STUDIES ON COLOMBIAN CRYPTOGAMS XX
A TRANSECT ANALYSIS OF THE BRYOPHYTE VEGETATION ALONG AN ALTITUDINAL GRADIENT ON THE SIERRA NEVADA DE SANTA MARTA, COLOMBIA

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SUMMARY

Along an altitudinal transect on the northern slope of the Sierra Nevada de Santa Marta, Colombia, 500–4100 m, five altitudinal bryophyte zones are distinguished – four forest zones and one páramo zone – based on ecosystem relevé analysis concerning species presence, substrate preference and percentage cover of bryophytes. Relevés were compared by using Sørensen's Index of Similarity and a simplified dendrogram technique, and zonation diagrams were constructed. Bryophyte zonation seems primarily correlated with climatic factors (precipitation, air temperature) as preliminary data suggest. Species presence and cover percentage appear to be of almost equal significance in distinguishing the different bryophyte zones of the tropical forests and are highest in the so-called "condensation zones". Work continues on other altitudinal transects in the Colombian Andes, in the framework of the ECOANDES project.

1. INTRODUCTION

This paper deals with the bryophytes along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia and forms part of an integrated ecosystem analysis of an altitudinal transect in the area, in the framework of the ECOANDES-project (Van der Hammen et al. in prep.). The prime goal of our investigation was to analyse the changes in bryophyte flora and vegetation in relation to altitude and to determine the altitudinal zones.

The Sierra Nevada de Santa Marta is an isolated, high-altitude mountain island situated in the dry coastal plain of northern Colombia. Its twin peak of 5776 m, only 48 km from the Caribbean coast, makes it the highest summit in Colombia and the highest coastal mountain in the world (Uhlig 1966). In the west the massif is bordered by the lowland swamps of the Magdalena plain and in the east and south by the semi-arid Guajira Peninsula and the Cesar valley, respectively.

The climate of the area is strongly influenced by the north-atlantic high-pressure cell, the southwestern portion of which extends to the southern Caribbean (Hermann 1971). Resulting northeastern winds blow almost continuously during the greater part of the year. In the period April-November the nucleus of these winds lies above the northern Caribbean, following the movement of the

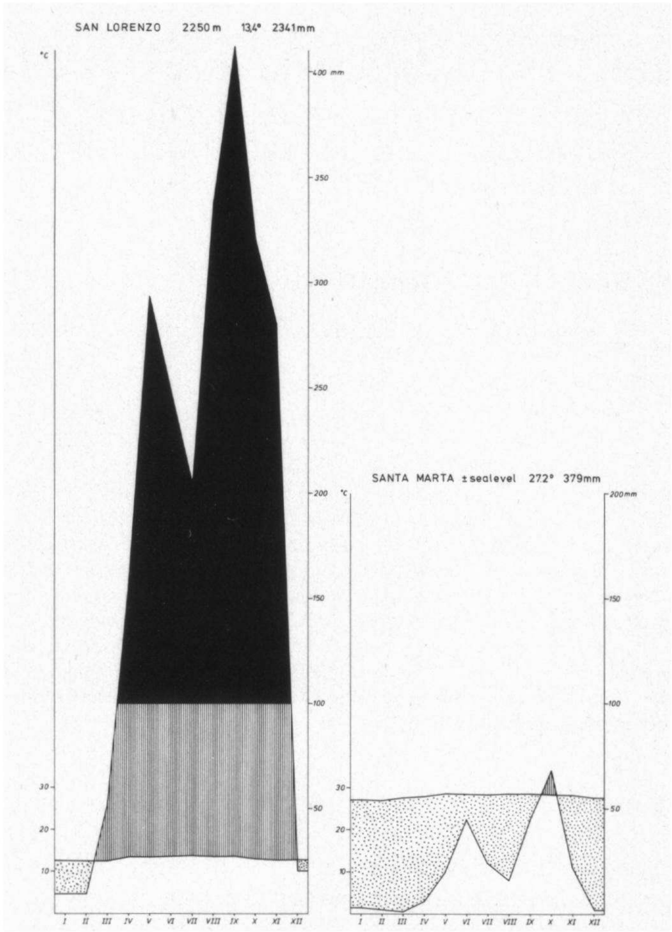

Fig. 1. Climate diagrams of the Sierra Nevada de Santa Marta area, showing differences in rainfall at the coast and at 2250 m (for explanation see WALTER 1970).

axis of the high-pressure cell to the north. High wind-velocities occur here from the earth surface to the higher troposphere. In the area of the Sierra Nevada winds have a much lower velocity and ascending air movements predominate. It is in this period that precipitation is high. From the end of November until March the nucleus of the northeastern winds lies in the southern Caribbean, in the lowermost layers of the troposphere, following the movement of the axis of the high-pressure cell southwards. A strong descendence of air movements results, preventing any rainfall. The annual rainfall distribution in the area is shown in *fig. 1*.

