Distribution and succession of vascular epiphytes in Colombian Amazonia
Benavides, A.M.

Citation for published version (APA):
Benavides Duque, A. M. (2010). Distribution and succession of vascular epiphytes in Colombian Amazonia

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
Synthesis

Distribution and success of vascular epiphytes in Colombian Amazonia
THIS THESIS REPORTS THE FIRST quantitative census how epiphytes are distributed over the main landscapes and along forest chronosequences in Colombian Amazonia. The sampling resulted in more than 2000 plant collections (not including trees or lianas) and comprised nearly 340 species, which belonged to 20 plant families (ferns and allies considered separately). Araceae, ferns, and Orchidaceae were the most diverse groups. The most commonly found and species-rich genera were *Anthurium* and *Philodendron*, which together accounted for 21% of the species records. About half of the epiphyte species were hemi-epiphytes, and most of these were (142 species) secondary hemi-epiphytes.

FACTORS DEFINING THE SPATIAL DISTRIBUTION OF EPIPHYTES. — The two independent studies of epiphyte species distribution (Chapters 2 and 3) convincingly showed that epiphyte species composition differed significantly over the main landscapes (i.e. floodplains, swamps, well-drained uplands and white sand areas). This landscape effect was found in both holo-epiphytes and hemi-epiphytes. At first sight this result is not surprising. In the past two decades several studies in Colombian Amazonia, and NW Amazonia have found clear landscape effects upon vascular plant species composition of different growth habits (e.g. trees, palms and ferns; Duivenvoorden and Duque 2010). The explanation for these patterns is often given in terms of the niche assembly theory (Grime 1977, Tilman 1980): species are distributed not randomly but as result of environmental constraints and competitive displacement. The fact that the landscape effect was well visible among holo-epiphytes suggests that soil physical and chemical factors may in an indirect way, at least to some extent, explain epiphyte distribution (Gentry and Dodson 1987b). More likely, however, atmospheric humidity in the forest, conditions of seasonal
and permanent inundations (especially influencing the lower strata in the forests), the faunal community (defining pollination, seed dispersal, herbivory and pathogen attacks), and the distribution of the phorophytes in combination with host preferences are among the principal variables defining the composition of epiphyte communities in this part of the Amazon basin.

In this light, the significant phorophyte effect on epiphyte composition (both holo-epiphytes and secondary hemi-epiphytes) (Chapter 3), and the way phorophyte composition remains influential even after cancelling out the landscape effect is remarkable. These results suggest that species-specific interactions between epiphytes and phorophytes drive the epiphyte species assemblage. Several studies outside Amazonia indicated that certain epiphyte species prefer phorophyte species. For example, in Chile some film fern species showed a preference for *Podocarpus nubigene* (Munoz et al. 2003) and in Puerto Rico, the orchid *Lepanthes caritensis* was only found on *Micropholis guyanensis* (Tremblay et al. 1998). Obtaining evidence for epiphyte-phorophyte associations at the level of individual species is difficult, because of the low aggregation levels in highly diverse NW Amazonian forests. The chances of finding combined occurrences of epiphyte species and host species are small, which quickly leads to a low power in statistical tests of association between two species. The Chiribiquete study in Chapter 3 thus exemplifies a case in which a multiple response is significantly related to a multiple explanation, whereas the pairwise associations between each of the individual response variables and each of the explanatory variables seem almost absent. Indeed, survey studies of species composition may not be the most suitable way of analyzing epiphyte-phorophyte interactions in upper Amazonia. Transplantation experiments and studies in large permanent plots, during
which the interactions between a limited numbers of species can be followed through several years, seem more appropriate.

SUCCESSION OF VASCULAR EPIPHYTE COMMUNITIES.—In Chapter 4, epiphyte succession was studied along a chronosequence of fallows. This implied that the phorophyte community structure which defines the substrate and space for settlement and further development of epiphytes, changed substantially over time. Indeed, from young fallows to fallows of about 30 yr old, the mean tree height increased from 9 to 15 m, basal area increased from 0.18 to 0.37 m$^2$, and the tree trunk volume from 1.4 to 5.7 m$^3$ (data from trees of DBH > 10 cm in 0.01 ha).

Along with forest structural changes, the species richness, density and biomass of both holo-epiphytes and hemi-epiphytes increased significantly from young fallows to aging fallows and mature forests. In general, this observation concurs with results from other studies which show that, in comparison with smaller trees, larger trees (which are often older) offer a larger sampling area, more habitat heterogeneity, and more prolonged time spans for colonization and seed interception (Zotz and Vollrath 2003; Laube and Zotz 2006a). Furthermore, the species composition of both holo- and hemi-epiphytes was highly explained by the geographic configuration of the plots. This showed that not only between landscapes, at regional scale (spanning distances of 10 to > 100 km) but also within one single landscape (well-drained uplands), at local scale (distances < 10 km), epiphyte species composition differed substantially.

