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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 coverage 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 & Lefkovitch 1989, Hietz & Hietz-Seifert 1995a, 1995b, Annalselvan & Parthasarathy 2001), or crown size (Yeaton & Gladstone 1982). In contrast, other studies conclude that epiphytes do not display marked host tree species preference (Benzing 1995, Hietz and Hietz-Seifert 1995b). This contradiction may arise, because many trees species are neither fully satisfactory nor totally unsatisfactory hosts to epiphytes. The reason is that host tree microenvironmental conditions (i.e., light and humidity) change with factors other than tree identity, such as size or age of the individual tree (Johanson 1974, Hietz & Hietz-Seifert 1995a).

Studies on host tree preference and colonization by climbers have documented relationships based on both climber abundance (Campbell & Newbery 1993, Talley et al. 1996a, Carse et al. 2000, Muthuramkumar & Parthasarathy 2001) and species composition (Talley et al. 1996b, Carsten et al. 2002). As with vascular epiphytes, climber host specificity may be related to tree features such as bark type (Talley et al. 1996b, Muthuramkumar & Parthasarathy 2001), bole height (Campbell & Newbery 1993, Muthuramkumar & Parthasarathy 2001), and tree diameter (Carse et al. 2000, Muthuramkumar & Parthasarathy 2001, Nabe-Nielsen 2001, Perez-Salicrup et al. 2001, Carsten et al. 2002). Some of these studies documented the inability of climbers to colonize certain tree species with particular morphological and physiological features, such as stem flexibility, branch shedding, and fast growing rates (Putz 1984a, 1984b, Talley et al. 1996a, 1996b, Carse et al. 2000, Muthuramkumar & Parthasarathy 2001, Carsten et al. 2002). In contrast, other researchers argue that clear relationships do not exist between most climbers and tree species (Perez-Salicrup et al. 2001).

In many neotropical cloud forests, vascular epiphytes often are abundant and diverse likely because of frequent and prolonged periods of cloud cover (Sugden & Robins 1979, Gentry & Dodson 1987a, Ingram et al. 1996, Haber 2000, Brown & Kappelle 2001). Woody lianas are more abundant in drier habitats (Haber 2000), and their diversity peaks in humid conditions but at lower altitudes than epiphyte diversity (Gentry 1988, 1991).

In the Argentinean subtropical montane cloud forest, most trees bear significant epiphytes loads (Brown et al. 2001). Most of these trees have rough bark and large horizontal branches, which may be favorable substrates for propagule establishment and subsequent growth (Brown 1990). No studies have been conducted, however, on the climber community in this cloud forest. The present study analyzes the community composition of both vascular epiphytes and climbers in a subtropical montane cloud forest in Argentina. I considered both epiphytes and climbers, because these plants rely on trees for support and compete for the same light and space. They thus may vary in density in relation to tree characteristics or tree identity. I addressed the following questions: Do tree species differ in their E-C community composition? Is E-C community composition related to host tree characteristics such as trunk diameter, crown dimensions, bole and total height, or foliar phenology?

MATERIALS AND METHODS

Study Site

This study was conducted in an old-growth subtropical montane cloud forest located at El Nogalar National Reserve near Los Toldos, Santa Victoria Department, Salta Province, northwest Argentina (22°30′S, 64°50′W), at 1800 m elevation on a river terrace. Dendrochronological dating of the largest trees suggests that the stand may have originated after a flood between 1810 and 1820 (R. Villalba unpubl. data). Topography-based isolines suggest an annual rainfall of ca. 1300–1600 mm, 80% of which falls in the wet season between November and April (Bianchi 1981). Mean annual temperature is 15°C at Los Toldos (ca. 100 m lower in elevation); frosts and snowfalls occur during the winter (Ramadori 1995). At a similar site in northwest Argentina, mist has been documented as an important source of humidity during the dry season, during which it exceeds rainfall for 5 months and constitutes ca. 470 mm/year (Hunzinger 1997). According to Stadmüller (1987), the absolute values of horizontal precipitation in tropical cloud forests range from 325 to 941 mm/year.

