SPECIES RICHNESS OF VASCULAR EPIPHYTES IN TWO PRIMARY FORESTS AND FALLOWS IN THE BOLIVIAN ANDES

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ABSTRACT. To study the impact of deforestation on vascular epiphyte diversity, we compared species richness in plots in primary forest and adjacent 15-year-old fallows in two different sites in the Yungas of Bolivia, including submontane forest near Sapecho (500–1200 m) and montane forest in the Parque Nacional Cotapata (1500–2500 m). Nearly 500 species of epiphytes (25 families, 110 genera) were recorded, and a 1.0 ha plot composed of eight subplots with a total surface of 0.32 ha of montane forest had up to 175 species. These forests rank among the richest worldwide in terms of epiphyte diversity. Fallows had 60–70% fewer species than neighboring natural forest. Numbers of species of orchids, bromeliads, Hymenophyllaceae, and Grammitidaceae were much lower in fallows than in primary forest, but hemiepiphytic aroids, Polypodiaceae and Aspleniaceae, were similar. Reduction of epiphytic species diversity in fallows can be explained by structural characteristics of the fallow trees, the lack of a dense moss cover, and the drier microclimate in the fallows.

Key words: epiphytes, vascular epiphytes, biodiversity, canopy studies, tropical rain forest, secondary vegetation, Bolivia

INTRODUCTION

The montane forests of the tropical Andes are among the world's richest ecosystems in terms of number of species (Barthlott et al. 1996). Vascular epiphytes, among them orchids, bromeliads, aroids, and ferns, are a key component of these forests, both in terms of species richness (Gentry & Dodson 1987, Ibisch 1996, Nieder et al. 1999) and their roles in water-balance and nutrient cycles (Nadkarni 1984, Coxson & Nadkarni 1995). These forests are now disappearing rapidly, as the result of increasing human pressures in the region. Deforestation in the tropical Andes is ca. 90% or ten times higher than in Amazonia (Henderson et al. 1991). The rapid destruction poses a major threat to the epiphytic vegetation and calls for measures to safeguard their existence.

Very little is known about effects on the epiphyte communities of these forests following deforestation nor about the ecology of the epiphytes in secondary forests (e.g., Hietz-Seifert et al. 1996, Engwald 1999). This investigation is the first one of its kind in the Central Andes. We investigated how the diversity of vascular epiphyte communities of Bolivian montane forests is affected by deforestation. We also documented the epiphyte diversity of secondary forest.

METHODS

Study Sites

The study was conducted in two different sites on the eastern slopes of the Andes in the Department of La Paz, Bolivia, the so-called "Yungas of La Paz" (FIGURE 1). The first study site is near the village of Sapecho (450 m; 15°27′–32′S, 67°18′–23′W), located along the Alto Beni River at the northeastern base of the Serranía Marimonos. Temperature in Sapecho averages ca. 24–25°C during the day, and annual rainfall varies from ca. 1500 mm in the valley to 2000 mm on the slopes. The rainy season of October–May alternates with a marked dry period of June–September (Elbers 1995). The natural forest on the slopes of the Serranía Marimonos is an evergreen or semi-evergreen submontane forest comprised of trees 30–40 m in height and a well developed shrub layer. Tree diversity averages ca. 120 species per ha (Seidel 1995).

Since the 1960s, the population of the Alto Beni region has increased considerably because of colonization by immigrants from the country's altiplano regions. The increased population has led to the conversion of large tracts of forests into agricultural fields. As a result, the lower slopes of the Serranía Marimonos are covered by a mosaic of arable fields and fallow land with trees up to 15 years old and a canopy height of 12–15 m (Krömer 2003). The most common pioneer trees of the fallows are *Cecropia* spp.,

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Jensen, W.A. 1962. Botanical Histochemistry. H.H. Freemann & Co., San Francisco.

Johansen, D.A. 1940. Plant Microtechinique. Paul Hoeber Inc., New York.

Kerstiens, G. 1996. Cuticular water permeability and its physiological significance. J. Exp. Bot. 47: 1813–1832.

Kraus, J.E. and M. Arduin. 1997. Manual Básico de Métodos em Morfologia Vegetal. Ed. Universidade Rural, Seropédica.

