INTRODUCTION

In a recently published paper, Heitz & Wolf (in Goldstein 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 phenophases, species turnover, or life history should also be considered. The present contribution tries to cover all 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 seeking out common research protocols for the sake of comparability of different studies. We will not cover eco-physiological 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 Been (1990).

ZONATION

Spatial orientation is the basis of community structure in scale-invariant. The obvious difference between the spatial arrangement of terrestrial and epiphytic plants is that the latter are distributed on their photophylls in a three-dimensional fashion. Zonation schemes have proven useful for standardizing descriptions of epiphyte occurrence on phorophytes. A second objective of the establishment of epiphytic zones on their photophylls should be to distinguish ecologically distinguished associations of epiphytes. In this respect, they represent models to be tested by identifying typical epiphyte communities in each zone. Under cluttered surfaces these two aims are probably incompatible, at least when epiphytinically and ecologically distinct epiphytes-bearing forests
are being compared. Nevertheless the following over-
view presents some suggestions for a pragmatic
procedure. The most common zonation scheme is
that proposed by Johannsen (1974). It is a simple
scheme, originally developed for large phanerophytes
in West African rain forests. The scheme is based on
obvious differences in the composition of the epip-
phytic vegetation of each zone. Subsequently, this
scheme has been used by many authors (e.g., Friis-
berg 1996; Briech 1996). It must be emphasized that
Johannsen’s zones are based on the principal structures
of phanerophytes and not on height above ground
per se (Fig. 1). Several modifications of the original
scheme have been used. Begho (1992), for example,
used height above ground as a criterion of zone de-
termination. This contradicts the original concept
because different types of branch diameters are lumped in one zone. The other extreme is the divi-
sion of a phanerophyte into zones on the basis of
branch and twig diameter. Although the overall
picture of zone structure on a tree may be rather com-
plicated (see Puppeln et al. 1993), 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 bran-
ches > 20 cm diameter, as in Hatz & Hitz-Sefer
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 pos-
sible, but the "Johannsen zones" should be used to
obtain a relatively simple model of epiphyte distri-
bution on their phanerophytes. We therefore suggest
using the original definition (Johannsen 1974): zone
I covers the basal parts of the trunk; zone II the trunk
up to the first ramifications, excluding isolated bran-
ches 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 estab-
lishing Johannsen zones at the very beginning of field
work for the phanerophytes 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 phanerophytes according to Johannsen. 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 phom-
phyte (after Briech 1996).
branches can typically be divided by thicks into Johanni sons III to V. Smaller unilaterale branches should be included in the respective Johnston zones. Extent of measurement is at distance from branch origin in the trunk and from branch tip, as well as height above ground and distance to the outer canopy margin, should be recorded.

In more cases, Johnston zones do not outside with distinguishable epiphyte communities in different forests. For Stege & Christiansen (1989) found no discernible between zone III and IV, and the typical epiphyte of zone III extended into zone II. Begg's three 'sections' each combine Johnston zones I, II, and III, and IV and V, respectively. In conclusion, arrangement schemes can only be a rough distinction of real distributions. The Johnston zone scheme can be helpful as a research tool because of its wide use as an 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.

**EPHYPITE SPECTRA OF PHOROMYTHES (SPECIES SPECIFICTY)**

Epiphytes and their phorophytes compete their life cycles in a situation of almost constant, second only to parasitic relationships, e.g., of maidens and their hosts. A thorough analysis of associations between epiphyte and phorophyte, but also among epiphytes will reveal biologically meaningful patterns. If so, the other hand mutual impacts is limited associations are expected to be quite small.

Phyophore-specific epiphyte species. Whether or not phyophore species play a role in determining the composition of epiphyte vegetation, is still an issue of debate. Fleiss & Wolf (in Garau et al. 1998) suggest that host tree species has little effect on epiphyte composition. In his classic study, West (1949), who used the term 'epiphyte sociology,' tried to prove that phyophore species was the most absolute single factor determining epiphyte community composition. The degree of independence of phyophore and epiphyte species changes along climatic gradients. Garden (1974) pointed out that in low favorable sites, phyophore orchids tend to be more connected into the 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 phyophore species. We conclude that a comparison of the epiphyte spectra of different phyophore species is desirable in most cases. At the beginning of such a study, comparable sample areas should be selected on different phyophore 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 segments) should lead to comparable, i.e. of epiphyte species on different phyophores.

**Relative abundance of different epiphyte species.** The problem of determining relative abundance of epiphyte species is treated by Fleiss and Wolf (in Gradstein et al. 1996). Until the development of more elaborate methods, epiphyte individuals are counted. In many cases and methods, in particular, the distinction of individuals may be difficult. So-called 'stems' (Sandford 1968), i.e., a collection of stems separated from other groups of stems of the same species, can be counted instead. Subsequently, the number of individual plants on different phyophores can be compared and tested for significant differences of variances, which is of course only meaningful if single trees (e.g., tree species) are comparable.

