

Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda

1. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire)

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Summary: Along a transect from 900 m to 3300 m elevation, various ecological parameters concerning epiphytic bryophytes have been studied. The most characteristic life form between 900 and 2300 m elevation is the dendroid, which is interpreted as an adaptation to better gas exchange under the unfavourable conditions (low light, high air humidity) of the rain forest. Above 2500 m, cushions are the predominant life form. The cushions are 2-5 cm high but can reach 50 cm at the forest line. In spectacular cases, moss balls are formed up to 1 m in diameter. PH measurements of the bark of host trees revealed values between 4.1 and 6.2, which is in accordance with results from South America and SE-Asia. The bryophyte cover on soil is very low (<5%) below 2700 m but raises to 90% in the subalpine ericaceous belt, but not in the subalpine *Senecio*-belt. The percentage cover of bryophytes on bark increases from 5 to 80% in the transect with increasing elevation, and the light intensity increases from <1% to 50%. The mean annual temperature decreases continuously from 20.6°C at 900 m elevation to 2.5° at 4500 m elevation. This allows a comparison of the growth conditions of bryophyte species occurring disjunct in the oceanic parts of the temperate regions and the tropical mountains. The phytomass of epiphytic bryophytes per m² and per ha increases synchronously in the transect. There is a sudden increase from 8 - 44 kg/ha in 900 - 1300 m to 100 - 600 kg/ha in elevations between 1900 and 2900 m. Maximum values of 6 tonnes/ha are found at the forest line, being 750 times higher than the lowest value in the lower part of the transect. The water storing capacity of epiphytic bryophytes is 20-60 l/ha at elevations between 900 and 1300 m, 130 - 2000 l/ha between 1900 and 2900 m and 18000 l/ha at the forest line. The latter is 18% of the estimated rainfall.

1. Introduction

As in the previous BRYOTROP projects in Peru (Frahm 1987a) and Borneo (Frahm 1990), the ecology and altitudinal zonation of (predominantly epiphytic) bryophytes have been studied along a transect on relevés at 200 m altitudinal distance. In Zaire, the transect could not be realized below 900 m elevation because of very large distances to the bottom of the Zaire basin, inaccessible roads and strong human influence on the vegetation. For a detailed description of

the transect see the contribution of E. Fischer in this volume. As shown in Fig.1, the transect started at 900 m at the slope of the Luhoro valley near the Irangi fieldstation and went up to 1500 m at top of Mt. Ilimo, the nearest accessible highest elevation, which has been not studied botanically before because of difficult access. Although a forest reserve, several small villages and cuttings were situated in between, but for the transect, intact areas could be selected in the appropriate elevations. Due to the situation of the transect on the slopes of a river valley, the

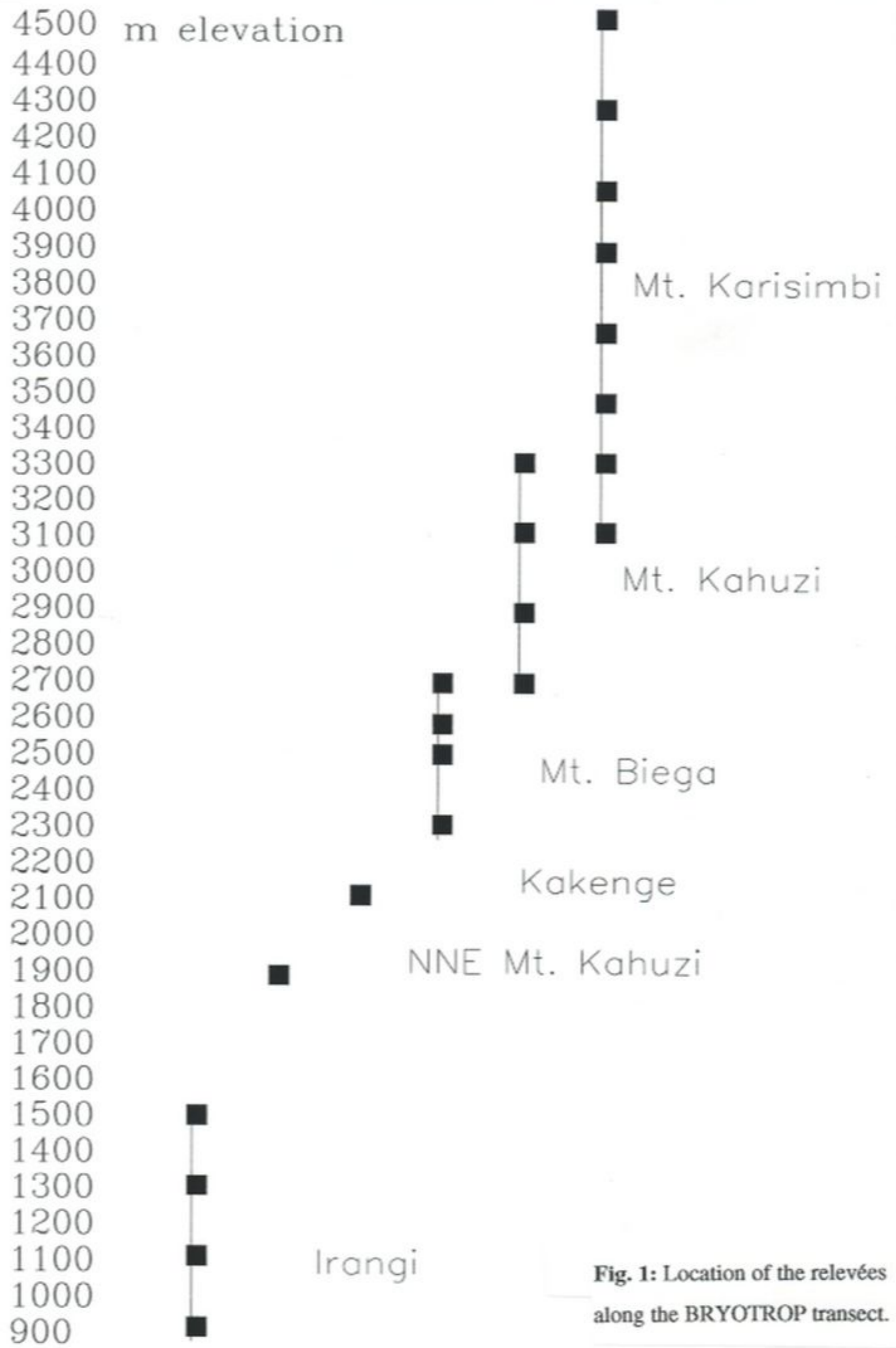


Fig. 1: Location of the relevées along the BRYOTROP transect.

zonation was reversed in this part of the transect. The forest close to the river were distinctly influenced by the humidity of the river; the valley itself was filled with clouds in the night and in the morning, whereas the upper slopes and the summit of Mt. Ilimo were more exposed to the sun. The cover of bryophytes was also distinctly higher around a waterfall at about 1000 m elevation.

The transect was continued on two isolated sites in 1900 m and 2100 m elevation. 1700 m could not be realized because of agriculture in the Luhoro valley outside the forest reserve. The 1900 m relevée shortly outside the park border of the Kahuzi park consisted of still nearly intact forest, although it was confined to a valley and local inhabitants started to cut trees. The 2100 m relevée was situated directly beside the park border and therefore probably not as typical. Furthermore it was influenced by elephants. In addition, comparative studies could be made in the Nyungwe forest in Rwanda between 1600 and 2400 m elevation. The relevées between 2300 m and 2700 m were situated at Mt. Biega, where, as on Mt. Kahuzi, relevées others than those covered by bamboo (*Arundinaria alpina*) were selected. In the Kahuzi-Biega park, almost 90% of the area between 2100 and 3000 m elevation consists of bamboo forest, true forest being scattered in small islands in between. Forests and bamboo stands show no intergradations but an abrupt change in a few meters. The reasons for the formation and alteration of bamboo stands or forests are not known. At 2700 m, the transect from Mt. Biega overlaps with that of Mt. Kahuzi. However, since the 2700 m relevée at Mt. Biega is situated just below the summit and for this reason is formed by subalpine *Philippia* forest, it is not taken into account here but used only for comparison. At Mt. Kahuzi, the transect is continued between 2700 and 3300 m. The uppermost relevée is situated again just below the summit and thus is influenced by the summit effect. In comparison with other mountains in Central Africa, the climatic forest line is situated higher than the summit of Mt. Kahuzi. To cover this restriction, additional studies have been undertaken at Mt. Karisimbi in Rwanda between 3100 and 4500 m elevation, although a direct comparison between Mt. Kahuzi and Mt.