Krauss, B.H. 1949. Anatomy of the vegetative organs of the pineapple, *Ananas comosus* (L.) Merr. II. The leaf. Bot. Gaz. 110 (3): 333–404.

Linsbauer, K. 1911. Zur physiologischen anatomie der epidermis und des durchlüftungsapparates der Bromeliaceen. Sber. Akad. Wiss. Wien 120: 319–348.

Luther, H.E. 2001. De Rebus Bromeliacearum III. Selbyana 22(1): 34–67.

Luther, H.E. and E.Sieff. 1994. De Rebus Bromeliacearum I. Selbyana 15(1): 9–93.

———. 1997a. De Rebus Bromeliacearum II. Selbyana 18(1): 103–148.

———. 1997b. De Rebus Bromeliacearum: Addenda et corrigenda. Selbyana 18(2): 215.

Matsukura, M., M. Kawai, K. Toyofuku, R.A. Barrero, H. Uchimiya and J. Yamaguchi. 2000. Transverse vein differentiation associated with gas space formation—fate of the middle cell layer in leaf sheath development of rice. Ann. Bot. 85: 19–27.

Mauseth, J.D. 1988. Plant Anatomy. The Benjamim Cunmings Publishing Co. Inc., California.

Medina, E. 1990. Ecofisiologia y evolucion de las Bromeliaceae. Bol. Acad. Nac. Ciênc. 59: 71–100.

Menezes, N.L., D.C. Silva and G.F.M. Pinna. 2000. Folha. Pp. 303–325 *in* B. Apezzato-da -Gloria and S.M. Carmello-Guerreiro, eds. Anatomia Vegetal. Universidade Federal de Viçosa, Viçosa.

Metcalfe, C.R. 1963. Comparative anatomy as a modern botanical discipline with special reference to recent advances in the systematic anatomy of monocotyledons. Adv. Bot. Res. 1: 101–147.

Mott, K.A. and O. Michaelson. 1991. Amphystomy as an adaptation to high light intensity in *Ambrosia*

cordifolia (Compositae). Am. J. Bot. 78(1): 76–79.

Netolitzki, F. 1935. Das tropische parenchyn. *In* K. Linsbauer, ed. Handbuch der Pflanzenanatomie. Gerbuder Borntraeger, Berlin.

Nobel, P.S. 1991. Physicochemical and Environmental Plant Physiology. Academic Press, San Diego.

Nobel, P.S., L.J. Zaragoza and W.K. Smith. 1975. Relation between mesophyll surface area, photosynthetic rate and illumination level during development for leaves of *Plectranthus parviflorus* Henckel. Plant Physiology 55: 1067–1070.

Pita, P.B. "Estudo anatômico dos órgãos vegetativos de *Dyckia* Schultes f. e *Encholirium* Mart ex Schultes f. (Bromeliaceae) da Serra do Cipó, MG." Master Dissertation, Instituto de Biociências, Universidade de São Paulo, 1997.

Pittendrigh, C. 1948. The Bromeliad-Anopheles-Malaria complex in Trinidad. I. The bromeliad flora. Evolution 2: 58–89.

Robinson, H. 1969. A monograph on foliar anatomy of the genera *Connellia, Cottendorfia* and *Navia*. Smiths. Cont. Bot. 2: 1–41.

Sajo, M.G., S.R. Machado and S.M. Carmello-Guerreiro. 1998. Aspectos estruturais de folhas de bromélias e suas implicações no agrupamento de espécies. Pp. 101–111 *in* E.M.C. Leme. *Canistropsis,* Bromélias da Mata Atlântica. Ed. Salamandra, Rio de Janeiro.

Sass, J.E. 1951. Botanical Microtechnique. The Iowa State College Press, Iowa.

Schimper, A. F. W. 1884. Ueber bau und Lebenweise der Epiphyten. Westindiens. Bot. Zbl. 17: 192–195.

Souza, R.C.O.S. and L.J. Neves. 1996. Anatomia foliar de quatro espécies de *Tillandsia*. Bromélia 3(2): 28–39.

Strasburger, E. 1924. Handbook of Practical Botany. George Allen & Nonwin, Ltd., London.

