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DISTRIBUTIONAL PATTERNS OF EPIPHYTES IN THE CANOPY AND PHOROPHYTE CHARACTERISTICS IN A WESTERN ANDEAN RAIN FOREST IN ECUADOR

DIRK RUDOLPH, GEORG RAUER, JÜRGEN NIEDER AND WILHELM BARTHLOTT

Botanisches Institut der Universität Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany

ABSTRACT. A total of 81 species of vascular epiphytes was collected from 22 selected branches of the middle and upper canopies of 16 phorophyte species. These phorophytes were characteristic and predominant species for the study area, a montane forest of the western slopes of the Ecuadorian Andes, 30 km southwest of Quito. With precise data of surface area (40.44 m^2), length (761.27 m) and the various inclinations of all these branches, a typical structure of the tree crowns can be expounded. High inclinations are characteristic of small branches in the outer tree crown, small inclinations are predominant in large branches forming the inner parts of the crown—independent of the tree species. Phorophyte branch characteristics influence substrate thickness for epiphytes; substrate depends on branch inclination and branch diameter. With increasing branch diameter, average substrate thickness and average body size of epiphytes increase.

The collection of 2,677 individuals of 81 epiphyte species and additionally 746 young and undeterminable individuals leads to a comprehension of the spatial distribution of epiphytic vegetation. Every branch can be divided into zones of different ages, these show different age levels of growing epiphytes. Younger twigs are colonized by a large number of juvenile individuals, older parts of branches are overgrown with fewer but generally more mature epiphytes. The number of species stays more or less constant with increasing branch age, but a turnover of certain species illustrates the succession of vascular epiphytes.

RESUMEN. Un total de 81 especies de epífítas vasculares fueron colectados de 22 ramas seleccionadas en el docel medio y superior de forofítas de 16 especies diferentes. Estas forofítas representan especies características y dominantes del área de estudio, un bosque montano de los Andes Ecuadorianos, 30 kilómetros al sudoeste de Quito. Datos exactos del area de superificie (40.44 m^2), longitud (761.27 m) y inclinaciones de todas las ramas, permiten la reconstrucción de la estructura típica de las copas de los árboles. Inclinaciones altas caracterizan las ramas pequeñas en las zonas exteriores de las copas, inclinaciones suaves predominan en grandes ramas formando la parte interior de las coronas. Esta estructura general aplica a todas las especies de forofitas. Las características de las ramas de las forofítas tienen una influencia determinada en el espesor del sustrato de las epífitas, la cual depende de la inclinación de ramas y su diámetro. El aumento de diámetro resulta en un crecimiento de espesor de sustrato y el tamaño medio de las epífitas.

La documentación de 2,677 individuos de 81 especies de epífitas (más 746 plantas juveniles no determinables) permite un concepto de la distribución espacial de la vegetación epífitica. Cada rama está compuesta de diferentes zonas de edad, que muestran un patrón correspondiente de epífitas de edades diferentes. Ramas juveniles están cubiertas por un gran número de individuos de epífitas juveniles, ramas de más edad están cubiertas de epífitas edultos. El número de especies queda constante en todas las zonas de las ramas, pero un cambio de especies indica un patrón de sucesión de epífitas vasculares.

INTRODUCTION

The abundance of epiphytic plants is a characteristic feature of humid tropical forests and is particularly apparent in neotropical montane rain forests. Ecological studies on epiphytes have been, however, not very numerous, probably due to the difficulties of gaining access to the forest canopy; classical studies being the works of Schimper (1888), Went (1940) and Johansson (1974). The interest in epiphytes has been revived only with the development of appropriate climbing techniques (Perry 1978), the growing interest in the biodiversity of tropical forests in general, and the canopy in particular (e.g., Erwin 1982). The result was the publication of illuminating studies: e.g., Gentry and Dodson 1987, Lüttge 1989, Benzing 1990.

A key problem in the analysis of epiphytic plants is their distribution on a phorophyte. Neotropical studies concerning epiphyte distribution have been carried out in Colombia (Sugden 1981, van Leerdam *et al.* 1990, Wolf 1993), Peru (Bennet 1986), Ecuador (Bøgh 1992), Guatemala (Catling & Lefkovitch 1989), Guyana (ter Steege & Cornelissen 1989) and Costa Rica (Lesica & Antibus 1991, Kernan & Fowler 1995).

What branches carry epiphytes? What preconditions have to be fulfilled for the growth of the epiphytic flora? How is life history of the epiphytic plants involved in their arrangement on a specific tree?

The spatial distribution of epiphytes seems to be a result of basically two determining factors.

