are higher in the forest clearing than in the understory, perhaps as a result of high atmospheric humidity and occurrence of heliophilic species. This quantitative survey approach is convenient for two reasons: it provides a defined view of actual field conditions and serves as a guide to posterior experimental corroboration.

RESUME - Létude de lêcologie des hépatiques êpiphylles en forét tropicale humide de basse altitude permet de mettre en evidence que Ic recouvrement par les Cpiphylles et l'action des herbivores soot generalement plus élevEs sur les feuilles larges; ils sont donc fonction de laire foliaire. Le développement des épiphylles et laire attaquee par les herbivores augmentent plus rapidement que Ia surface foliaire. II ny a pas de relation statistique entre I épiphyllie, et les herbivores et Ia forme de Ia feuille. Les recouvrements absolu et relatif par les épiphylles sont plus importants dans Ia forët clairsemée que daris Ia forCt dense, peut-etre a cause dune humidité atmospheriquc plus élevée et de Ia presence d'espèces héliophiles. Cette approche globale quantitative est utile pour deux raisoris: elle permet de définir les conditions actuelles in situ, et elle pourra servir de guide a une confirmation expérimentale ultérieure.

INTRODUCTION

The general ecology of epiphylly is just beginning to be studied. Studies such as those of Winkler (1968) and Olarinmoye (1974, 1976) can be considered pioneering. It is thus difficult to present an overview of current knowledge, but it can be divided into generally accepted and debated conclusions. There is a consensus that microclimatic conditions are of significance in epiphyllae ocurrence, abundance and diversity ('VinkIer 1968, Olarinmoye 1974, 1976, Richards 1984). Among the debated topics are intra- and interspecific competition, the nature of succession, the relationship between epiphyllae and host plants and the role of light and leaf characteristics (see Richards 1984 for a review). Two causes of this debate are the logistic difficulties that prevent prolonged studies (Winkler 1968) and the non quantitative nature of most research (Olarinmoye 1974, 1976, A. Kjeldberg, personal communication, 1987). This paper presents statistical analyses of the degree of cover by epyphyllae in relation to leaf age, size, shape and herbivory, as well as a comparison between epiphyllous cover from plants growing in a forest clearing and in the understory.

MATERIAL AND METHODS

The area of the Monte Verde Cloud Forest Reserve studied here is located in the tropical lower montane wet forest, in Northwestern Costa Rica. A detailed description is provided by Flartshorn (1983).

The leaf area covered by epiphyllae was estimated with a grid of points laced every cm), by using two variables: absolute cover or total number of points falling over epiphyllae, and relative cover: number of points falling over epiphyllae divided by total number of points falling over leaf. This second variable is a correction for leaf area. Absolute and relative areas lost to herbivores were evaluated similarly. To estimate number of points falling over missing leaf parts, another leaf of the same species and similar size was placed below. I.eaf size was measured with a ruler, and the area was calculated with the formula:

$$AREA = [(\pi) (X)(Y)] / 4$$

where X leaf length and Y leaf width.

Leaf shape was measured by dividing length by breadth, thus, higher quotients indicate longer leaves. This is a study of degree of epiphyllic cover, not presence; for this reason leaves that had no epiphyllae were excluded.

Leaf characteristics. - A single species of shrub (*Piper* sp.) was used, in order to decrease the number of factors that could affect the results. The host was selected because it is relatively common in the reserve and there were several individuals within a small area (about 50 m2). The leaves are puberullent with pinnate venation and measure about 9-15 by 3-7 cm. Young leaves were recognized for their lighter coloration, shiny surface devoid of debries and softer texture; no further age estimation was feasible and all leaves not having those characteristics were classified as old.

Forest clearing and understory. - Leaves of all species bearing epiphylls were collected as found, while walking in a forest clearing and in the nearby understory some 15 m away. Voucher specimens are deposited in the Herbarium, Universidad de Costa Rica.

A Spearman Rank Correlation was calculated for each variable pair (significance: * prob. < 0.05, ** = prob. < 0.01).

RESULTS

The epiphyllae found are leafy liverworts. The systematics of Costa Rican epiphyllae are currently under complete review by Profs. Maria 1. Morales and S. Winkler, and a list of species is not within the scope of this work.

	Sample	Mean	Standard deviation	Minimum	Maximum
Young leaves					
Area	216	74.6	30.3	35.6	165.8
Shape	210	2.8	0.5	0.9	4.2
Relative cover	218	0.3	0.3	0.01	2.7
Absolute cover	218	17.5	17.7	1	78
Relative herbivory	215	0.03	0.1	0	0.6
Absolute herbivory	215	2.0	7.4	0	46
Old leaves					
Area	270	77.8	28	20.1	165.8
Shape	256	2.7	0.5	0.9	4.2
Relative cover	273	0.3	0.3	0.01	2.7
Absolute cover	273	25	25	1	226
Relative herbivory	270	0.04	0.1	0	0.6
Absolute herbivory	270	3	7.5	0	58

Table 1 - Leaf characteristics, cover by epiphyllae and herbivory in young and old Piper sp. leaves.

