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EPIPHYTE DISTRIBUTION IN A SECONDARY CLOUD FOREST VEGETATION; A CASE STUDY OF THE APPLICATION OF GIS IN EPIPHYTE ECOLOGY

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Resumen. Proponemos el uso de Sistemas de Información Geográfica (SIG) como herramienta para clarificar las relaciones espaciales en el complejo ambiente de las epífitas. En un caso de estudio acerca de la distribución de epífitas en un bosque secundario de alta montaña en Colombia, la posición de epífitas (incluyendo Loranthäceas), arboles, copas y sotobosque fue anotado en un sistema de coordenadas tridimensional. Estos datos forman la información geométrica base para ser usados en el procesamiento, análisis y visualización de datos en SIG (en este estudio ArcInfo y ArcView). El objetivo principal de usar SIG en este estudio fue tratar de obtener algunas medidas espaciales de las epífitas y su contorno, que pudiesen servir para responder la pregunta ecológica de cómo la disponibilidad del sustrato y factores ambientales influencian la distribución espacial de las epífitas vasculares. Nuestros datos muestran una relación entre volúmen de hojas y la cantidad de epífitas en una escala vertical. La mayoría de epífitas crecieron en el área entre el sotobosque y el comienzo de la copa. Algunas manipulaciones de los datos en tercera dimensión fueron posibles, aunque los programas de SIG tienen limitaciones en este aspecto. Verdadero SIG tridimensional probablemente estará disponible en un futuro cercano, incrementando las posibles aplicaciones de éste método. En el presente artículo discutimos las posibilidades y restricciones del uso de SIG, e indicamos tres ventajas sobre métodos no-espaciales. Primero, inspección visual y visualización de los datos que permiten reconocer patrones tridimensionales complejos. Segundo, el cálculo de relaciones espaciales lo cual permite probar hipótesis sobre la estructura espacial de poblaciones. Tercero, modelar y manejar datos en una manera formal que permita usar y compartir datos más eficazmente. El uso de SIG permitirá adelantar estudios más detallados sobre epífitas y su interacción y dependencia de su ambiente y otras especies en el dosel.

Abstract. We propose the use of a geographical information system (GIS) as a tool to clarify spatial relationships in the complex environment of epiphytes. In a case study of the distribution of epiphytes (broadly defined to include Loranthaceae) in a Colombian secondary cloud forest, the position of epiphytes, trees, tree crowns and undergrowth were recorded in a three dimensional (3D) coordinate system. These data form the basic geometric information used for processing, analysis and visualization in a GIS (in this study ArcInfo and ArcView). The primary goal of using GIS in this study was to obtain some spatial measures for epiphytes and their surroundings which could help to answer the ecological research question of how substrate availability and environmental factors influence the spatial distribution of vascular epiphytes. Our data show a relationship between crown volume and the number of epiphytes on a vertical scale. Most epiphytes were growing between the undergrowth and the tree crowns. Some 3D calculations were possible, although GIS programs have limitations in 3D data analysis. True 3D GIS is expected to become available in the near future, and will increase the possible applications of this method. We discuss the possibilities and constraints of the GIS approach and point to three main advantages over non-spatial techniques. First, visual inspection and visualization of data will allow easier recognition of complex three-dimensional patterns. Second, calculation of spatial relationships will allow the testing of hypotheses about the spatial structure of populations. Third, formalized data modelling and data management will allow epiphyte data to be used and shared more efficiently. The use of GIS will contribute to more detailed studies on epiphytes and their interaction with, and dependence on their environment and other canopy-dwelling species. *Accepted 28 December 2000.*

Key words: *Vascular epiphytes, parasites, three-dimensional spatial analysis, GIS applications in ecology.*

INTRODUCTION

A forest canopy is a complex three-dimensional (3D) environment, imposing particular problems on ecologists studying spatial patterns and processes, such as epiphyte distribution and dispersal. Epiphytes are plant species that normally germinate on the surface of another living plant and go through their entire life cycle without becoming connected to the ground (Madison 1977). Strictly speaking, this definition does not include parasites (Moffett 2000) but we use the term epiphytes loosely in this paper to include Loranthaceae. Epiphytes are a conspicuous feature of tropical forest canopies, making a considerable contri-

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bution to overall biodiversity (Gentry & Dodson 1987), and influencing ecological processes (Veneklaas 1990, Coxson & Nadkarni 1995).

The growing concern for the depletion of biodiversity in rainforests is only one of the reasons for the increased interest in epiphyte ecology. Another intriguing aspect of epiphytes is the possibility of developing cultivation methods whereby the forest is left intact and the canopy is used as a nursing chamber for commercially interesting products (canopy farming) (Verhoeven & Beckers 1999). Exploiting this environment in a sustainable manner will require a high standard of knowledge of canopy ecosystem processes and population dynamics of the species involved. Also the epiphytes' role in the life-cycle of disease vectors, such as tank-bromeliads housing mosquito larvae (Pittendrigh 1948, Frank 1983), emphasizes the need to gain a better understanding of the ecology of these plants.

The patchy and dynamic character of the epiphyte habitat causes patterns of epiphyte occurrence to differ from those of terrestrial plants (Bennet 1986). The inaccessibility of forest canopies has been one of the reasons why these patterns have been largely understudied compared to those in terrestrial species. The development of canopy access systems has now taken away this limitation in many cases, and has allowed for a rapid increase in the number of epiphyte studies over the past twenty years (Nadkarni & Lowman 1995). A need remains though for the development of sampling strategies and data processing methods that capture the complexity of the epiphyte environment.

Epiphyte studies have covered a wide range of topics, such as the composition of the epiphytic vegetation, habitat requirements, population dynamics, plant physiology, and interactions with other biota (e.g., Benzing 1990). Many of these studies have a spatial component in their sampling and data analysis, or at least suggest this to be important. Defining and describing spatial positions, however, proves to be a difficult task, which has been approached in many different ways. In most of these approaches the epiphyte positions are related to the substrate, and measured either in relation to position in the phorophyte (host tree) (e.g., Johansson 1974, Ter Steege & Cornelissen 1989, Wolf 1993, Freiberg 1996) or to branch sizes (Rudolph *et al.* 1998), tree species (Migenis & Ackerman 1993), bark roughness (Kernan & Fowler 1995), or other substrate characteristics.