Tomlinson, P.B. 1969. Anatomy of Monocotyledons. III. *in* C.R. Metcalfe, ed. Commelinales-Zingiberales. Clarendon Press, London.

Turner, I.M. 1994. Sclerophylly: primary protective? Func. Ecol. 8: 1–32.

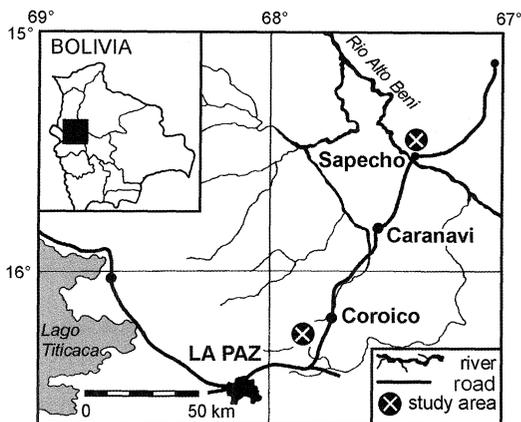Van Fleet, D.S. 1961. Histochemistry and function of the endodermis. Bot. Rev. 27: 165–220.

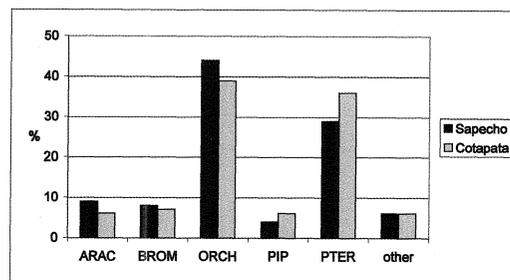FIGURE 1.   Location of the study sites in Bolivia.

FIGURE 2.   Percentage contribution of Araceae (ARAC), Bromeliaceae (BROM), Orchidaceae (ORCH), Piperaceae (PIP), ferns (PTER), and other families (other) to total vascular epiphyte diversity in Sapecho and Cotapata.

Ochroma pyramidale (Cav. ex Lam.) Urb., and *Inga* spp. (Seidel 1995, Acebey et al. 2003).

The second study site is in the Parque Nacional Cotapata (16°11′–13′S, 67°51′–54′W), located north of the road from La Paz to Coroico and extending 1100–5600 m in elevation. At 1500–2500 m, air temperatures average 13–19°C during the day and annual rainfall is ca. 2500 mm. The dry period, June–July, is less severe than in Sapecho (Bach et al. 2003, M. Schawe pers. comm.). The very steep slopes at these elevations, covered by evergreen montane forest made up of trees 15–25 m in height, have dense shrub and herb layers. The number of tree species per hectare is unknown but probably lower than in Sapecho. As the result of frequent landslides and the conversion of small forest patches for agricultural use, the lower slopes are covered by a mosaic of forests in different stages of succession including 15-year-old fallows with a canopy height of 8–12 m (Krömer 2003).

Sampling

Vascular epiphyte diversity in natural forest and in neighboring 15-year-old fallows was compared based on representative sampling of 1.0 ha plots of homogeneous forest (Gradstein et al. 2003, Krömer 2003). One fallow and five forest plots were sampled in Sapecho (500–1200 m elevation) and two fallow and three forest plots in Cotapata (1500–2200 m elevation). Canopy height in the fallows was 12–15 m in Sapecho and 8–12 m in Cotapata. In each of the forest plots, eight mature canopy trees were selected based on the epiphyte sampling protocol of Gradstein et al. (2003). All trees were sampled from the base to the outer portion of the tree crown by recording all vascular epiphyte species within the five vertical zones according

to Johansson (1974), using the single rope technique (Perry 1978). This technique allows for a nearly complete inventory of epiphyte diversity of the forest canopy (Flores-Palacios & García-Franco 2001). Because the epiphyte flora on shrubs and treelets in the forest understory usually differs from that on the large canopy trees, epiphytes on shrubs and treelets were sampled within a 20 × 20 m subplot around each sampled canopy tree, using collecting poles and binoculars (Shaw & Bergstrom 1997, Gradstein et al. 2003, Krömer 2003). Similarly, our inventories of the fallows, generally made up of trees that are too fragile to climb, were sampled in eight irregularly distributed 400 m² subplots in each 1.0 ha plot, using binoculars and collecting poles. About eight working hours were needed for complete inventory, including tree climbing and processing of specimens, of each subplot by two persons (one specialist and one field assistant).

