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Climatic habitat differences of epiphytic lichens and bryophytes

*Jan-Peter FRAHM**

Botanisches Institut, Meckenheimer Allee 170, 53115 Bonn, Germany

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Abstract – Conspicuously, some host trees (in temperate regions as well as in the tropics) are covered by epiphytic lichens, others by bryophytes, or we find bryophytes at the trunks and lichens in the crowns of trees. To determine the reasons for the dominance of bryophytes or lichens, humidity data loggers were installed over a period of one year on nearby lichen and bryophyte tree in the Vosges Mtns, France, as well in the Lower Rhine area, Germany. Since bryophytes and lichens are poikilohydric, only periods in which the plants are in wet state (rH > 80% rH) or in wet state during day light (assimilation phases) were taken into account. The results show clearly that the different relative humidity is at least in part responsible for the abundance of bryophytes or lichens. Bryophyte habitats are characterized by 20-30% longer wet phases and accordingly shorter phases of desiccation. The comparison of regions with different air humidity reveals that the lichen tree at the Lower Rhine had 27.5% less wet phases than the lichen tree in the Vosges Mtns., which possibly counts for the different cover (5% viz. 90%). The results of calculations of air quality based on the cover or frequency of epiphytic lichens from differently humid areas can therefore not be compared.

Epiphytes / lichens / bryophytes / bioindication / air humidity

Zusammenfassung – Auffälligerweise sind manche Bäume sowohl in temperaten Gebieten als auch den Tropen von epiphytischen Moosen, andere von epiphytischen Flechten besiedelt, oder wir finden Moose an den Stämmen und Flechten im Kronenraum. Um die Unterschiede zu bestimmen, welche die Dominanz von Moosen oder Flechten hervorruft, wurden Luftfeuchte-Datalogger für ein Jahr an nahe beieinander gelegenen mit Moosen bzw. Flechten bewachsenen Bäumen in den Vogesen (Frankreich) und dem Niederrhein (Deutschland) installiert. Da Moose und Flechten poikilohydrische Pflanzen sind, wurden die Phasen ermittelt, in denen die Pflanzen befeuchtet waren (rH > 80%) oder über Tag feucht waren (Assimilationsphasen). Die Ergebnisse zeigen daher, dass die relative Luftfeuchte zumindestens zum Teil für die unterschiedlich starke Bedeckung mit epiphytischen Moosen und Flechten verantwortlich ist. Der Vergleich zeigt, dass Moos-Standorte 20-30 % längere Feuchtephasen bzw. entsprechend geringere Trockenphasen haben als nahebei gelegene Flechtenstandorte. Im Vergleich unterschiedlich luftfeuchter Gebiete zeigt sich, dass der Flechtenbaum am Niederrhein 27,5% weniger Feuchtephasen hat als der in den Vogesen, was eine Erklärung für die unterschiedliche Bedeckung (5% bzw. 90%) sein kann. Daher sind an unterschiedlich luftfeuchten Standorten gewonnene Ergebnisse der Berechnungen der Luftgüte über Frequenz oder Abundanz von Flechten nicht vergleichbar.

Epiphyten / Moose / Flechten / Bioindikation / Luftfeuchte

* Correspondence and reprints: frahm@uni-bonn.de

INTRODUCTION

Bryophytes and lichens are the most common epiphytes and the only epiphytes in the extratropics. Reason is their poikilohydric life syndrome. The supply with nutrients and water by the atmosphere enables both (as well as some algae) to occupy this kind of habitat in contrast to homoiohydric plants, which are only to a small extent and only in the tropics able to occupy such a niche.

The predisposition for the growth of epiphytic lichens and bryophytes is the sufficient supply with water. Water does not necessarily mean rain fall, since bryophytes and lichens are also found as epiphytes in climates with low precipitation (*e.g.* on cacti in semi-deserts). They are able to take up dew over night and can also take up water from high air humidity (*e.g.* mist).

An often observed phenomenon is, that trees are overgrown either with bryophytes or with lichens. This can be observed either on trees in different regions or even on the same tree in different heights above the ground. The first case counts for temperate regions, where exposed trees (e.g. roadside trees) are covered with lichens in some regions (*e.g.* in lowlands) but with bryophytes (in montane regions). The latter case is met more rarely. According to own observations, the ericaceous trees in the subalpine belt of the African mountains can be densely covered with hepatics (*Herbertus, Chandonanthus*) in the lower part but with *Usnea* in the upper part. The same effect could be observed in subalpine shrubs in Venezuela.