Although all these factors may be ecologically relevant, such an approach does not describe positions in space, and may obscure alternative patterns. A widely used zonation scheme is that of Johansson (1974), which divides the tree into stem-base, stem, inner crown, middle crown and outer crown. A recent paper reviewing the available methods for ecological studies of epiphytes concludes that this zonation-scheme 'can only be a rough abstraction of real distributions ... and can be used as a model to be tested until computer-based three-dimensional analysis tools allow much more elaborate analysis in the future' (Nieder & Zotz 1998). Apart from an analysis tool, what seems to be missing is a systematic, repeatable method to measure, store, and present thematic and spatial information about epiphytes and their environment, including the amount of substrate available for epiphyte settlement (Nadkarni & Parker 1994). We have developed such a method using a geographical information system (GIS). To get a realistic model of epiphyte positions in canopies they should be placed in a 3D space, where environmental factors differ in all directions. Unfortunately, most of the commercial GIS software is not designed for real 3D analysis at the moment, although 3D visualization is becoming a common facility. However, the existing two-dimensional (2D) applications can be used to analyze 3D data to a certain extent.

This paper describes problems and solutions related to this GIS approach, including a discussion of data requirements and alternative sampling strategies. The general objective of the case study project was to study the influence of substrate availability and environmental factors on the distribution of vascular epiphytes in a secondary cloud forest in Colombia. Our first aim was to create a GIS database for the set of epiphyte data. This database should be able to return some spatial measures that are of ecological interest but were not measured in the field. These are the distances between epiphytes, the spatial relation of epiphytes to the surrounding vegetation, and the vertical distribution of epiphyte substrate. Our second aim was to create 3D images of the epiphytes and their environment, for visual inspection and presentation.

RELATIONAL DATABASES AND GIS

Some concepts of relational databases (Codd 1970) and GIS are introduced briefly here, explaining the terms used in the text. A GIS is basically a database system including a spatial component, on which spatial operations and queries can be performed. A GIS is defined in different ways, ranging from only the software for processing spatial information, to the complete field of geo-information science, including the organization, standards, people, and techniques (Heywood *et al.* 1998). In this study it is most suitably defined as software for managing spatial data, in combination with the data-handling methodology (for a general introduction on GIS, see Heywood *et al.* 1998).

An object can be defined as an instant of an object-class, e.g., a tree (one of the trees), an epiphyte, or an epiphyte-growing site. Usually this is a row in a table, and the columns are the object-attributes. Each object should be uniquely identifiable. The attribute(s) that safeguard this uniqueness are called the primary key. The objects can be related to objects from other object-classes (tables). These relationships can be one-to-one (e.g., a bromeliad ramet has one infloresense, and each inflorescence stems from one ramet only – these relationships usually ask for merging of the two tables), one-to-many (e.g., a tree can be inhabited by many epiphytes, but an individual epiphyte only lives on one tree), or many-to-many (e.g., one tree species can host more than one epiphyte species, and each epiphyte species can grow on more than one tree species). The latter relationship needs to be modelled with an 'intersection-table', containing all the existing combinations of, in the example, tree species and epiphyte species. Information is retrieved from the database by means of queries, for example 'which epiphyte species grow on tree species X?' or 'how many tree species host epiphyte species Y?' (for more information on querying and databases, see Elmasri & Navathe 1989, Date 1995, Watson 1999).

Two basic storage-structures are used in GIS. The first is called a field approach, and is based on a grid (also called lattice or raster). Attributes of the quadrats determine what property is present at any one location. The second storage structure, the vector structure, is based on the definition of objects (object-oriented or object-structured approach). The data on objects is divided into two parts: the thematic data and the geometric data. The thematic data (e.g., names, functions, values) is stored as attributes in tables, while the geometric or spatial data is stored in geometric files. The geometric information in both the field approach and the object-oriented approach has three aspects: position, shape and topology (relationship to other objects) (Molenaar 1998). Geometric GIS files are not graphic files, but can be used to create graphics, such as maps.

FIELD METHODS

The data set used was gathered in 1998 during 4 months of fieldwork in Colombia. Plots were laid out at c. 3000 m altitude, on the western slopes of the Cordillera Central (N 04° 50'17", W 75° 30'14"), in a twenty-year-old, secondary open forest on deserted pasture (Fig. 1). This area was selected because of its accessibility, its high abundance of vascular epiphytes, low stature, and structural heterogeneity. Trees reached up to 8 m in height, allowing species identification and precise mapping from the ground. The heterogeneity applies to the density and average height of the undergrowth and trees in the study area, and allowed for comparing epiphyte occurrence in different forest structures.

Eleven 5 m x 5 m non-adjacent plots with various vegetation structures were selected so as to include the widest range of density and height for trees and shrubs in the undergrowth. The plot borders were positioned north-south and east-west using a compass, the wes-

FIG. 1. A side view of plot B shown as an example of the forest structure in the study area. The arrows point to some of the bromeliads present.

tern border defining the X-axis and the northern border the Y-axis. Epiphytes, trees, and undergrowth were mapped according to their position in relation to these two axes. Height above the ground (z_g) of epiphytes and the top of trees and undergrowth constituted the measure used to calculate the z-coordinate in the orthogonal 3D coordinate system used in the GIS (see section on pre-processing below).

XY positions were determined by visually projecting the objects perpendicularly to the borders, which were subdivided into meters by sticks, leaving the remaining divisions to be estimated. Precision on both the xy plain and the z axis is c. 10 cm. The latter (z_g) was measured using a bamboo pole with 10-cm divisions.

Tree crown-projections were mapped. The crown data also included the height of the crown top and vertical extent of the crown foliage. For description of the undergrowth each plot was subdivided into 1 m x 1 m quadrats. An additional strip of 1 m x 1 m quadrats was laid out around the plots, in which only vegetation variables were recorded, to avoid edge effects in later analysis. The height of the undergrowth was taken as an average per quadrat. Some plots were not level, and one plot had a gully running through it. These differences in ground level were recorded with the aid of a level on a rope, along the plot borders. Apart from these spatial data, thematic variables of all objects were recorded (e.g., species, size, life-stage).