Presence-absence was scored for all species. Voucher specimens were deposited in the Herbario Nacional de Bolivia (LPB), with duplicates in the Herbarium of the University of Göttingen (GOET), Marie Selby Botanical Gardens (SEL), and the Jepson Herbarium, University of California, Berkeley (UC).

RESULTS

Almost 500 species of epiphytes, in 25 families and 110 genera, were recorded in this study: 255 in Sapecho (23 families, 87 genera) and 292 in Cotapata (24 families, 76 genera). Orchids were the leading family in terms of species number (Sapecho: 44%; Cotapata: 39%), followed by ferns (29%; 36%), Araceae (9.4%; 5.8%), and Bromeliaceae (7.8%; 7%) (FIGURE 2). Species assemblages in the two sites differed markedly. Only 54 species (11%) occurred both in Sapecho and Cotapata.

TABLE 1. Number of species, genera, and families of vascular epiphytes in natural forest (P) and fallow (S) plots of 1.0 ha in Sapecho and Cotapata, Bolivia. Plots arranged by increasing elevation.

Epiphyte taxa and elevation	Study plots, Sapecho			Study plots, Cotapata				
	S	PI	PII	PI	S1	PII	S2	PIII
Species	44	101	127	175	49	146	37	152
Genera	23	48	60	57	23	50	21	50
Families	9	16	18	23	11	18	10	19
Elevation (m)	550	600	625	1600	1650	1800	1900	2150

Epiphyte diversity in the fallows was much lower than in natural forest. It was ca. 47% lower at the family level, ca. 57% at the generic level, and 60–70% at the species level (Sapecho: ca. a 60% reduction in diversity; Cotapata: more than a 70% reduction) (TABLE 1, FIGURE 3). Reduction of species richness in fallows was severe in orchids (88%) and bromeliads (75%), less so in ferns and Piperaceae (genus *Peperomia*) (ca. 50%). Aroid diversity was affected strongly in Cotapata (79% reduction) but was not reduced in Sapecho, where aroids were the most speciose group of epiphytes in the fallows (43% of all species recorded). In contrast, ferns were the dominant group in the fallows of Cotapata (ca. 60% of all species recorded). Fern diversity in the fallows was restricted, however, and mainly included species of Polypodiaceae and Aspleniaceae. In contrast, Grammitidaceae, Hymenophyllaceae, and Lomariopsidaceae, each represented by large numbers of species in the forests, were virtually lacking in the fallows. Ericaceae and Gesneriaceae, each with only a few epiphytic species in the forest plots, were completely absent in the fallows.

DISCUSSION

Epiphyte Diversity in Primary Forest

According to a worldwide tally of vascular epiphytes by Kress (1986), an estimated 23,500 species or ca. 10% of all vascular plants are epiphytes. More than half of these occur in the neotropics, especially in the montane forests of the Andes, which are among the richest habitats worldwide in terms of vascular epiphytes (Gentry & Dodson 1987, Ibisch 1996, Nieder et al. 1999). The highest numbers of vascular epiphyte species at the regional level were recorded from two forest reserves in the Ecuadorian Andes: Reserva Biologica San Francisco, with 627 species (Bussmann 2001) and Reserva Otonga with 456 species (Nieder & Barthlott 2001). In comparison, epiphyte diversity in Cotapata with ca. 300 species recorded was relatively low, even though it equals the number of species recorded from the well studied forest reserves of La Selva

(McDade et al. 1994) and Monteverde (Ingram et al. 1995) in Costa Rica.

These comparisons of epiphyte diversity are problematic, however, in view of the differences in surface area inventoried, elevation, and collecting intensity. A comparison of our data with inventories carried out elsewhere at similar elevations and using similar plot sizes, showed that Cotapata may rank among the richest sites in the world in terms of vascular epiphyte diversity. With 175 species in 0.32 ha, forest plot "PI" (1600 m) is as speciose as plots inventoried by Ibisch (1996) in Bolivia and by Nowicki (2001) in Ecuador; and it is richer than plots inventoried in Andean forest of Venezuela (Kelly et al. 1994, Engwald 1999).