The north-south running altitudinal transect was located on the northern slopes of the massif: from 500 m up to 3300 m on a sharp ridge surmounting the Río Buritaca, and from 3300 m to 4100 m on the watershed of the upper headwaters of the Río Frío and the Río Diego. Orographic winds are responsible here for an almost permanently high atmospheric humidity and excessive rainfall during the greater part of the year.

Bryophytes are generally considered as important bioindicators marking climatic characteristics of the environment (cf. PÓCS 1982). Yet, papers describing altitudinal bryophyte zonations in the tropics are scarce (cf. PÓCS 1982, GRADSTEIN & WEBER 1982, BOWERS 1970). This is largely due to the as yet incomplete knowledge of the tropical bryophyte flora. Generally, altitudinal zonations in the tropics are based on phanerogams. For example, SEIFRIZ (1924) described the bryophyte and lichen distribution on Mt. Gedeh, Java in some detail, but the altitudinal zones were determined solely by one or more characteristic phanerogams. Similarly, his description of the altitudinal vegetation zonation of the Sierra Nevada de Santa Marta in Colombia (SEIFRIZ 1934) was based on prevailing phanerogams only. This zonation was subsequently used by WINKLER (1976) in his synthesis of liverwort distribution in the area. A rather sketchy description of altitudinal bryophyte zonation in the Colombian Andes, related to the four major altitudinal life zones commonly distinguished here (warm lowland, subandean, andean, páramo), was given by GRADSTEIN et al. (1977). According to MUELLER-DOMBOIS et al. (1981) such zones can be defined as "species assemblages that show some degree of homogeneity along a certain segment of the transect". In general, the steeper the gradient, the more distinct are these changes through which boundaries can be drawn and altitudinal zones determined. However, as the changes along a transect are not always abrupt, difficulties arise as to where to draw boundaries.

2. MATERIAL AND METHODS

2.1. Methods

Fieldwork was carried out in July, August and September 1977. For the ecosystem analysis, of which the bryophyte inventory formed a part, nineteen relevés were made along the altitudinal gradient at 200 m intervals (VAN DER HAMMEN et al. in prep.): fifteen forest relevés (500–3300 m) of 150-600 m^2 each and four páramo relevés (up to 4100 m), each covering 50–70 m^2. Size of the relevés was determined depending on vegetation structure (WESTHOFF & VAN DER MAAREL 1978). Local climatic data (*fig. 5d*) were obtained by using Lambrecht thermohygrographs type 252, which were placed in sheltered places 1.5 m above the ground.

Because of time limitations only habitats up to 3 m above ground surface were inventoried bryologically, including soil surface, rocks and stones, rotten logs and decaying wood, tree trunks, branches, leaves, trunks of palms and tree ferns, and lianas. Percentage cover was estimated for each species or, when this proved impossible, for genera or families. The various *Bazzania, Plagiochila* or Lejeuneaceae species, for instance, were often so exuberantly intermingled that it was impossible to determine the cover of individual taxa. Cover estimations are given for bryophytes growing on anorganic material (*fig. 2*) and those

