Annals of Botany Page 1 of 6
doi:10.1093/aob/mct085, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY
Founded 1887

VIEWPOINT

'Hemiepiphyte': a confusing term and its history

Gerhard Zotz[1,2,*]

[1]*University of Oldenburg, Institute of Biology and Environmental Sciences, Functional Ecology Group, Box 2503, D-26111 Oldenburg, Germany and* [2]*Smithsonian Tropical Research Institute, Box 0843-03092, Panama, Republic of Panama*
* *E-mail gerhard.zotz@uni-oldenburg.de*

Received: 31 January 2013 Returned for revision: 5 March 2013 Accepted: 8 March 2013

• *Background and Scope* Over more than 120 years of scientific study since Schimper's seminal work, the recognized categories of structurally dependent plants have changed several times. Currently, ignoring parasitic mistletoes, it is usual to distinguish four functional groups: (1) true epiphytes; (2) primary hemiepiphytes; (3) secondary hemiepiphytes; and (4) climbing plants, i.e. lianas and vines. In this Viewpoint, it is argued that the term secondary hemiepiphytes (SHs) is misleading, that its definition is hard to impossible to apply in the field and, possibly causally related to this conceptual problem, that the use of this category in field studies is inconsistent, which now hampers interpretation and generalization.
• *Conclusions* Categories will frequently fail to capture gradual biological variation, but terms and concepts should be as unambiguous as possible to facilitate productive communication. A detailed analysis of the conceptual problems associated with the term SH and its application in scientific studies clearly shows that this goal is not fulfilled in this case. Consequently, the use of SH should be abandoned. An alternative scheme to categorize structurally dependent flora is suggested.

INTRODUCTION

Clarity of terms and theoretical concepts is essential for productive communication among scientists and for scientific progress. Unfortunately, either terms are sometimes loosely defined, definitions vary with author and change with time or definitions are subsequently inconsistently or incorrectly applied in research projects. A case in point is the term 'hemiepiphyte'. More than a century ago, Went (1895) distinguished 'hemiepiphytes' from true epiphytes (both normally germinate on other plants), because only the former produce feeder roots that reach the ground. Schimper's (1903) definition of the same term was more specific by adding a temporal component. He defined 'hemiepiphytes' as structurally dependent plants that share germination in tree crowns with epiphytes, but later establish contact with the ground via aerial roots. Plants that germinate on the ground and later climb up trees showing successive dieback of the proximal stem portion were called 'pseudoepiphytes'. A completely different definition was introduced by Pessin (1925): he used the term 'hemiepiphyte' for facultative epiphytes, which 'derive their water and mineral elements from the substratum to which they are attached', which can be either the ground or the canopy soil. However, Pessin's suggestion has been by and large ignored in subsequent publications.

Later authors used the term hemiepiphyte for all dependent plants that have a root connection with the soil for some but not all of their life cycle, with Schimper's (1903) hemiepiphytes becoming 'hemiepiphyte praecoqua' (Hosokawa, 1943), 'protero-epiphytes' (Barkman, 1958) or 'primary hemiepiphytes' (Putz and Holbrook, 1986; Kress, 1986), while 'pseudoepiphytes' became 'hemiepiphyte postera' (Hosokawa, 1943), 'deutero-epiphytes' (Barkman, 1958) or 'secondary hemiepiphytes' ('SHs'; Kress, 1986; Putz and Holbrook, 1986). Although the terms proposed by Putz and Holbrook (1986) and Kress (1986), which were later endorsed by Benzing (1990) in his authoritative monograph on vascular epiphytes, can be currently considered standard in pertinent scientific publications, there were also repeated cases of criticism in subsequent years. Remarkably, the two authors of one of the papers that popularized the term SH partly revoked their definition in a later publication (Holbrook and Putz, 1996). There, they reserved the term hemiepiphyte for species that begin with an epiphytic stage (formerly called primary hemiepiphytes), arguing that SHs are actually vinelike in physiology and morphology. Not much later, Lüttge (1997) called the term SH 'not convincing' for a number of reasons. He argued that many so-called SHs, such as many aroid species in the genera *Monstera*, *Philodendron* and *Syngonium*, produce adventitious roots that re-establish contact with the soil, which would actually make them primary hemiepiphytes, although this does not match the original definition because they have not germinated on other plants. Similar reservations were also expressed by Mark Moffett in his excellent critique of the terms used in canopy biology (Moffett, 2000). He noted that the current use of hemiepiphyte confounds two radically different life cycle strategies. In order to resolve this situation, he suggested a new term 'nomadic vine' for SHs. However, his suggestion did not catch on, as I am only aware of a single subsequent publication that used the term (Kelly *et al.*, 2004).