Diaspore dispersal (Benzing 1981) determines the potential range of a specific plant and its potential abundance. Germination and the success of seedling establishment depend on the characteristics of the phorophyte substrate such as bark texture and chemistry (Frei 1972). Bryophytes, lichen cover and degree of mechanical stress as a consequence of branch inclination and diameter are important conditions for the vascular epiphyte's settling as well, and have much influence on the life history, the distributional patterns, and the diversity of epiphytes.

The following article presents the results of a study of epiphytes and phorophyte characteristics in a neotropical rain forest of Western Ecuador. It demonstrates the close relationship of phorophyte characteristics and epiphyte growth and distribution. Precise data on surface area and length of branches of different tree species are presented. Additional measurements of inclination and substrate thickness make it possible to describe the structure of tree crowns as diverse habitats for epiphytes. Furthermore, it facilitates comparison with other epiphyte-rich forest systems and contributes to a methodical analysis of the conditions which epiphytes need for seed establishment and development from seedling to fertile plant.

Study Area

The research was carried out in the *Reserva Florística Ecológica Río Guajalito,* situated on the western slopes of the Andes in the Ecuadorian province of Pichincha, 30 km southwest of Quito (elevation 1,780–2,000 m, 00°13′53″ S, 78°48′10″ W). The nature reserve consists of 320 ha of primary forest, 35 ha of secondary forest and about 45 ha deforested area, the latter close to the river Las Palmeras. The trees for the epiphyte studies were chosen in the central part which is a mountain ridge covering about 100 ha.

This part of the forest has a characteristic structure (Mutke *et al.* in prep.). Three strata of tree heights can be differentiated. The upper level consists of trees of 22–35 m (occasionally higher than 40 m). Common species are *Croton* cf. *dacryoides, C. suribus* (Euphorbiaceae), *Myrcianthes rhopaloides* (Myrsinaceae), *Cedrela odorata* (Meliaceae), various Lauraceae of the genera *Nectandra, Endlichera,* and *Rhodostemonodaphne, Pochota squamigera* (Bombacaceae), *Ficus cervantesiana,* and *F. citrifolia* (Moraceae). The middle level with trees of 14–21.5 m is characterized by species like *Sapium verum* and *Hieronyma* sp. (Euphorbiaceae), *Styrax* sp. (Styracaceae), *Cybianthus* cf. *peruvianus* (Myrsinaceae), *Guarea kunthiana* (Meliaceae), *Nectandra* spp. (Lauraceae), and *Catoblastus* sp. (Arecaceae). Frequent species of the lower level are *Palicourea* spp. (Rubiaceae), *Cornus peruviana* (Cornaceae), *Saurauia tomentosa* (Actinidiaceae), and *Cyathea caracasana* (Cyatheaceae).

The forest is a lower montane forest (Acosta-Solis 1977) composed of montane and lowland species. Western Andean forests of this elevation can be regarded as transition-zones (Møller-Jørgensen *et al.* 1989). Epiphytes are abundant throughout the forest. This can at least in part be attributed to high precipitation and a very short dry period. FIGURE 1 shows the climate of a meteorological station (Las Palmeras) at a distance of 4 km from Río Guajalito on the same altitudinal level (Grijalva 1991). Monthly averages of precipitation range from 11 mm (June) to 429 mm (April). A short dry season (June–July) possibly limits the occurrence of epiphytes. The average atmospheric humidity amounts to 88.1% (min. 67.3%, max. 98%). Average temperature over the year is 16.4 degrees Celsius (Grijalva 1991). Differences between night and day can reach 11 degrees in shadowed areas (unpubl. data). The differences must be even higher in the outer and sunlit canopy.

Methods

Fieldwork was carried out between October and December 1994. Canopy access was realized with a modified mountaineering technique (Perry 1978). In the trees, plant specimens were sampled while being up in the canopy. Twenty-two branches of 17 different host trees of the middle and upper canopy (zones 3, 4 and 5, see Johansson 1974) were cut, lowered to the ground and checked completely for epiphytes. Typical tree species reaching the middle and upper canopy were selected. Only branches with a relatively typical architecture for the tree species were chosen. We tried to exclude those (rare) branches with unusually rich or unusually poor epiphytic vegetation, which are absolutely not characteristic of the study area.

Structure, shape and extension of branches was recorded, in particular the length of segments, angles of forks and diameters. Inclination of sections was measured before the branch was cut.

Thickness of substrates (mainly bryophytes and dead organic matter) was measured to the nearest 0.5 cm. The surface available for settlement by vascular epiphytes was determined as the upper half of the surface of branches, treating them as cylinders. The few individuals of epiphytes growing on the lower half were ignored.