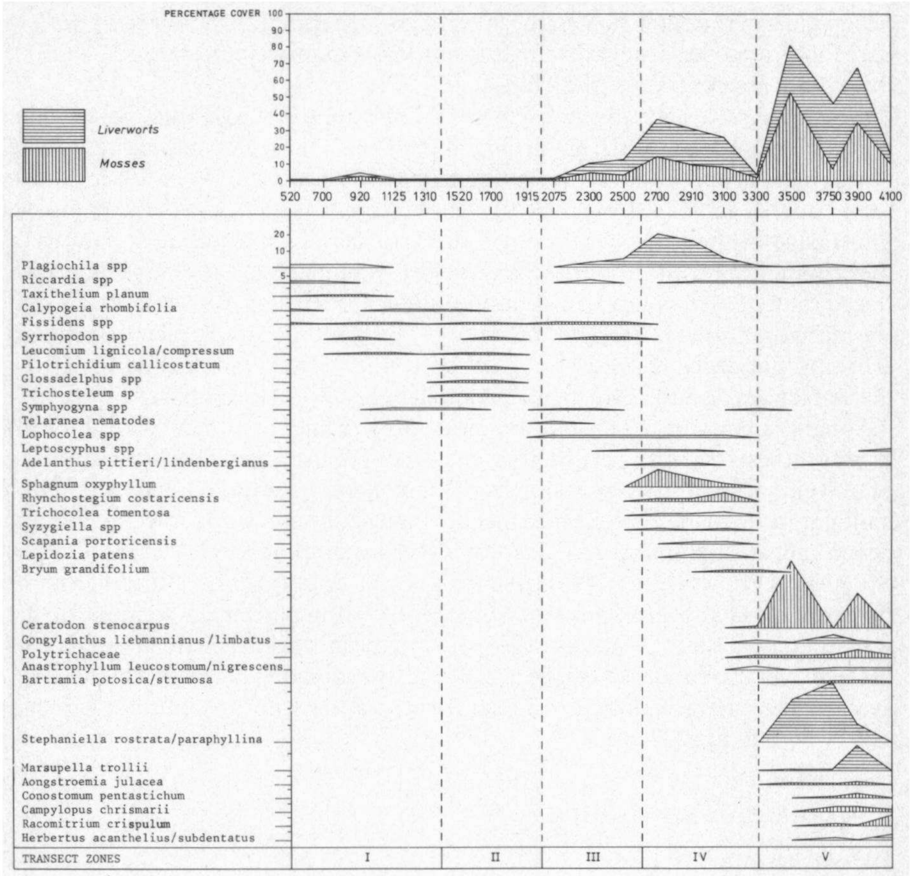

Fig. 2. Percentage cover diagram for bryophytes growing on soil and/or rock ("SR-group"). Species recorded only once not included.

growing on organic material (*fig. 3*). After BOWERS (1970) these two groups are named "SR-group" (growing on soil and rock) and "TL-group" (growing on trees and logs), respectively. In addition, a dendrogram technique generating clusters of samples at various degrees of similarity (according to MUELLER-DOMBOIS & ELLENBERG 1974) was used to determine changes in species presence with elevation. Because many relevés do not show any similarity, calculations could be made with a desk calculator instead of a computer in a reasonably short time. The procedure was as follows: similarities between relevés with respect to species presence were calculated by using the relatively simple and widely tested Sørensen's Index of Similarity (*table 1*). In the established matrix of similarity indices (IS) the highest IS-value is searched for, locating the two relevés that are most similar in their quantitative species content. In *table 1* these are relevés 37 and 39. The values of these two relevés are isolated and averaged.