Species richness of vascular epiphytes in the submontane rain forests of Sapecho is more difficult to assess because of the lack of data from similar forest types. Species richness is, however, usually lower than in the montane forests of Cotapata but significantly higher than in Amazonian lowland rain forests (ter Steege & Cornelissen 1989, Ek et al. 1997, Engwald 1999, Acebey & Krömer 2001).

Orchids are the leading epiphyte family in terms of species richness, and they contribute up to 50% of total diversity (Ibisch 1996, Kelly et al. 1994, Engwald 1999). Much of that diversity
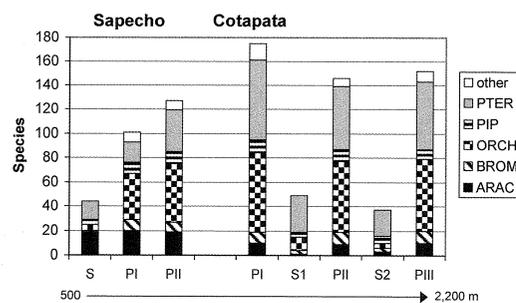

FIGURE 3. Number of epiphytic species of Araceae (ARAC), Bromeliaceae (BROM), Orchidaceae (ORCH), Piperaceae (PIP), ferns (PTER), and other families (other) in natural forest (P) and fallows (S) in Sapecho and Cotapata. Plots arranged by increasing elevation.

is the result of a few speciose neotropical genera, e.g., *Epidendrum, Maxillaria, Pleurothallis,* and *Stelis.* Ferns are the second-ranked group with a diversity almost equal to orchids in Cotapata. Fern diversity relative to orchids, however, varies in neotropical regions. In Ecuador, species richness of orchids is at least five times higher than ferns (Jørgensen & León-Yánez 1999), whereas in Bolivia it is only three times as high (Ibisch 1996). Although data support a greater richness of orchids in Ecuador, they may also indicate higher diversity of ferns in Bolivia. Araceae are nearly as speciose as Orchidaceae in lowland forests; but in montane forests, species richness of the aroids is usually much reduced, with the exception of some montane areas in Ecuador (Nieder & Barthlott 2001). Other epiphyte families such as Bromeliaceae, Piperaceae, Ericaceae, and Gesneriaceae, taken together, usually contribute less than 10% to total epiphyte species richness, and occasionally up to 25%, e.g., in Otonga (Nowicki 2001) and Monteverde (Ingram et al. 1995).

Epiphyte Diversity: Primary Forest vs. Fallow

Forest destruction usually results in a considerable loss of species and a major reduction in total species number. This reduction may be more severe for vascular epiphytes than for other groups of plants (Turner et al. 1994). In rain forest fragments of Singapore, epiphytes were reduced by 62%, as compared with a 29% reduction of total species richness. Thus epiphyte diversity was affected twice as severely as that of all vascular plants taken together. The severe reduction of species richness of epiphytes following deforestation is corroborated by our study. In the 15-year-old fallows in Sapecho and Cotapata, species reduction (60% and 70% respectively) was as severe as in the fragmented forests of Singapore. It was slightly higher than in 25–50 year old secondary forests in Venezuela, where Engwald (1999) found a reduction of 55%.

The marked differences in species reduction among individual epiphyte groups recorded in this study, e.g., in orchids (ca. 90%) and ferns (ca. 45%), corroborate the findings from Singapore (Turner et al. 1994) but differ from the results of Engwald (1999), who documented a ca. 60% reduction of both groups in the secondary forest of La Carbonera in Venezuela. Species reduction in Grammitidaceae, Hymenophyllaceae, Araceae, and Bromeliaceae was much less in La Carbonera than recorded in this study. The smaller reduction of these epiphyte families in secondary forest at La Carbonera in Venezuela

may be the result of the older age of this forest and the presence of relict trees. In Mexico, remnant trees of the natural forest may be very rich in hemiepiphytic Araceae and Bromeliaceae and may contribute considerably to the diversity of open, secondary habitats (Hietz-Seifert et al. 1996). Another difference between our study and that in Venezuela, which is more difficult to explain, involves the much greater reduction of Piperaceae (genus *Peperomia*) in La Carbonera than in our field sites. Our results are closer to those from Mexico, where species richness and abundance of Piperaceae were unaffected in disturbed habitats as compared with the natural forest (Hietz-Seifert et al. 1996).