Only few attempts have been made to explain this effect. Already Ule (1908) stated that in the Amazon lowlands, epiphytic lichens are more commonly found in open situations along rivers but to a lesser extend in the forest. Vareschi (1980) argued that lichens are found more frequently in wind exposed habitats. This effect can be observed along mountain ridges, in mountain passes, in the canopy of forests and along the edges of forests. He explained this effect by the fact that lichens need stronger winds to supply the phycobiont with CO_2, which must be pressed into the thallus.

The observation that the different lichen or bryophyte cover is found along the same tree excludes other factors for explanation of differences of epiphytes such as different bark structure, different bark chemistry, different macroclimate (especially precipitation), different tree habitats and focuses the problem to different ecological microclimatic factors along the same tree, especially light, temperature and humidity, which can be determined by help of dataloggers. As parameter for comparison, the relative humidity (rH) was chosen. This is based on the consideration, that for a poikilohydric plant, the length of the period is essential, during which the plant is turgescent, that means metabolic active. Light is no delimiting factor, especially not on free standing trees, especially with regard to the relatively low compensation point of bryophytes and lichens. Also temperature is no critical factor since high temperatures are usually combined with dry phases and thus not relevant for poikilohydric plants and differences of few degrees Celsius as realized between different microclimatic stations have little influence on the photosynthesis.

MATERIALS AND METHODS

Air humidity was measured by dataloggers (TinyTalk, Orion Co.), which were fixed on the bark of tree trunks in 3 m height on lichen viz. bryophyte covered trees in the same area. Since the humidity sensors do not work when exposed to rain, the dataloggers were mounted under small shields made from thin aluminium plates. In one place, a double set of dataloggers was mounted to get an estimate of the measuring differences of the individual loggers. The differences ranged between 0% and 10% within a period of two to three months. A main problem with humidity loggers is, that water can condense at the sensors, which is expressed in the readings by values > 100%. Although these values indicate saturated air humidity, it can take some time until the condensed water is evaporated. Therefore the measured values can be slightly higher than in reality. Measurements were made every hour over a period of one year, thus covering all seasons. Since the memory of the dataloggers was limited to 1 700 readings, the data had to be downloaded to a notebook in intervals of one to three months.

The measurements from one year are probably not representative for a longer period, because we can have drier and wetter, hotter or colder years in temperate regions. However, the data are not used to determine the absolute but the relative differences between the stations.

The stations were situated

1. In the Vosges mountains, France, at 645 and 660 m elevation, annual precipitation about 1 800 mm. The dataloggers were placed

a. on a single, exposed tree trunk of *Juglans regia* situated in a stream valley at 645 m elevation. The tree trunk is covered (90%) with abundant bryophytes such as *Antitrichia curtipendula, Hypnum cupressiforme, Leucodon sciuroides, Zygodon viridissimus, Frullania dilatata, Radula complanata* and *Metzgeria furcata.*

b. on a trunk of *Quercus robur* within an open oak stand at 660 m elevation 15 m higher and 100 m apart from the first station, densely covered (90%) by lichens such as *Usnea florida, U. filipendula, Parmelia sulcata, Pseudevernia furfuracea*. The only moss is *Ulota bruchii.*

c. for one measuring period of two months from May to July, an additional data logger was mounted on *Fraxinus excelsior* situated at 645 m elevation along a stream within a dense spruce forest, about 100 m apart from the walnut tree. This tree was also covered but more densely with bryophytes such as *Antitrichia curtipendula, Neckera crispa, Hypnum cupressiforme, Radula complanata* and *Frullania tamarisci.*

Although the host trees are different species with a different bark structure and bark chemistry, the differences between purely lichen covered and purely bryophyte covered trees in short distance under the same macroclimatic conditions are amazing and cannot be explained only by the different bark.

2. The second station was situated in the Lower Rhine area, Germany, at 20 m elevation, annual precipitation about 600 mm. The dataloggers were fixed in both stations on trunks of *Populus xcanadensis*, thus better comparable with regard to the same species of host tree as in the Vosges Mountains.

a. in a small plantation of poplars within meadows. The trunks were sparsely covered (5%) with lichens such as *Physcia tenella, Xanthoria parietina* and *Parmelia sulcata*.

b. at the eastern edge of a dense forest, where the trunk was covered (40%) by *Dicranoweisia cirrata* and *Hypnum cupressiforme*. During the study period, small amounts of *Orthotrichum affine* established in addition.