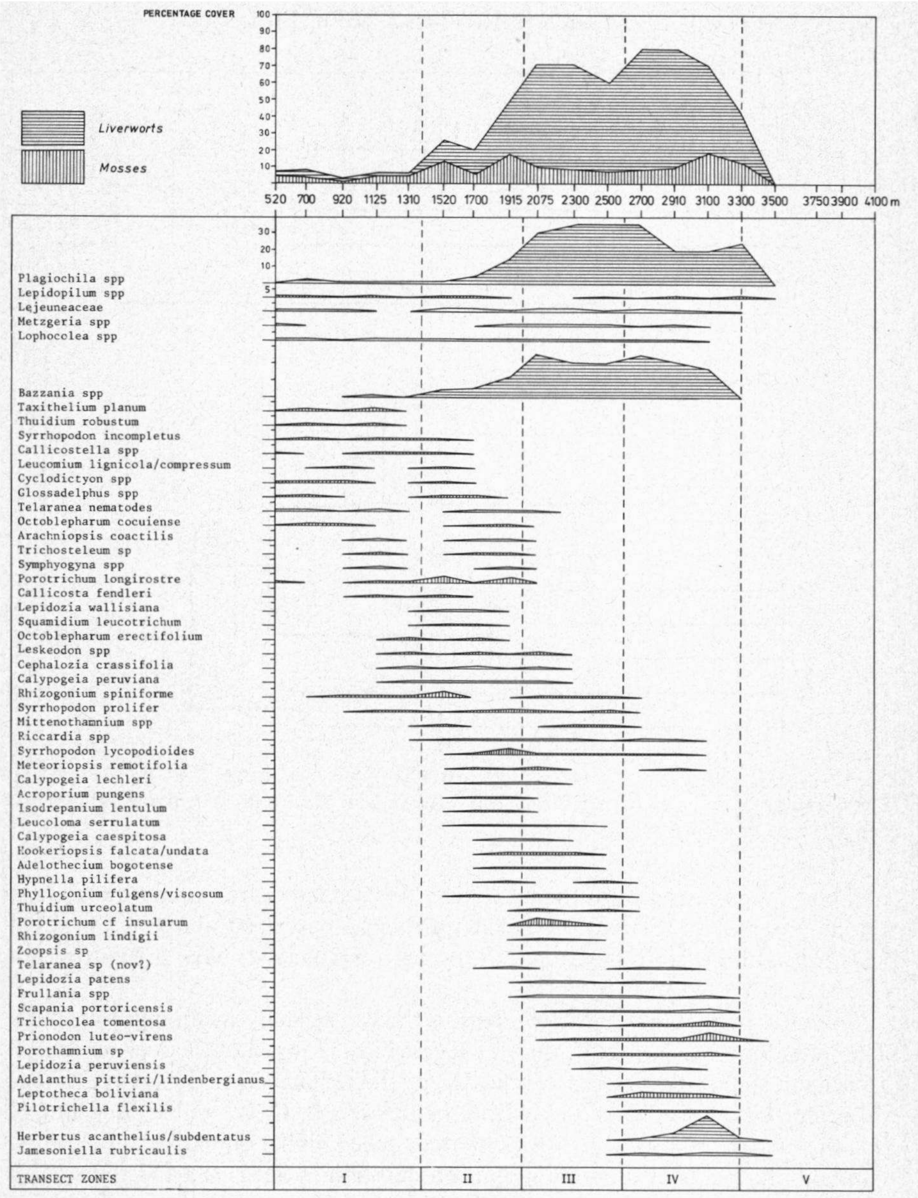

Fig. 3. Percentage cover diagram for bryophytes growing on dead and/or living wood ("TL-group"). Species recorded only once not included.

This implies a reduction of the two colums (under relevé 37 and 39) in the similarity matrix to one. This column is returned to the IS-matrix in place of the relevé with the smaller number (37) while the position of the relevé with the larger

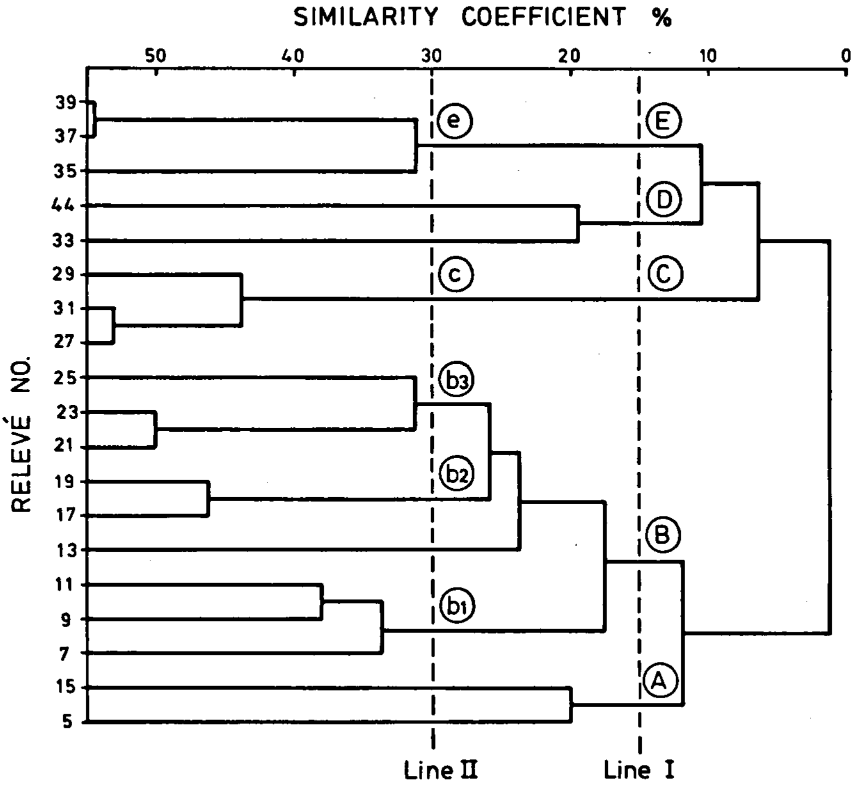

Fig. 4. Dendrogram based on relevé similarity values (*table 1*). Threshold values at 15% (line I) and 30% (line II) similarity.

number (39) is cancelled in the matrix. In this second matrix again the highest IS-value is looked for and the calculation cycle described above is repeated. This procedure is continued until all relevés are clustered. Now a dendrogram can be constructed (*fig. 4*).