Forest vegetation is characteristic of the upper montane forest belt and presents ca. 17 species per ha (Brown et al. 2001). The main vascular epiphyte families are Polypodiaceae, Bromeliaceae, Orchidaceae, Piperaceae, Cactaceae, and Bignoniaceae (Brown 1986). Climber families present within the study site are Asteraceae, Begoniaceae, Cucurbitaceae, Dioscoreaceae, Loasaceae, and Vitaceae.

Data Collection

I sampled all living trees larger than 10 cm diameter at breast height (dbh) in a 1-ha plot in September and October 1999. For each individual tree, I visually estimated percent cover of E-C species by studying the entire trunk and crown

TABLE 1. Characteristics of the six common tree species larger than 20 dbh in a 1-ha plot at El Nogalar National Reserve, Salta, Argentina.

Tree species	Density (ind/ha)	Mean dbh (range) (cm)	Mean crown diameter (m)	Mean bole height (m)	Mean tree height (m)	Foliar phenology*	Bark type
Allophylus edulis	9	24 (21–29)	7	4	16	1	Squamous
Blepharocalyx salicifolius	28	31 (21–64)	6	7	20	1	Rough
Cedrela lilloi	24	52 (21–164)	8	13	25	1	Rough
Juglans australis	44	36 (20–74)	7	14	27	1	Rough
Myrcianthes pseudo-mato	31	33 (21–51)	8	5	19	2	Exfoliating-smooth
Podocarpus parlatorei	35	79 (21–129)	10	10	25	2	Rough

Note: * 1 = deciduous, 2 = evergreen

from at least four different spots on the ground with binoculars (10×42). For each tree, I estimated the total E-C percent cover with respect to the total bark surface of the tree and I estimated the relative cover of each E-C species with respect to the total cover. For this, I multiplied the cover of each E-C by the total E-C cover and divided it by 100%. Thus for each E-C species present on at least two of the sampled trees, I calculated mean relative percent cover per individual tree and per tree species. Although subjective estimates, this method likely is unbiased and provides a comparative measure for the analysis conducted. Cover data rather than presence/absence data was used, because I considered it to be more representative of the relative ecological importance of the species. Identification of species was made based on the work of De la Sota (1977), Gentry (1993), Jankowski et al. (2000), and reference collections at the Miguel Lillo herbarium (LIL), Universidad Nacional de Tucumán, Argentina. Of the 328 individual trees represented by 16 species within the plot, 157 individuals had less than 10% of E-C total cover, and 10 tree species were represented by few individuals, introducing significant noise in preliminary multivariate analyses and making interpretation difficult. For further descriptions and analysis, I therefore considered only tree individuals >20 cm dbh with ≥10% E-C total cover of the most abundant tree species. The tree species studied were *Juglans australis* Griseb. (Juglandaceae), *Podocarpus parlatorei* Pilg. (Podocarpaceae), *Myrcianthes pseudo-mato* (D. Legrand) Mc Vaugh (Myrtaceae), *Blepharocalyx salicifolius* (Kunth) O. Berg (Myrtaceae), *Cedrela lilloi* C. DC. (Meliaceae), and *Allophylus edulis* (A. St.-Hil., Cambess. & A. Juss.) Radlk. (Sapindaceae).

For each tree >20 cm of diameter, I recorded total tree height, bole height, dbh, and crown dimensions. I measured tree and bole height with a clinometer. Bole height was measured from the tree base to the first ramification. As an index of crown dimensions, I estimated crown projection onto the forest floor and measured the diameter in a north-south direction. TABLE 1 describes the main characteristics of the tree species studied, including foliar phenology and bark type. Foliar phenology was classified in two categories according to Meyer (1963): 1 = deciduous, and 2 = evergreen tree species. Bark type was assigned four ordinal categories: exfoliating, smooth, rough, and squamous. Rough-barked trees have longer and deeper cracks than squamous ones.