Variable	Old leaves		Young leaves	
	N	Mean Rank	N	Mean Rank
Area**	94	171.4	40	102.2
Relative cover**	95	214.6	40	160.2
Absolute cover**	95	218.4	40	131.4
Relative herbivory**	95	172.5	40	155.2
Absolute herbivory**	95	181.4	40	141.1

** $p < 0.0001$ Mann-Whitney U Test.

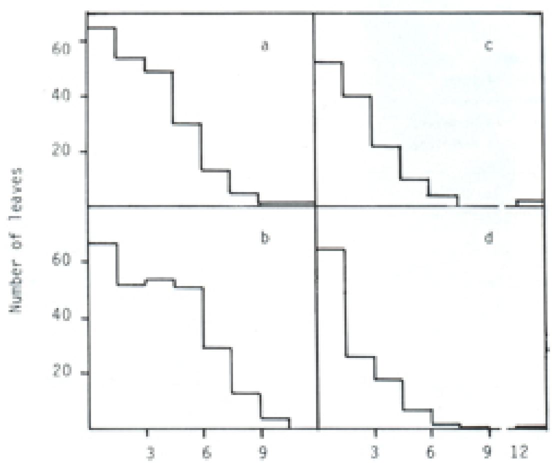
Table 2 - Mean rank values for leaf area, cover by epiphyllae and herbivory in old and young Piper sp. leaves. N = sample size.

LEAF CHARACTERISTICS

A correlation does not imply the presence of a cause-effect relationship, but the opposite is true (Sokal and Rohlf 1969) and I will firstly mention the variables that were not correlated. In young leaves, the absolute cover is unrelated to leaf shape and to absolute and relative herbivory, as absolute herbivory is unrelated to leaf area and shape and to relative cover. In old leaves, the following variables are independent: area and absolute herbivory and relative cover; absolute herbivory arid relative and absolute cover; shape and relative herbivory and relative cover, and relative herbivory and relative cover.

In the young leaves (Table 1), there are correlations between relative cover and area (Contingency Coeficient 0.373**), relative cover and shape (0.302**) and absolute cover and area (0.253*). Leaf shape is also a funtion of area (0.497**). lost leaves have a low relative cover (Fig. la).

Old leaves (Table 1) produced correlations between absolute cover and area (0.583**), absolute cover and shape (0.290**), relative herbivory and area (0.204*) and area and shape (-0.446**). Most leaves have a low relative cover (Fig. 1b).



Area covered by epiphyllae

Fig. 1 - Relative cover by epiphyllae on young (a) and old (b) leaves of leaves of a forest clearing (c) and in the understory (d).
Piper sp., and on leaves of a forest clearing (c) and in the understory (d)

When leaves of the two age classes (Fig. 1 a, b) were compared, the six variables were found to differ significantly (table 2). Area, relative and absolute cover, relative and absolute herbivory are higher in old leaves, which in turn are less elongated (old leaves N = 84, mean rank = 82.4, young leaves N = 38, mean rank = 125.7, p < 0.0001). Both young and old leaves have epiphyllae covers below 12 (Fig. 1 a, b).

	Mean	Standard deviation	Minimum	Maximum
Understory				
Area	65.7	153.2	3.2	0.002
Length	13.7	21.4	2	221
Breadth	6.4	4.3	1.5	45
Shape	2.2	2.7	0.2	24.6
Relative cover	0.1	0.3	0.003	2.4
Absolute cover	7	15	1	77
Clearing				
Area	75.3	80.3	0.8	411.9
Length	16.3	9.6	1	47
Breadth	6.2	2.7	1	13.8
Shape	2.6	1.5	1	7.7
Relative cover	0.2	0.2	0.02	1.3
Absolute cover	15	21	1	113

Table 3 - Leaf characteristics and cover by epiphyllae in a forest understory and a clearing. Sample sizes: N = 120

Variable	Clearing	Understory
Area	133.9	116.4
Length**	142.4	107.2
Breadth	123.0	128.2
Shape **	149.0	100.1
Relative cover*	135.6	114.5
Absolute cover **	143.2	106.3

*p < 0.05, p<0.0l Mann-Whitney U Test.

Table 4 - Mean rank values for leaf area, length, breadth and shape and cover by epiphyllae in a forest clearing and in the understory. Sample sizes: clearing N = 130, understory =120.