The next important step is to identify the ecologically meaningful clusters. This was done by setting of more or less arbitrary threshold values at 30 and 15 percent similarity. These are indicated by the vertical dashed lines in the dendrogram. Line I identifies five major clusters (A, B, C, D, and E) and line II five clusters (b_1, b_2, b_3, c and e), which can be called higher-similarity subclusters. Now, a relevé cluster diagram (zonation diagram in MUELLER-DOMBOIS et al. 1981) can be constructed (*fig. 5a*). To determine the zones the rule has been adopted that at least three limits occur in the relevé cluster diagram. The resulting transect zones are shown and defined at the bottom of this diagram.

2.2. Material

Bryophyte and data collecting in the field was carried out by D. Griffin III (Gainesville), A. M. Cleef (Utrecht), O. Rangel (Bogotá) and G. B. A. van Reenen.

Table 1. Similarities between relevées calculated with Sørensen's Index of Similarity (IS). Values in percentages. Relevée numbers on left side and at top.

	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41
5	x	14,3	0,0	36,4	0,0	20,0	5,3	14,3	6,7	7,1	9,1	7,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0
7		x	30,8	36,4	13,3	20,0	15,8	14,3	6,7	0,0	0,0	7,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0
9			x	38,1	28,6	0,0	5,4	7,4	13,8	7,4	19,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
11				x	34,8	28,6	13,0	22,2	21,1	11,1	20,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
13					x	9,5	25,6	20,7	38,7	6,9	26,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
15						x	13,6	5,9	0,0	17,7	7,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
17							x	46,2	37,0	11,5	21,7	8,0	8,3	0,0	0,0	0,0	0,0	0,0	0,0
19								x	45,5	23,8	22,2	13,0	10,5	0,0	0,0	0,0	0,0	0,0	0,0
21									x	50,0	31,6	14,3	15,0	5,3	0,0	0,0	0,0	0,0	0,0
23										x	33,3	25,0	21,1	16,7	5,3	0,0	0,0	0,0	0,0
25											x	23,5	18,8	6,7	6,3	0,0	0,0	0,0	0,0
27												x	50,0	52,9	16,7	6,5	0,0	0,0	12,1
29													x	37,5	5,9	0,0	6,7	0,0	6,5
31														x	12,5	0,0	0,0	0,0	13,8
33															x	6,9	6,7	15,4	19,4
35																x	24,0	38,1	0,0
37																	x	54,5	37,0
39																		x	8,7
41																			x

Identification was carried out with the help of specialists but epiphyllous liverworts remained unnamed thus far and are therefore not taken into account in the description of the zonation. D. Griffin III identified most of the mosses. Other specialists, whose help with critical identifications is gratefully acknowledged, are for the Hepaticae: J. Aguirre, Bogotá (Lejeuneaceae), H. Inoue, Tokyo (*Plagiochila*), J. Meenks, Utrecht (*Riccardia*), T. Pócs, Vácrátót (*Lepidozia*) and J. Vána, Praha (*Marsupella, Lophozia, Cephalozia* and *Anastrophyllum*); for the Musci: M. Crosby, St. Louis (*Callicosta*) and J.-P. Frahm, Duisburg (*Campylopus* and *Chorisodontium*).

The classification of taxa follows the "Catalogue of the Hepaticae of Colombia" (GRADSTEIN & HEKKING 1979) and the "Lista Comentada de los Musgos de Colombia" (FLORSCHÜTZ-DE WAARD & FLORSCHÜTZ 1979). The collections are deposited in COL, with duplicates in U and FLAS. A complete list of all determined bryophytes collected in the transect, including author's names, collection numbers and exact data on substrate and altitude, will be published in a separate paper dealing with the phytogeography of the Santa Marta bryoflora.