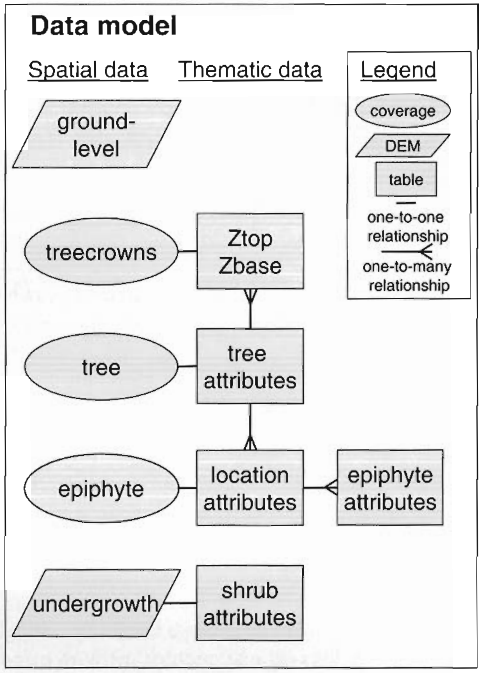


FIG. 2. Outline of the data model used in this study, clarifying the relationship between data in different tables. All spatial features are linked through their position in a common coordinate system. DEM is an abbreviation of Digital Elevation Model.

DATA PROCESSING

The process of entering and using data in GIS was divided into several phases, as outlined below. The software packages used for data storage and analysis were ArcInfo (version 7.2.1., Esri) and ArcView (version 3.2, Esri). Pre-processing was performed in ArcInfo because of its extensive functionality. ArcView was used for the analysis and visualization. Two extra ArcView extensions, Spatial Analyst (version 1.0, Esri) and 3D Analyst (Version 1.1, Esri), were used for handling the grids (quadrat data) and the 3D graphics respectively.

Pre-processing. In the pre-processing phase, the raw data were put into the correct GIS format, and the database was constructed. All the plots have a separate data set with the same structure (Fig. 2). Tables were stored per plot, because the software package used (ArcInfo) cannot handle composite keys (two or more attributes forming a key together, in this case plot-id and id within plot). Because more than one epiphyte could be growing at a site, the site data and epiphyte data were stored in separate tables, with a one-to-many relationship between them (Fig. 2).

Epiphyte positions and tree-bases were stored in a vector file ('point-coverage' in ArcInfo). The drawings of crowns were scanned, transformed into the correct plot-coordinate system, and digitized. This resulted in a polygon-coverage with polygons representing crowns, or sometimes parts of crowns or overlap-areas. These polygons were joined into regions that represented whole crowns (Fig. 3a).

As only 2 dimensions are supported in ArcInfo coverages, the third dimension, i.e., the height, was stored as an attribute in the thematic tables. From here it was used in 3D calculations. However, some problems did arise when reducing 3D space to 2 dimensions. Objects that differed only in their vertical location ended up having the same position in the 2D representation, as was the case with the tree crowns. Distinguishing these objects from each other in spatial queries, however, was possible after some adaptations (see Analysis). Apart from the height values, the thematic tables contained the measured thematic attributes of the objects.

The height values of the objects had to be transformed to values with a common reference plane, because the ground surface was not level within the plots (Fig. 3b). Using the ground-level measurements as input, a digital elevation model (DEM), a grid containing height values, was created of the ground surface. The ArcInfo DEM-building module Topogrid was used for the interpolation between the measured points.

All height measures were corrected with the help of the ground DEM. The position of a tree stem was projected onto the ground DEM. The height value of the DEM in this point was used as a correction factor, which was applied to epiphyte and crown heights to produce a corrected height attribute. This could be done because the values for the height of epiphytes within a tree were always related to the values for the height of the other epiphytes in that tree. With a different measuring method, where all epiphyte heights are measured relative to the ground, each epiphyte would have to be corrected individually. In this study this was only necessary for those epiphytes that were not growing in trees.

The undergrowth characteristics were assigned to the center-points of the 1 x 1-m quadrats. The height of these points was also corrected with the ground DEM, and a new DEM was created by interpolation of the corrected height values. Topogrid was not used here because it emphasizes hydrological terrain properties, which is not a good representation of an undergrowth surface. Instead, a simple weighted-distance interpolation was used, estimating the parameters by judging the appearance of the output grid.

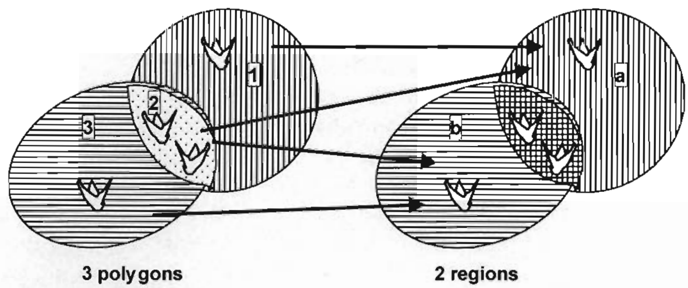
Data-action models. In GIS it is good practice to capture the data processing in so-called data-action models or flowcharts. In these schemes all data processing steps are represented, thus preserving the processing knowledge, allowing for easy comprehension and repetition with other data or parameters. There are even special programs (e.g., Arisflow, Aris 1999) to create such flowcharts and manage execution of the processes all in one. Flowcharts for the data processing of this project can be found at the URL (http://cgi.girs.wageningen-ur.nl/cgi/products/epiphytestudies/ABSTRACTepigisart.htm).

ANALYSIS AND RESULTS

A total of 1537 angiosperm epiphytes was found in the 11 plots, belonging to the families Bromeliaceae (894 individuals), Orchidaceae (364 individuals), and Loranthaceae (73 individuals). Identification to species, or even genus, could not be made for all epiphyte individuals. Especially orchids and small seedlings (< 5 cm) of the other groups were difficult to identify. The bromeliad species found were *Racinea tetrantha* (Ruiz & Pav.) M.A. Spencer & L.B.Smith, *Racinea penlandii* (L.B. Smith) M.A. Spencer & L.B. Smith, *Tillandsia compacta* Griseb, and *Tillandsia* sp. Circa 96 % of all Bromeliaceae were identifiable to one of these species.