All vascular epiphytes were sampled and their precise positions on the surveyed surfaces were

TABLE 1. Tree species with number, length, and surface area of the surveyed branches.

Family	Species	Surveyed branches	Length [m]	Surface area [m²]
Cornaceae	*Cornus peruviana* MACBR.	2	49.17	2.5348
Cunoniaceae	*Weinmannia macrophylla* H.B.K.	1	24.28	1.2386
Euphorbiaceae	*Croton* cf. *dacryoides**	1	43.83	2.8293
Euphorbiaceae	*Croton suribus**	1	48.10	2.9859
Euphorbiaceae	*Sapium verum* HEMS.	2 (of 2 trees)	61.02	3.7790
Lauraceae	*Endlicheria* spec.	1	115.46	6.7397
Lauraceae	*Nectandra* spec. 1	1	37.94	2.2783
Lauraceae	*Nectandra* spec. 2	1	13.52	1.4294
Meliaceae	*Cedrela odorata* L.	2	25.35	1.3315
Moraceae	*Ficus cervantesiana* STANDLEY & WILLIAMS	1	22.84	2.7681
Moraceae	*Ficus tonduzii* STANDLEY	1	56.28	1.8729
Myrtaceae	*Myrcianthes* cf. *rhopaloides* (HBK) MCVAUGH	2	29.20	1.5982
Rubiaceae	*Elaeagia utilis* (GOUDOT) WEDDELL	2	27.97	0.7425
Sapindaceae	*Allophyllus* cf. *excelsus* (TRIANA et PLANCH.) RADKL.	1	96.59	4.2655
Styracaceae	*Styrax* spec.	1	34.43	1.6769
Theaceae	*Freziera* spec.	2	75.29	2.3661
11 families	16 species	22 branches	Σ 761.27 m	Σ 40.4367 m²

* = genus in revision, pers. comm. Brian Smith.

recorded. The plant size was measured as the distance between plant tip (without inflorescence) and the branch surface were the plant was anchored.

Most of the species were identified and deposited in the herbarium QCA of the *Universidad Católica del Ecuador* in Quito.

RESULTS AND DISCUSSION

EPIPHYTES. Eighty-one species (2,677 individuals) were recorded on the 22 branches. Furthermore, four other species have been found, but it was not possible to distinguish between individuals in the mat-forming species *Sphyrospermum cordifolium* and *S. sodiroi* (Ericacaceae), *Hymenophyllum fucoides* (Hymenophyllaceae) and *Elaphoglossum peltatum* (Dryopteridaceae). So 81 (from 85) species taken into consideration for the following statistical analysis, especially plant height and spatial distribution.

To estimate the representativeness of the collection (epiphytes and phorophytes), we tried to accomplish an inventory for the whole Reserva; 166 species of vascular epiphytes, including 44 hemiepiphytes, were collected from many trees in different parts of the mountain ridge. Of these, 132 (79.5%) were angiosperms and 34 (20.5%) were pteridophytes.

Considering the 122 holoepiphytes (epiphytes passing their whole life on a phorophyte, in contrast to hemiepiphytes, which are forms that have a vascular connection with the ground for only a part of their life cycle [Kelly 1985]), the 85 holoepiphytic species of epiphytes (20 ferns) are a reduced number on the branches which were sampled. This can be explained by the absence of 23 presumably very rare orchid species on the sampled branches. Seven species of ferns, six species of bromeliads, and the common orchid *Xylobium* sp. grew only on tree stems or in branch forks (in zones 1 and 2 *sensu* Johansson 1974).

The epiphyte species richness and diversity and other important questions concerning the relation of species number and surface area, pollination and seed dispersal or population dynamics will be extensively discussed in a future paper.

PHOROPHYTES. We surveyed 22 complete branches of 17 different host trees of the middle and upper canopy. The phorophytes belong to 16 species of 11 families (TABLE 1).

PHOROPHYTE CHARACTERISTICS. **Surface area and branch inclination.** A phorophyte supplies its epiphytes with the physical basis of their existence. Tree structure determines quantity and quality of potential space for epiphytes. Surface area, inclination, branch diameter and substrate thickness were determined for each part of all 22 selected branches. Their surface area is 40.44 m² and their total length is 761.27 m (TABLE 1).

TABLE 2. Length and surface area at different inclinations.

Inclination [°]	Length [%]	Surface area [%]
0–10	20	39
15–30	10	17
35–50	16	18
55–70	15	10
75–90	39	16

Thirty-nine percent of the total surface area is provided by nearly horizontal sections of branches, 39% of the total length of branches is represented by nearly vertical branches (75 to 90 degrees inclination). Yet, because of usually small diameters, they provide not more than 16% of surface area (TABLE 2).