EVALUATION

For evaluation of the data, the logged values were transferred into Microsoft Excel®, and all readings above 80% humidity were counted. This approach was chosen to determine the approximate "**wet period**" during which the epiphytes are turgescent. The idea was to get an estimation of the length of the period, in which bryophytes as well as lichens are metabolic active. This is only the case when the plants are turgescent. The 80% value is based for bryophytes on own measurements of the relative humidity (rH) at a time, when the plants start to dry up. Such measurements were made in different elevations in tropical rain forests in Borneo (Frahm, 1990), where bryophytes were turgescent at 78% rH but dried up at 75% or 72%. Principally, this critical value depends on the osmotic value which may differ seasonally, from species to species and in species of different habitats. Even if the turgescence periods of the species on a tree are slightly different, the periods with rH > 80% are a good approximation and are used to characterize the relative differences of habitats.

For lichens, Schöller (1991) stated anabiosis below 70% rH and Schöller & Jahns (1992) presented measurements of the thallus humidity and in dependence on air humidity and stated a decrease of thallus humidity below 80% rH for the lichen species *Cladonia portentosa*. Jahns & Ott (1983) presented results of microclimatic measurements of lichen habitats. They included daily curves of thallus humidity and air humidity. Depending on habitat and day of the year, the thallus humidity drops at air humidities between 75 and 90%, in average slightly above 80%. As stated by Jahns & Fritzler (1982), the time of desiccation is species specific and depends on growth form as well as thallus anatomy. Lange *et al.* (1991) measured water contents of thalli of *Alectoria* spec. and air humidity in the Namib desert. The increase of thallus weight (and thus uptake of water vapour) started at 80% rH. Therefore periods > 80% rH were also used for indication of turgescence periods of lichens.

The wet period, however, falls largely into the night hours caused by cooling over night and reaching the dew point, in which no photosynthesis is possible. The competitive power of epiphytes depends on growth and growth is only possible during net-photosynthesis. Therefore the dark hours were deducted from the total wet period, which are seasonally different, being 8 hours in June but 16 hours in December. For that purpose, sunrise and sun set was determined for both localities (Vosges: 6° 40´E, 47°50´N, Lower Rhine 6° 28´E, 51° 26´N) for the first day of every month on the internet (www.wetterochs.de/wetter/sunset.html). The calculation of the **light period** is thus not absolutely correct since the time of sunrise and sunset varies about 45 minutes during a month, however, since the data loggers only measured in hour intervals, this error is compensated.

RESULTS

1. Vosges Mountains

Air humidity measurements were undertaken from July 20, 1998 to July 22, 1999 over a period of 8673 hrs. Due to technical problems with the logger in the bryophyte habitat, data in both habitats were only recorded from Sept. 25 to

December 31 and from May 15 to July 22, thus only for 3950 hours (almost half a year). During the last measuring phase, a third logger was installed in a more humid bryophyte habitat.

At the lichen station with continuous measurements over the year, an air humidity of more than 80% was reached at 6,453 hrs, thus in 77.4% of the time. The percentage varied seasonally: between September and December as well between May and July, the critical value for the turgescence was 64-67% but 72% between March and May, 82% in December and 95% from January to March.

At the bryophyte station, an air humidity of more than 80% was reached in 94-95% of all hours from September to December and 77% of all hours between May and July, thus 10% higher as at the lichen station in early summer, more than 10% higher in autumn and 30% higher in the winter months. The number of hours with more than 80% humidity was 2722 in the lichen station but 3462 in the bryophyte station, thus 22% higher in the bryophyte station (Fig. 1). In opposite, the desiccation period during half year in which both loggers were recording was 1228 hrs in the lichen station and 488 hrs in the bryophyte station, thus 78% times higher in the lichen station.

An example for the daily differences between both habitats is given in Fig. 2.

Saturated air humidity is found on both trees during night and during the morning hours until 9 a.m. At the bryophyte tree, the humidity decreases from hour to hour and reaches it minimum in the afternoon hours between 6 p.m. and 7 p.m. with values between 50% and 60% rH but raises in the evening hours to 100% at 9 p.m. The humidity at the lichen tree drops more rapidly from 9 a.m. to 12 a.m.; the values are all the day below the values of the bryophyte tree and (due to evening sun) reach saturation not before 11 p.m. During winter time, the humidity is frequently saturated over a period of several days in both stations.