Data Analysis

For a general description of the relationships between E-C species and host tree species, I performed an Indicator Species Analysis (Dufrêne & Legendre 1997). This method produces Indicator Values (IV) calculated as the product of the relative abundance and relative frequency of each E-C species for every tree species in the following equation:

$$IV_{ij} = A_{ij} \times B_{ij} \times 100, \quad \text{where}$$

$$A_{ij} = \text{E-Ccover}_{ij}/\text{E-Ccover}_i$$

$$B_{ij} = \text{Ntrees}_{ij}/\text{Ntrees}_j$$

E-Ccover$_{ij}$ is the mean percent cover of E-C species *i* across tree species *j*. E-Ccover$_i$ is the sum of the mean percent covers of E-C species *i* over all tree species. Ntrees$_{ij}$ is the number of trees species *j*, where E-C species *i* is present, and Ntrees$_j$ is the total number of trees of that species (Dufrêne & Legendre 1997).

IV ranges from 0% (no indication) to 100% (perfect indication). Perfect indication occurs when a given E-C species has the highest percentage cover in a particular tree species and also is present in all individuals of that tree species. I used a Monte Carlo test (1000 permutations) to evaluate the statistical significance of the observed maximum IV for each E-C species.

To explore changes in E-C community composition across host tree species, I performed an ordination of E-C community data, using nonmetric multidimensional scaling (NMDS, see Kruskal & Wish 1978). The NMDS ordination was based on a matrix of Bray Curtis distances (Legendre & Legendre 1998) between individual host trees calculated from percent cover data for each E-C species. In computing similarity between two trees, the Bray Curtis index compares the cover of each E-C species present. Trees that share species with comparable coverages are considered more similar; and as a result, those trees are closer in the multivariate space (Jogman et al. 1995). The advantage of NMDS over other ordination methods is that no assumptions are made about how species are distributed along environmental gradients (Kenkel & Orlóci 1986). I used a two-dimensional configuration, because the final stress, which indicates how accurately the graph configuration represents the Bray Curtis matrix (the lower the better), was 18.23 and did not decrease substantially in the three-dimensional configuration, where it was 15.28.

I used the non-parametric Kruskall-Wallis analysis to test for overall differences among host tree species in terms of scores along the two NMDS axes. Pairwise non-parametric Mann-Whitney *U*-tests identified groups of host tree species along the two NMDS axes; and non-parametric Kendall correlation coefficients between E-C species percent cover data and NMDS axis scores determined which E-C species were most important in separating host trees in the ordination space (Sokal & Rohlf 1995). To determine how the characteristics of individual host trees related to E-C community composition, I calculated Kendall correlation coefficients among individual tree characteristics (dbh, crown diameter, tree and bole height, foliar phenology) and NMDS axis scores. After making these correlations, I used the Bonferroni correction to limit false hypothesis acceptance based on chance alone (Legendre & Legendre 1998).

Indicator Species Analysis, Monte Carlo test, and NMDS were performed with PC-ORD 3.0 (McCune & Mefford 1997). Kruskall-Wallis analysis, pairwise non-parametric Mann-Whitney test, and Kendall correlation coefficients were performed with STATISTICA 5.1 (StatSoft 1998).

RESULTS

I recorded a total of 23 vascular E-C species with five climbers and 18 epiphytes on a total of 171 individual trees >20 cm dbh. Among the epiphytes were 11 ferns, three bromeliads, one cactus, one orchid, one herb (Piperaceae), and one shrub (Asteraceae) (see APPENDIX).

Indicator Species Analysis showed a significant association between the host tree *Podocarpus parlatorei* and the following epiphyte and climber species: *Asplenium auritum, A. praemorsum, Campyloneurum aglaolepis, Dryopteris patula, Polytaenium lineatum, Pecluma oranense, Pleopeltis macrocarpa, Senecio epiphyticus,* and *Cissus tweedieana* (TABLE 2). The liana *Macfadyena unguis-cati* was significantly associated with the host tree *Juglans australis*; *Tillandsia sphaerocephala* with *Cedrela lilloi*; and *Peperomia lorentzii* with *Allophylus edulis* (TABLE 2). *Campyloneurum aglaolepis, Pecluma oranense, Macfadyena unguis-cati,* and *Peperomia lorentzii* had the highest total and per tree species mean percent coverages (APPENDIX).