The relative amount of surface area and branch inclination depends on species-specific growth forms and individual differences between phorophytes. Nevertheless, middle and upper canopy branches show in all species a characteristic structure. The inner parts of the tree crown are usually dominated by branches with large diameters and accordingly abundant surface area. The middle crown shows more inclined branches, with smaller diameters and less surface area. The outer canopy consists of thin branches and twigs with small diameter and small surface area, and usually vertical growth.

There is a clear relation between branch inclination and diameter (compare TABLE 2, showing the relation of length and surface area). The surveyed surfaces show a higher inclination in branches with comparatively smaller diameters and likewise less substrate. The surface of large branches with relatively small inclinations is covered with more substrate than a comparable surface of smaller branches with a relatively high inclination. Therefore, the quality of surfaces is just as important as their quantity, because they offer different conditions for the settling of epiphytic vegetation.

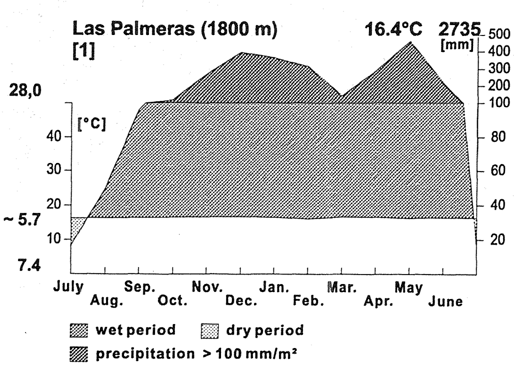

FIGURE 1. Climate of Las Palmeras, 4 km southeast of Río Guajalito (source: Instituto Nacional de Meteorología y Hidrología, in: Grijalva 1991).

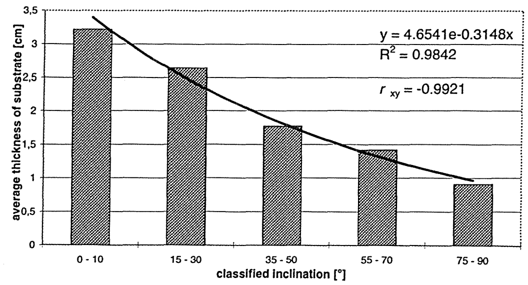

FIGURE 2. Average thickness of substrate and inclination of the branches.

Substrate thickness. The substrate on branches is provided predominantly by lichens and mosses. The inner layer may consist of dead, humus-like material. Apart from so-called twig orchids or some juvenile epiphytes of other families, which settle on bare branches (usually in the periphery of the tree crown), vascular epiphytes depend upon a substrate layer for seedling establishment, mechanical support of the roots and water and mineral supply. How is the substrate typically distributed along a branch?

Not suprisingly, the average thickness of substrates decreases exponentially with increasing inclination (FIGURE 2). Inclination and substrate thickness show a strong inverse correlation (r_{xy} $= -0.9921$).

The average thickness of substrate increases with branch diameter (FIGURE 3). Up to a diameter of 10 cm ($r_{xy} = 0.9731$), substrate thickness grows exponentially, but from 10.5 cm on, average substrate thickness does not increase, it grows not beyond 6 cm. The highest value for absolute substrate thickness was 20 cm at a branch diameter of 22 cm (individual case). Surfaces without substrate or only a flat layer of lichens or liverworts exist only on twigs in the

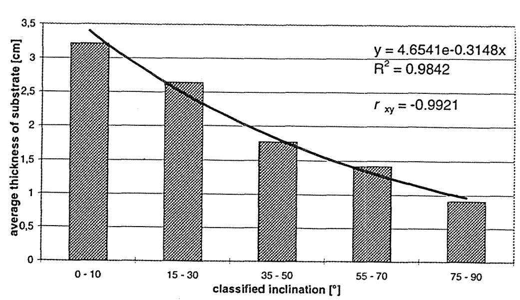

FIGURE 3. Average thickness of substrate and diameter of the branches.

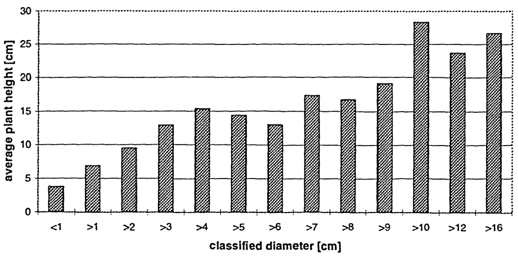

FIGURE 4. Average height of epiphytes at different diameters of branches.