3. BRYOPHYTE ZONATION

Based on the percentage cover diagrams (*figs. 2–3*) and the relevé cluster diagram (*fig. 5a*), five altitudinal bryophyte zones can be distinguished: four forest zones and one páramo zone. Further subdivision into subzones is sometimes possible. As is shown in *fig. 5*, the altitudinal zones based on the cluster analysis of relevés are rather similar to those determined from the percentage cover, except for the boundary at 1600 m. At this altitude the relevé cluster diagram reveals a sharp boundary, whereas in the percentage cover diagram there is a broad zone between about 1400 m and 2000 m. However, in the relevé cluster diagram this zone would also become apparent when a two-cluster limit would have been considered (see Methods). Such anomaly is not very surprising since the relevé cluster diagram is based on species presence, hence qualitative characters only, whereas in the percentage cover diagram quantitative differences are taken into account as well.

The prominent changes in quantity of individual species reflect the boundaries between the zones most clearly (*figs. 5b* and *5c*). Thus, five bryophyte zones can be distinguished, which can be described as follows:

ZONE I (500–1400 m). This zone is characterized by a very low cover of both the "TL-group" and the "SR-group". A low terrestric cover of bryophytes is a common feature in undisturbed tropical lowland forests (RICHARDS 1979) and is probably caused by the smothering effect of fallen sclerophyllous leaves, forming a continuous terrestric layer inhibiting bryophyte growth (PÓCS 1982). Bryophytes characteristic for the entire warm and humid neotropical lowland region are found in this zone, such as *Syrrhopodon incompletus, Thuidium robustum* (= *T. antillarum*?) and *Leucomium lignicola* (= *L. compressum*?). Their altitudinal ranges usually extend to about 1700 m (cf. *figs. 2* and *3*) but the increase of the "TL-group" from 1400 m upwards together with a number of newly arriv-

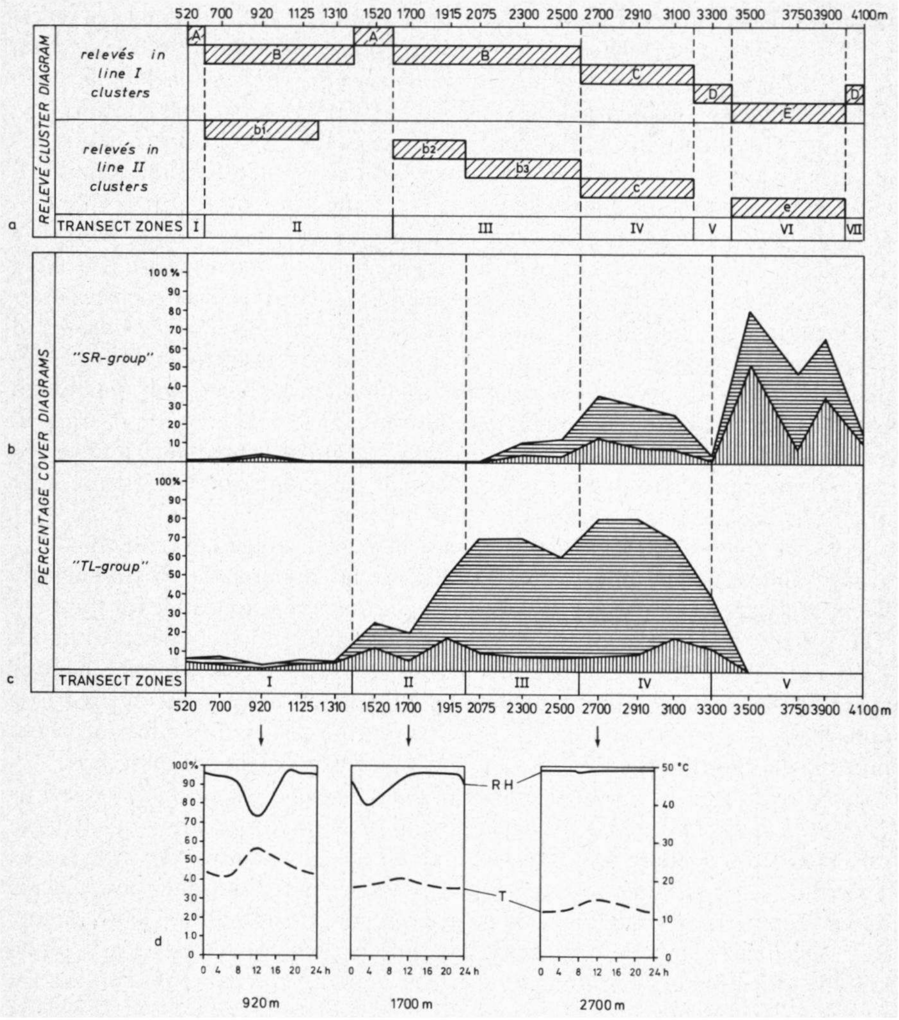

Fig. 5. Bryophyte zonation and climate along the Sierra Nevada de Santa Marta transect. a: relevé cluster diagram, based on species presence. b: total percentage cover diagram for the "SR-group" (*fig. 2* for details). c: total percentage cover diagram for the "TL-group" (*fig. 3* for details). d: air humidity and air temperature during 24 hours in relevées at 900 m, 1700 m and 2700 m. Data lacking for zone V (páramo).