Tree species segregated along the first and second axes of the NMDS ordination of E-C percent covers (Kruskall-Wallis, first axis: H = 58.74, $P < 0.01$; second axis: H = 91.56, $P < 0.01$) (FIGURE 1A). Pairwise Mann-Whitney *U*-tests identified two distinct groups along the first axis: (1) *Juglans australis* (high scores) and (2) all other species (low scores) ($P < 0.01$; FIGURE 1B). Three groups were discriminated along the second NMDS axis: (1) *Myrcianthes pseudomato* (high scores); (2) *Blepharocalyx salicifolius, Cedrela lilloi,* and *Juglans australis* (intermediate scores); and (3) *Podocarpus parlatorei* (low scores); with *Allophylus edulis* being part of both groups 1 and 2 (pairwise Mann Whitney *U*-tests, $P < 0.01$) (FIGURE 1C).

Kendall's correlation analysis between E-C species percent cover and tree individuals' scores along the first NMDS axis revealed ten significant correlations (TABLE 2). *Macfadyena unguis-cati* showed a positive relationship with the first axis scores, while the other nine species showed negative relationships. Of these ten E-C species showing significant correlations with the first axis scores, nine species also had significant Indicator Value (IV) in the Indicator Species Analysis. Thirteen E-C species had a significant negative correlation with the second NMDS axis; and of these species, 11 also had significant IV (TABLE 2).

Bole height and foliar phenology respectively had positive and negative correlations with the first NMDS axis. Crown diameter, dbh, and total tree and bole height were all negatively correlated with the second NMDS axis (TABLE 3).

DISCUSSION

Host tree species differed in their epiphyte and climber (E-C) species composition and coverage. Tree characteristics apparently influencing

TABLE 2. Indicator values (IV) for epiphyte-climber (E-C) species. Bold numbers indicate maximum IV for each E-C species on each tree species and are accompanied by significance levels from a Monte Carlo test. Kendall correlation coefficients between E-C species percent covers and tree individuals scores along each non-metric multidimensional sealing (NMDS) axis are reported.

	Indicator values of study trees							
E-C species	Aled	Blsa	Celi	Juau	Myps	Popa	Axis 1	Axis 2
Asplenium auritum	3	1	4	0	0	**52****	−0.211**	−0.362**
Asplenium praemorsum	6	3	13	0	0	**47****	−0.162*	−0.413**
Caiophora lateritia	0	0	0	0	1	2	−0.070	0.008
Campylocentrum grisebachii	2	2	1	1	0	6	−0.035	−0.073
Campyloneurum aglaolepis	1	13	16	0	1	**50****	−0.248**	−0.646**
Cissus tweedieana	0	0	0	0	0	**14****	−0.109	−0.161
Cyclanthera tamnifolia	0	1	1	0	0	8	−0.076	−0.174*
Dioscorea glandulosa	0	0	2	0	0	9	−0.126	−0.065
Dryopteris patula	0	1	3	0	0	**66****	−0.203**	−0.455**
Macfadyena unguis-cati	2	14	15	**37****	2	20	0.488**	−0.423**
Microgramma squamulosa	2	10	8	0	3	11	−0.272**	−0.127
Pecluma filicula	0	0	0	0	0	6	−0.047	−0.109
Pecluma oranense	6	12	14	0	0	**63****	−0.285**	−0.537**
Peperomia lorentzii	**29****	20	12	5	9	20	−0.315**	−0.252**
Pleopeltis macrocarpa	2	11	8	3	0	**43****	−0.170*	−0.528**
Polypodium lasiopus	0	0	0	0	0	6	−0.009	−0.065
Polypodium tweedianum	0	3	1	0	0	0	−0.026	−0.093
Polytaenium lineatum	0	1	1	0	0	**15***	−0.069	−0.273**
Rhipsalis floccose	0	2	4	0	0	7	−0.066	−0.219**
Senecio epiphyticus	12	12	8	0	3	**47****	−0.329**	−0.445**
Tillandsia recurvata	0	0	8	3	0	0	0.090	−0.087
Tillandsia sphaerocephala	0	11	**19***	2	0	9	−0.011	−0.317**
Tillandsia usneoides	0	3	14	2	0	4	−0.101	−0.138

