Distribution and succession of vascular epiphytes in Colombian Amazonia

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General introduction.

Vascular epiphytes
— salient features and ecology

Distribution and succession of vascular epiphytes in Colombian Amazonia
GREEN PLANTS HAVE GREATLY DIVERSIFIED SINCE they first appeared about one billion years ago (Bowman et al. 2007). At present, green plants are one of the most conspicuous life forms on Earth. Whereas most plant species have evolved to grow mechanically independent from other plants, especially in wet tropical areas many vascular plant species can be found that depend on other plants for support. These mechanically dependent species belong to climbers, (half-) parasites, and epiphytes (Schimper 1888; Ruinen 1953; Barkman 1958).

Epiphytes may be divided into holo-epiphytes, primary hemi-epiphytes, and secondary hemi-epiphytes functional types (Kress 1986). Holo-epiphytes never have root contact with the soil and hemi-epiphytes are connected to the soil during part of their life-cycle at which stage they resemble vines (i.e. herbaceous climbers). Primary hemi-epiphytes germinate on other plants, usually trees, only to become terrestrially-rooted through aerial roots. Secondary hemi-epiphytes germinate in the soil to lose contact later in their life cycle, but some adventitious feeder roots may maintain contact with the ground.

The epiphyte habit is a successful adaptation to conditions in the tropical forest, judging from the large number of epiphyte species, the large number of epiphyte individuals, and the great amount of epiphyte biomass in these forests (Benzing 1990). In total there are an estimated 25000 species of vascular epiphytes worldwide (Madison 1977; Kress 1986; Benzing 1990). Over 70% of all epiphytes are orchids (sensu Madison 1977), followed by Bromeliaceae, Araceae and Polypodiaceae. Worldwide and at a national level (Peru, Guianas), epiphytes represent about 10% of the total vascular plant diversity (Ibisch et al. 1996; Ek 1997). At the landscape level (> 100 ha) or in small plots (< 1.0 ha) vascular epiphytes often represent up to ca. 30% or 50% of all plant species, respectively (e.g. Gentry and Dodson 1987ab;

Epiphytic biomass is greatest in high elevation mountain cloud forests where epiphytic vegetation is dominated by bryophytes. Here, green epiphyte and suspended soil dry weight may total more than a staggering 40 tons/ha (Hofstede et al. 1993). In most mountain forests, epiphyte biomass is lower, typically not surpassing several tons/ha, and in lowland rainforest epiphyte biomass is even lower (Edwards and Grubb 1977; Nadkarni 1984ab; Hofstede et al. 1993; Köhler et al. 2007). For forests with abundant epiphyte vegetation, the suggestion has been made that epiphytes contribute significantly to ecosystem functions and to microhabitat diversity on which a diverse fauna depends (Nadkarni 1984b; Nadkarni and Matelson 1989; Veneklaas 1990; Nadkarni and Matelson 1992; Richardson 1999; Acebey et al. 2003; Holscher et al. 2004).

Epiphytes are adapted to life in the canopy by means of reproductive and eco-physiological traits. The overall majority of epiphytic plants have spores, dust-like or winged seeds, which are most likely dispersed by wind. While most winged seeds tend to disperse within a few meters from the parental plant, long-distance dispersal may also occur (Cascante-Marín et al. 2006a). Distant wind-dispersal is probably most successful on dry windy days (Horn et al. 2001), prevailing during the dry season in seasonal forests. In aseasonal wet tropical lowland forests, however, such conditions are relatively rare. Here many epiphytes have fruits adapted to animal consumption, dispersed principally by frugivorous birds, bats and monkeys (Kelly 1985; Barthlott et al. 2001; Vieira and Izar 1999). Accordingly, Wolf and Flamenco-S. (2003) attribute the dominance of zoochoric aroids in wet tropical lowland rain forests to continuously climatic wetness in these forests.
Besides seed dispersion, many epiphyte species show the ability to propagate vegetatively. Asexual rhizomes, shoots or adventitious roots may either develop short internodes that form massive clumps (ramets) or long internodes. Long internodes allow an individual plant to forage for essential resources, but also to multiply and disperse meristems into newly available habitats (Ray 1988, 1990, 1992). Interestingly, hemi-epiphytic aroid shoots may exhibit an abrupt shift from short to long internodes, becoming flagellar. Flagellar shoots may have a more rapid growth than non-flagellar stems. Flagellar shoots are not only formed by terrestrial creeping stems but can also be produced by adult individuals, which are already attached to a tree. This mechanism confers hemi-epiphytic aroids the ability to rapidly become mobile, presumably in response to changes in the environment (Ray 1992).