The low epiphyte diversity in the fallows of Sapecho, Cotapata, and elsewhere may be explained by several factors. In contrast to natural forest trees, fallow trees are usually uniform in stature, smooth-barked, having little-branched crowns with oblique (instead of horizontal) branches. This type of crown architecture is unfavorable for establishment of epiphytes (Ibisch 1996). Secondary forests appear to offer fewer suitable microhabitats to epiphytes than do primary forests, whose old canopy trees provide a complex mosaic of microhabitats or "physical mosaic" (Benzing 1995), which promotes the development of species-rich epiphyte communities.

Another major factor is the drier microclimate in the fallows, caused by the more open canopy and stronger radiation in these young secondary forests (Acebey et al. 2003). Not all epiphyte groups are negatively affected by decreased relative air humidity, however. In the fallows of Sapecho, hemiepiphytic aroids thrive in the well lit understory of the young secondary forests, probably because of their succulent stems and firm connection to the soil. Species of Polypodiaceae, e.g., *Pleopeltis astrolepis* and *Polypodium polypodioides,* also are well adapted to the relatively dry environment and may outnumber those growing in the natural forest, e.g., in Cotapata and in Mexico (Hietz-Seifert et al. 1996).

A third factor is the cover of bryophytes. In moist montane forests, trunks and branches of canopy trees usually are densely covered by thick layers of bryophytes. These bryophyte layers may provide a suitable substrate for the germination and establishment of vascular epiphytes (Nadkarni 1984, Gradstein 1992, Zotz & Vollrath 2003). In fallow vegetation, the bryophyte cover usually is much reduced as compared with the natural forest, because of the drier microclimate and structural characteristics of the secondary forest trees (Acebey et al. 2003). Thus the reduced bryophyte cover may have a

negative impact on the diversity of vascular epiphytes in the fallows.

CONCLUSIONS

With up to 175 species of vascular epiphytes recorded from 0.32 ha of forest in Parque Nacional Cotapata, the moist montane forests on the eastern slopes of the Andes of Bolivia rank among the richest in terms of epiphyte diversity in the world.

Deforestation results in a major loss of epiphytic diversity: 15-year-old fallows (500–2000 m elevation) have 60–70% fewer species than neighboring natural forest. Loss of species is very severe in orchids, bromeliads, and certain families of ferns (Hymenophyllaceae, Grammitidaceae). In Aspleniaceae, Polypodiaceae, and (at lower elevations only) hemiepiphytic aroids, however, species richness is not reduced in the fallows.

Reduction of epiphytic species diversity in the fallows may be the result of the structural characteristics of the fallow trees, drier microclimate, and reduced bryophyte cover.

ACKNOWLEDGMENTS

LITERATURE CITED

Acebey, A. and T. Krömer. 2001. Diversidad y distribución vertical de epífitas en los alredededores del campamento río Eslabón y de la laguna Chalalán, Parque Nacional Madidi, Dpto. La Paz, Bolivia. Rev. Soc. Boliviana Bot. 3: 104–123.

Acebey, A., S.R. Gradstein and T. Krömer. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. J. Trop. Ecol. 19: 9–18.

Bach, K., M. Schawe, S. Beck, G. Gerold, S.R. Gradstein and M. Moraes. 2003. Vegetación, suelos y clima en los diferentes pisos altitudinales de un bosque montano de los Yungas, Bolivia—primeros resultados. Ecol. Bolivia 38: 3–14.

Barthlott, W., W. Lauer and A. Placke. 1996. Global distribution of species diversity in vascular plants: toward a map of phytodiversity. Erdkunde 50: 317–327.

Benzing, D.H. 1995. The physical mosaic and plant variety in forest canopies. Selbyana 16: 159–168.

Bussmann, R.W. 2001. Epiphyte diversity in a tropical Andean forest—Reserva Biológica San Francisco, Zamora-Chinchipe, Ecuador. Ecotropica 7: 43–59.