Karisimbi is not possible. The part of the transect in Zaire is situated in an area with plutonic rocks providing an acidic substrate. Accordingly, the subalpine belt is formed by *Erica-Philippia* stands. This vegetation type is lacking on Mt. Karisimbi except for a small spot found by E. Fischer SW of the Susa River in 3400 - 3500 m. The upper montane forest on Mt. Karisimbi at 2700 to 3000 m consists of *Hagenia*, followed by a *Hagenia-Hypericum* belt from 3000 to 3300 m. At 3300 m, *Hagenia* is vanishing and *Hypericum* is associated with first *Senecios* to 3600. From 3600 to 3900 m, giant *Senecios* form the subalpine belt, associated with *Lobelia* between 3900 and 4200, where the alpine belt starts. Because of different geology and different height of Mt. Karisimbi, the observations can therefore be compared with Mt. Kahuzi only with much care.

2. Methods

As in the previous studies in Peru and Borneo, at every 200 m altitudinal distance a relevée was chosen of approximately 25 x 25 m size, rarely smaller (e.g. in subalpine forests) or larger, up to 1 ha (100 x 100 m). The relevées were situated in undisturbed primary forests with no (or not recognizable) human influence. According to the topographic situation, they were differently exposed or inclined. Within these relevées, the following parameters were measured or estimated:

1. The estimated percentage of bryophytes on soil and rocks.
2. The estimated percentage of epiphytic bryophytes.
3. The estimated percentage of vascular epiphytes. Lichens were not considered, as their occurrence seems to be related more to exposed habitats than to any other parameter.
4. The maximum circumference of stems of trees.
5. The maximum leaf length of tree species.
6. The maximum cover of epiphytic bryophytes.
7. The fresh and dry weight of epiphytic bryophytes on half a square meter taken from a tree trunk between 0.5 and 2.0 m height. For this purpose, the bryophytes were removed from the bark with a knife around the tree. Usually three

different trees were treated in this way. For calculations, the mean value was used. According to the diameter of the stem, the length of the area on which the bryophytes were scratched off, varied between ca. 40 cm and ca. 2 m or more. The material was air dried, in the very humid conditions in the lower part of the transect also pretreated on a dryer operated by a kerosine stove. Therefore the values of the dry weight taken in the field will slightly differ from those found in a laboratory in a drying stove at 105°C. The difference between the two methods has not been determined, however, the difference will be negligible compared to the large variation of the phytomass from tree to tree, which is usually no more than 10% but can be as much as 50%.

From the dry weight measured on half a square meter, the phytomass per hectare was estimated. This was calculated based on the area on the tree trunk cleared of bryophytes. It was then estimated, how many more bryophytes were growing on the same tree and then on all trees growing in the area, which could easily be seen from this position. This area differed between 10x10 m in subalpine forests to 40x40 m in montane forests. This factor was then multiplied by the dry weight for half a square meter and calculated to one hectare.

8. The light intensity in bryophyte habitats in the forest (on soil, stems or branches) on the most shady and the most sunny place. At the same time, the light intensity was measured outside the forest in the open (rarely on absolutely open places with direct sunlight on trails or clearings). The measurements were performed with a luxmeter. The results are not directly correlated with the wave lengths of the maximum light uptake by the bryophytes and are thus not directly usable in physiological experiments, but the maximum viz. minimum percentage of the daylight available in bryophyte habitats of the relevée characterizes the stand.

9. Temperature and air humidity in bryophyte habitats of the relevée, taken with an electronic psychrometer directly above the bryophytes. Although these measurements give only an idea of the present values, the determination of the air humidity allows the determination of the conditions under which the bryophytes are turgescient

and at what air humidity they start drying up. This gives an impression of the time span used by bryophytes for aspiration or respiration. Continuous measurements of day/night curves of temperature and humidity have additionally been made with data loggers in 850 and 2300 m elevation (see the contribution of R. Lössch in this volume).

10. The mean annual temperature of the relevée, taken as soil temperature measured at 30 cm depth. This method used by Lauer (1976) is a very valuable tool for comparisons of relevées and to get annual mean values with only one measurement. A hole of 30 cm depth was prepared with a metal rod, in which an alcohol thermometer fixed on a piece of string was introduced. Afterwards the hole was covered with soil. After ten minutes, the thermometer was pulled up with the string and the reading taken. The measurements are very consistent, and the same results were obtained at the same elevation on different mountains such as the Mt. Biega, Mt. Kahuzi and even on Mt. Karisimbi.

11. The structure of the bark of the trees.

12. The pH of the bark of trees. For this purpose, 50 ml. plastic bottles were filled with bark taken with a knife on a tree at 1.5 - 2 m height and the bottle was filled with distilled water. Measurements were taken after 24 hrs with an electronic pH-meter. The accuracy of this method as compared with other treatments has been discussed previously (Frahm 1990) and is as exact as +/- 0.2 pH values.

13. The life forms of the epiphytic bryophytes. Life forms are not only morphological but also physiological adaptations to conditions of different habitats and elevations. They are especially important for water uptake, water storage and gas exchange. Changing life forms therefore reflect very well changing ecological conditions quite accurately. Although there are proposals for a classification of life forms of temperate bryophytes as well as special proposals for tropical bryophytes, the determination of life forms in the field is difficult. As a result of some practical experience in different parts of the tropics, the following life forms are recognized in the epiphytes of the tropical rainforests:

a. Crusts. Bryophytes, predominantly liverworts, appressed to the bark of trees. Example: *Lejeu-*

- neaceae, but also certain species of *Radula*.
- b. Dendroids. This includes not only dendroids in a narrow sense like Pterobryaceae (*Porothamnium Porotrichum*, *Lopidium* etc.) but also all other species (including hepatics) which stand away from the trunks of trees and branches, e.g. species of *Plagiochila*. It also includes unbranched mosses such as tails. The most important feature of this life form is that the plants hang free into the air and thus have a perfect gas exchange, probably the reason for this life form. They are turgid when wet but never covered with water reducing the gas exchange. On the other hand, such plants quite easily dry up and thus are characteristic only for humid habitats.
- c. Pendants are similarly surrounded by air like dendroids but are highly characteristic for areas with extreme high air humidity.
- d. Tufts, which are characteristic for higher elevations as adaptation to water storage. Turfs are included here, since there are problems separating both life forms in certain cases, e.g. to distinguish between a loose tuft or a more compact turf of *Dicranum* or *Campylopus*. Also the separation into small and high turfs seems not appropriate, since it splits young and small from old and tall plants of the same species.
- e. Wefts .

14. The estimated coverage of the canopy and the estimated height of the trees.

3. Results

3.1 Thickness of epiphyte cover (Fig. 2)

As well as the phytomass and the percentage cover of epiphytic bryophytes, the thickness of the epiphyte cover is also a useful indicator of the changing ecological conditions within a transect. Whereas liverwort crusts, liverwort wefts and pleurocarpous mats form only a low, hardly measurable bryophyte cover, the tallest bryophytes are formed by dendroids and cushions. Dendroids are characteristic of lower altitudes. They are not only formed by pleurocarpous mosses (Neckeraceae, Pterobryaceae) but also by hepatics such as species of *Plagiochila* with a high number of species and a high abundance. The dendroid life form has a great advantage for bryophytes at lower altitudes in the tropics. The

plants are not covered by rainwater (as in bryophytes growing in crusts) and therefore do not suffer from a reduction of gas exchange, and are not pressed together and therefore have the largest surface enabling a high gas exchange. The rate of gas exchange is very important for those plants growing under unfavourable light conditions. Thus this life form helps to balance growth under low light intensity by a optimized gas exchange. The length of the dendroids varies between 2 and 5 cm in elevations between 900 and 2300 m and is not significantly related with increasing altitude.