The establishment of epiphytes at new sites depends on characteristics related to architectural traits and physico-chemical properties of the host tree (phorophyte), among others (Frei and Dodson 1972; Hietz and Briones 1998; Merwin et al. 2003; Aguirre et al. 2010). As a rule, more holo-epiphyte species, individuals and biomass are found on larger and older trees (Zimmerman and Olmsted 1992; Hietz-Seifert et al. 1996; Zotz et al. 1999; Dunn 2000; Hsu et al. 2002; Zotz and Vollrath 2003; Burns and Dawson 2005; Hietz 2005; Werner et al. 2005; Wolf 2005; Flores-Palacios and Garcia-Franco 2006). The positive correlation with tree size relates to larger sampling area, higher chances on settlement because of longer time spans, larger habitat diversity, more surface area for colonization and seed interception, and higher levels of factors that facilitate germination and establishment such as organic soil accumulation and moisture (Zotz and Vollrath 2003; Laube and Zotz 2006a). Nevertheless, tree size does not seem to affect hemi-epiphyte establishment in the same way, since they are able to colonize a wide range of phorophyte sizes by means of clasping leaves.
closely adpressed to the trunk or adventitious roots (Burns and Dawson 2005; Lozano Orihuela and Waechter 2010).

With respect to the eco-physiological adaptations of epiphytes it has been noted that water supply is perhaps the most constraining factor for both holo- and hemi-epiphytes (Andrade and Nobel 1997; Nieder et al. 2000; Zotz and Hietz 2001). Although many holo-epiphytes exhibit morpho-ecophysiological adaptations to water shortage, which is common in the canopy (e.g. pseudobulbs, trichomes, velamen, succulence, phytotelm morphology, CAM), their distribution is often limited to the more humid zones within the phorophytes (Arevalo and Betancur 2004; Krömer et al. 2007; Martinez-Melendez et al. 2008; Reyes-García et al. 2008; Higuera and Wolf 2010; Zhang et al. 2010). Hemi-epiphytes may experience difficulties to reach the dryer, outer canopy of large trees because feeder roots have hydraulic limitations to height (Fisher et al. 1997; Zotz et al. 1997; Lopez-Portillo et al. 2000; Meyer and Zotz 2004).

Holo-epiphytes grow slowly and tend to have a long life span (Nadkarni 2000). For that reason, it is likely that substrate instability, due to tree- or branch fall or detaching bark, is a major factor of mortality among holo-epiphytes (Bennett 1986; Ibisch et al. 1996; Laube and Zotz 2006a; Zotz and Schultz 2008). Other factors, such as herbivory of meristematic tissue can be important, but have been scarcely studied (Schmidt 2000; Winkler et al. 2005; Cascante-Marín et al. 2009b).

SPATIAL DISTRIBUTION PATTERNS.—The distribution of epiphytes amongst trees (horizontal) and within trees (vertical) depends on niche differentiation (competition) and dispersal (Wolf and Zotz 2009). The relative importance of both processes, known as demand ecology versus supply ecology (Oksanen 1988) or niche assembly- versus dispersal assembly perspective (Hubbell 1997), is still debated. For example, see the
ongoing discussions around McArthur and Wilson’s Island Biogeography Theory and Hubbell’s recent Neutral Theory of Biodiversity and Biogeography that assume ecological (near-) equivalency and neutrality of species in a given habitat (MacArthur and Wilson 1967; Hubbell 2001). There is consensus that for epiphytes both perspectives play a role, but to what extent remains unclear (Wolf 1994; Wolf 1995; Oliveira et al. 2009).

In the footsteps of the classical study by Pittendrigh (1948), epiphyte distributional patterns have been explained by emphasizing species adaptations to environmental gradients (Zotz 1997; Hietz et al. 2003; Zotz 2004; Reyes-García et al. 2008). Niche (vertical) segregation in epiphytes appeared related to species-specific adaptations to the environmental and structural conditions along a tree (Wolf 1994; Cardelus and Chazdon 2005; Krömer et al. 2007). Other studies showed that certain epiphyte species were more abundant at specific sites inside the forest, for example those of high humidity (Sanford 1968; Sugden and Robins 1979; Flores-Palacios and Garcia-Franco 2008). Similarly, certain epiphyte species in subtropical forests and dry forests showed a non-random distribution over phorophytes (Callaway et al. 2002; Munoz et al. 2003; Burns and Dawson 2005). On the other hand, ecologists who studied spatial patterns of offspring and properties of the seed supply of epiphytes suggested that dispersal assembly largely structured epiphyte communities (Bader et al. 2000; Van Dunné 2002a; Wolf 2005; Cascante-Marín et al. 2006a; Cascante-Marín et al. 2009a).