CURRENT USE OF THE TERM 'HEMIEPIPHYTE' IN RESEARCH PAPERS

With the exception of Pessin (1925), the term '(primary) hemiepiphyte' has been consistently used for over a century.

These plants (e.g. many species in the genera *Clusia* and *Ficus*) share the vulnerable early stages with true epiphytes, which is adequately expressed by the morpheme 'epiphyte'. Such an unambiguous use in the literature is not at all true for SHs, which are most common among Araceae (Williams-Linera and Lawton, 1995), but also frequent in some fern groups (e.g. Dubuisson *et al.*, 2003). The original definition of an SH (e.g. Kress, 1986) had the following components (1) germinates on the ground; (2) climbs up a tree; (3) shows dieback of the older stem and severs all (!) connections to the soil. The third requirement is particularly important, because otherwise these plants are simply vines: roots are suited as well as shoots for long-distance water transport (Zotz *et al.*, 1997). Hence, it is functionally irrelevant whether roots connect to the shoot at ground level or a few metres above. Even worse, few researchers seem to have investigated whether the alleged SHs fulfil this crucial requirement at all. As observed by Moffett (2000), this uncertainty is not surprising because adventitious feeder roots, which may or may not reach the ground, are hard to trace. However, beyond the problem with the practical application of the definition of an SH in the field, the definition itself has not been applied consistently. A survey of 42 publications after 1986 (Table 1) that deal with SHs documents a substantial amount of confusion. Only 12 of these papers explicitly state that SHs are, or rather are assumed to be, disconnected from the soil as required by the original definition. Many studies are vague (e.g. 'may lose connection') or give no definition at all; others even state paradoxically, and in contrast to the accepted definition, that SHs are always connected to the soil via adventitious roots throughout their life. For example, *Heteropsis* species have been called SHs (Balcázar Vargas and van Andel, 2005), although plants invariably die when their aerial roots are removed in commercial harvesting (Balcázar Vargas and van Andel, 2005), which is hardly an indication of successful epiphytic growth. The frequent observation that the same species is alternatively called vine, liana or hemiepiphyte, even in publications of the same lab (Muñoz *et al.*, 2003; Salinas *et al.*, 2010), is also indicative of a certain conceptual confusion.

A SUGGESTION

Ignoring parasitic mistletoes, there are four basic categories of structurally dependent plants, two of which start their life in trees, i.e. true epiphytes and (primary) hemiepiphytes, while two germinate on the ground and climb up, i.e. lianas/vines and SHs. These groups can be further sub-divided. For example, depending on the degree of fidelity to the epiphytic habitat, Benzing (1990) classified epiphytes into obligate or holoepiphytes (occurring almost exclusively as epiphytes), facultative epiphytes (occurring both epiphytically and on the forest floor) and accidental epiphytes (almost exclusively rooted to the forest floor). However, these definitions are also vague, because epiphytes become increasingly facultative as environmental conditions in tree canopies converge on terrestrial environmental conditions (Benzing, 1990; Burns, 2010). Secondary hemiepiphytes *sensu* Putz and Holbrook (1986) bridge the gap between true epiphytes and vines/lianas, and, not surprisingly, both liana (Parren *et al.*, 2005) and epiphyte (Zotz and Bader, 2011) researchers have had problems accommodating them in their conceptual framework. Dubuisson *et al.* (2003) suggested distinguishing SHs, which fulfil the definition of Kress, from those plants with shoot dieback, albeit with continued root contact with terrestrial soil ('true lianescence'), but there is a prominent problem: for all practical purposes, most pronounced in lush montane vegetation, it is very difficult to detect whether a plant that has lost the basal part of its shoot still has soil contact via adventitious roots or not. Moreover, without repeated observations on a larger sample of individuals, it will remain unclear (1) whether this situation is stable in time and (2) whether individual observations are representative for the entire population or species.