Note: * $P < 0.05$. ** $P < 0.01$. Tree abbreviations. Aled = *Allophylus edulis*, Blsa = *Blepharocalyx salicifolius,* Celi = *Cedrela lilloi,* Juau = *Juglans australis,* Myps = *Myrcianthes pseudo-mato,* and Popa = *Podocarpus parlatorei.*

these differences were bole height and foliar phenology. These characteristics likely create a range from dry and well lit to humid and dark microenvironment within the canopy. Drier and brighter microenvironments were provided by *Juglans australis,* which presented tall-boled and leafless individuals with the longest deciduous period (pers. obs.). These conditions apparently were suitable for the climber *Macfadyena unguis-cati,* which had the highest coverage on the tree surfaces and also was frequent on individual *J. australis* trees. The preference of this liana for such environment is supported by observations showing that this species grows in very bright environments, when cultivated for ornamental purposes (Jankowski et al. 2000). In contrast, individuals of the other five tree species presented shorter boles and were either evergreen or had shorter leafless periods than *J. australis* (pers. obs.), implying darker and moister microenvironments. At least eight epiphyte species were both abundant and frequent under these conditions. Epiphytic associations with humid host microenvironments are consistent with geographical distribution patterns, as vascular epiphytes reach their peak abundance and diversity in humid regions (Gentry & Dodson 1987a). The contrast can be partially explained by the fact that lianas, being rooted in the ground, are more tolerant than epiphytes to the drier canopy microenvironments.

Others tree characteristics, such as tree size and bark type, also were influential in discriminating tree species with different E-C community composition. Larger and taller individuals of the rough-barked species (*Podocarpus parlatorei, Juglans australis, Cedrela lilloi,* and *Blepharocalyx salicifolius*) were covered by 11 E-C species, which also were frequent on their individual trees. In particular, *Tillandsia sphaerocephala* presented the highest abundance and was frequent on *C. lilloi.* This bromeliad, common on the outer and thinner branches of the crown (branches raging from 5 to 20 cm dbh, pers. obs.), therefore is likely a light-demanding species. Similar branch diameter thicknesses were mentioned for this same species in a similar site of northwest Argentina (Meyer 1963, Brown 1990) and for other *Tillandsia* species in a Mexican cloud forest (Hietz & Hietz-Seifert 1995a). Bromeliads, which have water storage capacity within their leaves, may be able to per-