One of the reasons for the ongoing discussion about the relative importance of niche assembly versus dispersal assembly is that both processes lead to spatial aggregation of species. As long as the ecology of epiphytes, especially at the seedling stage, is poorly understood and few data are available on the historical biogeography of sites, spatial aggregation may therefore not simply be explained as the result of dispersal limitation and
mass effect mechanisms (Schmida and Wilson 1985; Bennett 1986; Bader et al. 2000; Van Dunné 2002b; Wolf 2005). To elucidate this point further, I draw attention to one often studied but still elusive aspect of epiphyte ecology: the preference of certain epiphytes or all epiphytes for certain species of phorophytes or certain (large) individual trees. Since phorophytes are not distributed randomly in the forest, such a preference would lead to spatial aggregation of epiphytes. Presumably because of the high diversity of trees in the tropical rain forests, few studies have evaluated the phorophyte-epiphyte relationship in detail (Cardelus et al. 2006). In Panamanian rainforest, the distribution of 69-81% of the epiphyte species on three abundant host trees was indistinguishable from random (Laube and Zotz 2006b). These authors suggested that the other species did have a positive or negative association with their hosts. In case of strong host-preference or host-avoidance, we expect that in the Amazonian lowland rain forest epiphyte species are closely associated to landscape units such as floodplains, swamps and tierra firma, since these units have characteristic phorophyte assemblages (Duivenvoorden and Lips 1993, 1995; Duivenvoorden and Duque 2010). On the other hand, if the epiphyte distribution depends mostly on environmental factors such as forest humidity and light conditions, epiphytes are also expected to be associated with landscape units (Ter Steege and Cornelissen 1989; Leimbeck and Balslev 2001). This example shows some of the pitfalls of correlative studies on epiphyte distribution patterns.

TEMPORAL DISTRIBUTION PATTERNS.—The development of the epiphyte community on tree- or branch segments over time depends on species colonization rates, growth, survival and turnover rates. Holoepiphyte and primary hemi-epiphyte recruitment in newly available habitats is characteristically low as it is limited by low and uncertain seed supply or seedling establishment (Ackerman et al. 1996; Nadkarni 2000;
Cascante-Marín 2006). In addition, many epiphytes require organic soil accumulation for establishment, which especially at lower elevations is also a slow process (Nadkarni 2000; Merwin et al. 2003). Secondary hemi-epiphytes, however, germinate in the terrestrial soil and the successful occupation of a host tree is therefore not hampered by slow and uncertain seed recruitment on bark or on the presence of accumulated canopy soil. After germination, secondary hemi-epiphytes are capable to colonize trees by means of vegetative recruitment pathways (Schnitzer et al. 2008), which can promote rapid tree colonization because of advantages such as higher survival and growth rates (Lasso et al. 2009). Moreover, in secondary hemi-epiphytes host tree colonization is not limited to young saplings since adult plants may descend to the forest floor to forage for host trees as well, potentially distributing ramets over several host trees.

Whereas the holo-epiphyte and primary hemi-epiphyte recruitment is slow, the subsequent epiphyte turnover rate at a particular branch- or tree segment is relatively rapid compared to woody terrestrial plants that have much longer life cycles. Holo-epiphytic bromeliads in the outer canopy may reproduce in only a few years, but inner canopy bromeliads tend to grow slower and may take between 10 to 19 years to produce an inflorescence (Hietz et al. 2002). Longevity in most species of monocotyledons such as orchids and bromeliads is, moreover, enhanced because they form adventitious roots that build long-living clumps of ramets. The capacity to enhance the life-span of an individual plant through ramets is also observed in many epiphytic dicotyledons, such as Cactaceae and Piperaceae and in ferns.

Higher turnover rates of epiphyte species over time is a product of the combination of niche filling mechanisms related to species-specific adaptations to the environment and a high mortality, for example in consequence of substrate instability (Hietz et al. 2002; Laube and Zotz
Studies in montane rain forests have shown that during forest succession there is a shift from drought tolerant epiphyte species to species that appear better adapted to a more humid microclimate, particularly in the understory (Barthlott et al. 2001; Wolf 2005). Colonization patterns between holo- and hemi-epiphytes might differ substantially, nevertheless. The increasing branch area of expanding canopies in developing forest yields a continuous supply of newly available substrate in the outer canopy for holo-epiphytes. Hemi-epiphytes, however, are more restricted to the lower forest stratum, where over time the availability of trunk surface area may increasingly limit their establishment and growth.