Coxson, D. and N.M. Nadkarni. 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems. Pp. 495–546 in M. Lowman and N.M. Nadkarni, eds. Forest Canopies. Academic Press, San Diego.

Ek, R.C., H. ter Steege and K.C. Biesmeijer. 1997. Vertical distribution and associations of vascular epiphytes in four different forest types in the Guianas. Pp. 65–89 in R.C. Ek, ed. Botanical Diversity in the Tropical Rain Forest of Guyana. Tropenbos, Wageningen.

Elbers, J. 1995. Estudio de suelos en la zona de colonizacíon Alto Beni, La Paz, Bolivia. Ecol. Bolivia 25: 37–69.

Engwald, S. 1999. Diversität und Ökologie der vaskulären Epiphyten eines Berg- und eines Tieflandregenwaldes in Venezuela. Books on Demand, Hamburg.

Flores-Palacios, A. and J.G. García-Franco. 2001. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. Selbyana 22: 181–191.

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

Gradstein, S.R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. Pp. 234–258 in J.W. Bates and A.W. Farmer, eds. Bryophytes and Lichens in a Changing Environment. Clarendon Press, Oxford.

Gradstein, S.R., N.M. Nadkari, T. Krömer, I. Holz and N. Nöske. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. Selbyana 24(1): 105–111.

Henderson, A., S.P. Churchill and J.L. Luteyn. 1991. Neotropical plant diversity. Nature 351: 21–22.

Hietz-Seifert, U., P. Hietz and S. Guevara. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biol. Conserv. 75: 103–111.

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

Ingram, S.W., K. Ferrell-Ingram and N.M. Nadkarni. 1995. Epiphytes of the Monteverde cloud forest reserve. Selby Botanical Gardens Press, Sarasota, Florida.

Johansson, D. 1974. Ecology of vascular epiphytes in a West African rain forest. Acta Phytogeogr. Suecica 59: 1–129.

Jørgensen, P.M. and S. León-Yánez. 1999. Catalogue of the Vascular Plants of Ecuador. Missouri Botanical Garden Press, St. Louis.

Kelly, D.L., E.V.J. Tanner, E.M. Niclughadha and V. Kapos. 1994. Floristics and biogeography of a rain forest in the Venezuelan Andes. J. Biogeogr. 21: 223–241.

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

Krömer, T. 2003. Diversität und Ökologie der vaskulären Epiphyten in primären und sekundären Bergwäldern Boliviens. Cuvillier Verlag, Göttingen.

McDade, L.A., K.A. Bawa., H.A. Hespenheide and G.S. Hartshorn. 1994. La Selva—Ecology and Natural History of a Neotropical Rain Forest. Chicago University Press, Chicago, Illinois.

Nadkarni, N.M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16: 249–256.

Nieder, J., S. Engwald and W. Barthlott. 1999. Patterns of neotropical epiphyte diversity. Selbyana 20: 66–75.

Nieder, J. and W. Barthlott. 2001. Epiphytes and Canopy Fauna of the Otonga Rain Forest (Ecuador). Results of the Bonn-Quito Epiphyte Project, funded by the Volkswagen Foundation, Vol. 2 of 2. Books on Demand, Hamburg.

Nowicki, C. 2001. Epífitas vasculares de la Reserva Otonga. Pp. 115–160 in J. Nieder and W. Barthlott, eds. Epiphytes and Canopy Fauna of the Otonga Rain Forest (Ecuador). Results of the Bonn-Quito Epiphyte Project, funded by the Volkswagen Foundation, Vol. 2 of 2. Books on Demand, Hamburg.

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

Seidel, R. 1995. Inventario de los árboles en tres parcelas de bosque primario en la Serranía de Marimonos, Alto Beni. Ecol. Bolivia 25: 1–35.

Shaw, D.S. and D.M. Bergstrom. 1997. A rapid assessment technique of vascular epiphyte diversity at forest and regional levels. Selbyana 18: 195–199.

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

Turner, I.M., H.T.W. Tan, Y.C. Wee, A.B. Ibrahim, P.T. Chew and R.T. Corlett. 1994. A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. Conserv. Biol. 8: 705–712.