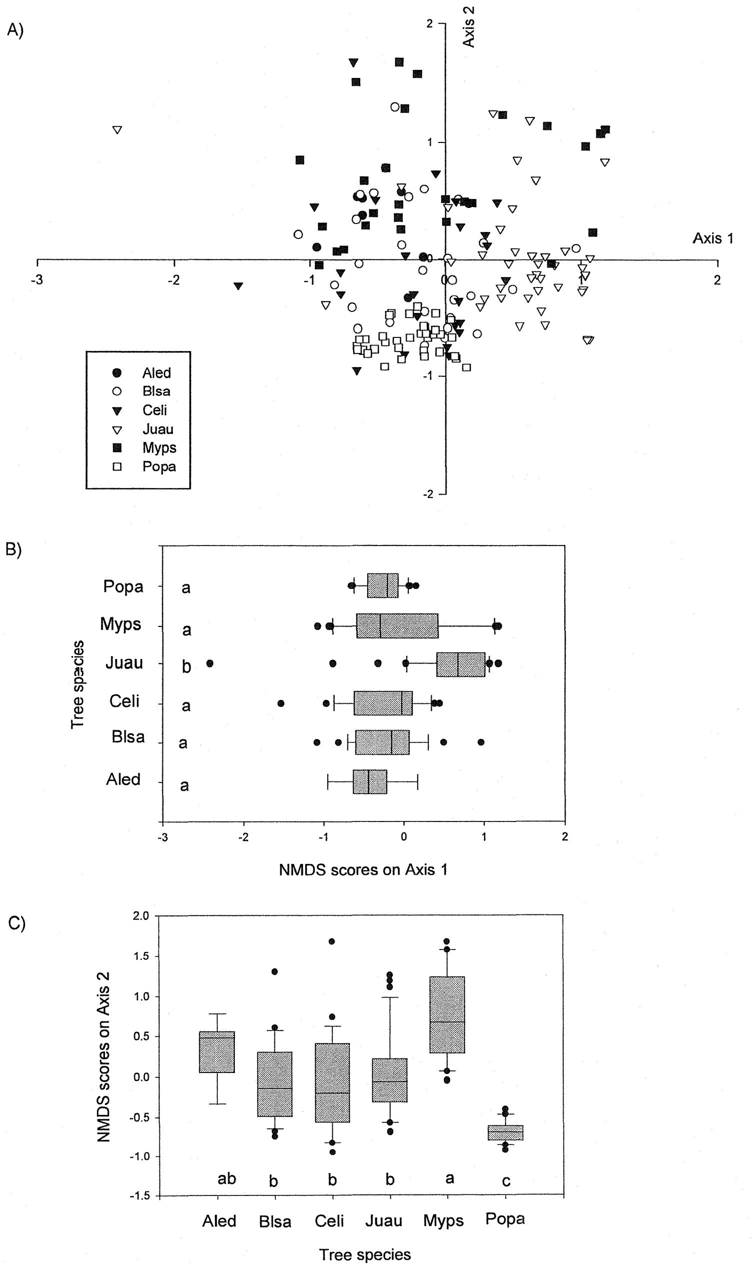

FIGURE 1. Analysis of study tree data. **A.** Non-metric multidimensional scaling (NMDS) ordination diagram of tree individuals based on epiphytes and climbers percent cover. **B., C.** Medians, quartiles, and standard error bars of NMDS scores for host tree species on first and second axes, respectively. Groups (same letters) are based on pairwise Mann-Whitney *U*-tests. Tree abbreviations. Aled = *Allophylus eduli,* Blsa = *Blepharocalyx salicifolius,* Celi = *Cedrela lilloi,* Juau = *Juglans australis,* Myps = *Myrcianthes pseudomato,* and Popa = *Podocarpus parlatorei.*

TABLE 3. Kendall correlation coefficients between tree characteristics and tree individuals scores in the non-metric multidimensional scaling (NMDS) ordination.

Tree features	Axis 1	Axis 2
Bole height	0.232**	−0.198*
Diameter of crown	−0.117	−0.236**
Diameter at breast height	−0.087	−0.390**
Foliar phenology	−0.222**	−0.069
Tree height	0.081	−0.207**

Note: * $P < 0.05$. ** $P < 0.01$.

sist at sunny sites without suffering drought stress. In general, the large number of E-C species associated with rough-barked trees may reflect favorable conditions (e.g., bark porosity and moisture) for seed anchorage and subsequent growth (as suggested by Johanson 1974, Zimmerman & Olmsted 1992, Brown 1990). In addition, E-C associations with larger and likely older trees may reflect the longer time available for E-C colonization and establishment and perhaps a larger variety of microhabitats represented by different branch diameters, crotches, and knotholes (Zimmerman & Olmsted 1992, Hietz & Hietz-Seifert 1995a). In contrast, *Myrcianthes pseudo-mato* individuals had no abundant E-C species, probably because of their smooth and exfoliating bark that may be unsuitable for epiphytic colonization and may render ascension by climbers difficult. This pattern has been documented for epiphytes and tree species with defoliating bark in other forests (Johanson 1974, Hietz & Hietz-Seifert 1995b, Carlsen 2000). Finally, *Peperomia lorentzii* was both abundant and frequent on *Allophylus edulis* individuals. Their squamous bark may have less rain tracks or drainage channels than roughed-barked species, making it less likely for seeds of *P. lorentzii,* which are ca. 1 mm long (Meyer et al. 1977), to wash away or die by excess of water.

The present study lacks spatial and phylogenetic independence, as all tree individuals grew close together, and those of the same species were treated as independent. To make generalizations about tree traits and E-C community composition, more tree species are required to replicate tree foliar phenology, bark type, and tree size in different species. The low tree species richness of this forest (16/ha), however, does have the advantage of producing a comparatively large sample of individuals per tree species in a relatively uniform environment. The most significant emerging pattern is that E-C community composition differs according to host tree species and that some of this variation may be interpreted in terms of the characteristics of each tree species.

