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METHODS OF ANALYZING THE STRUCTURE AND DYNAMICS OF VASCULAR EPIPHYTE COMMUNITIES

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Resumen. Si posible, la colecta de epífitas vasculares debe ser combinado con el estudio de la estructura y la dinámica de las comunidades de estas plantas creciendo en las copas de los arboles. Se recomenda el uso de zonas "Johansson" para el analisis espacial de su distribución. Hay que documentar conjuntos típicos de epífitas en árboles distintos (forofitos) y simultaneamente determinar las abundancias relativas de las distintas especies. Aprovechando la concentración de epífitas en ciertos forofitos preferidos, basta incluir un número limitado de árboles en el analisis demográfico representativo. El establecimiento de lotes permanentes es altamente recomendado. El presente trabajo complementa las recomendaciones dados por Hietz & Wolf (en Gradstein *et al.* 1996).

Abstract. The sampling of vascular epiphytes can be used for data collection on epiphyte community structure and dynamics. The use of Johansson's zonation scheme is recommended in order to allow a simple spatial analysis of epiphyte distribution. Phorophyte specific epiphyte spectra and relative abundance of different epiphyte species should be determined. Clumped occurrence of epiphytes usually means that only a limited number of phorophytes and epiphytes have to be sampled for a representative study of epiphyte vegetation. Documentation of epiphytic plants in permanent plots is higbly desirable for information on long-term community changes in epiphytes and on life history and population biology of individual species. This review complements the "guidelines for sampling" by Hietz & Wolf (in Gradstein *et al.* 1996).
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Key words: Epiphytic plants, zonation, phorophytes, epiphytic communities, vegetation dynamics.

INTRODUCTION

In a recently published paper, Hietz & Wolf (in Gradstein *et al.* 1996) describe some basic guidelines for sampling and setting up inventories of epiphytic plants. They focus on methods of determining species composition, species abundance, seasonal variation, and species identification. We think that additional aspects of epiphyte biology such as spatial distribution within phorophytes, species turnover, or life history should also be considered. The present contribution tries to cover this end of the range of possible investigations by providing a critical overview of the methodological frameworks that have been used up to now. This evaluation should be particularly useful for the novice in the field, but we also attempt to advance the discussion among researchers in working out common research protocols for the sake of compatibility of different studies. We will not cover ecophysiological traits of vascular epiphytes, although they are undoubtedly important features in the context of a causal analysis of epiphyte distributions. In this field of research, the reader is referred to recent reviews by Lüttge (1989, 1997) and Benzing (1990).

ZONATION

Spatial orientation is the basis of community structure in sessile organisms. The obvious difference between the spatial arrangement of terrestrial and epiphytic plants is that the latter are distributed on their phorophytes in a three-dimensional fashion. Zonation schemes have proven useful for standardized descriptions of epiphyte occurrence on phorophytes. A second objective of the establishment of epiphyte zones on their phorophytes should be to distinguish ecologically differentiated associations of epiphytes. In this respect, they represent models to be tested by identifying typical epiphyte communities in each zone. Under close scrutiny these two aims are probably incompatible, at least when geographically and ecologically distinct epiphyte-bearing forests are being compared. Nevertheless the following overview presents some suggestions for a pragmatic procedure. The most common zonation scheme is that proposed by Johansson (1974). It is a simple scheme, originally developed for large phorophytes in West African rain forests. The scheme is based on obvious differences in the composition of the epiphytic vegetation of each zone. Subsequently, this scheme has been used by many authors (e.g., Freiberg 1996, Ibisch 1996). It must be emphasized that Johansson-zones are based on the principal structures of phorophytes and not on height above ground per se (Fig. 1). Several modifications of the original scheme have been used. Bøgh (1992), for example, used height above ground as criterion of zone determination. This contradicts the original concept because different types of branch diameters are lumped in one zone. The other extreme is the division of a phorophyte into zones on the basis of branch and twig diameter. Although the overall picture of zone structure on a tree may be rather complicated (see Papulin *et al.* 1995), the principle of using branch diameter is useful, especially if branch diameter classes are formed (e.g., branches < 5 cm, branches between 5 and 20 cm diameter and branches > 20 cm diameter, as in Hietz & Hietz-Seifert 1995), because the quality of epiphytic substrates largely depends on age and physical properties of branches.