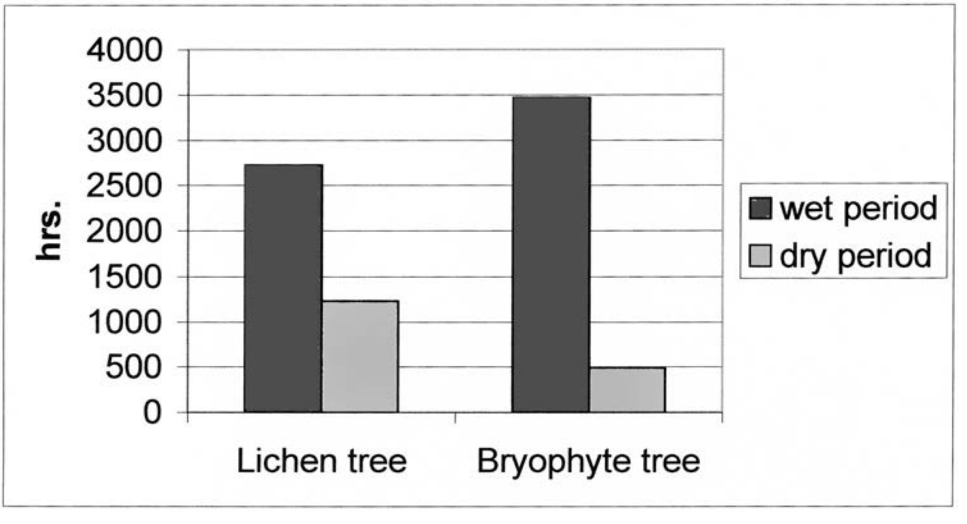

Fig. 1. Numbers of hours of wet periods (> 80% rH) viz. dry periods (< 80% eH) over a period of 3950 hours on a lichen covered and a bryophyte covered tree in the Vosges Mtns., France. The lichen habitat has distinctly fewer wet and more dry phases as compared with the bryophyte habitat.

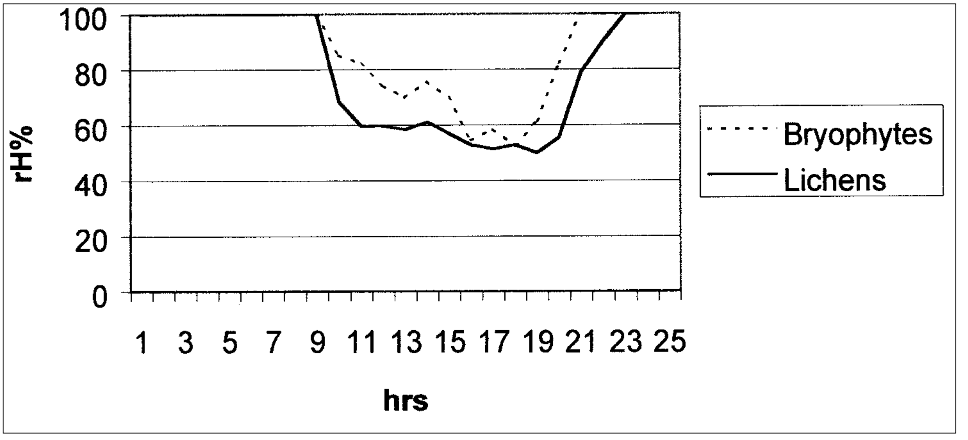

Fig. 2. Curve of percentage of relative humidity (rH) on lichen tree and bryophyte tree during July, 18, 1999 in the station Vosges Mountains.

At the second bryophyte station (with *Neckera crispa* etc.), the bryophytes stayed wet during 84% of the time between May, 15 and July, 22, whereas the turgescence period at the first bryophyte station (*Leucodon* etc.) was 77% of the time but only 67% of the time at the lichen station.

The photosynthetic active period (light plus humidity > 80%) increases similarly to the turgescence period from the lichen tree to the mesic bryophyte tree and the humic bryophyte tree (Fig. 3).