I suggest resolving the current conceptual problem by discarding the term SH entirely and using Moffett's (2000) 'nomadic vine' for all climbing plants that germinate on the ground and may lose the older parts of their stem in the process of ascending – in contrast to true vines and lianas. This would remove a number of shortcomings. In contrast to the term SH, the new term does not imply a relationship with (primary) hemiepiphytes, which arguably does not exist, but rather emphasizes the similarity to other climbing plants. As pointed out by Moffett (2000), it also accommodates the possibility of occasional germination of SH species in canopy soil. Moreover, it neither implies nor discards a continuous root connection with the soil, although this should be investigated whenever possible. The suggested change would, however, discontinue the predominant practice of making conjectures in this regard without data. The change would also get rid of the ambiguity associated with the frequent use of 'hemiepiphyte' without modifier in the literature (e.g. Mucunguzi, 2007; Hokche *et al.*, 2008), because it also makes the use of the modifier 'primary' obsolete. Finally, calling SHs *sensu* Putz and Holbrook (1986) 'nomadic vines' and not hemiepiphytes will also help to abandon the common practice of lumping them with true epiphytes and (primary) hemiepiphytes in many published inventories in spite of their very different ecology associated with germination either in epiphytic or terrestrial situations. This obscures rather than clarifies possible generalities in later comparisons across studies. This statement is not meant to suggest ignoring 'non-epiphytes' in epiphyte, or 'nomadic vines' in liana surveys; on the contrary, the ideal survey actually uses a comprehensive approach which includes, but does not mingle, the different components of the structurally dependent flora, an excellent example being Kelly's work (e.g. Kelly *et al.*, 2004).

To conclude, the use of the term secondary hemiepiphyte should be discontinued for all the reasons given above. Four basic terms with clear definitions suffice to describe structurally dependent flora: epiphytes and hemiepiphytes as originally defined by Schimper (1903), 'nomadic vines' (Moffett, 2000) and climbing plants *sensu strictu* (lianas and vines).

TABLE 1. *Use of the term 'secondary hemiepiphyte' (SH) in the literature*

Publication	Germination on the ground	Stem dieback	(a) Always with root connection to the ground	(b) Temporarily without connection to ground	(c) No connection to the ground	(d) May lose connection	Not defined	Comments
After 1986								
Addo-Fordjour *et al.* (2009)								Only (primary) hemiepiphytes mentioned
Aguirre *et al.* (2010)							X	
Arévalo and Betancur (2006)	X	X			X			Refer to Benzing (1990)
Balcázar Vargas and van Andel (2005)	X	X	X					'keeping their roots connected to the soil during their entire life cycle (Kress, 1986)'
Balcázar-Vargas *et al.* (2012)	X	X	X					Defined only for *Heteropsis* species
Benavides *et al.* (2006)	X	X				X		Not clearly defined
Benzing (1990)	X	X			X			Defined in glossary
Boyce and Wong (2012)	X	X		X				Have both feeder roots and anchor roots
Croat (1988)	X	X				X		SH often heteroblastic
Dubuisson *et al.* (2011)							X	
Gentry and Dodson (1987)	X	X			X			Refer to Kress (1986)
Holbrook and Putz (1996)	X							SHs not distinguished from vines
Jácome *et al.* (2004)							X	Not defined, only aroids
Kelly *et al.* (2004)								Only (primary) hemiepiphytes mentioned, otherwise climbers, use of the term nomadic vines
Kersten and Silva (2006)	X	X			X			Refer to Benzing (1990)
Krömer *et al.* (2007)	X	X			X			Refer to Kress (1986)
Lingán (2006)							X	
López-Portillo *et al.* (2000)	X	X	X					'stem may die back until only feeder roots connect . . . '
Lüttge (1997)	X	X		X	X			'not convincing' – should be called (a) 'SHs' or in case (b) 'primary hemiepiphytes'
Mania and Monteiro (2010)	X	X			X			
Mantovani (2000)	X	X			X			Refer to Putz and Holbrook (1986)
Martin *et al.* (2004)							X	
Mayo and Sakuragui (2011)							X	
Menini Neto *et al.* (2009)	X	X			X			Refer to Benzing (1990)
Meyer and Zotz (2004)	X	X	X					
Moffett (2000)	X	X		X	X			Term should be abandoned – suggests 'nomadic vine'
Mora *et al.* (2006)							X	
Moran *et al.* (2010)							X	
Mucunguzi (2007)								Only (primary) hemiepiphytes mentioned
Nieder *et al.* (2000)	X	X			X			Refer to Benzing (1990)