Cushions alternate with dendroids at higher altitudes. In the Mt. Kahuzi transect, cushions are found from 2500 m on. Cushions have a much higher phytomass and thus are significant in areas of higher precipitation. They also have a high water storing capacity. Although the water storing effect is much stressed in bryophytes, there is no real ecological need for water storage in such perhumid regions, since water storage usually means keeping water for dry (daily or seasonal) periods and the enlarge the phase of photosynthesis into climatic periods which are not suitable for poikilohydric plants. Thus water storage is an synecological effect for balancing the water factor in an ecosystem, but in an autecological view (as in *Sphagnum*) not essential in wet habitats. As in *Sphagnum*, water storage of epiphytes may have an effect on nutrient supply in the way that water with nutrients is soaked up by epiphytic bryophyte cushions, of which part evaporates, however, as pure water, leaving the nutrients in the bryophytes.

Bryophyte cushions along this transect are usually 2-5 cm high in elevations between 2500 and 2900 m, but can reach up to 50 cm near the forest line in 3100-3300m. Maximum values are found at the forest line, at Mt. Kahuzi in a *Podocarpus* stand at 3100 m, at Mt. Karisimbi in a *Hagenia* stand at the same elevation.

In a very spectacular case, epiphytic bryophyte cushions can form balls of up to 1 m in diameter, and can easily be more than 5 times as large in diameter as the branches on which they are growing.

Moss balls are a phenomenon which can be observed also at Mt. Karisimbi (at comparable

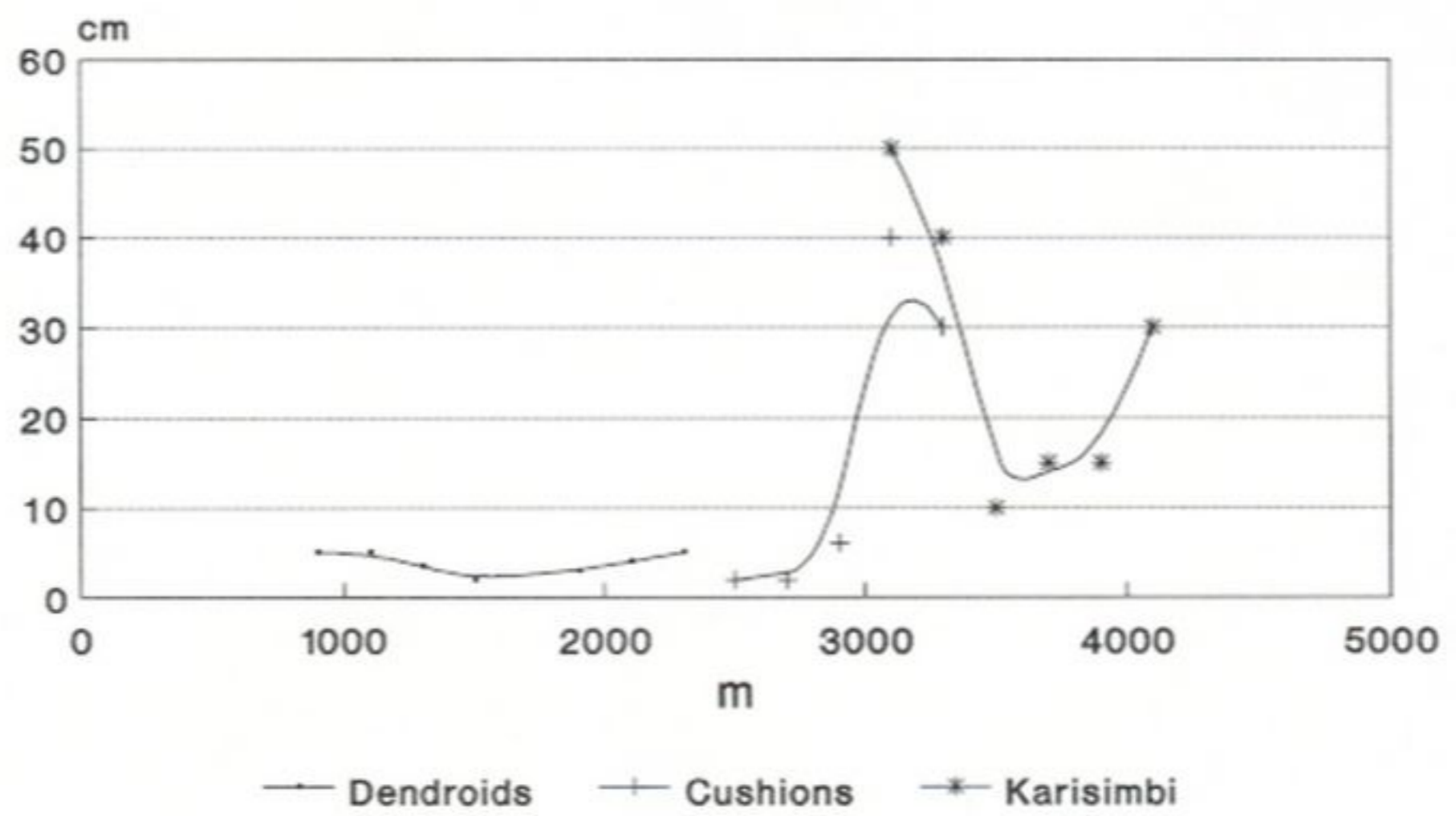


Fig. 2: Thickness of epiphyte cover.