**HOW MANY TREES HAVE TO BE SAMPLED?**

If a researcher is interested in the epiphyte spectrum of a particular phyophore species, a study survey by Zois & Benten (unpublished) may give some insight into the number of trees to be surveyed for a representative sample. On Borno Caledon Island (Pomera), Zois and Heesma studied the epiphytes on Acacia globosa, a small tree restricted to marshy habitats, registering of epiphytes occurring on more than 1000 trees. They found 49 species of vascular epiphytes, with very uneven abundance: 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
more 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 largerrees 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 (Dudigence 1925, Johansson 1974, Yeaton & Gladierine 1982). Although succession is a chronological phenomenon, the growth of phycophyte 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 phycophyte age should be undertaken (e.g., by core extraction and identification of tree-rings, realized for instance in Achatz eosmata phycophytes in Bolivia by Ibsch 1960). Epiphyte species numbers can be plotted against branch diameter and/or branch age (e.g., in Hext & Hext-Soloff 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 impractic (e.g., binocular scanning). A promising method for long-term observations was used by Hext (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 disorientation of tree crowns and trunks. The expected life history characteristics of vascular epiphytes are discussed in detail by Bursing (1998, Chapter 5).
Selling (1980) lists the following parameters as necessary information in describing a life history strategy: 
(1) seed pool, seeding and adult mortality; (2) age of first reproduction; (3) reproductive life span; (4) fertility, i.e., proportion of individuals reproducing at a particular age; (5) fecundity (number of seeds); (6) seedling age at germination; (7) reproductive effort, i.e., allocation of resources to reproduction at 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. Diverse epiphytes are also ideally suited for experimental studies because of their relatively small size and more manageable, i.e., removal and transplantation is quite easy in many cases (e.g., Acker- man et al. 1990). A problem arises rather often when – particularly in dense epiphyte populations – it prove impossible to dislodge one individual from another. The use of "stotch" (Stanford 1985) as an operational unit is not advisable in a demographic study. Inevitably, this will reduce the number of species suited for long-term, observational population studies. In experimental demographic studies, however, this is not a complicating factor. Beringer (1984), for example, investigated the population dynamics of Tillandsia costa by feeding a representative set of epiphytes 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 counting the population afterwards (Beringer 1980). Many epiphytes may have a longer potential life expectancy than their substrates. If mortality in older plants is indeed almost exclusively due to tree falls or breaking branches, as suggested by several authors (Beringer 1990; Zotz 1995), then it is necessary to study a large number of populations for different species in long-term studies to obtain reasonable estimates of causes and rates of mortality of mature plants. In a study with the epiphytic orchid Dendrochilum engleri (Zotz, unpubl.), two out of 12 study plots (1 branches with an epiphyte population) were lost in three years. Depending on the dynamics of a particular forest, we would recommend including not fewer than 50 independent plots in a demographic study. Further- more, considering the stochastic nature of stream- line 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 meas- ured destructively, but we suggest establishing indi- vidual estimates (e.g., 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, Crowley (1990) pointed out the importance of "empty quarters" in population biology studies. Since epiphytes have to be "perospective" in space and time due to the instabil- ity of their substrate, it is important to document successful establishment at new microsites. This could be done using traps made from a source tree (Acker- man et al. 1990).

COMMUNITY ECOLOGY

An ecological "community" is the assemblage of potentially interacting species in a given ecosystem (Pianka 1994). Vascular epiphytes develop two- dimensional relations they interact not only with their phanerophytes (see above) but also with each other. The two basic processes in epiphytic inter- relationships are competition and facilitation. Com- petition in the natural forest is relatively easy to document with the help of "preservative" manipula- tions, but very difficult to prove without them (Can- nett 1980). 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 Vigna umbellata by large bromeliads) may be possible. Comparison of frequen- cies of species and individuals will lead to further insights into competitive processes. As in the analy- sis of successive stages, branch ring trunk segments of different age can partially substitute for long-term observation. Especially rewarding are comparisons of juvenile and adult plants on different branch sections (e.g., Zotz 1995). The differences in the numbers of juvenile specimens present on young branches with small diameter and mature epiphytes or older branches result from either differential ecological niches of different species or from interspec- cific 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 orchids (Davidson 1988). Some species of epiphytes
in our garden among them ferns, orchids and Avoid often present no obvious benefit to ants and act as commensals or "spatial parasites" of our garden. (Thiers & Fieseler 1988, but see Yu 1994). closer observation of succession of garden plants and typical associations under this aspect should reveal information on the use of special resources by opportunistic epiphytes. Another example are the human accumulations in some trail-bucket ferns which function as nectar beds for a number of epiphytic species (Noske 1998). In general studies on mutual facilitation of epiphytes should be conducted in areas where epiphytic vegetation is limited, allowing the distinction of clumps of indistinguishable nailing 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 & Winter (in Gradstein et al. 1980) form the necessary basis of any investigations of epiphytic diversity. Our intention was to provide additional tools for the phytogeographer in order to open some wide windows on the complex and fascinating world of epiphytic vegetation. The "guidelines for sampling" by Hietz & Winter 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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