Continued

TABLE 1. *Continued*

Publication	Germination on the ground	Stem dieback	(a) Always with root connection to the ground	(b) Temporarily without connection to ground	(c) No connection to the ground	(d) May lose connection	Not defined	Comments
Nieder *et al.* (2001)								'which at some stage of their life cycle grow on the ground'
Oberbauer and Noudali (1998)								*Monstera tenuis* = vine
Obermüller *et al.* (2012)							X	
Orihuela and Waechter (2010)								Refer to Putz and Holbrook (1986)
Patiño *et al.* (1999)	X	X		X		X		
Primack and Corlett (2005)								Only (primary) hemiepiphytes mentioned
Salinas *et al.* (2010)	X		X					'later move upward'
Salinas and Armesto (2012)							X	Not defined, refer to Salinas *et al.* (2010)
Tenorio *et al.* (2012)							X	Not defined, only aroids
Van Andel (2003)							X	Not defined, lumped with lianas
Williams-Linera and Lawton (1995)	X	X			X			Establish terrestrially and subsequently sever 'all connections with the ground'
Zotz and Andrade (2002)	X	X		X				
Before 1986								
Kelly (1985)	X	X			X			
Miehe (1911)								Only (primary) hemiepiphytes mentioned
Kress (1986)	X	X			X			Severing 'all connections with the ground'
Putz and Holbrook (1986)	X	X			X			'later lose rooting contact with the soil'
Barkman (1958)	X	X			X			Calls SHs deutero-epiphytes
Gentry (1986)								Distinguishes two types of climbers, hemiepiphytes and 'true' lianas
Hosokawa (1943)	X	X			X			
Oliver (1930)								Refer to Schimper (1903)
Pessin (1925)								'(facultative epiphytes), derive their water and mineral elements from the substratum'
Schimper (1903)								only primary hemiepiphytes, SH = 'pseudoepiphyte'
Strong and Ray (1975)								*Monstera gigantea* is a vine [in Jacome *et al.* (2004) it is a hemiepiphyte]
Sudgen (1985)								Only (primary) hemiepiphytes mentioned
Went (1895)								SH is an 'epiphyte' with feeder root reaching the ground

Publications before the influential paper by Putz and Holbrook (1986) are given in the second part of the list.

LITERATURE CITED

Addo-Fordjour P, Anning AK, Addo MG, Osei MF. 2009. Composition and distribution of vascular epiphytes in a tropical semideciduous forest, Ghana. *African Journal of Ecology* **47**: 767–773.

Aguirre A, Guevara R, García M, López JC. 2010. Fate of epiphytes on phorophytes with different architectural characteristics along the perturbation gradient of *Sabal mexicana* forests in Veracruz, Mexico. *Journal of Vegetation Science* **21**: 6–15.

Arévalo R, Betancur J. 2006. Vertical distribution of vascular epiphytes in four forest types of the Serrania de Chiribiquete, Colombian Guayana. *Selbyana* **27**: 175–185.

Balcázar Vargas MP, van Andel T. 2005. The use of hemiepiphytes as craft fibres by indigenous communities in the Colombian Amazon. *Ethnobotany Research and Applications* **3**: 243–260.

Balcázar-Vargas MP, Peñuela-Mora MC, van Andel TR, Zuidema PA. 2012. The quest for a suitable host: size distributions of host trees and secondary hemiepiphytes search strategy. *Biotropica* **44**: 19–26.

Barkman JJ. 1958. *Phytosociology and ecology of cryptogamic epiphytes*. Assen, The Netherlands: Van Gorcum & Co.

Benavides AM, Wolf JHD, Duivenvoorden JF. 2006. Recovery and succession of epiphytes in upper Amazonian fallows. *Journal of Tropical Ecology* **22**: 705–717.

Benzing DH. 1990. *Vascular epiphytes. General biology and related biota*. Cambridge: Cambridge University Press.

Boyce PC, Wong SY. 2012. The Araceae of Malesia I: introduction. *Malayan Nature Journal* **64**: 33–67.

Burns KC. 2010. How arboreal are epiphytes? A null model for Benzing's classifications. *New Zealand Journal of Botany* **48**: 185–191.

Croat TB. 1988. Ecology and life forms of Araceae. *Aroideana* **11**: 4–55.

Dubuisson JY, Hennequin S, Rakotondrainibe F, Schneider H. 2003. Ecological diversity and adaptive tendencies in the tropical fern *Trichomanes* L. (Hymenophyllaceae) with special reference to climbing and epiphytic habits. *Botanical Journal of the Linnean Society* **142**: 41–63.

Dubuisson J-Y, Hennequin S, Bary S, Ebihara A, Boucheron-Dubuisson E. 2011. Anatomical diversity and regressive evolution in trichomanoid filmy ferns (Hymenophyllaceae): a phylogenetic approach. *Comptes Rendus Biologies* **334**: 880–895.