It is, however, clearly undesirable to use as many different zonation schemes as there are differences in epiphyte composition structure in different habitats. Branch diameters should be recorded wherever possible, but the "Johansson zones" should be used to obtain a relatively simple model of epiphyte distribution on their phorophytes. We therefore suggest using the original definition (Johansson 1974): zone I covers the basal parts of the trunks, zone II the trunk up to the first ramifications, excluding isolated branches originating on the trunk, zone III is the basal part of the large branches (one third of their total length), zone IV the second third, and zone V the outer third of their total length. We suggest establishing Johansson zones at the very beginning of field work for the phorophytes in question. Growing sites of each epiphyte specimen should be documented with relation to fixed points, e.g., branch bases and branch tips. Epiphyte vegetation of single large

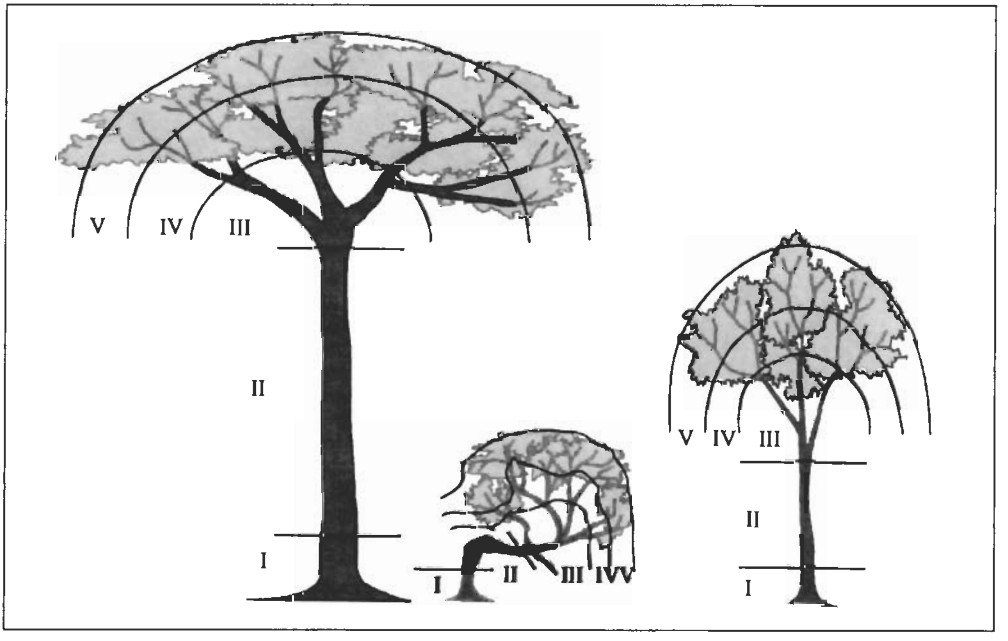

FIG. 1. Zones on phorophytes according to Johansson. Zonation reflects tree structure, not height, above ground, and not characteristics of single branches. Zones 3 to 5 form hemispheres in the canopy of the phorophyte (after Ibisch 1996).

branches can typically be divided by thirds into Johansson zones III to V. Smaller collateral branches should be included in the respective Johansson zones. Exact location measured as distance from branch origin at the trunk and from branch tip, as well as height above ground and distance to the outer canopy margin, should be registered.

In most cases, Johansson zones do not coincide with distinguishable epiphyte communities in different forests. Ter Steege & Cornelissen (1989) found no distinction between zones IV and V, and the typical epiphytes of zone III extended into zone II. Bøgh's three "sections" each combine Johansson zones I, II and III, and IV and V, respectively.

In conclusion, zonation schemes can only be a rough abstraction of real distributions. The Johansson zone scheme can be helpful as a research tool because of its wide use in epiphyte literature. It allows easy graphic representation of epiphyte distribution in the canopy and can be used as a model to be tested, until computer-based three-dimensional analysis tools allow much more elaborate analyses in the future.