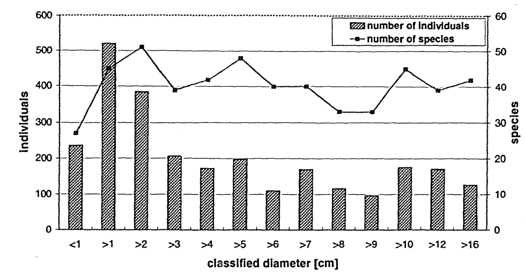

FIGURE 5. Species and individuals of identified plants at different diameters of branches (lacking undetermined plants see FIGURE 6).

periphery of the tree crowns. They were not considered in the above mentioned figures.

BRANCH DIAMETER AND PLANT HEIGHT. FIGURE 4 shows the average epiphyte height—measured as the distance between stem tip and branch surface—at different branch diameters. With increasing diameters the average height of the epiphytes increases. There are mainly two reasons: the properties of branches and the age of epiphytes. Sufficient mechanical support and substrate cover are preconditions of the epiphytic existence (see FIGURE 3). It is striking that average substrate cover and average epiphyte size both reach a maximum at 10.5 to 12 cm branch diameter. The upper limit of substrate thickness might be caused by a static factor, resulting from the relationship of surface area to inclination of the branch, a certain limit of stability for the thickness of the moss and humus layer.

Many epiphytes are slow-growing (Zotz 1995) and need several years to reach a considerable size, keeping in line with their phorophyte's growth. Branch diameter correlates to phorophyte age (Ibisch 1996). Most of the large and presumably old epiphytes are restricted to thick branches.

SPATIAL DISTRIBUTION OF VASCULAR EPIPHYTES. The distribution of species and individuals is shown in FIGURE 5. Whereas the number of species almost remains more or less constant from diameters of 1.5 cm and greater (which is consistent with the results of Freiberg [1996] in Guiana), the number of individuals reaches a maximum in the branch diameter category of 1.5–2 cm, and decreases on thicker branches (a phenomenon that Catling *et al.* [1986] also found in orchids in Belizean grapefruit trees).

To estimate and to understand the colonizing of very thin branches, we have to consider those young individuals which could not be identified to species level. Seven hundred forty-six juvenile plants were collected (21% of all collected individuals), with stem heights between 1 and 6 cm and were simply classified as orchids, bromeliads or ferns. FIGURE 6 shows their distribution at different branch diameters. They are extremely numerous on twigs with diameters of 0.5–1 cm (203 individuals) and 1.5–2 cm (191 individuals). Up to a diameter of 10 cm they are less frequent with a mean of 37, and rare on larger branches. The frequency differences between bromeliads and orchids correspond approximately to that of adult plants, whereas juvenile ferns are generally rare.

The number of species varies between 33 and 51 at diameters from 1.5 to >16 cm (mean 41.4). Twigs between 0.5–1 cm diameter show a minimum of only 27 species (FIGURE 5, without the numerous and undetermined juvenile plants). Yet, it can be expected that at a very early stage (young twigs) only the settling of some epiphyte species seems to be possible. From about 1.5 cm branch diameter, the number of species varies within limits but stays more or less constant. The highest species number at branch diameters of 2.5–3 cm represents a transition-zone. In this zone species settling on twigs occur as well as characteristic species on older branches. It is perhaps comparable to the most species rich zone of Catling *et al.* (1986).

More than ⅔ of all collected species appear in all diameter classes (>1.5 cm) they can be found as young plants on twigs and as adults on old branches. FIGURE 7 shows the distribution of *Til-*

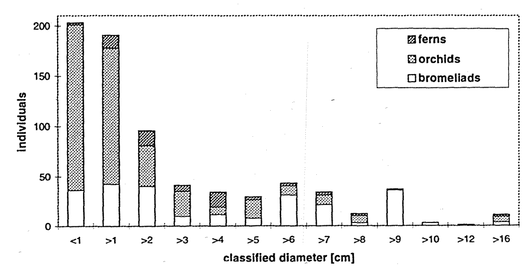

FIGURE 6. Juvenile undetermined plants/three taxonomic groups at different diameters of branches.

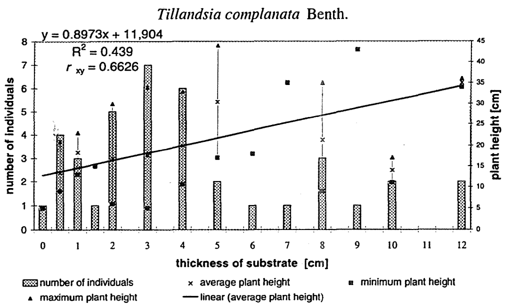

FIGURE 7. Distribution of *Tillandsia complanata* Benth. (45 individuals on 10 phorophytes).