The position of epiphytes relative to the vegetation. Several distance measures of epiphytes relative to crowns were compared (Fig. 4). To combine epiphyte positions and crowns, a graphical overlay was used in Arcview (Fig. 3c). This technique places the map of the crowns on top of the map of the epiphytes, so that it is known for each epiphyte within which crown it lies on the xy-projection. This is a straightforward analysis as long as an epiphyte is situated under one crown only. In this study many epiphytes were situated in overlap areas, resulting in epiphytes in two or more crown regions (Fig 3a). This multi-valued result caused problems in the overlay (Fig 3c). The GIS program can only return one region per epiphyte, and which of the overlapping crowns is chosen is determined by the order in which the regions are stored in the coverage file, an order which cannot be changed. However it is unambiguous which polygon the epiphyte is situated in, and this has to be used to perform the overlay. The thematic data is only attached to the regions, but the polygon can be assigned the values of the crowns. Again, this is a many-to-many relationship (many polygons form a region, and a region consists of many polygons). As the coverage tables cannot be sorted, there is usually no control of the assignment of values of a region to a polygon. By sorting the intersection table (which connects the polygon and region tables) on the basis of the values in the region table, this could only be controlled to a certain extent. At least in this way the values from the crown with the highest top and those from the crown with the lowest base, the two most interesting measures in this case, could be assigned to the polygon table, and thus to the epiphytes. Simple subtraction ($z_{crowntop} - z_{epiphyte}$ and $z_{crownbase} - z_{epiphyte}$) then gives the distance between epiphytes and crown top and base (Fig. 3c).

Overlapping crowns:



polygon-table:

poly-id	shape	area
1	poly	1.4
2	poly	0.4
3	poly	1.2

Intersection-table:

poly-id	region-id
1	a
2	a
2	b
3	b

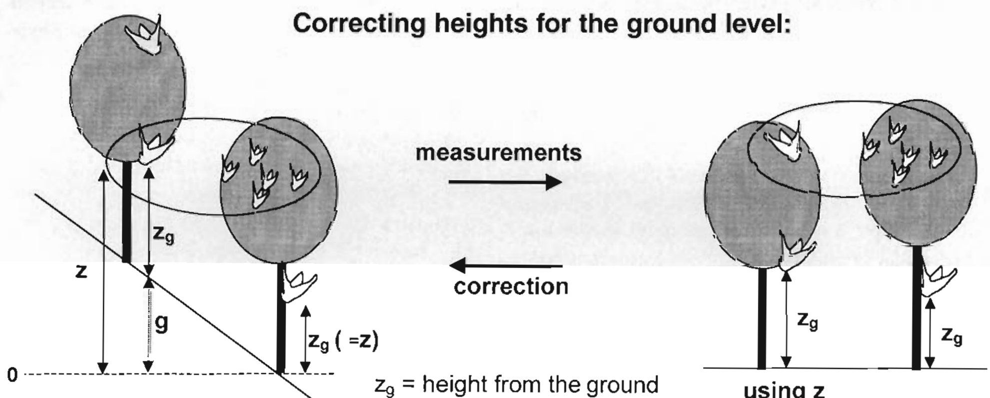
Region-table:

region-id	area	tree-species	DBH	Ztop	Zbase
a	1.8	Clethra sp.	8	6.2	4.4
b	1.6	M. thaezans	4	4.0	3.2

Polygon-table X with double attributes from the region table

poly-id	region-id	region-id2	Ztop	Ztop2	Zbase	Zbase2
1	a	a	6.2	6.2	4.4	4.4
2	a	b	6.2	4.0	4.4	3.2
3	b	b	4.0	4.0	3.2	3.2

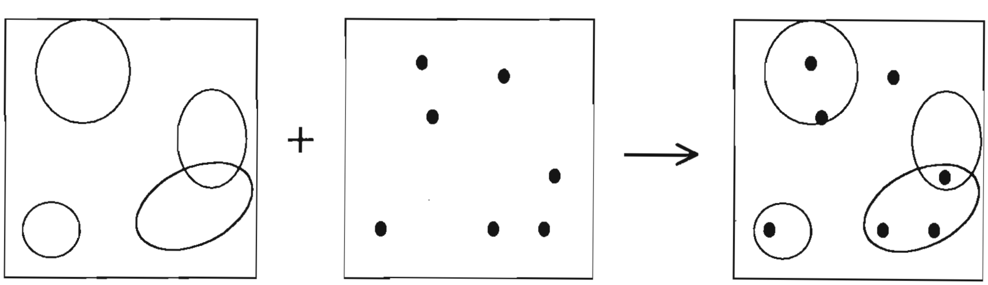
Correcting heights for the ground level:



z_g = height from the ground

$z_g + g = z$ = height from 0

Overlay:



Distances of epiphytes to the undergrowth surface were calculated using the undergrowth DEM. This gave the height of the undergrowth under/above each epiphyte. The subtraction formula in this case was $z_{epiphyte} - z_{undergrowth}$, negative values implying a position inside the undergrowth (Fig 4).

Comparing height measures. The three aditional height measures mentioned above, as well as the distance above ground, were normally distributed (D'Agostino test, Zar 1999) in nearly all plots individually, as well as in the pooled data of all plots. Only the distribution of heights above ground did not have a normal distribution in two of the plots. The distribution of the height values of the pooled data (all epiphytes) was more leptokurtic than the other measures (a kurtosis of 1.2 compared to 0.2 for distance under crown top, 0.3 for distance under crown base and 0.5 for height above undergrowth, see also Fig. 7).

The distribution of crown volume and substrate. The height distribution of foliage volume, i.e., undergrowth and tree crowns, was estimated for each plot. The volumes were calculated per 1-m layer, the division of the layers being parallel to the ground surface. All space between ground surface and undergrowth surface was considered to be filled with shrubs. The volume of a crown was modelled as a box: the ground projection multiplied by the measured thickness. For every layer, the amount of space under the undergrowth and the amount of crown-box volume were calculated. The correlation between the amount of foliage volume and the amount of epiphytes was determined using Spearman's rank correlation, per plot, per layer within a plot, and per layer of the same height between plots, but no significant correlations were found ($\alpha = 0.05$). The distribution of foliage volume is shown in Fig. 8.

Differences of substrate availability between plots do have some influence on epiphyte numbers. A significant correlation was found between basal area and the number of epiphytes ($P < 0.01$). Total foliage volume per plot was not significantly correlated with epiphyte numbers, nor was the volume per layer, between plots, at most heights. However, in the most epiphyte-rich layer (1–2 m from the ground) such a correlation was found ($P < 0.05$).