EPIPHYTE SPECTRA OF PHOROPHYTES (SPECIES SPECIFICITY)

Epiphytes and their phorophytes complete their life cycles in a situation of closest contact, second only to parasitic relationships, e.g., of mistletoes and their hosts. A thorough analysis of associations between epiphyte and phorophyte, but also among epiphytes, will reveal biologically meaningful patterns. If on the other hand mutual impact is limited associations are expected to be quite variable.

Phorophyte-specific epiphyte spectra. Whether or not phorophyte species play a role in determining the composition of epiphytic vegetation, is still an issue of debate. Hietz & Wolf (in Gradstein *et al.* 1996) suggest that host tree species has little effect on epiphyte composition. In his classic study, Went (1940), who used the term "epiphyte sociology," tried to prove that phorophyte species was the most decisive single factor determining epiphyte community composition. The degree of interdependence of phorophyte and epiphyte species changes along climatic gradients. Sanford (1974) pointed out that in less favourable sites epiphytic orchids tend to be more restricted to those phorophytes offering the right bark conditions. In humid climates, the usual thick cover of mosses and lichens allows the growth of the same epiphytes regardless of phorophyte species. We conclude that a comparison of the epiphyte spectra of different phorophytes is desirable in most cases. At the beginning of such a study, comparable sample areas should be selected on different phorophyte species, i.e., trees of roughly the same size, identical branch lengths and similar height in the forest. Sampling of whole trees or representative parts of them (trunk, large branch systems) should lead to comparative lists of epiphyte species on different phorophytes.

Relative abundance of different epiphyte species. The problem of determining relative abundance of epiphyte species is treated by Hietz and Wolf (in Gradstein *et al.* 1996). Until the development of more elaborate methods, epiphyte individuals should be counted. In many ferns and monocots, in particular, the distinction of individuals may be difficult. So-called "stands" (Sanford 1968), i.e., a collection of stems separated from other groups of stems of the same species, can be counted instead. Subsequently, the numbers of individual plants on different phorophytes can be compared and tested for significant differences of variances, which is of course only meaningful if sample sizes (e.g., tree sizes) are comparable.

HOW MANY TREES HAVE TO BE SAMPLED?

If a researcher is interested in the epiphyte spectrum of a particular phorophyte species, a recent study by Zotz & Bermejo (unpublished) may give some insight into the number of trees to be surveyed for a representative sample. On Barro Colorado Island (Panama), Zotz and Bermejo studied the epiphytes on *Annona glabra*, a small tree restricted to marshy habitats, registering all epiphytes occurring on more than 1000 trees. They found 49 species of vascular epiphytes, with very uneven abundances: the five most abundant species accounted for 82%, the 10 most abundant for almost 95% of all individuals. Hence, focusing on these common species does not sacrifice much information, while considerably reducing the amount of field work compared to a complete inventory of all epiphyte species, which would have to include all trees (the "species-area curve" shows no sign of saturation, data not shown). We therefore asked the question, using the original data set, how many trees had to be sampled so that the