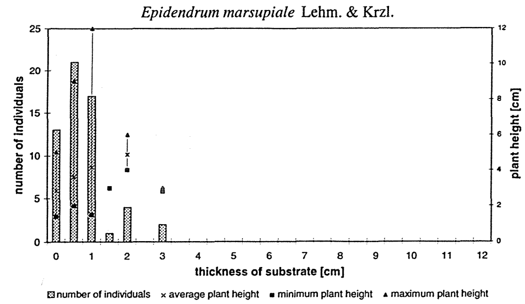

FIGURE 8. Distribution of *Epidendrum marsupiale* Lehm. and Krzl. (58 individuals on 12 phorophytes).

landsia complanata Benth., representing the majority of the collected epiphyte species occuring in all classes of substrate thickness (depending on diameter classes, see FIGURE 3). We found 45 individuals on 10 phorophytes. With increasing branch diameter the average plant height increases ($r_{xy} = 0.6626$) and the number of individuals decreases. This distribution corresponds to the general tendencies shown in FIGURES 4–6. *T. complanata* is able to germinate directly on the bark surface of thin twigs of the outer canopy'esumably some of the undetermined juvenile plants in FIGURE 6 represent this species. *T. complanata* grows quite slowly and needs five years or more to flower (Ibisch 1996).

However, other species are also typical pioneers on the youngest twigs, but they reach their reproductive period after a more or less short time (several months up to few years). An example is given with the orchid *Epidendrum marsupiale* Lehm. and Krzl. in FIGURE 8. Fifty-eight individuals on 12 phorophytes have been found on bark surface of younger twigs up to a substrate thickness of 3 cm. Maximum plant height has been measured at substrate thickness of just 1 cm. Further examples with a similar distribution are *Campylocentrum polystachyum* (Lindl.) Rolfe, *Stelis pusilla* H.B.K. or some species of *Lepanthopsis* and *Trichosalpinx.* These taxa never have been observed on older branches. Probably the increasing substrate thickness is unsuitable to these species. Further important reasons might be microclimatic differences between inner and outer canopy, or interspecific competition.

A third group of species characteristically has never been found on twigs, e.g. *Sobralia crocea* (P. & E.) Rchb. f., *Epidendrum geminiflorum* H.B.K., some species of *Elleanthus* and *Pleurothallis* and various ferns. They need thick substrate (>1 cm) for seed establishment, and they are not adapted to the youngest twigs in the outer canopy (see Rauer *et al.* in prep.).

This spatial distribution of these groups of species indicates a succession of vascular epiphytes. Some species replace other species in time, settling on the host tree which forms a steadily growing substrate basis (compare with Dudgeon 1923, Barkman 1958, Catling *et al.* 1989, Ibisch 1996). Van Leerdam *et al.* 1990 show a clear sequence of the growth-form composition in tree crowns; this partly applies to the vascular species of the first and the third group of our studies, but can only be considered as tendency.

The subsequent decrease in number of individuals means that on thicker branches, fewer individuals of a given species persist. A general competition for space (intra and interspecific) results in the reduced number of individuals on older branches. The widespread distribution of many juvenile plants on smaller but longer twigs is at first not influenced by mechanisms of competition because of the higher spatial separation. In the course of time, a partial loss of individuals must have occurred.

Obviously, thin branches are preferential settling areas for juvenile epiphytic plants. This can also be illustrated with the seed dispersal by wind, which is very common for epiphytes (73% of all collected species). The high relation of length and surface area of small twigs of the outer tree crown can be effective as 'net' or 'lattice.' In contrast to this, the bigger branches of the inner tree crown (>4 cm diameter) are of little importance for seed establishment. They offer less free space and are mostly overgrown with older epiphytes.

Furthermore, the currents of air around a branch, directly leading to whirls, are of great importance for the success of seed establishment: the characteristic whirls around small twigs effect the deposition of seeds and spores with higher probability than the differing currents of air around bigger branches with more surface area (Chamberlain and Chadwick 1972).

Finally, it is possible to characterize a branch of the middle and upper canopy as habitat with zones of different ages. The outer tree crown consists of young small twigs, settled by many juvenile individuals of epiphytes. The inner tree crown is formed by older and bigger branches, occupied by fewer but mostly adult individuals of epiphytes. This dynamic and steadily growing system involves intermediate forms on branches of intermediate diameters. A certain species turnover represents the succession of vascular epiphytes; the different spatial distribution of some species leads to the understanding of species composition on branches of different age levels.