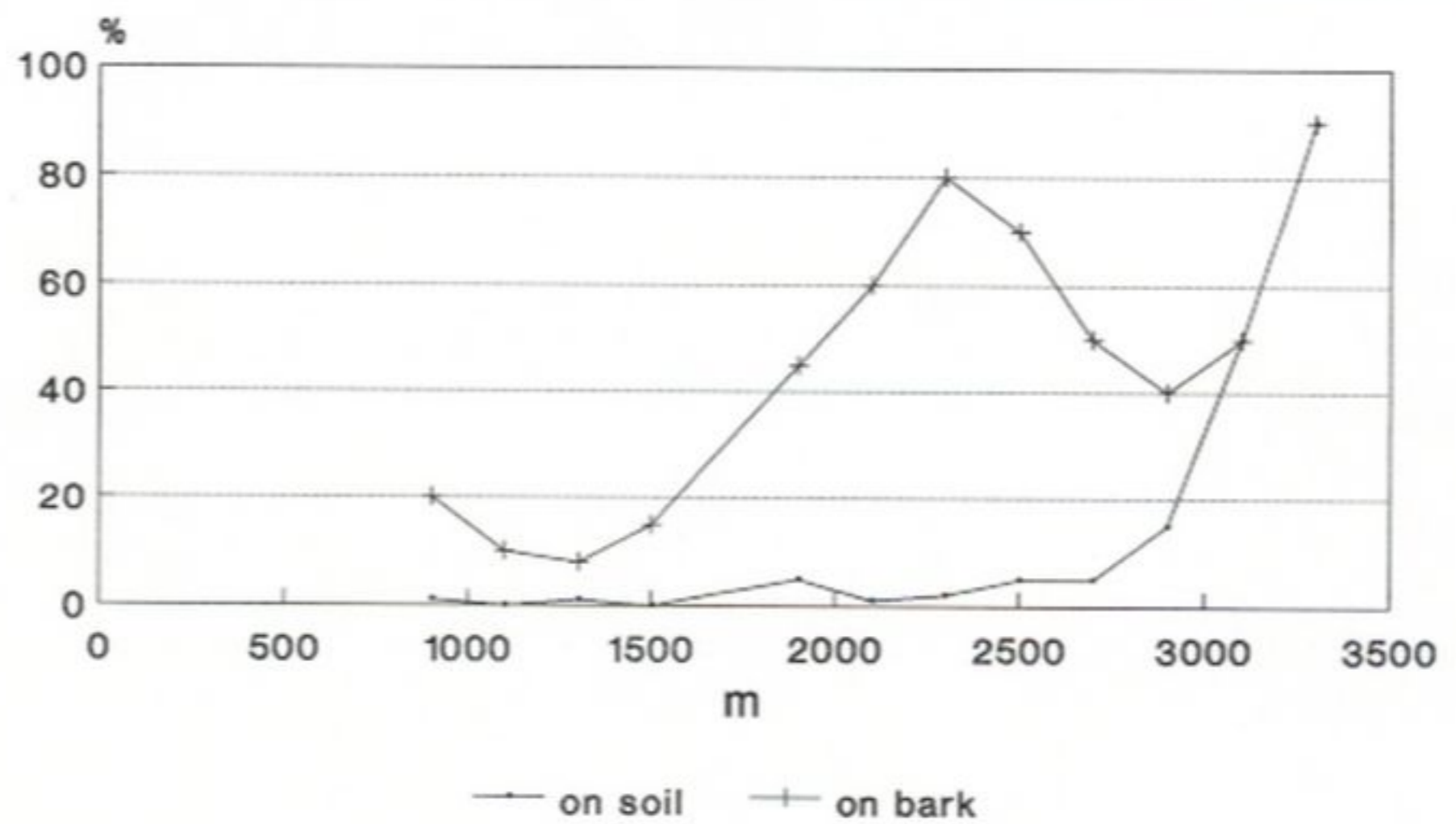


Fig. 3: Bryophyte cover.

elevation) between 2900 and 3300 m but also at much lower altitude at the humid W-edge of the Nyungwe forest in Rwanda at 1800-2000 m. In the Mt. Kinabalu-transect, moss balls were found in the "mossy forest" at 2300 m. They seem therefore to be an indicator of high precipitation, just as pendulous mosses are indicators of frequent mist layers, and occur independently of the altitudinal zonation. Interestingly, moss balls seem to be lacking in the neotropics. It could be that suitable species able to form moss ball are not present. The moss balls in Central Africa have a very different composition. In Nyungwe forest, they are only formed by mosses, predominantly *Dicranoloma billardieri*, but also *Campylopus hildebrandtii*. At Mt. Karisimbi, moss balls are found mainly on branches of *Hagenia abyssinica* and consist mainly of *Antitrichia kilimandjarica* and species of *Chandonanthus*. At Mt. Kahuzi, "moss" balls are formed by liverwort species of the genera *Chandonanthus*, *Herbertus* and *Plagiochila*. The origin of the typical ball shape is not known and thus it would be interesting to study the ontogeny of moss balls, especially to know whether there is a species succession in the moss balls and which species form the starting point for a moss ball. Moss balls with 1m in diameter can reach such a weight that such moss balls fallen to the forest floor cannot be lifted up by one person. In the final stage, they fall down because of their weight, breaking off the branch on which they are growing. It can be assumed that moss balls play an important role for the nutrient cycle in the forest. As canopy epiphytes, they are mainly supported with nutrients by rain water. By filtering the nutrients from the rain water, they incorporate the nutrients in the phytomass and humify the forest floor when fallen down. In contrast, water not stored by moss balls may only partly be soaked up by the forest floor and may (especially on slopes) run off, the nutrients being lost to that particular ecosystem.

3.2 pH Measurements of the bark of host trees. The first pH-measurements of the bark of host trees from the tropics were published from Amazonia by Lisboa (1976) ranging between 4.0 and 6.0. From Borneo, a number of trees in the Kinabalu Park were studied with pH values

ranging from 4.6 to 6.2 (Frahm 1990), indicating that all epiphytic bryophytes are probably acidophilous. This result is confirmed in Zaire, where measurements of the bark of host trees were made along the whole transect. The trees were kindly identified by E. Fischer.

900 m (Irangi)
Julbernartia saerettii (Caesalpiniaceae) 5.6
Staudtia stipitata (Myristicaceae) 5.3
Gilbertiodendron dewrevii (Caesalp.) 5.3

1100 m (Irangi)
Cynometra alexandri (Caesalpiniaceae) 5.1
Zanthoxylum gillettii (Rutaceae) 5.1
Musanga cecropioides (Moraceae) 5.6
Anthonota acuminata (Caesalpiniaceae) 5.3
Piptadeniastrum africanum (Mimos.) 4.7

1500 m (Irangi)
Ocotea keniensis (Lauraceae) 4.1

1900 m (Nyungwe Forest, Rwanda)
Parinari excelsa (Chrysobalanaceae) 4.7
Newtonia buchananii (Mimosaceae) 4.5
Albizia gummifera (Mimosaceae) 5.5
Chrysophyllum gorungosanum 5.6
Symphonia globulifera (Guttiferae) 4.6
Strombosia scheffleri (Olacaceae) 4.6

2300 m (Mt. Biega)
Agauria salicifolia (Ericaceae) 4.1
Hagenia abyssinica (Rosaceae) 6.2
Macaranga kilimandscharica (Euph.) 5.3
Nuxia floribunda (Loganiaceae) 5.6
Arundinaria alpina (Poaceae) 6.0
Ocotea usambarensis (Lauraceae) 5.6

2500 m (Mt. Biega)
Podocarpus latifolius (Podocarpaceae) 4.9
Balthasarea schrieberii (Theaceae) 4.5
Syzygium guineense (Myrtaceae) 5.2
Rappanea melanophleos (Myrsinaceae) 4.9

2600 m (Mt. Biega)
Myrica salicifolia (Myricaceae) 5.9
Philippia johnstonii (Ericaceae) 4.7
Erica rugegensis (Ericaceae) 4.9

The values measured have a conspicuously

narrow range between 4.1 and 6.2 and - like in the pH-measurements from South America and SE-Asia cited above, show a range of acidic conditions. The lowest value is found in *Agavea salicifolia*, the highest in *Hagenia abyssinica*. Interestingly, these two host trees are the only ones which show a different epiphytic bryophyte flora. This is the only case observed where a host-specific bryophyte flora has been found along the BRYOTROP transects. The bryophyte flora on *Agavea* is characterized by the consistent occurrence of a bryophyte community consisting of *Campylopus hildebrandtii*, *Orthodontium sp.*, *Hypnum sp.* and *Bazzania sp.* (see also the contribution of Frey & Kürschner in this volume). All species are strongly acidophytic. In contrast, on *Hagenia* species such as *Hylocomiopsis cylindricarpa*, *Homalothecium sp.*, *Tortula fragilis*, *Neckera ssp.* etc. are found, which indicate a bryophyte community of more neutrophilous species. Beside, the type of bark is totally different on both species of host trees. *Agavea* has a corky bark which is very much furrowed, allowing dust to accumulate and store water whereas the bark of *Hagenia* is constantly stripping off. Interestingly, *Hagenia* and *Agavea* are often found growing together at the same altitude showing clearly that dust impregnation (which would approximate the pH values of the bark of both species) plays no important role. Similarly, a correlation between the pH values of the bark of species of the same family and a correlation with the elevation is not apparent. Also the values measured in the drier Nyungwe Forest in Rwanda are comparable to those taken in the Kahuzi-Biega park in Zaire.