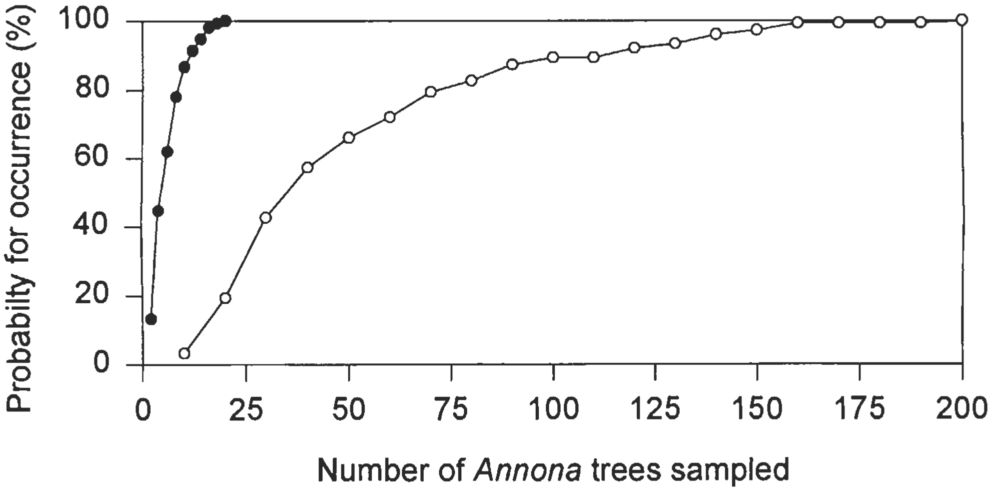

FIG. 2. Probability of the occurrence of the 5 (closed circles) or 10 (open circles) most common species of vascular epiphytes on a particular host tree (*Annona glabra*) as a function of the number of trees sampled. Trees were chosen at random from 606 epiphyte-bearing trees of the *A. glabra* population on Barro Colorado Island, Panama. The data represent 200 iterations.

most common species of epiphytes were included in the survey. The results are shown in Fig. 2. With 50% certainty, sampling only five trees would be sufficient to include the five most abundant species, while more than 30 trees should be sampled to include the 10 most abundant. Due to the patchy and highly clumped distribution of epiphytes, higher degrees of certainty can only be reached with considerable extra effort. For larger trees in particular this is probably not a realistic option.

DYNAMICS: COMMUNITY CHANGES

Species turnover in time or along discrete spatial units may be an important factor in epiphyte diversity, considering the material instability of the substrates epiphytes grow on, and the large-scale change in spatial structure and microclimatic gradients of the epiphytic habitat by branch loss or gap formation. Different successional stages of epiphytic vegetation have often different species compositions (Dudgeon 1923, Johansson 1974, Yeaton & Gladstone 1982). Although succession is a chronological phenomenon, the growth of phorophyte branches allows a substitution of space for time to some extent. The spatial sequence of epiphyte vegetation on branches reflects a time sequence. Where possible, efforts to determine phorophyte age should be undertaken (e.g., by core extraction and identification of tree-rings, realised for instance in *Alnus acuminata* phorophytes in Bolivia by Ibisch 1996). Epiphyte species numbers can be plotted against branch diameter and/or branch age (e.g., in Hietz & Hietz-Seifert 1995).

The establishment of permanent plots would, however, still be highly desirable. In any case, exact documentation of sample sites e.g., with photographs, should allow re-checking of the epiphyte vegetation after the original research. Destruction in the course of research is also a problem and often inevitable to some extent. Non-destructive sampling is either costly (e.g., crane systems, permanent rope access) or rather imprecise (e.g., binocular scanning). A promising method for long-term observations was used by Hietz (1997); by repeatedly taking photographs of epiphytes in a Mexican montane forest, he was able to document the fate of more than 5000 individuals over a two-year period without any disturbance.

LIFE HISTORY AND POPULATION BIOLOGY

The life cycle of epiphytes has to adapt itself to the idiosyncrasies of tree crowns and trunks. The expected life history characteristics of vascular epiphytes are discussed in detail by Benzing (1990, Chapter 5).