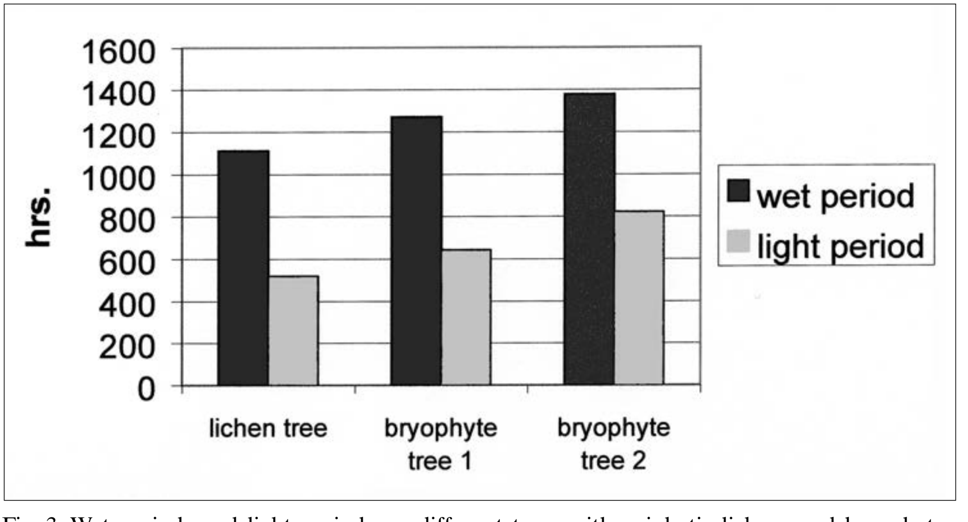

Fig. 3. Wet periods and light periods on different trees with epiphytic lichens and bryophytes from May 15 to July 22, 1999 in the Vosges Mtns, France.

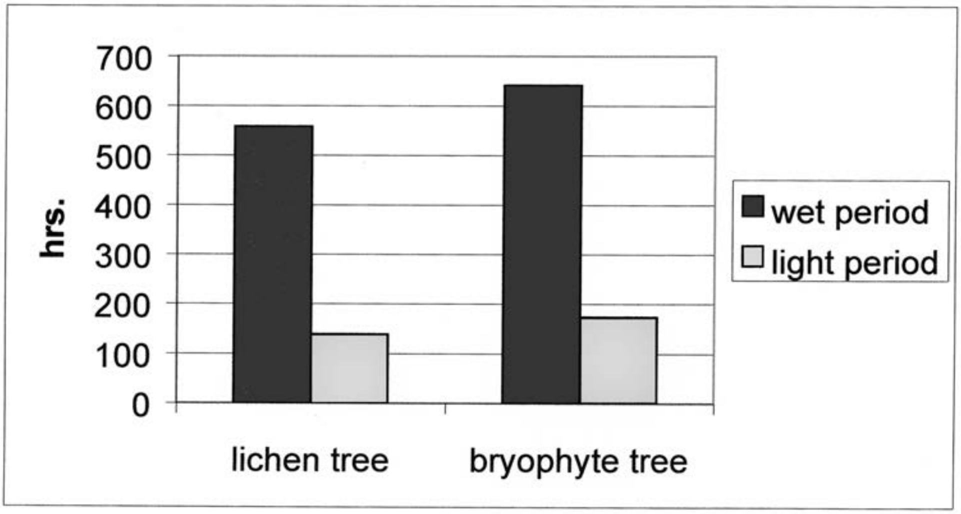

Fig. 4. Turgescence period and photosynthetic active period on different trees with epiphytic lichens (station 1) and bryophytes (station 2 and 3) from December 3-31, 1998 in the Vosges Mtns., France.

During winter time, the relative differences between the lichen and bryophyte tree as well as wet and light periods are the same as in summer time. Only the light periods are shorter due to the shorter day length (Fig. 4). This means that growth rates are not necessarily higher in winter season, because of the higher humidity is compensated by the shorter light period and the lower humidity in summer time is compensated by longer photo period.

2. Lower Rhine

Humidity was measured from July 15, 1998 to July 31, 1999, thus over a complete year or 9,141 hrs. The data from the last measuring period were shortened to exactly one year or 8,764 hrs. The fact that spare loggers were used in both stations compensated the loss of data of two loggers over two periods.

An air humidity >80% was reached at the lichen tree during 4,687 hrs or 53.4% of the time, at the bryophyte tree during 6,748 hrs or 76.9% of the time (Fig. 5). The wet period at the bryophyte tree was thus 31% longer.