3.3 Bryophyte Cover (Fig. 3)

The percentage cover of bryophytes on soil and rotten wood and on bark along the transect is shown in fig. 3. On soil, the bryophyte cover is generally very low in the lower part of the transect up to 2700m. Usually it does not exceed 5%. The reason is presumably the high rate of decomposition of the litter in the lower, warmer parts of the transect, and the thick layer of litter of large leaves in the upper parts of the transect. The result of lower levels of litter is demonstra-

ted along the banks of the summit trail to Mt. Kahuzi, where larger quantities of bryophytes, especially of mosses, are found. A similar effect has been observed along the summit trail to Mt. Kinabalu in Borneo. A noteworthy exception is found directly beside the Luhoro River. Although situated below the 900 m relevée, the percentage cover can go up to 40%. This effect is probably due to the availability of rocky substrates, relatively light habitats and the humidity of the river. At 3100 and 3300 m, the percentage cover of bryophytes on soil raises to 40-50% in the Podocarpus forest and up to 90% in the Erica belt. The same value is present in the summit region of Mt. Biega. Due to the summit effect, the Erica-belt is found here at 2700 m.

Interestingly, there is no bryophyte layer on soil in the subalpine Senecio-belt of Mt. Karisimbi. The bryophyte species forming dense mats at Mt. Biega and Mt. Kahuzi are all acidophytes (*Breutelia ssp.*, *Sphagnum ssp.*, *Campylopus ssp.*, *Dicranum ssp.*) and correlated with the subalpine *Erica-rugegensis* - *Philippia* heath. At Mt. Karisimbi, such heath has been found by Dr. Fischer only at the small spot at 3400m. Elsewhere the subalpine belt above the (indistinct) forest line at about 3300 m (where *Hagenia abyssinica* is gradually disappearing) consists of *Hypericum* and *Senecio* between 3300 and 3600 m and *Senecio* and *Lobelia* between 3600 and 4200 m. Based on the observation of acidophytic bryophytes in the *Erica-Philippia* stands it was supposed that the *Senecio* stands are the result of basic substrate and that the lava of Mt. Karisimbi is for the most part basic with the exception of the *Erica* stand, which might grow on a small acidic lava extrusion. An analysis of soil from Mt. Karisimbi, however, carried out at the Esterhazy's teachers College by Mrs. Agota Kocka (the results were kindly provided by T. Pócs) showed that the pH is surprisingly low (3.86 in KCl 3.86, 4.31 in H₂O), but on the other hand, the nutrient contents is very high (Mg 455 ppm, Na 480 ppm, Ca 600 ppm, K 1428 ppm). The high bryophyte cover in the *Erica* stand seems therefore to be a result of low nutrients in the litter and lacking competition by flowering plants.

The percentage cover on bark is again lowest in the lower part of the transect between 900 and

1500 m, ranging between 5 and 20%. The lowest values are, however, not found at 900 m, as might be expected. The reason is a conversion of the zonation due to the topography. Since the transect starts at the bottom of a humid river valley with high humidity caused by the river and frequent cloud layers in the valley, and goes up to a relatively dry mountain ridge, the highest values are found at the lowest point and the lowest values are found at the highest point. Above 1500 m, the percentage cover of bryophytes on bark goes up and reaches 80% at 2300 m. There is a small decrease at higher elevations, probably caused by the structure of the forest. In the high montane belt, the main vegetation in the African mountains consists of bamboo. True forests exist only in small patches within the bamboo thickets. The highest values are found at the forest line and in the subalpine belt. At Mt. Karisimbi, the same values are reached in the subalpine belt.

The curve of the bryophyte cover (fig. 3) is strongly correlated with the curve of the light intensity (fig. 4) with the exception of the lowermost part of the transect (Luhoro river valley) for the reasons given above.

3.4 Light intensity

The light intensity increases with the elevation. Fig. 4 shows the light intensity as percentage of the direct sunlight at the most shady and most light bryophyte habitats. The light intensity was less than 1% at 900 m elevation and 1-4% in elevations between 1100 and 1500 m. Between 1900 and 2900 m, it varies between 4 and 10% and reaches up to 50% at the forest line. As mentioned in the chapter on the bryophyte cover, the percentage cover and the percentage light intensity are correlated. This may lead to the conclusion that the bryophyte cover is increasing because of the increasing available light. However, there are also potential bryophyte habitats in the lowlands with as much light intensity as at higher elevations (such as roadsides, edges of forests, gardens, plantations) which do not show a comparable bryophyte cover. Therefore the light factor cannot be regarded as the only limiting factor for the zonation of bryo-

phytes along an altitudinal transect (Frahm 1987b).

3.5 Mean annual temperature

The mean annual temperature shows a gradual decrease within the transect (fig. 5, here continued up to the summit of Mt. Karisimbi in 4500 m elevation). Except for small irregularities in the Luhoro river valley caused by the damper (and therefore perhaps cooler) climate, the temperature decreases 0.6 - 1.0 °C per 100 m elevation. With respect to many bryophyte species which occur in the tropical mountains as well as in temperate regions of the northern hemisphere (as relicts from warmer climatic periods in the Tertiary) and the southern hemisphere (as potential origin of these species), the mean annual temperatures enables to compare the climatic conditions in the different disjunct parts of their ranges. Mean annual temperatures of approximately 8 °C as in the oceanic lowlands of western Europe are realized in the equatorial latitudes roughly at the forest line in 3300 m. Mean annual temperatures of about 5 °C as in Central Europe in about 1000 m elevation are present at Mt. Karisimbi in 4100 m, see tab. 1 and 2..

This means that bryophyte species found disjunct in the tropical mountains and in extratropical regions occur in comparable climatic conditions. In the tropics, they are, however, associated with species which do not occur in extratropical regions. It is an open question whether these species are not able to survive in the extratropics or do not occur in extratropical regions "by chance". The latter implies lower competition as well as historical reasons, e.g. extinction during the Pleistocene.

3.6 Tree height and canopy (fig. 6)

As factors influencing much of the ecological conditions within the forest, the tree height and the percentage cover of the canopy has been estimated in the relevés along the transect. The tree height changes gradually along the transect. In the lower part between 900 and 1900 m, the tree height is up to 45 m. A break in the curve