GIS graphics. A 2D representation of the data is easily created from the spatial files (Fig. 5a). However, a more informative presentation can be given if the data can be viewed three-dimensionally (Fig. 5b). 3D graphics were created using the ArcView 3D Analyst extension. This allows for the addition of height values (present in the thematic tables) to the spatial files, creating 3D spatial files (called shapeZ-files in ArcView). Although these cannot be queried three-dimensionally, they can be represented graphically. Epiphytes were represented as points. The legend symbols can be set by any attribute in the epiphyte table, e.g., species or size. The crowns were drawn as the 'ground-projection' lifted to the height of the crown base and extruded to form a cylinder with the measured crown thickness. The ground and the undergrowth were represented as 3D surface models.

Drawing the stems and branches of the trees was slightly more complicated. These were not measured optimally in this research because no branching-points were recorded. Still, even with the limited number of

FIG. 3. (a, top) Relationship between the polygons and the regions of the tree crowns. The two epiphytes in polygon 2 are situated in two overlapping regions. Since only one of the regions can be associated with an epiphyte, the height values from the region table cannot be compared with the epiphyte data directly. To do this, we had to add the thematic data to the crown polygons. Polygon 2 should receive data from both regions, and this could not be done automatically. The intersection table was first sorted using the attribute Z_{top} (height of the top of the crown). Then, the first region encountered in the intersection table (highest crown) was used to assign the region attributes to the polygons. Next the intersection table was sorted again, in descending order, using Z_{base} (height of the base of the crown), and the region attributes (with a suffix to distinguish them from the previous attributes) of the lowest crown were assigned to the polygons, resulting in polygon table X. (b, middle) The effect of a change in ground height on the relationship between spatial position (x,y,z) and measured height (z_g). This effect is corrected by adding the ground height (g), relative to a base (0), to the measured height ($z_g + g = z$). (c, bottom) The concept of an overlay operation. Two geometric files are combined (as if maps were put on top of each other), and a new table created, so that the mutual relationship between the objects in both files becomes clear.

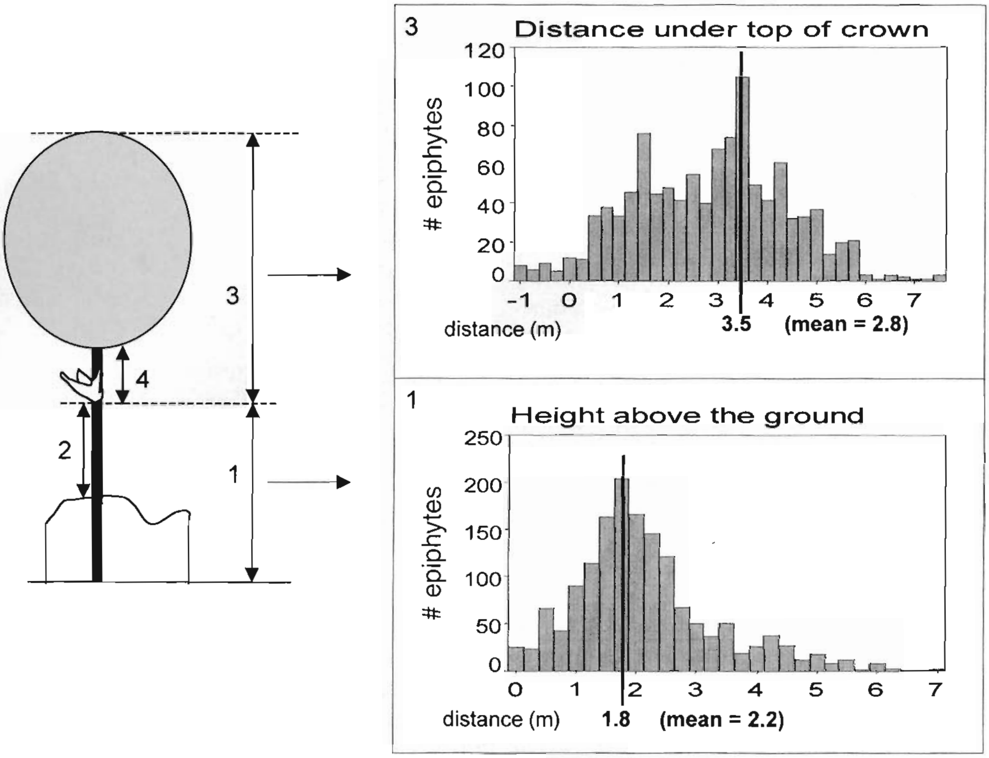
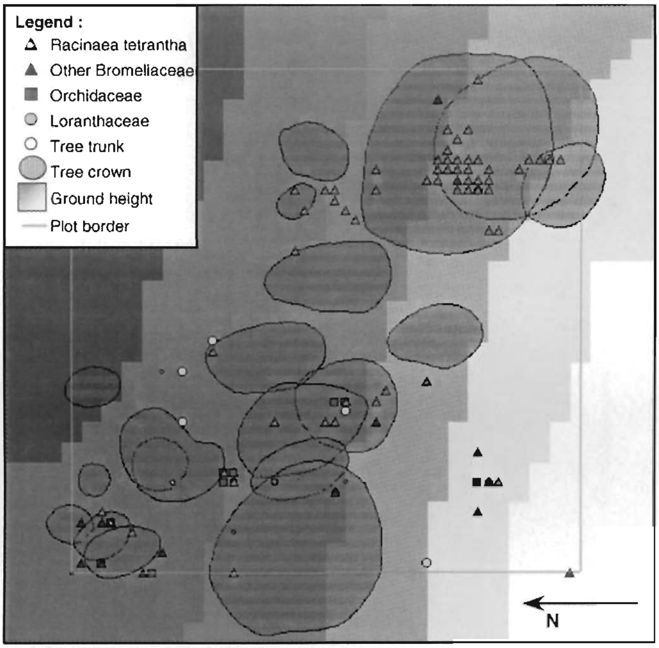


FIG. 4. Four height measures. 1 = height from the ground, 2 = height above the undergrowth, 3 = distance under the crown top, 4 = distance under the crown base. The histograms show the distribution of all the epiphytes recorded in all plots.

parameters taken, lines could be drawn to represent the trunks and main branches. The trunk is represented by a line between the position of the tree on the ground and the center of the corresponding crown. If a tree has more than one crown, 'branches' ending in the crown centers are connected to the trunk at a height of the crown thickness under the crown base (Fig. 6). Diameter at breast height (DBH) and tree species were used to set the line properties. These lines, unlike the former shapes, are only graphics; they exist only in the illustration and not in a spatial file. The ArcView-script used, and the 3D graphics, can be viewed at the URL mentioned above.