(The wet period at the bryophyte tree in the Lower Rhine region as about as long as that of the lichen tree in he Vosges Mountains. Therefore it is impossible to argue that trees are covered with bryophytes if the wet period is, for instance, more than 5,000 hrs a year. Other factors as the humidity seem to modify the effect. In this case, the habitat of the bryophyte tree in the Lower Rhine got less light intensity than the lichen tree in the Vosges Mtns, which may explain the difference in the cover in spite of about the same wet period. The wet periods differed seasonally but again distinctly different in both habitats. From April to June, the wet phases were only 20-30% of the time at the lichen tree and 50-60%

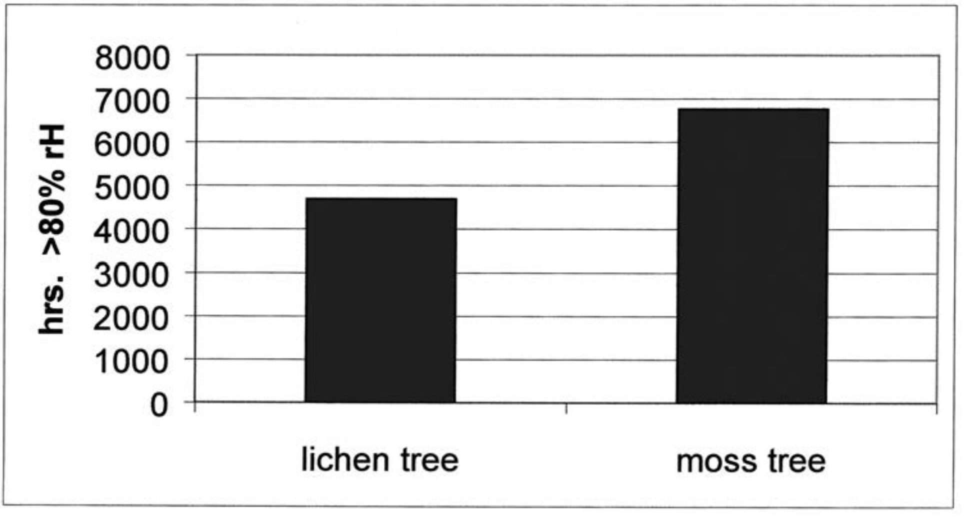

Fig. 5. Wet periods (in hrs) on a lichen tree and bryophyte tree in the Lower Rhine area over a period of one year.

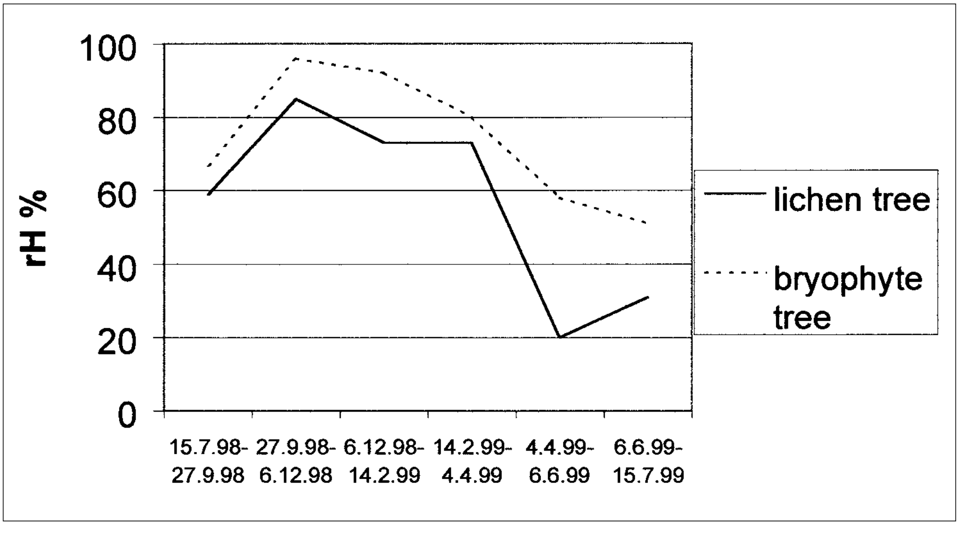

Fig. 6. Percentage of wet periods (rH > 80%) depending on the season at the bryophyte tree (upper line) and lichen tree (lower line) in the stations Lowe Rhine.

at the bryophyte tree. In contrast, the wet phases were 85% viz. 96 in autumn and 73% viz. 80-90% in winter and spring (Fig. 6).