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Literature Cited

Acosta-Solis M. 1977. Conferencias Fitogeograficas. Instituto Geografico Militar, Quito, Ecuador.

Barkman J.J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum, Assen, Netherlands.

Bennett B.C. 1986. Patchiness, diversity, and abundance relationships of vascular epiphytes. Selbyana 9: 70–75.

Benzing D.H. 1981. Bark surfaces and the origin and maintenance of diversity among angiosperm epiphytes: a hypothesis. Selbyana 5: 248–255.

———. 1990. Vascular Epiphytes. Cambridge University Press, Cambridge, Massachusetts.

Bøgh A. 1992. Composition and distribution of the vascular epiphyte flora of an Ecuadorian montane rain forest. Selbyana 13: 25–34.

Catling P.M., V.R. Brownell and L.P. Lefkowitch. 1986. Epiphytic orchids in a Belizean grapefruit orchard: distribution, colonization, and association. Lindleyana 1(3): 194–202.

Catling P.M and L.P. Lefkowitch. 1989. Associations of vascular epiphytes in a Guatemalan cloud forest. Biotropica 21(1): 35–40.

Chamberlain A.C. and R.C. Chadwick. 1972. Deposition of spores and other particles on vegetation and soil. Ann. Biol. 71: 141–158.

Dudgeon W. 1923. Succession of epiphytes in the *Quercus incana* forest at Landour, Western Himalayas. Preliminary note. J. Ind. Bot. Soc. 3: 270–272.

Erwin T. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopterist Bulletin 36: 74–75.

Frei J.K. 1972. The chemical effect of certain bark substances on the germination and early growth of epiphyte orchids. Bull. Torrey Bot. Club 99: 301–307.

Freibrg M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in Guiana. Biotropica 28(3): 345–355.

Gentry A.H. and C.H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Miss. Bot. Gard. 74: 205–233.

Grijalva E. 1991. Estudio biológico de especies nativas para reforestar áreas comprendidas entre 1,300 y 2,600 m. Tesis de Licenciatura, PUCE, Quito, Ecuador.

Ibisch P.L. 1996. Neotropische Epiphytendiversität—das Beispiel Bolivien. Wiehl, Martina Galunder-Verlag. 357 pp.

Johansson D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeographica Suecica 59: 1–136.

Kelly D.L. 1985. Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life forms and life histories. J. Biogeogr. 12: 223–241.

Kernan C. and N. Fowler. 1995. Differential substrate use by epiphytes in Corcovado National Park, Costa Rica: A source of guild structure. J. Ecol. 83: 65–73.

van Leerdam A., R.J. Zagt and E.J. Veneklaas. 1990. The distribution of epiphyte growth-forms in the canopy of a Columbian cloud-forest. Vegetatio 87: 59–71.

Lesica P. and R.K. Antibus. 1991. Canopy soils and epiphyte richness. Nat. Geogr. Res. & Expl. 7(2): 156–165.

Lüttge U., ed. 1989. Vascular Plants as Epiphytes:. evolution and ecophysiology. Springer Verlag. Berlin, Heidelberg, New York.

Møller-Jørgensen P., H. Borgtoft Pedersen and J. Jaramillo. 1989. Estudios botánicos sobre la taxonomia del bosque montano. Mayo 1986–Abril 1989. Dep. de Ciencias Biológicas, PUCE, Quito, Ecuador.

Mutke J. Zur baumvegetation eines westandinen bergregenwaldes in Ecuador: struktur, floristik, biogeographische beziehungen. Thesis. Bot. Inst. Bonn, (Mutke *et al.* in press.)

Perry D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.

Schimper A.F.W. 1888. Die Epiphytische Vegetation Amerikas. G. Fischer, Jena.

Sugden A.M. 1981. Aspects of the ecology of vascular epiphytes in two colombian cloud forests: habitat preferences of Bromeliaceae in the Serrania de Macuira. Selbyana 5(3–4): 264–273.

ter Steege H. and J.H.C. Cornelissen. 1989. Distribution ecology of vasclar epiphytes in lowland rain forest of Guyana. Biotropica 21(4): 331–339.

Went F.W. 1940. Soziologie der epiphyten eines tropischen Urwaldes. Annals du Jardin Botanique de Buitenzorg 50: 1–98.

Wolf J.H.D. 1993. Ecology of epiphyte communities in montane rain forests, Colombia. Diss. pp.233.