DISCUSSION

Height distributions. Height above the ground is nearly always found to be an important factor for epiphyte occurrence (e.g., Pittendrigh 1948, Wolf 1993, Serna Isaza 1994). However, the environmental conditions that determine the occurrence of epiphytes high in the crown may also prevail elsewhere in the forest. High light intensities at forest edges, or at canopy valleys (Herwitz *et al.* 1994), can allow canopy epiphytes to occur down to ground level, if the right substrate is found there (De Granville 1978). The frequently used tree-zones, after Johansson (1974), are also based on structure rather than height from the ground. Height above the ground may not be the most ecologically relevant measure for describing epiphyte height. A better alternative is the distance from the top of the crown, or one of the other vertical measures calculated (distance to crown base and undergrowth, Fig. 7). The most relevant distance measure will have a narrower, i.e., more leptokurtic, distribution and a lower variability across different vegetation structures (i.e., the sampled plots). In this study the alternative height measures should therefore not



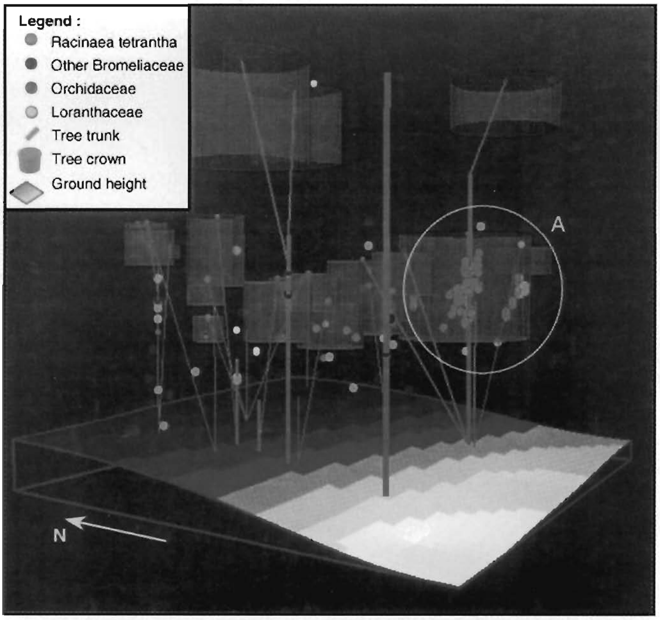


FIG. 5. (a, top) 2D and (b, bottom) 3D graphical representation of plot A. Arrows indicate north. The undergrowth DEM is left out here because it made the picture less clear. Individuals of *R. tetrantha* are shown as turquoise dots, and a cloud of this species is indicated at A. For dynamic views of 3D colour images see URL (http://cgi.girs.wageningen-ur.nl/cgi/products/epiphytestudies/ABSTRACTepigisart.htm).

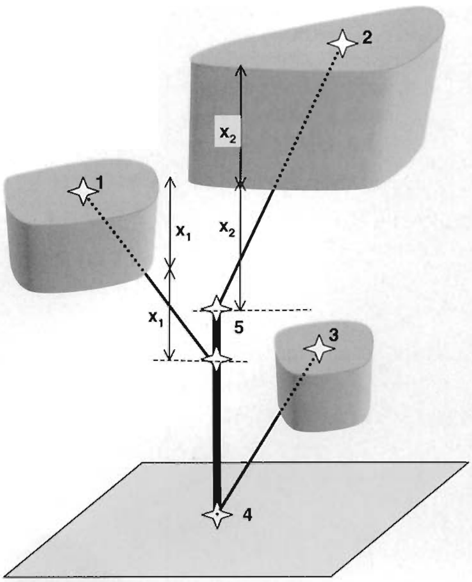


FIG. 6. The rules applied for drawing the trunk and main branches in FIG. 5b. The trunk is represented by a line between the position of the tree on the ground (4) and if, as in this example, a tree has more than one crown, 'branches' ending in the crown centers (1 and 2) are connected to the trunk at 5, at a height of the crown thickness x under the crown base. If only one crown is present, or if the crown is less than 3 m high, the stem is drawn directly from the ground (4) to the crown center (3).

replace height from the ground as the best measure for expressing vertical epiphyte positions.

The spatial relationship of the epiphytes to the surrounding vegetation was only investigated in the vertical direction, because of practical constraints. Although this does not fully consider the structure of the vegetation, even these simple measures do give an additional dimension to the information on epiphyte position. True 3D GIS could easily return distances in any direction, including the shortest distance to the crown periphery.

The transition of height values from height-above-ground to height-above-a-horizontal-plane has not produced any direct research results, but has made sure that the spatial data were correct. It is an operation that makes the method independent of the geomorphology of the research area, and thus more universally applicable.

Distribution of crown volume and substrate. It seems that the mean epiphyte height does not correspond with an increase of crown volume (Fig. 7a and Fig. 8). This observation is supported by the absence of significant correlations between substrate and epiphyte quantities per layer in any of the plots. In fact, the mean and optimum of epiphyte occurrence lie above the undergrowth and under the crowns (Fig. 4), so most epiphytes grow in a relatively open area (*cf.* Fig. 5a). The quality and age of the substrate may be one factor influencing the position of epiphytes. However, environmental factors such as light, moisture availability, and wind (seed supply) are also likely to play an important role (Bader 1999).

The effect of substrate availability (basal area) suggests that the number of available seeds was not the main limiting factor for successful establishment of individuals. Increased moisture availability stemming from the evapotranspiration of the undergrowth may have been the most important factor determining the position and local abundance of epiphytes.