Zotz, G. and B. Vollrath. 2003. The epiphyte vegetation of the palm Socratea exorrhiza—correlations with tree size, tree age, and bryophyte cover. J. Trop. Ecol. 19: 81–90.

HOST TREE PREFERENCE OF VASCULAR EPIPHYTES AND CLIMBERS IN A SUBTROPICAL MONTANE CLOUD FOREST OF NORTHWEST ARGENTINA

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ABSTRACT. In a subtropical montane cloud forest of northwest Argentina (22°S, 1800 m elevation), vascular epiphyte and climber communities were described in 1 hectare to assess relationships between the epiphytes and climbers and their host tree species. In addition, inferences were made regarding associations between epiphytes and climbers and tree morphological-functional groups. A total of 23 epiphytes and climbers were registered on 171 trees. Tree species differed in their epiphyte and climber composition and coverage of a non-metric multidimensional scaling ordination. Tree species were differentiated by foliar phenology and bole heights. These factors likely create a range of microenvironments within the canopy from humid and dark to dry and well lit. The most abundant climber (*Macfadyena unguis-cati*) was associated with trees having drier and brighter microenvironments (particularly *Juglans australis*), and at least eight epiphyte species were associated with trees with moister and darker microenvironments. Tree species also differed according to tree and crown diameter, total tree and bole height, and bark type. Taller tree species with rough bark, larger diameters and crown dimensions were associated with at least eleven epiphyte and climber species. Overall, epiphyte and climber community composition differed among host tree species and may be explained in part by measurable host tree characteristics.

Key words: climbers, epiphytes, lianas, microenvironments, neotropical montane forests, Yungas

INTRODUCTION

Vascular epiphytes (sensu Moffett 2000) and climbers (herbaceous vines and woody lianas) are non-tree components of tropical forests that contribute significantly to biodiversity (Gentry & Dodson 1987a, 1987b, Gentry 1991, Haber 2000, Nabe-Nielsen 2001). In mature wet tropical forests, these plant groups can account for ca. 35% of the species richness in 0.1 ha plots (Gentry & Dodson 1987b). Epiphyte abundance is higher in mature forests (Gentry & Dodson 1987b, Barthlott et al. 2001), and climber abundance is higher in secondary and disturbed ones (Hegarty & Caballé 1991, Dewalt et al. 2000, Haber 2000, Laurance et al. 2001). Vascular epiphytes and climbers serve as valuable food sources and habitat structure for forest animals, such as arthropods, amphibians, reptiles (Richardson 1999), mammals (Brown 1986, Diller O'Dell 2000), and birds (Nadkarni & Matelson 1989).

Climbers and epiphytes, which often rely on trees for support, depend on the microenvironment created by bark surfaces and canopy openness. Differences in tree characteristics, such as size, foliar phenology, and/or bark type, are likely to produce different microenvironmental conditions and thus differences in epiphyte-climber (E-C) community composition. These tree characteristics influence epiphyte and climber cov-

erage differentially. Tree diameter and bark type may reduce the growth of climbers depending on their method of ascension (Putz & Chai 1987) and may favor epiphytes by providing space and time for their establishment and growth (Hietz & Hietz-Seifert 1995a). Tree deciduousness may increase the seasonal light availability for both climbers and epiphytes. All of these features modify water retention and humidity on tree surfaces (Johanson 1974). While such characteristics may have little effect on climbers that root in the ground, they may reduce water availability for epiphytes. Although epiphytes and climbers tend to occupy the same space on their hosts and therefore compete with each other, most published studies analyze these groups separately.

Several studies on host tree specificity of vascular epiphytes yielded contrasting results (Benzing 1990). Some epiphyte taxa, such as orchids, seem to show preference for particular tree genera (Díaz Santos 2000), and certain epiphyte communities are differentiated by tree species (ter Steege & Cornelissen 1989, Brown 1990, Wolf 1993, Ayarde 1995, Hietz & Hietz-Seifert 1995b, Carlsen 2000). In some cases, epiphyte host preference seems to be related to tree characteristics, such as bark roughness or smoothness (Johanson 1974, Zimmerman & Olmstead 1992, Hietz & Hietz-Seifert 1995b, Carlsen 2000), tree diameter (Catling & Lefkov-