The daily curves of humidity are usually similar to the Vosges (*cf.* Fig. 2), see fig. 7, in the way that we have saturated air humidity over night to the morn-

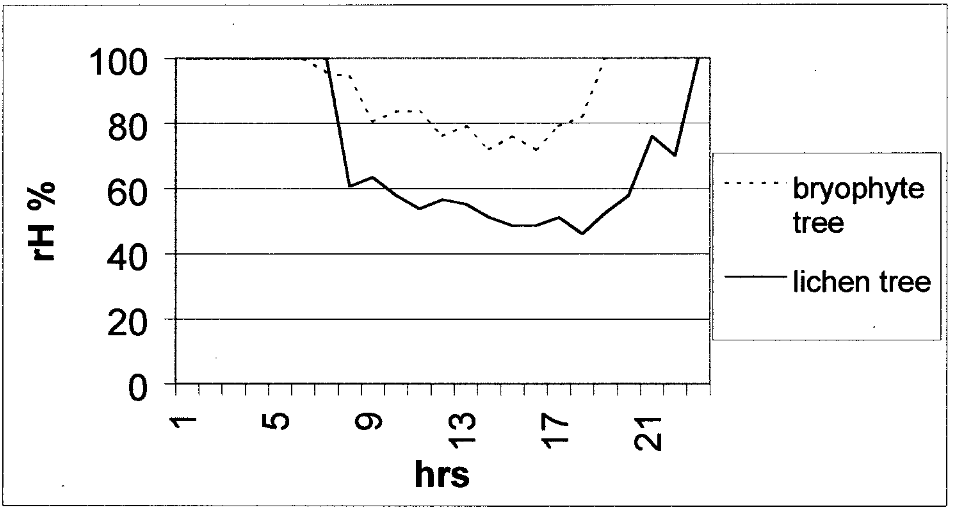

Fig. 7. Daily curve of humidity on March 3., 1999 at the bryophyte stations (upper line) and the lichen station (lower line) in the Lower Rhine.

ing hours with a decrease at sunrise, various lower values over the day (depending on insolation or clouds) and increase of values during the evening hours with the lowering of the temperature. Typically, the bryophyte habitat has always the higher humidity.

3. Comparison Vosges Mtns – Lower Rhine area

The stations in the Vosges Mtns and the Lower Rhine area differ largely by the cover of lichens and bryophytes. Whereas the trees in the Vosges Mtns are almost fully covered with lichens viz. bryophytes, the trees in the Lower Rhine area, although differing principally by lichen or bryophyte cover, have much less cover. Cover is, however, an expression of growth and the latter a function of growth periods (net-phyotosynthetic phases). Therefore the attempt was undertaken to explain the differences in cover by the different length of photosynthetic phases. This is based on the observation, that bryophyte and lichen cover increase with altitude in the mountains (longer phases of higher humidity due to cloud, mist and more frequent reaching of the dew point) or in certain topographic situations (depressions, valleys, gorges). For this purpose, the datalogger values from the lichen trees from the Vosges Mtns and the Lower Rhine (only the lichen tree logger worked for the full year in the Vosges Mtns). It turns out that the wet phase of the lichen tree in the Vosges Mtns was 6,453 hrs per year but that of the lichen tree in the Lower Rhine was only 4,684 hrs. (Fig. 8) thus only 72.5% of the period in the Vosges Mtns.