Describing spatial patterns. Sampling epiphytes in predefined tree-zones (Johansson 1974) can improve the comparability of data from different sources, but the position of ecologically meaningful zone boundaries will differ between forest types (Nieder & Zotz 1998). Dickinson *et al.* (1993), who mapped all epiphyte communities on an emergent tree (drawing the tree with the communities on it), could confirm the zonations in epiphyte communities only for the outer canopy, while the inner canopy showed complex patterns.

Registering epiphyte positions independently of any presumed zones or categories, purely spatially, may be one method to overcome the limitations of zonation systems, especially with the development of methods to link various ecological parameters to the sites in GIS. If the position and shape of the phorophytes is stored in the same 3D coordinate system as the position of epiphytes, the data can still be translated to a zonation system. In this way comparisons can be made with data from previous studies.

When studying epiphyte clustering within one or a few trees, the distribution of the substrate becomes an important factor, but one that is difficult to describe or quantify. The primitive tree model used in this study (a wide cylinder on a narrow cylinder) would not suffice for most detailed analyses. More advanced tree(-shell) models have been developed, like that of Koop (1989). Such a model could also be very useful in making more precise estimations of substrate (branch surface) quantities. A more detailed quantification of foliage distribution, such as the method for measuring vegetation occupancy by Van der Meer (1997), is recommended.

An alternative method for analyzing spatial patterns of epiphytes, on a detailed scale, was described by Hazen (1966), who considered the spatial distribution as distances along a branch. He transforms the branch to a straight line by inserting the length of side branches at the points where they branch off, and then analyzes the randomness of epiphyte distribution by their position on this line. However the assumption necessary for this one-dimensional approach, 'that interaction occurs along a branch, not between neighbouring branches...' (Hazen 1966), does not seem justified. Vester & Gardette (1996) proposed 'three-dimensional mapping', mapping 'large individuals ... individually and patches of small individuals or colonies ... by indicating form, extension and position of the patch.' Unfortunately this method is not described in sufficient detail, leaving unclear whether a truly 3D mapping method has been developed, or whether 2D maps of the tree-shape (see also Dickinson *et al.* 1993) are meant, and in what way these maps are to be analyzed. The use of GIS is a promising approach for performing such mapping in practice.

Possibilities other than GIS. Using GIS was not the only option for the epiphyte information system, but it was the most suitable type of software for this application. For graphic representation a wide range of

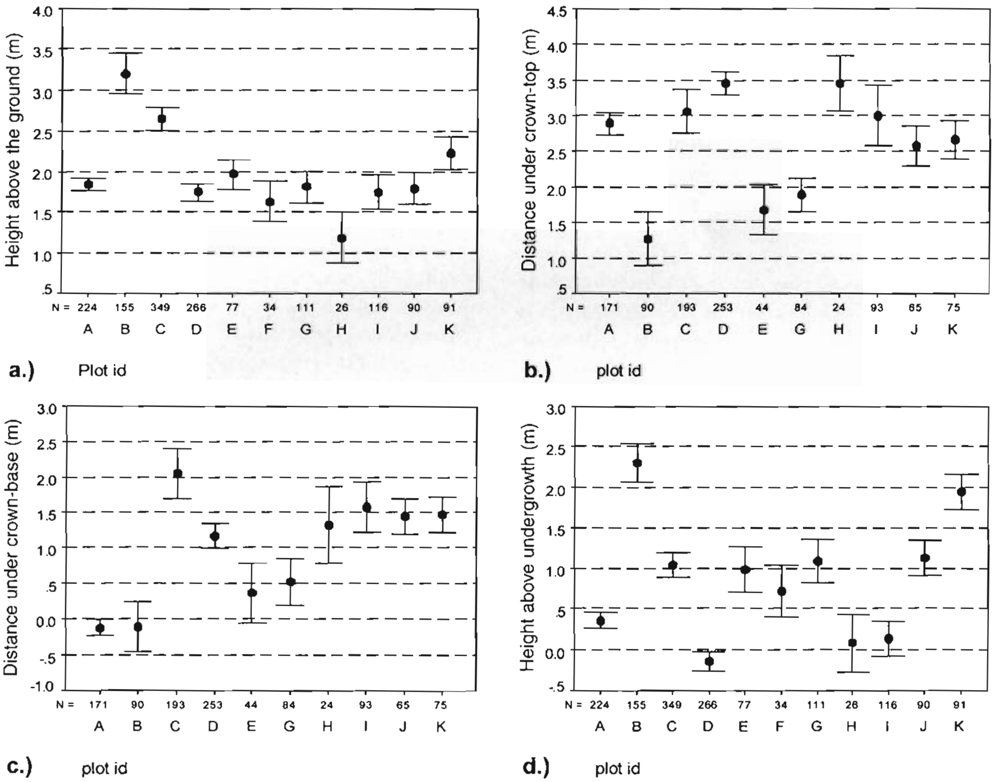


FIG. 7. Mean and standard error of the height of epiphytes in each plot. a) Height from the ground, b) distance under the top of the crown, c) distance under the base of the crown, d) height above the undergrowth. Less epiphytes are included in graphs b and c because not all epiphytes were found underneath crowns. In plot F, no epiphytes were found under crowns.

software is available, also for 3D objects. However, these applications generally lack the possibilities for spatial operations and extensive querying, and are therefore not suitable for statistical analysis of the data, which is usually the primary objective.

Some applications have been developed for specific 3D spatial analysis. An interesting example is the program FOREYE (Koop 1989), which simulates hemispherical photographs from a modelled forest consisting of crown shells. These simulations give an indication of the light climate at a certain position in the forest, which is valuable information for plant-growth studies. However, these specialized programs have a limited array of possibilities, as well as strict input requirements, and are therefore not suitable for a general information system.

There may be some confusion about the mentioned absence of real 3D functionality in GIS. 3D views of landscapes can be created from surface models in most GIS packages, and analysis functions for such surfaces also exist. However, surface models are only $2^1/_2$D, i.e. only one Z value can be present at every xy-coordinate (Heywood *et al.* 1998). They are suitable to represent single surfaces, such as ground levels, but it is clear that this restriction makes it impossible for such a surface model to give a detailed representation of a forest canopy.