FOREST UNDERSTORY AND CLEARING

In leaves collected in the forest understory (Table 3), there are no correlations in all combinations of cover, and shape and herbivory, while there are correlations between area and absolute (Contingency Coefficient 0.20*) and relative (0.50**) cover. The leaves from the clearing (Table 3, Fig. 1 c, d) showed no correlation between cover, shape and herbivory, although there were also some correlations, as follows: absolute cover and length *(0.51**),* width (0.40**) and area (0.49**). Length was also correlated with width *(0.59**).* shape (0.38**) and area (0.88**), as was width with shape (0.40**) and area (0.87**).

Four variables had higher mean rank values in the clearing than in the forest understory (Table 4): absolute cover, relative cover, length and shape. Most clearing and understory leaves had less than 9 % cover.

DISCUSSION

LEAF CHARACTERISTICS

Leaves of the investigated species tend to elongate and increase their area with age, as normal in many other species (Flores 1989). Leaf area increase is slower than the increase in epiphyllic cover and in area lost to herbivores, since both absolute and relative cover and herbivory are higher in old leaves. This results are consistent with the idea that in epiphyllae there is a strong selection for rapid growth, as discussed by Richards (1984). The concentration of defensive compounds is higher in young leaves (Coley 1987), which would explain why, in this case, the higher proportion of lost lamina occurs in old leaves, although their size is also important: proportionally, larger leaves lose less area.

It has been proposed that herbivory may favour epiphylly (A. Kjeldberg, personal communication, 1987), but this is not true for our data, even when all the combinations of absolute and relative cover and herbivory are tested. This does not appear to be the result of sampling error: this evaluation of herbivory is consistent with that of studies which used more sophisticated measuring devices (Dirzo 1987). Besides, the results shown in the present paper fall within the range known for *Piper* in Costa Rica (Marquis 1987). These measurements of cover by epiphyllae are also in general agreement with those obtained independently by A. Kjeldberg (personal communication, 1987), who used a different method.

Absolute cover with epiphyllae is higher in larger leaves, independently of their age, which supports the idea that cover degree is partially a function of the available area (Winkler 1968, Richards 1984). Epiphyllous cover is strongly associated with age during the first year of leaf life (Winkler 1988, personal communication) and this suggests that our sample consisted chiefly of leaves that were more than one year old. Why longer old leaves have less cover is ignored, but it may be simply the result of another factor which in turn is correlated to leaf shape. Relative cover correlates positively with area and shape only in young leaves, suggesting that larger, younger leaves favour establishment of epiphyllae.

Similarly, epiphyllae seem to be favoured by large leaves, as found in palm leaves in New Guinea and fern fronds in El Salvador WinkIer 1968, Richards 1984).

FOREST UNDERSTORY AND CLEARING

The intensity of light that reaches leaves is variable (Richards 1984) and instead of attempting to measure incident light, I evaluated its effect indirectly by comparing epiphyllae from a clearing and from the forest understory. This non- experimental approach has at least one important disadvantage: concomitant factors such as rain and wind are not excluded and data interpretation becomes more difficult. In the clearing the leaves are more elongated and have a higher mean length. At both sites larger leaves have more absolute epiphyllae cover, but relative cover is higher only in larger leaves of the understory. As age was not estimated for these leaves, it is ignored if it reflects a faster growth of epiphyllae in the understory. Olarinrnoye (1974, 1976) listed low air humidity, high light incidence and strong rain as factors that negatively affected epiphyllae. These conditions are expected in the forest clearing rather than in the understory (Richards 1952. Smith 1987), but the results show the opposite: both absolute and relative epiphyllic cover are higher in the clearing. A. Kjeldberg (personal communication, 1987) also found in Monte Verde that those *Piper* sp. leaves which received more sun light had more cover. Among the possible causes for higher cover values in this clearing are the following: a) Olarinmoye's (1974, 1976) studies were done in a strongly seasonal lowland area in Africa and important differences in humidity have been found between lowland and the much more favourable conditions of the mist highland forests ('4Vinkler 1968, Richards 1984). In Monte Verde, atmospheric humidity is relatively high throughout the year and should not be a limiting factor, even in forest clearings.

b) Some taxa are more heliophilic (Richards 1984) and may require higher amounts of light. Ileliophily might result from a need to meet high photosynthetic demands to provide the host with nitrogen, an interesting and overlooked possibility that would explain why more atmospheric nitrogen is fixed in leaves carrying epiphyllae. Such hypothesis is not mutually exclusive with the alternative explanation mentioned by Richards (1984): leaves that bear epiphyllae have a more congenial environment for Cyanophyceae and nitrogen fixin bacteriae.

CONCLUSIONS

1. The level of epiphylly and herbivory are generally higher in larger leaves, which indicates that both behave as functions of area.

2. Epiphyllic growth and area consumed by herbivores increase more rapidly than leaf area.

3. There is no statistical relationship between epiphylly, and herbivory and leaf shape.

4. Absolute and relative epiphyllic cover are higher in the forest clearing than in the understory.

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