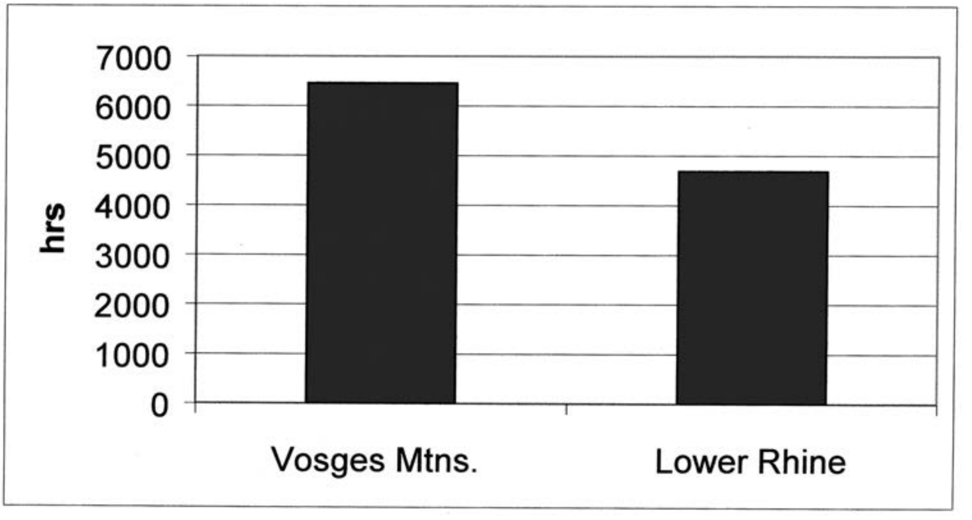

Fig. 8. Hours of wet periods (> 80% rH) over a year on lichen trees in the Vosges Mtns and the Lower Rhine.

DISCUSSION

The results of air humidity measurements on nearby lichen and bryophyte habitats in the lowlands and montane region of Central Europe show clearly that epiphytic lichens and bryophytes require different habitats defined by different periods of desiccation (or turgescence, respectively). Epiphytic lichen covers are characteristic for habitats with longer desiccation periods, those of bryophytes for shorter desiccation periods. The results of the data logger measurements show that the bryophyte habitats have shorter desiccation periods and 22% longer phases of turgescence in the Vosges Mountains and 31% longer wet phases (on the same host tree species and nearby, macroclimatic identical localities) at the Lower Rhine. This confirms field observations, according to which bryophytes are more competitive in more humid habitats than lichens and disappear if the desiccation periods get too long, which are, however, tolerated by lichens. It can be assumed that similar microclimatic differences separate bryophytes on tree trunks and lichens in the canopy. The values presented here are taken from one year (summer 1998 to summer 1999) and may be not representative (there is in fact no representative curve of temperature or humidity in Central Europe but the characteristic of the climate is its inconsistency) and vary from year to year, but the relative differences, here expressed in percentages, seem (according to the "law" of relative habitat constancy) to be the same.

The result is important for several reasons:

1. The cover of epiphytic bryophytes and lichens is at least in part determined by air humidity. Methods to determine "air quality" by frequency such as the German VDI method (VDI 1995) for epiphytic lichens include this parameter in the evaluation. By this way, investigated trees in more humid regions, which are more densely covered with epiphytes, get higher values and thus the region a better air quality certificated. This concerns mountains and also trees in depressions or valleys, which are differentiated by longer periods of high air humidity but not necessarily by less immissions. Therefore results from mountains cannot be compared with those from lowlands. As a consequence, a correction factor has to be introduced which concerns the different air humidities of the study areas or habitats. This would require more work, since the present results are based just on the comparison of two different localities in different elevations and thus show a trend but no exact data. A consequence, however, could be not to include percentage cover or frequency in such evaluations (because these are based on differences of humidity) but simply the species number (diversity index).

2. At the beginning of the use of epiphytic lichens as indicators of air quality, the lack or low numbers and low cover of epiphytic lichens in cities was discussed. Is this an expression of high immissions or have these lichens reduced chances to survive in cities because of the lower air humidity (drought hypothesis, cf. Coppins, 1973; Thiele, 1974)? The present study reveals that air humidity determines the cover of epiphytes simply by the fact that longer periods of high air humidity mean also longer periods of turgescence, assimilation and growth rates. As a consequence, data from regions with different air humidity such as downtown areas and suburbs cannot be compared with respect to air quality. Reason is, that the common base for comparison (the same number of wet phases) is lacking. However, different species numbers can be used as biodiversity index and as expressions for different life quality with the argument that regions with higher biodiversity are biologically more valuable, also in terms of life conditions for man.

3. The use of only lichens as indicators for air quality is limited to relatively dry regions or habitats, which are free of epiphytic bryophytes. Such studies were developed for urban or industrial areas at a time of high SO_2-emission rate with few epiphytic species and lack of epiphytic bryophytes. Such studies do not work anymore in the same regions after the severe reduction of SO_2-emissions and also not in more humid regions (*e.g.* montane regions). Using the presently used methods for epiphytic lichens, wide regions (*e.g.* Pre-Alps, where even roadside trees are densely covered with bryophytes but not with lichens) cannot be included in such studies. With respect to an evaluation of epiphytes on a large geographical scale, it is therefore proposed to include bryophytes in such studies to extend the ecological range of this method and to combine both, lichens and bryophytes, in a common method which is no more based on calculations of frequency but on species numbers and indicator species.

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