Graphical representation. The possibility of creating 3D maps can be important for the data analysis as well as the presentation. Studying epiphyte clustering quantitatively is difficult. However, by examining the field data in a virtual view, looking at a plot from different angles without interference from the vegetation, patterns in the spatial distribution of the epiphytes may become apparent (Fig 5b). In a way, this is just a modern 3D variety of the classic methods used by early researchers like Pittendrigh (1948). Drawing epiphytes in trees and forests by side views can provide considerable insight into epiphyte patterns. However, a good side view is difficult to obtain in many forests and the method is 2D, with all the restrictions of such a reduction in dimensions.

Presenting data is an important phase in any research, determining to a great extent the way the results are appreciated. 3D pictures can provide clarifying illustrations with research results. As an example, Fig. 5b clearly shows a clustering of *Racinea tetrantha*, in this case a cloud of juveniles around a large adult, the presumed parent.

Sampling and data requirements. The data requirements of a GIS depend on both the research questions and on the models used. Tree models especially should be considered carefully before data are collected. Detailed studies may require data on individual branches (branching point, main vertices (bending points) and tip, thickness at different lengths), while less detailed studies, such as this one, may only need the shape of the crown shell (see Koop 1989).

In this study we registered the height of the undergrowth by estimating an average for each quadrat, but, although interpolating block averages is a valid method, this approach smoothes extreme features and results in a loss of information. We therefore recommend measuring undergrowth height at specific points, such as highest and lowest points and points close to drastic changes, although this has to be designed carefully because it may introduce a bias to the sampling. It is not necessary to space these point regularly.

Of course there are also circumstances where sampling cannot be optimal because of insufficient knowledge of the system under study. In this research, the sampling plots were too small to effectively study species clustering. Although some small-scale clusters were recognizable (see Fig. 5b), the effects of dispersal distances could not be distinguished. In larger plots however, registering each individual epiphyte is impractical. If clustering of species is being studied, counts of epiphytes in small sub-plots could yield sufficient information to distinguish these patterns, and storage in GIS on this scale would be most appropriate in a grid format (VanDunné, unpublished data). 3D grid environments, with volume pixels (voxels) (Raper & Kelk 1991), could be a worthwhile tool in this approach, although affordable commercial packages are as yet unavailable.

Monitoring. The systematic and repeatable traits of the methodology make GIS a useful monitoring tool, allowing for repeated sampling of epiphytes in permanent plots, for instance in deriving demographic population parameters. In cases where epiphytes cannot be labelled (e.g., if they are out of reach), such monitoring can be complicated if epiphyte positions cannot be measured unambiguously. The dynamic character of trees can cause confusion if trees are used as a reference to define positions. A 3D coordinate system does not cause such problems, and should be defined in the field and in the data by a position (some fixed marker) and a measurable direction (e.g., north-south, east-west). When registering plant development, measurements should be such that epiphytes that are close together can be repeatedly recognized as individuals, also if neighboring plants disappear in the course of time. The 2D and 3D graphics can also serve as an aid in the field for recognizing individual plants.

Conclusion. Even with the present limitations, the application of GIS in epiphyte studies offers three important advantages over methods which are not spatially explicit. First, visual inspection and visualization of data allow easier recognition of complex three-dimensional patterns. Second, calculation of spatial relationships allows the testing of hypotheses about the spatial structure of populations. Third, formalized data modelling and data management allow epiphyte data to be used and shared more efficiently. The use of GIS will facilitate more detailed studies on epiphytes and their interaction with, and dependence on both their environment and other canopy dwelling-species. In the future, real 3D GIS will almost certainly become available (Raper & Kelk 1991, Hack & Sides 1994, Breunig 1999), adding many extra possibilities to the method presented here.

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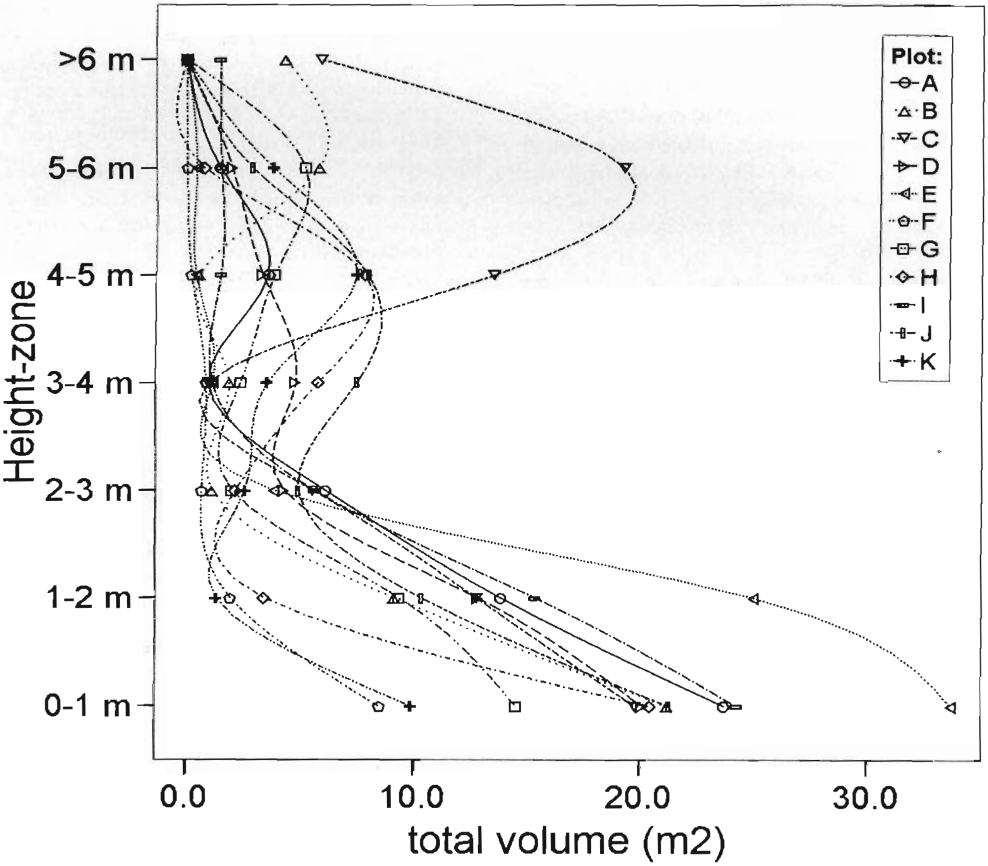

FIG. 8. Volume of the vegetation at different heights in the plots, measured per 1-m layer.

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