Solbrig (1980) lists the following parameters as necessary information in describing a life history strategy: (1) seed pool, seedling and adult mortality; (2) age of first reproduction; (3) reproductive life span; (4) fertility, i.e., proportion of individuals reproducing at a particular time; (5) fecundity (number of seeds); (6) fecundity-age regression; (7) reproductive effort, i.e., allocation of resources to reproduction as opposed to growth or tissue maintenance. To date, however, no epiphyte species has been studied in such detail. The basic design of a demographic investigation can be observational and/or experimental. Long-term observational studies are highly desirable, but epiphytes are also ideally suited for experimental studies because of their relatively small size and hence manageability, i.e., removal and transplantation is quite easy in many cases (e.g., Ackerman *et al.* 1996). A problem arises rather often when – particularly in dense epiphyte populations – it proves impossible to delimit one individual from another. The use of "stands" (Sanford 1968) as an operational unit is not admissible in a demographic study. Inevitably, this will reduce the number of species suited for long-term observational population studies. In experimental or destructive studies, however, this is not a complicating factor. Benzing (1981), for example, investigated the population dynamics of *Tillandsia circinnata* by felling a representative set of cypress trees in three successive years, including all living individuals of the epiphyte colonies. It is also possible to focus on growth and survival of the early stages of development by attaching seeds or small seedlings to potential host trees, repeatedly censusing the population afterwards (Benzing 1990). Many epiphytes may have a longer potential life expectancy than their substrate. If mortality in older plants is indeed almost exclusively due to tree falls or breaking branches, as suggested by several authors (Benzing 1990, Zotz 1995), then it is necessary to study a large number of populations on different trees in long-term studies to obtain reasonable estimates of causes and rates of mortality of mature plants. In a study with the epiphytic orchid *Dimerandra emarginata* (Zotz, unpubl.), two out of 12 study plots (= branches with an epiphyte population) were lost in three years. Depending on the dynamics of a particular forest, we would recommend including not fewer that 50 independent plots in a demographic study. Furthermore, considering the stochastic nature of disturbance and the slow growth of most epiphytes, a study should be designed to last not less than 3 years, preferably more. Vegetative growth could be measured destructively, but we suggest establishing indirect measures of size (length of stems, leaf area) which correlate with biomass, and estimating growth by repeated in situ determinations of these parameters with the same individuals. Finally, Crawley (1990) pointed out the importance of "empty quadrats" in population biology studies. Since epiphytes have to be "fugitives" in space and time due to the instability of their substrate, it is important to document successful establishment at new microsites. This could be done using transects from a source tree (Ackerman *et al.* 1996).

COMMUNITY ECOLOGY

An ecological "community" is the assemblage of potentially interacting species in a given ecosystem (Putman 1994). Vascular epiphytes develop two-dimensional relations: they interact not only with their phorophytes (see above) but also with each other. The two basic processes in epiphytic interrelationships are competition and facilitation. Competition in the natural habitat is relatively easy to document with the help of "provocative" manipulations, but very difficult to prove without them (Connell 1983). Because of the slow development of epiphytic vegetation, field experiments will have to be carried out over many years. Sometimes direct observation of negative effects of one species on others (e.g., overgrowth of twig orchids by large bromeliads) may be possible. Comparison of inventories of species and individuals will lead to further insights into competitive processes. As in the analysis of successional stages, branch and trunk segments of different ages can partially substitute for long-term observation. Especially rewarding are comparisons of juvenile and adult plants on different branch sections (e.g., Zotz 1997). The difference in the numbers of juvenile specimens present on young branches with small diameter and full-grown epiphytes on older branches result from either differential ecological niches of different species or from intra- and interspecific competition. The first possibility can be verified or excluded by comparison of growing sites of the species in question.

Facilitation is even less investigated. Among the few well-studied examples of facilitation are ant gardens (Davidson 1988). Some species of epiphytes in ant gardens (among them ferns, orchids and aroids) often present no obvious benefit to ants and act as commensals or "spatial parasites" of ant gardens (Davidson & Epstein 1989, but see Yu 1994). Closer observation of succession of ant garden plants and typical associations under this aspect should reveal information on the use of spatial resources by opportunistic epiphytes. Another example are the humus accumulations in some trash-basket ferns which function as nursery beds for a number of epiphyte species (Benzing 1990). In general, studies on mutual facilitation of epiphytes should be conducted in areas where epiphytic vegetation is limited, allowing the distinction of clumps of individuals; rewarding objects are branch fork "nests" and similar structures.

CONCLUSIONS

The study of the structure and dynamics of vascular epiphytes requires a variety of methodological approaches, as the above should have demonstrated. We would like to emphasize that the "guidelines for sampling" given by Hietz & Wolf (in Gradstein *et al.* 1996) form the necessary basis of any investigation of epiphyte diversity. Our intention was to provide additional tools for the epiphytologist in order to open some more windows on the complex and fascinating world of epiphytic vegetation. The "guidelines for sampling" by Hietz & Wolf and our suggestions should complement each other and help researchers to design their work in such a way as to allow better mutual comparisons.

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