ACKNOWLEDGMENTS

I thank Pilar Vaquera and Osvaldo Díaz for their help in the field; Marcelo Echenique for both his field and logistic support; Alberto Slanis and Hugo Ayarde from Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Argentina, for plant identifications; Alejandro Brown for advising me throughout several stages of the project; Roxana Aragón, Jeremy Lichstein, Saara DeWalt, Mark Moffet, and four anonymous reviewers for providing helpful comments on the manuscript. Finally, I am grateful to Ricardo Grau, who encouraged me to write this article and made numerous corrections. Financial support was provided by PRO-YUNGAS (Argentinean Conservation Program for the Upper Bermejo River Basin).

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APPENDIX. Vascular epiphyte and climber (E-C) species recorded on two or more tree individuals in a 1-ha plot at El Nogalar National Reserve, Salta, Argentina, listed by botanical family, life form, and total and per tree species mean percentage coverage. Bold numbers indicate maximum coverage for each E-C species.

Epiphyte-climber species	Family	Life form	Total	Aled	Blsa	Celi	Juau	Myps	Popa
Asplenium auritum Sw.	Aspleniaceae	E	0.30	0.21	0.09	0.19	0.01	—	**1.20**
Asplenium praemorsum Sw.	Aspleniaceae	E	0.53	0.33	0.29	0.74	0.01	—	**1.78**
Caiophora lateritia (Hook.) Klotzsch	Loasaceae	C	0.005	—	—	—	—	0.01	**0.02**
Campylocentrum grisebachii Cogn.	Orchidaceae	E	0.04	0.04	0.03	0.04	0.03	—	**0.09**
Campyloneurum aglaolepis (Alston) de la Sota	Polypodiaceae	E	5.34	0.83	5.93	7.03	0.59	0.57	**15.04**
Cissus tweedieana (Baker) Griseb.	Vitaceae	C	0.02	—	—	—	—	—	**0.10**
Cyclanthera tamnifolia Griseb.	Cucurbitaceae	C	0.02	—	0.02	0.01	0.01	0.005	**0.07**
Dioscorea glandulosa (Griseb.) Kunth	Dioscoraeceae	C	0.03	—	0.01	0.03	—	0.01	**0.09**
Dryopteris patula (Sw.) Underw.	Dryopteridaceae	E	0.94	—	0.18	0.67	—	0.01	**3.98**
Macfadyena unguis-cati (L.) A.H. Gentry	Bignoniaceae	C	5.74	0.84	4.91	4.79	**10.95**	0.75	6.17
Microgramma squamulosa (Kaulf.) de la Sota	Polypodiaceae	E	0.97	0.57	1.40	**1.46**	0.18	0.90	1.44
Pecluma filicula (Kaulf.) M. G. Price	Polypodiaceae	E	0.10	—	—	—	—	—	**0.48**
Pecluma oranense (de la Sota) de la Sota	Polypodiaceae	E	2.88	1.03	2.20	2.56	0.10	0.11	**10.09**
Peperomia lorentzii C. DC.	Piperaceae	E	2.96	**5.94**	4.33	2.53	1.37	2.14	4.11
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.	Polypodiaceae	E	0.92	0.42	1.05	0.73	0.43	0.03	**2.49**
Polypodium lasiopus Klotzsch	Polypodiaceae	E	0.02	—	—	—	—	—	**0.09**
Polypodium tweedianum Hook.	Polypodiaceae	E	0.02	—	**0.10**	0.02	—	—	—
Polytaenium lineatum (Sw.) J.E. Sw.	Vittariaceae	E	0.11	—	0.10	0.05	—	—	**0.40**
Rhipsalis floccosa Pfeiff.	Cactaceae	E	0.05	—	0.04	0.10	—	—	**0.14**
Senecio epiphyticus Kuntze	Asteraceae	E	0.92	0.76	0.92	0.63	0.07	0.45	**2.66**
Tillandsia recurvata (L.) L.	Bromeliaceae	E	0.02	—	0.01	0.07	**0.02**	—	—
Tillandsia sphaerocephala Baker	Bromeliaceae	E	0.39	—	0.66	**0.95**	0.16	0.02	0.49
Tillandsia usneoides (L.) L.	Bromeliaceae	E	0.24	—	0.21	**0.65**	0.18	0.03	0.30

Note: E = epiphyte. C = climber. Tree abbreviations: Aled = *Allophylus edulis*, Blsa = *Blepharocalyx salicifolius,* Celi = *Cedrela lilloi,* Juau = *Juglans australis,* Myps = *Myrcianthes pseudo-mato,* and Popa = *Podocarpus parlatorei.*

Selbyana 24(2): 206–214. 2003.