ing bryophytes at this altitude, mentioned below (zone II), justify to draw the upper boundary at 1400 m (see above).

Zone I can be further subdivided into two subzones with a boundary at about 1000 m. The lower subzone is characterized by a small increase of the epiphytic cover, predominantly caused by *Plagiochila* spp., and by the terrestric presence of *Plagiochila* and the hygrophytic *Riccardia hymenophytoides*, one of the few *Riccardia* species which occur at lower altitudes (Meenks, pers. comm.). In spite of the decrease of the "TL-cover" in the upper subzone, the appearance of several "TL-species" from 1000 m upwards is notable, such as the mosses *Callicosta fendleri, Porotrichum longirostre, Syrrhopodon prolifer, Rhizogonium spiniforme, Trichosteleum* sp., *Callicostella* sp. and the liverwort *Arachniopsis coactilis.*

ZONE II (1400-2000 m). In this zone the cover of the "SR-group" remains unchanged, while the cover of the "TL-group" increases, slightly in the beginning, more sharply from 1700 m upwards. Small creeping liverworts, such as *Cephalozia crassifolia, Arachniopsis coactilis* and *Calypogeia* spp. are found here. The liverwort *Lepidozia wallisiana* and the mosses *Syrrhopodon leprieurii, Fissidens prionodes, Acroporium pungens, Isodrepanium lentulum* and *Octoblepharum erectifolium* from the "TL-group" and species of *Glossadelphus, Pilotrichidium* and *Trichosteleum* from the "SR-group" are restricted to this altitudinal range. Remarkable is the absence of *Rhizogonium spiniforme* which certainly was found below as well as above this range, Also the abundance of the mosses *Phyllogonium fulgens, P. viscosum* and *Porotrichum logirostre,* whose distribution go beyond this range, are striking here. All in all these data indicate the presence of a rather well-defined altitudinal bryophyte zone.

ZONE III (2000–2600 m). In this zone a high percentage cover of the "TL-group" and an increasing cover of the "SR-group" are notable. Predominantly liverworts, e.g. species of *Bazzania* and *Plagiochila,* are responsible for this high "TL-cover", at the cost of the mosses which reduce in cover between about 1900 and 2300 m (*fig. 3*). When the liverwort cover decreases, mosses recover again (2900–3100 m). The overwhelming abundance of epiphytic liverworts is apparently an important factor in eliminating the detoriating effect of heavy rain showers which often occur in these types of tropical mountain forests. According to PÓCS (1976, 1980), species of *Bazzania* and *Plagiochila,* as well as *Trichocolea, Lepidozia* and *Frullania,* common in this zone, are very effective rain interceptors. After reception one part of the rainwater re-evaporates and a second part is retained by the epiphyte; the surplus rainwater slowly drips down keeping the environment moist even in periods when there is no rain or fog. Apparently suitable conditions are thus created for terrestric bryophyte growth. Other factors favouring terrestric bryophyte growth are the continuous supply of humus provided by the epiphytic bryophytes (PÓCS 1976) as well as the relatively small size of the leaves and leaflets of trees at these altitudes not hindering bryophyte growth.

The small decrease of the "TL-cover" at 2500 m is possibly due to the location of the relevé on the more exposed eastside of the mountain ridge and the thin soil layer resulting in a more open vegetation.

ZONE IV (2600–3300 m). Both the "SR-group" and "TL-group" reach peak values in this "mossy forest" as such a zone is often referred to in the literature. As can be observed from *figs. 2* and *3,* a number of species with high covers are predominantly restricted to this range. It is also striking that substrate preference of the species diminishes. *Trichocolea tomentosa, Lepidozia patens* and *Plagiochila bursata,* mostly occurring as epiphytes, are growing here on the soil. The opposite is also true, as *Herbertus acanthelius* and *H. subdentatus,* which are common on soil and rock in humid páramos (VAN REENEN 1982 and below), are quite abundant here as epiphytes. This phenomenon was also observed for vascular plants (Cleef, oral comm.). It is normally explained by an extremely high humidity, which, in the area investigated, is also indicated by the presence of *Sphagnum oxyphyllum* on vertical, mostly rocky substrates. This uncommon type of habitat for *Sphagnum* was also reported from the Gálapagos Islands, on crater walls receiving unusually large amounts of drizzle (ITOW & WEBER 1974).