Zotz G. 1995. How fast does an epiphyte grow? Selbyana 16(2): 150–54.

Selbyana 19(1): 34–43

ARE ISOLATED REMNANT TREES IN PASTURES A FRAGMENTED CANOPY?

SERGIO GUEVARA[1], JAVIER LABORDE AND GRACIELA SÁNCHEZ

Instituto de Ecología, A.C., Apartado Postal 63, Xalapa 91000, Veracruz, México,
Tel.: +(28) 42-18-38 Fax: +(28) 18-78-09, e-mail: guevaras@sun.ieco.conacyt.mx

ABSTRACT. It is generally thought that pastures are inhospitable habitats for rain forest organisms. This largely results from (i) using low resolution images when studying fragmented landscapes and (ii) ignoring the actual characteristics of pastures. In a highly fragmented landscape of Los Tuxtlas, Mexico, numerous remnants of the forest canopy are left when pastures are created. Most of these are undetected in deforestation studies and dismissed as irrelevant in fragmentation studies. Using aerial photographs and field verification, we analyzed the spatial distribution and physical and biotic characteristics of isolated trees in pastures, a common landscape element in this region. In 30 pastures there were 98 species of isolated trees, 76 of which were primary rain forest species. Isolated tree density averaged 3.3 tree/ha (range: 0.4–11.9) and decreased with slope. Variation in the species composition, density and canopy physiognomy of isolated trees greatly increases the biotic and physical heterogeneity of pastures. These remnant trees function as 'stepping stones' for native fauna and 'safe sites' for flora, favoring their maintenance in fragmented landscapes. We propose that, together with other forest remnants, isolated trees in pastures compose a physically discontinuous but functional canopy in the Los Tuxtlas landscape.

RESUMEN. Por lo general se considera a los potreros como habitats inhóspitos para organismos de selva, lo cual se debe en gran parte al uso de imágenes con baja resolución, así como al desconocimiento de las características de los potreros. En un paisaje muy fragmentado de la región de Los Tuxtlas, México, encontramos numerosos remanentes de selva al interior de los potreros. La mayoría no son detectados en estudios de desforestación y son ignorados en los de fragmentación. Mediante fotografías aéreas y verificación en terreno, se analizan las características físicas y bióticas de árboles aislados en potreros, mismos que constituyen un elemento del paisaje común en ésta región. En 30 potreros fueron registradas 98 especies de árboles aislados, 76 de ellas de la selva madura. La densidad de árboles aislados promedió 3.3 árboles/ha (intervalo: 0.4–11.9), decreciendo con la pendiente del terreno. La variación en densidad, fisonomía de copas y especies de árboles aislados aumenta considerablemente la heterogeneidad biótica y física de los potreros. Estos árboles operan como 'sitios de relevo' para la fauna y como 'sitios seguros' para la flora nativas. Proponemos que en conjunto con otros remanentes de selva, los árboles aislados en potreros componen un discontinuo pero funcional dosel en el paisaje de Los Tuxtlas.

INTRODUCTION

The deforestation of tropical rain forest (TRF) in the Americas is well documented (see review by Toledo 1992). The dramatic reduction of the original area covered by TRF, in addition to the spatial isolation of remnant fragments by the surrounding pastures and crop fields, presently represent the main threats to TRF biodiversity. However, the consequences of TRF fragmentation as well as the ecological dynamics of these fragmented landscapes in the humid tropics are still poorly understood.

Most studies on TRF fragmentation focused on the fragments per se, from the border to the interior, ignoring the characteristics of the habitat or types of habitats which surround these fragments (Saunders *et al.* 1991). Consequently, it is generally unknown how TRF organisms perceive, use or respond to habitat characteristics outside remnant fragments (Guevara 1995). In order to evaluate and understand the effects of TRF fragmentation on biodiversity and ecological dynamics, an accurate description of landscape structure is a necessary first step. For this purpose information about species composition, abundance and spatial arrangement in pastures is particularly important. The types of elements present in a given landscape and their spatial arrangement define landscape structure (Forman & Godron 1986); i.e., "the distribution of energy, materials, and species in relation to the sizes, shapes, numbers, kinds and configurations of components" (Turner 1989). Landscape structure strongly influences important ecological processes within and among landscape components. The ecological dynamics of both the components and the mosaic which they usually form is known as landscape dynamics (Forman & Godron 1986, Turner 1989).

The exactness with which one can describe the structure of a landscape depends on the scale of the map used (Turner 1989). Studies of TRF deforestation commonly employ coarse or regional scales (e.g., 1:250,000), which are inappropriate for detecting the fine grained compo-

[1] To whom correspondence should be addressed.