AIM AND OUTLINE OF THIS THESIS

The innovation of rope-climbing and other canopy-access techniques such as walkways, platforms, cranes and hot-air balloons to gain access to the forest canopy resulted in a burgeoning of interest in canopy research (Perry 1984; Parker et al. 1992; Moffett 1993; Dial and Tobin 1994; Nadkarni and Parker 1994; Laman 1995; Mitchell et al. 2002). However, epiphyte studies have been greatly biased for holo-epiphytes, mountain forests, and undisturbed forests. For example, as far as I know, no data are available on the life-span or growth rate of hemi-epiphytes under field conditions. This is surprising since in terms of biomass and number of individuals hemi-epiphytes are comparable to or surpass holo-epiphytes in American wet tropical lowland forest, the largest extension of tropical forest in the Neotropics (Nieder et al. 2000; Leimbeck and Balslev 2001). Overall, there are few epiphyte studies in the wet tropical lowland forests of Amazonia. Wolf and Flamenco (2003) list a total of 47 Neotropical vascular epiphyte inventories, and of those fewer than ten took place in the Amazon area. Finally, in the tradition of the classical work on vascular epiphytes by Schimper (1888), tropical epiphyte studies have focused on forests that are
least disturbed by man (e.g. Went 1940; Johansson 1974; Benzing 1990). So far, epiphytes in disturbed forests have attracted only limited attention, with some exceptions (e.g. Turner et al. 1996; Barthlott et al. 2001; Krömer and Gradstein 2003; Wolf 2005). Compared to trees, epiphytes appear particularly vulnerable to disturbance of the forest, especially the shade-epiphytes in the understory and inner canopy (e.g. Barthlott et al. 2001; Wolf 2005; Cascante-Marín et al. 2006b). In tropical tree plantations and recovering clear-cut forests, epiphyte immigration is a slow and spatially heterogeneous process (Madison 1979; Catling et al. 1986; Barthlott et al. 2001; Merwin et al. 2003). More insight in the response of epiphytes to anthropogenic disturbance is particularly needed to facilitate the incorporation of the epiphytic component in sustainable forest management.

The aim of this thesis is to study the distribution patterns of vascular epiphytes in lowland rain forests of the Colombian Amazon, both in space and time. Spatial distribution patterns were the subject of the first two studies and the next two addressed time. These studies provide, for the first time, quantitative information about the species diversity and abundance of epiphytes in the lowlands of Colombian Amazonia.

Based on earlier studies about forest-landscape relationships (Duivenvoorden and Lips 1995; Duque et al. 2001), Chapter 2 focussed on the question how the epiphyte distribution differed between the main landscape units (floodplains, swamps, well-drained uplands, and so-called white sand areas) in the Metá area. Chapter 3 addressed how the epiphyte distribution relates to the principal landscape units in a different area (the Chiribiquete area, about 100 km NW of the Metá area). This study allows an independent check to confirm the conclusions from Chapter 2. Furthermore, in Chapter 3 holo-epiphytes and hemi-epiphytes are analysed separately, to better understand the potential role of the soil substrate.
Finally, the study in this chapter adds the phorophyte dimension to the issue, because the epiphytes were sampled in the same forest plots where the trees and lianas were sampled. This provided the opportunity to examine how host-preferences might contribute to between-landscape epiphyte assemblage building. Four questions were addressed in Chapter 3: (1) is the composition of epiphyte communities related to the composition of phorophytes, (2) is this relationship perhaps due to the strong link between tree species composition and landscapes found previously in this same area (Duivenvoorden and Lips 1995; Duque et al. 2001), (3) do phorophytes still explain epiphyte species composition after having controlled for the effect of landscape units, and vice versa, and (4) is it possible to show that individual epiphyte species prefer certain phorophyte species?

Temporal patterns of epiphyte distribution, studied in regenerating fallows (2–30 yr old) and mature forest in the Amacayacu National Park and Ticuna indigenous territory, were the subject of the next two chapters. Expectedly, epiphyte species may differ in their response to the environmental change which takes place as a consequence of forest succession. Also, differential abilities to colonize new habitats in the growing fallows may yield consistent and non-random patterns of epiphyte species turnover along the chronosequence of the developing forest matrix. Chapter 4 addressed the question if holo- and hemi-epiphyte species show such non-random successional patterns. Chapter 5 is a direct follow-up of that study. It focused on the question why hemi-epiphytic aroids show such a quick recovery in young fallows. Fallows can be seen as a model of tree fall gaps in natural forests. Therefore, Chapter 5 implicitly deals with the issue of gap recruitment by hemi-epiphytes. Through descriptive and experimental field studies, and concentrating on the differential role of recruitment by seeds or clonal mechanisms the following questions were
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addressed: (1) what is the relative contribution of seed and vegetative recruitment in the recovering aroid assemblages, (2) what is the speed of stem displacement in the successional habitats, (3) do creeping stems of aroids have a preferential growth direction, and (4) do early-successional species show higher stem displacement rates than late-successional species? Finally, Chapter 6 provides a synthesis highlighting the new insights obtained from all studies.