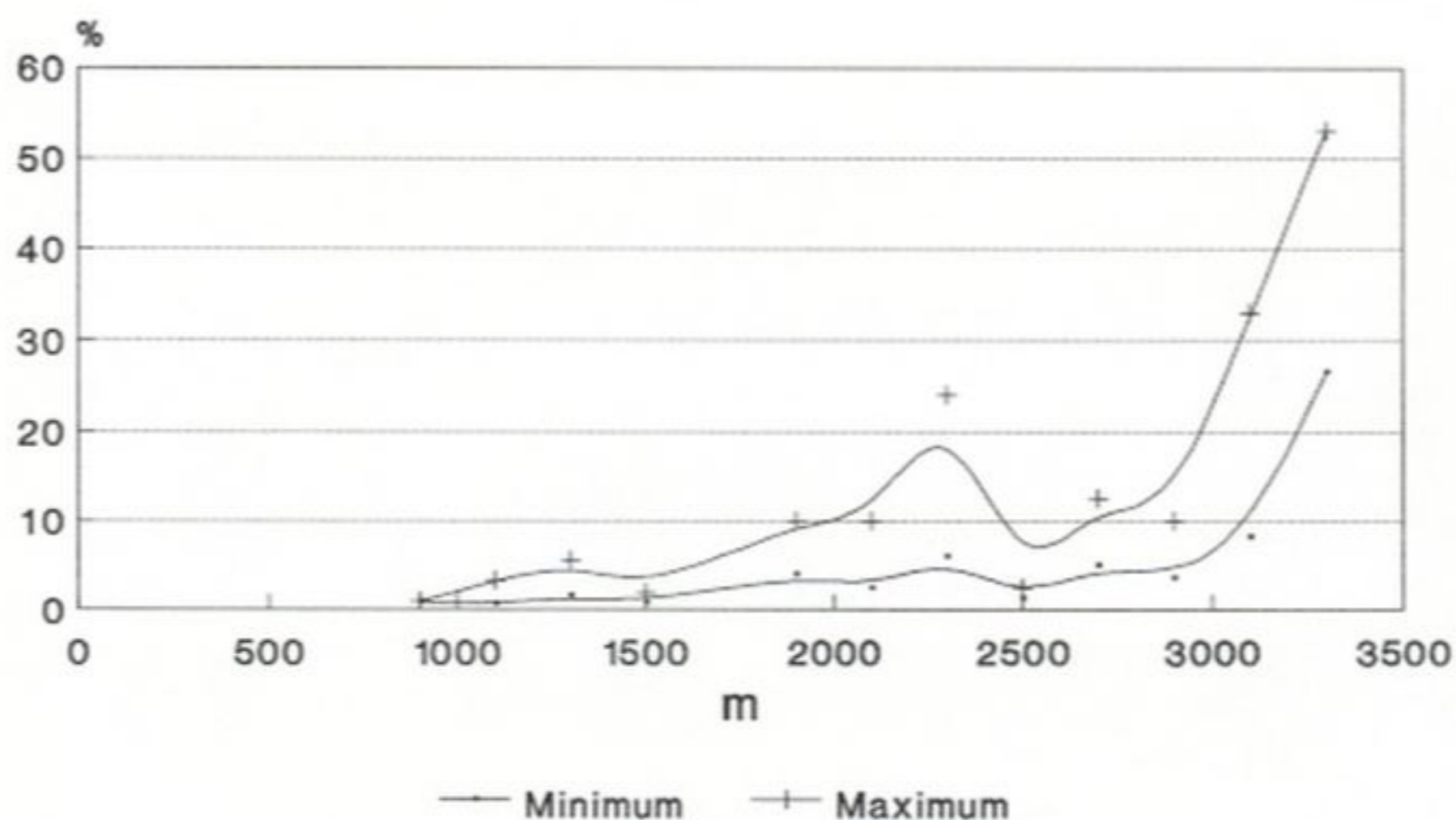


Fig. 4: Light Intensity.

Elevation in transect	mean annual temperature °C	comparable station in Europe
2300 m	15	Rome
2500	14	Marseille
2700 m	12	Lugano, Bozen
2900 m	11	Paris, London, Grenoble
3100	10	Brussels
3300	9	Glasgow, Berlin
3500	8	Hamburg, Bergen
3900	7	Stockholm
4100	5	Helsinki, Reykjavik
4500	2,5	Tromsø

Tab 1: Comparison between mean annual temperature along the transect with stations in Europe.

	in Europe	in Zaire/Rwanda
Lepidozia cupressina	10.8 (Ireland)- ca.7.0 (Vosges)	9-14
Adelanthus decipiens	ca. 11 (Ireland)	8-14
Campylopus pilifer	10.9 (Paris) - 18.0 (Almeria)	9-18
Hypnum cupressiforme,	5,9 (Oslo)-13,9 (Santander)	7-15

Tab. 2: Mean annual temperatures for disjunct tropical montane- temperate bryophytes

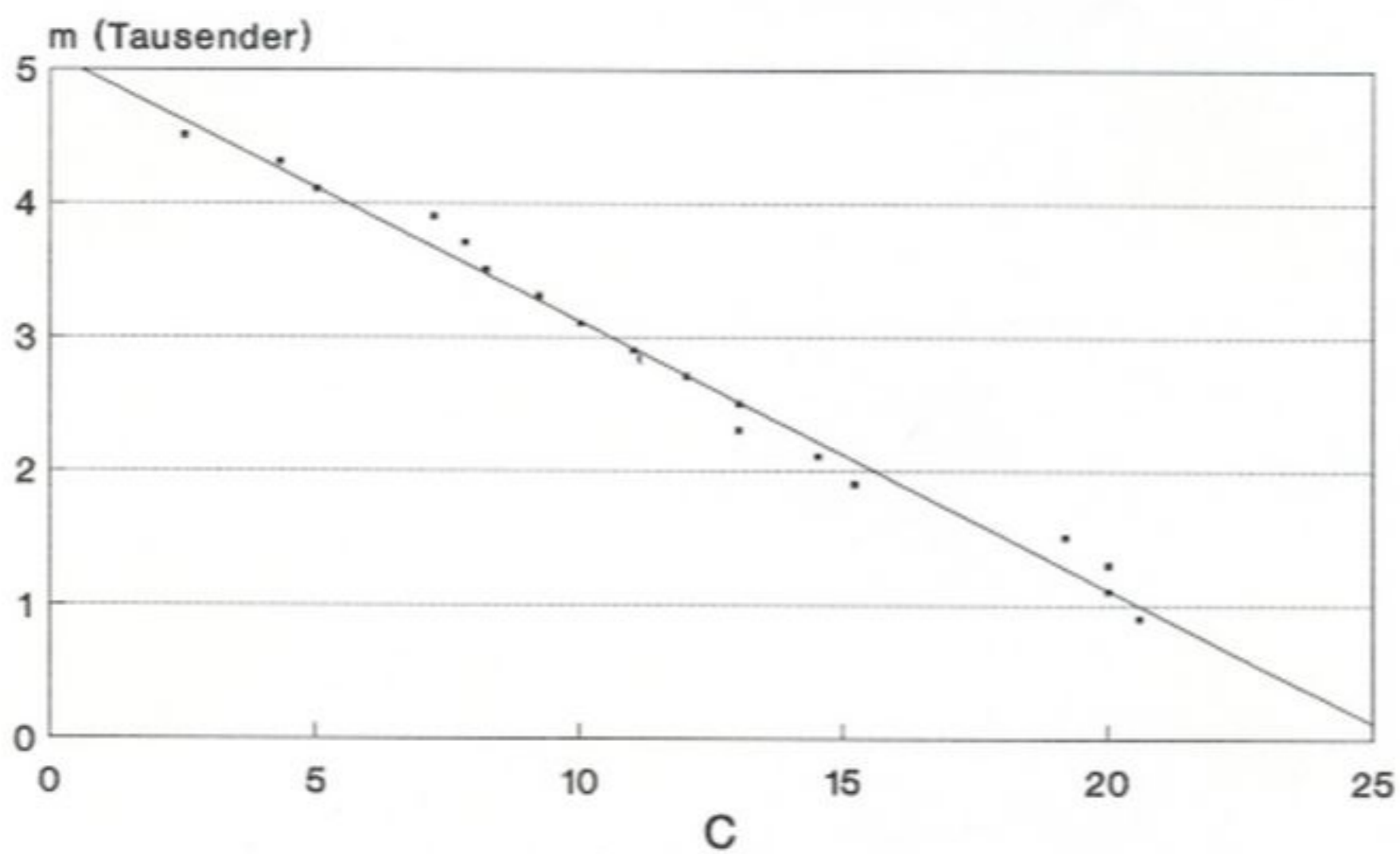


Fig. 5: Mean annual temperature.