Gentry AH. 1986. Species richness and floristic composition of Chocó region plant communities. *Caldasia* **15**: 71–91.

Gentry AH, Dodson CH. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* **74**: 205–233.

Hokche O, Berry PE, Huber O. 2008. *Nuevo catálogo de la flora vascular de Venezuela*. Caracas: Fundación Instituto Botánico de Venezuela.

Holbrook NM, Putz F. 1996. Physiology of tropical vines and hemiepiphytes: plants that climb up and plants that climb down. In: Mulkey SS, Chazdon RL, Smith AP. eds. *Tropical forest plant ecophysiology.* New York, Chapman & Hall, 363–393.

Hosokawa T. 1943. Studies on the life-form of vascular epiphytes and the epiphyte flora of Ponape, Micronesia (I). *Transactions of the Natural History Society of Taiwan* **33**: 35–55.

Jácome J, Galeano G, Amaya M, Mora M. 2004. Vertical distribution of epiphytic and hemiepiphytic Araceae in a tropical rain forest in Chocó, Colombia. *Selbyana* **25**: 118–125.

Kelly DL. 1985. Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life forms and life histories. *Journal of Biogeography* **12**: 223–241.

Kelly DL, O'Donovan G, Feehan J, Murphy S, Drangeid SO, Marcano-Berti L. 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *Journal of Tropical Ecology* **20**: 643–666.

Kersten RA, Silva SM. 2006. The floristic compositions of vascular epiphytes of a seasonally inundated forest on the coastal plain of Ilha do Mel Island, Brazil. *Revista De Biología Tropical* **54**: 935–942.

Kress WJ. 1986. The systematic distribution of vascular epiphytes: an update. *Selbyana* **9**: 2–22.

Krömer T, Kessler M, Gradstein SR. 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. *Plant Ecology* **189**: 261–278.

Lingán J. 2006. Araceae endémicas del Perú. *Revista Peruana de Biología* **13**: 698–705.

López-Portillo J, Ewers FW, Angeles G, Fisher JB. 2000. Hydraulic architecture of *Monstera acuminata*: evolutionary consequences of the hemiepiphytic growth form. *New Phytologist* **145**: 289–299.

Lüttge U. 1997. *Physiological ecology of tropical plants*. Berlin: Springer.

Mania LF, Monteiro R. 2010. Florística e ecologia de epífitas vasculares em um fragmento de floresta de restinga, Ubatuba, SP, Brasil. *Rodriguésia* **61**: 705–713.

Mantovani A. 2000. Leaf orientation of epiphytic aroids: effect on water and temperature balances of the leaves. *Leandra* **15**: 91–103.

Martin PH, Sherman RE, Fahey TJ. 2004. Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. *Biotropica* **36**: 297–317.

Mayo SJ, Sakuragui CM. 2011. Typification and interpretation of *Philodendron imbe* Schott ex Kunth (Araceae). *Taxon* **60**: 1764–1767.

Menini Neto L, Forzza RC, Zappi D. 2009. Angiosperm epiphytes as conservation indicators in forest fragments: a case study from southeastern Minas Gerais, Brazil. *Biodiversity and Conservation* **18**: 3785–3807.

Meyer CFJ, Zotz G. 2004. Does growth and survival of aerial roots limit the vertical distribution of hemiepiphytic aroids? *Biotropica* **36**: 483–491.

Miehe H. 1911. Javanische Studien. *Abhandlungen der mathematisch-physischen Klasse der Königlich Sächsischen Gesellschaft der Wissenschaften* **32**: 299–431.

Moffett MW. 2000. What's 'up'? A critical look at the basic terms of canopy biology. *Biotropica* **32**: 569–596.

Mora M, Bernal R, Croat T, Jacome J. 2006. A phytogeographic analysis of Araceae of Cabo Corrientes (Choco, Colombia) and comparable lowland tropical American floras. *Annals of the Missouri Botanical Garden* **93**: 359–366.

Moran RC, Labiak PH, Sundue M. 2010. Phylogeny and character evolution of the bolbitidoid ferns (Dryopteridaceae). *International Journal of Plant Sciences* **171**: 547–559.

Mucunguzi P. 2007. Diversity and distribution of hemi-epiphytes and facultative herbaceous epiphytes in Kibale National Park, Uganda *African Journal of Ecology* **45**: 57–64.

Muñoz AA, Chacon P, Perez F, Barnert ES, Armesto JJ. 2003. Diversity and host tree preferences of vascular epiphytes and vines in a temperate rainforest in southern Chile. *Australian Journal of Botany* **51**: 381–391.