In three ways the dynamics of the holo-epiphytes differed from that of the hemi-epiphytes. First, the hemi-epiphytes (which were mostly aroids) showed a remarkably higher abundance and biomass in the youngest fallows compared to the holo-epiphytes. We hypothesized that the high initial biomass and abundance of hemi-epiphytes was due to germination of seeds in the seed bank, to sprouting of fragments of hemi-epiphytes,
which had fallen out of the trees when the forests was cut down and had survived the burning, or possibly even from relatively rapid colonization via clonal growth, entering the young fallows from the surrounding forests. Secondly, in the course of succession, the relative increase of holo-epiphytes exceeded that of secondary hemi-epiphytes. This suggested that, once established, the holo-epiphytes experienced no limits to local recruitment and growth within the expanding canopy of the developing fallows. Contrary to this, secondary hemi-epiphytes would hardly experience an increase in opportunities for continued local recruitment because the soil surface area available for colonization remains constant (or even decreases slightly) through time. Finally, the variation in species composition of holo-epiphyte species could not be related to time, whereas that from hemi-epiphytes was significantly associated to forest age, even after cancelling out any effect of the spatial configurations of the sampled plots. To explain the lack of succession in holo-epiphytes, it was assumed that the increasing branch area in the expanding canopies in developing fallows yielded a growing supply of substrate allowing a continuous arrival of new holo-epiphyte species. In contrast, the hemi-epiphytes, which occurred predominantly at tree bases, expansion in the developing fallows might be increasingly limited by trunk space, potentially leading to species turnover due to competition. Chapter 5 enlarges on the question why hemi-epiphytes, and especially aroids, recovered so quickly in chagras and young fallows. Apart from man-made chagras and fallows, the field studies also included natural treefall gaps. In field experiments, aroid germination rates under open conditions were low, implying that seed recruitment would be largely confined to closed-canopy forests. Therefore, the idea of quick aroid recovery in gaps through seed recruitment was rejected. Instead, stem cuttings of five study species experimentally placed in chagras all showed
resprouting capacity, indeed suggesting that aroid fragments may persist in gaps. Secondly, near the forest edges a high abundance of creeper plants was found with flagellar shoots which grew rapidly, indicating that aroids are foraging for essential resources and dispersing meristems clonally. Finally, hemi-epiphytic aroids in the forest edge up to 30 m from the gap exhibited habitat selection, growing towards the gap. Thus, we concluded that hemi-epiphyte aroids improved their capacity to colonize gaps rapidly through vegetative recruitment.

CONCLUSIONS AND RECOMMENDATIONS

The high epiphyte species turnover within and between landscape demonstrated that the scale at which such studies are conducted has important implications for the interpretation of results. At between-landscape scales, the results presented in this dissertation strongly suggested that niche assembly mechanisms, related to eco-physiological adaptations to environmental constraints, structure epiphyte communities (both holo-epiphytes and hemi-epiphytes). At local scales, dispersal limitation would explain the low abundance of holo-epiphytes in young fallsows, and even plays a certain role in the way hemi-epiphytes colonize gaps through vegetative recruitment mechanisms. The results reported in this thesis emphasized that the abundance, diversity, and species composition of the epiphyte communities depended strongly on the dynamic environment provided by the forest (assemblage of phorophytes). As a consequence, compared to trees, the epiphytic life-form would appear particularly sensitive to disturbance and forest transformation. Further research is needed to detect the environmental constraints and competitive mechanisms causing the nonrandom distribution in epiphytes. In view of the scarcity of epiphytes studies in proportion to the high diversity and enormous geographical extension of the Amazon basin, it is important to carry out more epiphyte inventories using standardized methods (e.g. Wolf
et al. 2009), and in different landscapes. In these, it is fundamental to improve the taxonomic knowledge of the epiphyte community to be able to determine more precisely their distribution and to extrapolate findings. Also, long-term epiphyte monitoring studies should be established, which allow detailed studies of species interactions (host-preferences), as well as measurements how variation in micro-environmental conditions (light, nutrient and water flux) influence the performance of epiphytes. For the future, ecophysiological studies in combination with experimental research on dispersal, germination, establishment, growth, causes of mortality, and relocation over different micro-environmental conditions are perhaps most likely to yield valuable insights in epiphyte community assembly.