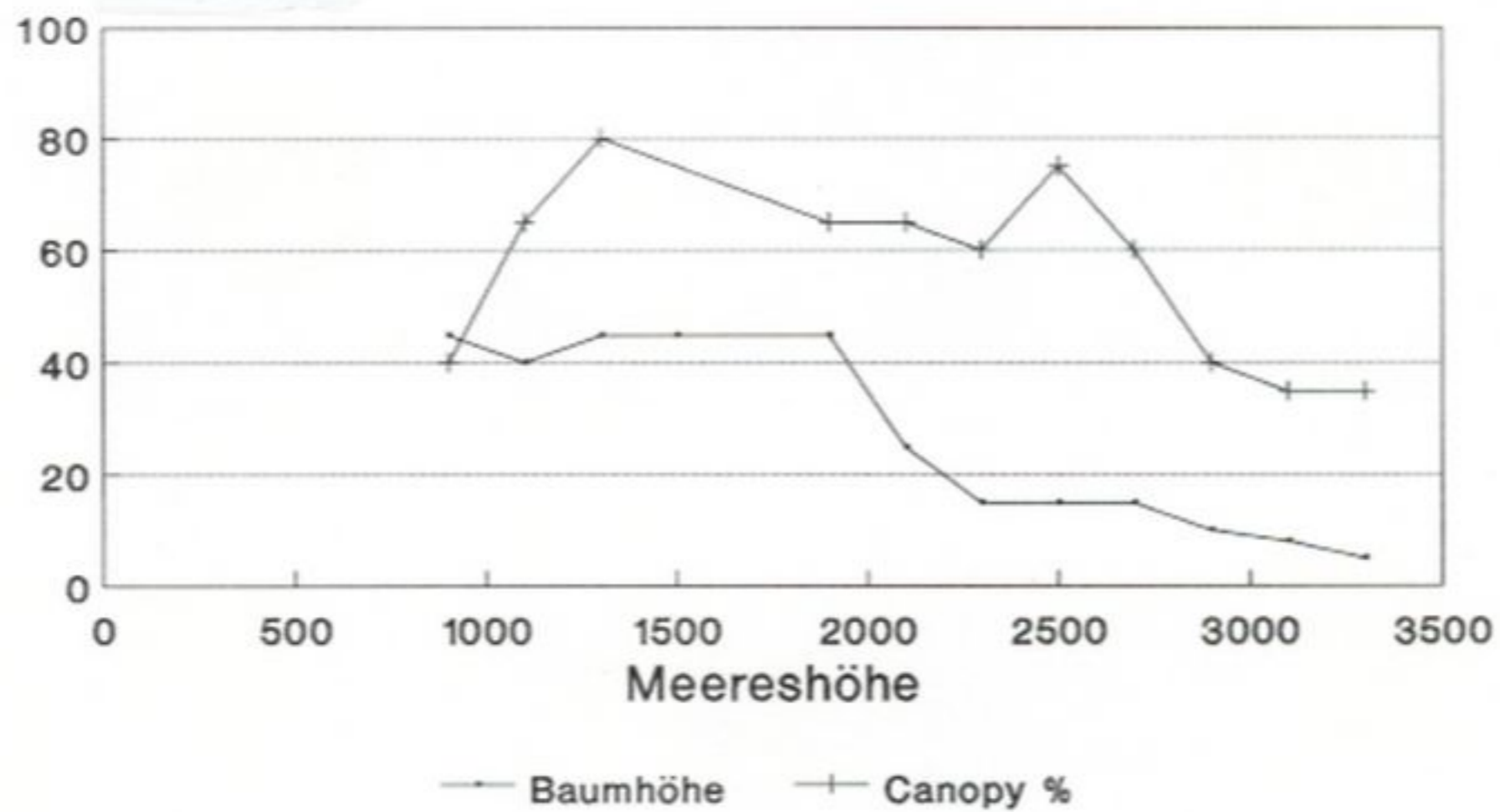


Fig. 6: Tree height and canopy.

the upper montane belt and includes only small patches of forest. This forest consisting of *Hagenia abyssina* or mixed stands of *Podocarpus*, *Psychotria*, *Syzygium* or *Agauria* is much lower than upper montane forests in other parts of the tropics in comparable elevation. At the forest line, the trees are as low as 10 meters and the subalpine *Erica* heath is up to 5 m high.

The canopy varies according to the selection of relevés and might also be influenced by the species composition of trees. It varies between 60 and 80% in elevations between 1100 and 2700 m but decreases towards the forest line to 35-40%. The values of the canopy are conspicuously inversely proportional to the values of the light intensity: the decrease in the canopy values between 1100 and 2300 m is correlated with the increase of the light intensity measured at the forest floor, a more closed canopy at 2500 m corresponds to the low light intensity at this relevé and decrease of the canopy cover above relates to the increase of the light intensity. This is a good test for the exactness of the canopy cover estimations and high evidence of simple canopy cover estimations for the light climate of the interior of a forest.

3.7 Phytomass of epiphytic bryophytes

The phytomass of epiphytic bryophytes per m² and per hectare along the transect is shown in fig. 7. Both curves are synchronous, although not completely. The values per m² are not necessarily characteristic for all trees of the relevé, since the trees can show very different growth of epiphytic bryophytes. Especially at lower altitudes, the bryophyte cover can vary much from tree to tree and there is no real representative cover. The values of phytomass per hectare, although based on estimations and derived from single measurements, give more representative data. As in the values for bryophyte cover, there is a reversal of the profile in the lower part of the transect of the Luhoro river valley, where the phytomass of epiphytic bryophytes is 20 g/m² at 900 m at the bottom of the valley but only 14 g/m² at the ridge at 1500 m. There is a sudden increase to 70 g/m² at 1900 m, a phenomenon found in all previous studies in Peru and Borneo

at elevations above 1500 m. In contrast to the previous studies, there is, however, no increase of this value in the upper montane forest, which consists of "mossy forest". The reason is that the upper montane forest in the Mt. Kahuzi transect consists only of small spots of forests within wide bamboo thickets. As in the other transects in Peru and Borneo, maximum values are reached at the forest line or in the subalpine belt.

The phytomass of epiphytic bryophytes in kg/ha is 20 kg at 900 m. It goes down to about 8kg/ha at 1500 m for the reason mentioned above and increases at 1900 m to 44 kg/ha. At higher elevations, the trees are more densely and equally covered with epiphytic bryophytes and thus the values of epiphytic bryophytes per hectare increase to 100 - 600 kg/ha in elevations between 1900 and 2900 m, although the values per m² oscillate only between 35 and 70 g. Highest values of 6 tonnes per hectare are again found at the forest line viz. in the subalpine belt. The phytomass of epiphytic bryophytes is here 750 times (!) higher than the lowest value found in the lower part of the transect! It illustrates very dramatically the importance of the rôle of bryophytes as indicators for the different ecological conditions in such a transect through tropical rainforests.

The only previous determination of the phytomass of epiphytic bryophytes in Africa has been performed by Pócs (1980) in Tanzania. Although the values cannot be directly compared with the values from Zaire because of a different latitude, different climatic conditions and consequently a different altitudinal zonation of the vegetation, they provide a view about the conditions in other parts of the African tropics. Pócs (l.c.) indicated the phytomass in an elfin forest on a summit (although situated at 2140 m only but due to the different latitude and the summit effect more or less comparable with the summit region of Mt. Kahuzi) with 11 tonnes/ha, nearly double as much as on Mt. Kahuzi. Also the phytomass given for the lower submontane rain forest in Tanzania of 1773 kg/ha is much higher than in Zaire. The phytomass measured is indicated, however, by Gradstein & Pócs (1989) as bryophyte phytomass, but in the original publication and by Pócs (1982) as epiphyte phytomass and