Nieder J, Engwald S, Klawun M, Barthlott W. 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane Plot) of Southern Venezuela. *Biotropica* **32**: 385–396.

Nieder J, Prosperi J, Michaloud G. 2001. Epiphytes and their contribution to canopy diversity. *Plant Ecology* **153**: 51–63.

Oberbauer SF, Noudali M. 1998. Potential carbon gain of shingle leaves in juveniles of the vine *Monstera tenuis* (Araceae) in Costa Rica. *American Journal of Botany* **85**: 850–854.

Obermüller F, Silveira M, Salimon C, Daly D. 2012. Epiphytic (including hemiepiphytes) diversity in three timber species in the southwestern Amazon, Brazil. *Biodiversity and Conservation* **21**: 565–575.

Oliver WRB. 1930. New Zealand epiphytes. *Journal of Ecology* **18**: 1–50.

Orihuela RLL, Waechter JL. 2010. Host size and abundance of hemiepiphytes in a subtropical stand of Brazilian Atlantic Forest. *Journal of Tropical Ecology* **26**: 119–122.

Parren MPE, Bongers F, Caballé G, Nabe-Nielsen J, Schnitzer SA. 2005. On censusing lianas: a review of common methodologies. In: Bongers F, Parren MPE, Traoré D. eds. *Forest climbing plants of West Africa. Diversity, ecology and management.* Wallingford, UK: CABI Publishing, 41–58.

Patiño S, Gilbert GS, Zotz G, Tyree MT. 1999. Growth and survival of aerial roots of hemiepiphytes in a lower montane tropical moist forest in Panama. *Journal of Tropical Ecology* **15**: 651–665.

Pessin LJ. 1925. An ecological study of the polypody fern *Polypodium polypodioides* as an epiphyte in Mississippi. *Ecology* **6**: 17–38.

Primack R, Corlett RT. 2005. *Tropical rain forests*. Oxford: Blackwell Publishing.

Putz FE, Holbrook NM. 1986. Notes on the natural history of hemiepiphytes. *Selbyana* **9**: 61–69.

Salinas F, Armesto JJ. 2012. Regeneration niche of three epiphytic species of Gesneriaceae from Chilean rainforests: implications for the evolution of growth habits in Coronanthereae. *Botanical Journal of the Linnean Society* **170**: 79–92.

Salinas F, Arroyo MTK, Armesto JJ. 2010. Epiphytic growth habits of Chilean Gesneriaceae and the evolution of epiphytes within the tribe Coronanthereae. *Annals of the Missouri Botanical Garden* **97**: 117–127.

Schimper AFW. 1903. *Plant geography upon a physiological basis*. Oxford: Clarendon Press.

Strong DR, Ray TS. 1975. Skototropism in *Monstera gigantea*. *Science* **190**: 804–806.

Sudgen AM. 1985. Leaf anatomy in a Venezuelan montane forest. *Botanical Journal of the Linnean Society* **90**: 231–241.

Tenorio V, Sakuragui CM, Vieira RC. 2012. Stem anatomy of *Philodendron* Schott (Araceae) and its contribution to the systematics of the genus. *Plant Systematics and Evolution* **298**: 1337–1347.

Van Andel TR. 2003. Floristic composition and diversity of three swamp forests in northwest Guyana. *Plant Ecology* **167**: 293–317.

Went FW. 1895. Über Haft- und Nährwurzeln bei Kletterpflanzen und Epiphyten. *Annales du Jardin Botanique de Buitenzorg* **12**: 1–72.

Williams-Linera G, Lawton RO. 1995. The ecology of hemiepiphytes in forest canopies. In: Lowman MD, Nadkarni NM. eds. *Forest canopies.* San Diego: Academic Press, 255–283.

Zotz G, Andrade JL. 2002. La ecología y la fisiología de las epífitas y las hemiepífitas. In: Guariguata MR, Kattan GH. eds. *Ecología y conservación de bosques neotropicales.* San José, Costa Rica, Libro Universitario Regional del Instituto Tecnológico de Costa Rica, 271–296.

Zotz G, Bader MY. 2011. Sampling vascular epiphyte diversity – species richness and community structure. *Ecotropica* **17**: 103–112.

Zotz G, Patiño S, Tyree MT. 1997. Water relations and hydraulic architecture of woody hemiepiphytes. *Journal of Experimental Botany* **48**: 1825–1834.