VASCULAR EPIPHYTES IN THE TEMPERATE ZONE— A BIBLIOGRAPHY

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ABSTRACT. Vascular epiphytes typically are associated with tropical rain forests, whereas their occurrence in temperate forests is little appreciated. This bibliography lists nearly 200 citations dealing with the biology of this group at latitudes beyond the tropics of Cancer and Capricorn. Papers on ecology, physiology, anatomy, morphology, and natural history are included, while purely taxonomic accounts are excluded. The bibliography also is available electronically (request to be sent to the author).

RESUMEN. Epífitas vasculares son típicamente asociados con los tropicos, menos apreciado es su presencia en los bosques templados. Esa bibliografía presenta casi 200 citas relacionadas con la biología de este grupo. Se incluye artículos sobre ecología, fisiología, anatomía, morfología y historia natural, pero en general se excluyó publicaciones puramente taxonómicas o florísticas. Esta bibliografía es disponible en forma electronica (pedidos al autor).

Key words: accidental epiphytes, biogeography, drought, ferns, frost, temperate forests

INTRODUCTION

This bibliography of the scientific literature on vascular epiphytes that occur beyond the tropics is intended to stimulate research in these poorly studied plants. In spite of the great scientific interest in vascular epiphytes in recent years, this attention is confined geographically almost completely to lower latitudes. When it comes to descriptive epiphyte biogeography outside the tropics, let alone an understanding of the mechanisms responsible for the relative paucity of vascular epiphytes in most temperate areas, we have not progressed much since A.F.W. Schimper published his seminal monograph on epiphytes in 1888.

The steep gradients in the diversity and the abundance of vascular epiphytes from the tropics to higher latitudes have been mentioned by Schimper (1888). He also noted the pronounced asymmetry of this latitudinal trend: the rich epiphyte floras of New Zealand and Chile rival those of many tropical regions (e.g., Hofstede et al. 2001). The most species-rich region in respect to vascular epiphytes in the north-temperate zone is the Himalayas (Schimper 1888), but locally abundant epiphyte populations also occur in temperate East Asia (Kolbeck 1995), Central Europe (Zotz 2002), the British Isles (Tansley 1939), or the Pacific Northwest of North America (Sillett 1999).

The observed latitudinal trend is generally attributed to hypothesized limitations by frost or drought (Schimper 1888, Gentry & Dodson 1987, Benzing 1990). Clearly, these hypotheses are not mutually exclusive. Unfortunately, however, neither factor alone or in combination has been tested experimentally. Moreover, possible influences of historical events (e.g., Pleistocene extinctions) or other ecological factors (e.g., prevalence of conifers in the northern hemisphere) on the extant global distribution of vascular epiphytes rarely have been put forward, while certainly deserving more attention.

Geographically, this bibliography covers all studies from latitudes beyond the tropics of Cancer and Capricorn. To avoid unnecessary overlap, however, with earlier bibliographies (Watson et al. 1987, Nadkarni & Ferrell-Ingram 1992), studies from subtropical areas such as southern Florida are generally excluded. References are not limited to those focusing on holoepiphytes. Many terrestrial plants grow occasionally on living trees, and in the temperate zone, these "accidental epiphytes" frequently constitute the majority of epiphytically growing tracheophytes. Consequently, reports on accidental epiphytes make up a large proportion of the citations.

The citations compiled here were collected by a thorough search of journals, books, proceedings, and online search engines. All citations have been read by the author. This was particularly important because vascular epiphytes are frequently mentioned in the bryological literature without being indexed in search engines. The same is true for book chapters. Thus, quite a few of the citations do not primarily deal with vascular epiphytes; they focus on non-vascular epiphytes or are (descriptive) vegetation studies with some ecological information on vascular epiphytes. Considering the paucity of informa-