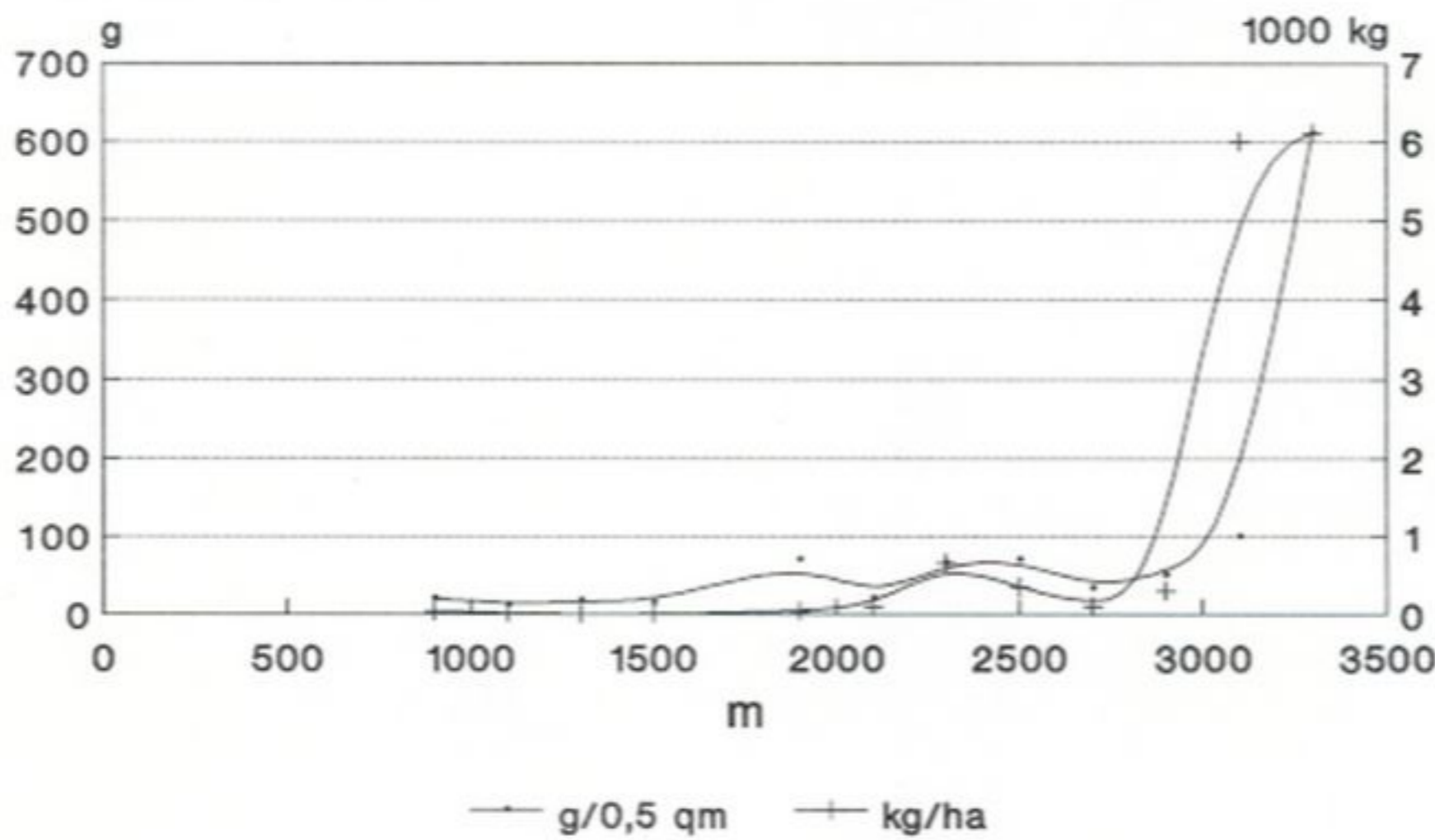


Fig. 7: Phytomass, dry weight.

includes other epiphytes as well which would explain the higher value.

3.8 Water storing capacity

Practical tests for determination of the water storing capacity of epiphytic bryophytes were not performed in the Mt. Kahuzi transect. The reason is that the water storing capacity of bryophytes has been revealed to be very uniform across different parts of the world. In Borneo, bryophytes stored between 2.6 and 3.4 times as much water compared with their dry weight with the exception of the lowland dipterocarp forest, where a factor of 5 was measured, due to the prevalence of *Leucobryaceae* and *Calymperaceae* with special morphological structures for storing water. In Tanzania, Pócs (1980) gave a factor of 2.55. In temperate bryophytes, the water storing capacity was studied by Mägdefrau & Wutz (1951). The factor of wet weight compared with dry

weight was given as 14 in *Leucobryum*, 8-12 in *Sphagnum*, 8-11 in *Scleropodium purum* and 2.5 - 3.8 in *Polytrichum formosum* and seems generally to be higher than the values obtained in the tropics by Pócs (1980) and Frahm (1990). The indication that *Leucobryum* has a higher water storing capacity as *Sphagnum* and that *Scleropodium* has the same as *Sphagnum* make these results questionable. Therefore for a rough calculation, the amount of water stored in bryophytes is regarded as three times the dry weight. In this calculation it has to be born in mind that the value of the water storing capacity is hypothetical. It is based on absolutely dry bryophytes, which is unlikely to be realized in the field. On the other hand, this calculation does not consider the interception water kept between the plants in bryophytes tufts and therefore our values can be of practical value.

Based on this consideration, the amount of water stored in epiphytic bryophytes is 20 - 60 l/ha at elevations between 900 and 1500 m, a value

which is ecologically not relevant and which compares to the low significance of epiphytic bryophytes in the interior of the rainforest. Between 1900 and 2900 m, 130 to nearly 2000 l/ha of rainwater can be stored in epiphytic bryophytes per hectare and at the forest line, about 18000 l/ha.

Unfortunately there are no climatic data available for the Kahuzi park. It can be estimated that the precipitation is comparatively low. The forest at the park gate at 2200 m hardly gives the impression of a rainforest but of a mesic montane evergreen forest. Therefore the precipitation can be estimated as less than 2000 mm/year. Precipitation at higher altitudes will be accordingly low. If a mean value of 4000 mm is considered at 3100 m, this would be (1mm = 10,000l/ha) 40,000,000 l/ha /yr or 109,589 l/ha/day. Of these approximately a hundred thousand litres per day, 18.000 l can be stored at the forest line in epiphytic bryophytes, which is 18%. At lower altitudes, even if the highest value of 2000 l/ha at 2300 m is taken into account, 2% of the rain fall could be stored if 4000 mm yearly precipitation is estimated or 1%, if 2000 mm is estimated. The importance of the water storing capacity and the ecological rôle of bryophytes is therefore not as high as usually stressed. If the high bryophyte cover of 90% on soil in the subalpine belt is considered, there is certainly an important effect of bryophytes on the water balance of the ecosystem. This concerns, however, only the subalpine belt or the forest line. In the upper montane forest below there is only a low percentage cover of bryophytes on ground and also a low water storing capacity of epiphytic bryophytes.

Water storing capacity is furthermore dependant on the amount of rainfall. Low rainfall can be stored more easily and more completely than strong rainfall. The stronger the rainfall the less is the percentage of water stored by bryophytes, and only in ecosystems with a moderate precipitation, can the bryophytes take up all available water and reduce the outflow to zero.

Most of the water stored by epiphytes evaporates, since 80% of the precipitation in a rainforest evaporates (Larcher 1976). Thus epiphytic bryophytes function to stabilize evaporation, to saturate the air humidity and to keep intact the cycle

of evaporation and rainfall. This is particularly so with bryophytes on soil, which evaporate most of the water, and this is especially the fact for low rainfall, which is stored totally by bryophytes. According to Larcher (1976), *Sphagnum* can keep 15 mm of rainfall before the excess reaches the ground, what means that bryophytes can make no significant contribution to the ground water. Rainwater of light or medium rainfall is stored and evaporates, and only excess water of heavy rainfall seeps into the ground, and this only in less steep areas. The view of a mossy forest as a sponge that keeps rainwater and slowly releases it to the ground water is thus not quite concrete and cannot be generalized. It applies only to very humid regions where the rainfall is higher than the amount of water stored by bryophytes.

From Tanzania, Pócs (1980) calculated that the water storing capacity of epiphytes including interception water was over 50% of the annual rainfall. This value cannot be confirmed for Zaire. Pócs included interception water. In our test, the surplus water in the bryophyte material was shaken off for weighting. To test how interception water influences the results, a "moss" ball (consisting mainly of *Herbertus* spec. collected in 3300 m at Mt. Kahuzi) was soaked with water and balanced with interception water. The dry weight of the moss ball was 494 g. The highest weight measured immediately after soaking (before the water dripped off and thus lowered the weight) was 1800 g, which is 3.6 as high as the dry weight. Thus inclusion of interception water does not raise the water storing capacity dramatically, but only 20%.

Generally, the percentage of rainfall stored by epiphytic bryophytes is not a suitable parameter. It depends too much on the amount of precipitation (which varies great, and also the phytomass is not proportional to the amount of precipitation) and does not include the amount of water used by the vegetation. So it could be that epiphytic bryophytes may store most of the water needed by the higher vegetation, although the percentage of the annual rainfall stored may be low in areas with high precipitation.

I thank B.J. O'Shea for correcting the English text.

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