Apparently we are dealing here with a so-called "condensation-zone" (CLEEF 1981) extending from about 2700 m to 3100 m. Although prolonged climatological data are not available, hygrographic measurements made during the fieldwork indicate that a constantly high air humidity of almost 100% RH during 24 hours is one of the factors characterizing such a zone (*fig. 5d*). At lower altitudes air humidity values of up to 100% RH alternate with a lowering to 70–80% RH during morning hours.

At 3300 m timberline is reached and the last, isolated shrubs are encountered. The low, open character of vegetation through which winds can easily enter as contrary to the more closed stands at lower altitudes – with exception of the relevé at 2500 m – has possibly caused the strong decrease of both the "SR-group" and the "TL-group" as well as the occurrence of *Plagiochila ovata, P. pinnatidens, Rozea subjulacea* and *Chorisodontium mittenii,* not found elsewhere along the transect.

ZONE V (3300 m upwards). From 3300 m upwards we are dealing with the open páramo. The percentage cover of the "SR-group" is increasing considerably, while the "TL-group", in absence of trees and shrubs, is lacking. Especially *Stephaniella paraphyllina. S. rostrata, Ceratodon stenocarpus* and, at 3900 m, *Marsupella trollii* are present with high covers. The absence of *Ceratodon stenocarpus* at 3750 m and 4100 m is possibly caused by the rocky substrate of these two relevés.

According to CLEEF (1981) the páramo climate is basically humid. The presence of *Stephaniella paraphyllina* and *Gongylanthus liebmannianus* however, and the absence of bamboos indicate a relatively dry environment (GROLLE 1969, CLEEF 1981).

Also this zone can be further subdivided. The absence of *Racomitrium crispulum, Campylopus chrismarii, Conostomum pentastichum, Herbertus acanthelius* and *Herbertus subdentatus* below 3600 m allow for subdivision of the páramo zone in two subzones. Furthermore, the cover increase of the two hygrophytic *Herbertus* species as well of *Racomitrium crispulum* and *Rhacocarpus purpurascens* at the upper limit of the transect at 4100 m suggest the beginning of a next "condensation-zone" at this altitude.

4. CONCLUDING REMARKS

The boundaries between the zones described above are defined particularly by distinct changes in total epiphytic as well as terrestric bryophyte cover (*figs.*

5b and *5c*). In their transect studies on Hawaii, MUELLER-DOMBOIS et al. (1981) regarded the presence of overlapping and spatially associated groups of species with restricted distributions primarily responsible for the recognition of transect zones. Such species assemblages are also found among the bryophytes (group of organisms not investigated by Mueller-Dombois et al.) of the Santa Marta transect and, especially, in the "SR-group" (*fig. 2*) they coincide well with the zonation based on total cover. In the "TL-group" (*fig. 3*) this correlation is less distinct except in the "condensation zone". In general, cluster analysis based on species presence yields a zonation rather similar to that based on total cover (*fig. 5*).

From the scarce climatological data available (cf. *figs. 1* and *5d*) we may arrive at the preliminary conclusion that high bryophyte cover values are primarily initiated by high rainfall and high air humidity. Low temperatures, characteristic for the high tropical mountain forests (cf. *fig. 5d*) and resulting in a low reevaporation, seem to be important as well. PÓCS (1982), in his rainfall-epiphyte correlation theory, indicates that epiphytes are an adaptation to "utilize water-resources which are generally surplus for the host plants". By keeping the atmosphere moist in periods with less rainfall and by the production of humus, epiphytes contribute to the development of a terrestric bryophyte layer. It follows that in tropical forests the highest cover values for terrestric bryophytes are usually found in the zones with the highest and most constant air humidity, i.e. the "condensation zones".

The above conclusions concerning the relations between bryophyte zonation and ecological conditions have been hampered by the incompleteness of data concerning local climatic conditions. It is to be expected that more extensive climatic data become available from other altitudinal transects in the Colombian Andes studied in the framework of the ECOANDES project, on which work is now in progress.

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