Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda.

3. Photosynthetic gas exchange of bryophytes from different forest types in eastern Central Africa.

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Abstract. During the BRYOTROP-Expedition to Zaire and Rwanda bryophytes were collected from a rainforest habitat at 800 m a.s.l. and from bamboo forest and tree-heath environments between 2200 and 3200 m. The microclimates influencing the mosses are different at the altitudinally separated locations. Conditions are rather constant with 24 °C, 100 % rel. hum. and PAR below 100 μmol photons m^{-2} sec^{-1} at the lowland station, rather versatile in the mountains with six times higher daily sums of PAR, temperatures between 10 and 25 °C and relative humidities between 60 and 1oo %. In the bamboo forest epiphytic mosses dry out during the day to less than 70 % of their water content, but regain saturation from the vapor-saturated air during night.

Bryophyte photosynthesis and respiration were studied by Warburg manometry with moisture saturated samples. Temperature curves of gas exchange peaked between 22 and 30 °C. Optima of the lowland species were somewhat higher than those from samples collected at the mountain sites. Habitat separation of characteristics of photosynthesis was more pronounced with respect to light responses. Saturation gas exchange rates were reached by all species still below 400 μmol photons m^{-2} sec^{-1}. But the slopes of the curves in the low-light range were distinctly steeper, and the light compensation points smaller in the lowland than in the highland species (compensation points of the former: 3 - 12 μmol photons m^{-2} sec^{-1}, of the latter: 8 - 20 μmol photons m^{-2} sec^{-1}).

It is emphasized that bryophytes in the rainforest understory experience extremely high ambient CO_2 concentrations near the floor. This, their low light requirements for photosynthesis, and the permanently optimal temperature and humidity conditions for maximal carbon gain enable them to live successfully, but with less biomass development in this dark and damp environment. By contrast, bryophytes from the bamboo forest and tree-heath environments can utilize light conditions combined with variable temperatures and humidities similarly as species from extratropical vegetation types.

In tropical regions bryophytes are conspicuous and contribute considerably to the ecosystems biomass particularly in mountain forests. In lowland forests species diversity is lower (Richards 1984) and the bryoflora consists mostly of tiny, often epiphyllous bryophytes (Frahm 1987a, b, 1990b; Schuster 1988). It seems that the humid, warm environment is less favourable for bryophyte growth than humid, but temperate or even cold environments. This may be because respiration is rather high under high temperatures and the light intensity too low in the understory of tropical forests so that too a small net carbon gain results (Frahm 1987b).

Photosynthetic rates of bryophytes are generally lower than those of higher plants (Kallio and Karenlampi 1975a; Vallane 1984, Masarovikowa and Elias 1987). An overview of the literature shows that most detailed studies on bryophyte carbon metabolism have been made with mosses from arctic, boreal and temperate regions (Proctor 1982). Data on carbon gain of subtropical or tropical mosses are scarce and focus, as a rule, mostly upon worldwide occuring, not particularly tropical species (e.g. Longton 1979; Rao et al. 1979). In particular the bryophyte ecology of the African regions is poorly studied. The expedition "Bryotrop III" aimed to investigate thoroughly the floristics, systematics and ecology of mosses and liverworts which occur along the vertical profile from the tropical upper lowland forest of the Congo Basin in Eastern Zaire up to the mountain tops of the volcanoes which border the Central African Rift Valley. Some microclimatic measurements were done also and samples of bryophytes were collected, transferred to the laboratory in Europe and checked for photosynthetic responses to light and temperature.

The results of these studies will increase the body of information about CO_2 gain of tropical bryophytes in general and shall clarify, whether a functional separation exists between species from the warm-humid shade sites in the lowland forests and species from the temperate-perhumid, but more light-exposed elfin-forests and from the interior of the bamboo forests which both are the characteristic vegetation of the mountains.

Material and methods

Collections of bryophytes were made in September 1991, December 1992 and May 1993 in the Kahuzi-Biega National Park/Zaire (Kiwu Province) at the localities Irangi (800 m a.s.l.), Kasirusiru at the foot hills of Mount Biega (2200 m), Tshivanga, the headquarter of the National Park (2200 m), and Mount Kahuzi (3200 m). The Irangi Forest reserve is an upper lowland rain forest dominated by *Uapaca* and *Gilbertiodendron* trees, where bryophytes occur mostly as epiphytes (Fischer 1993a). The hill slopes near Kasirusiru and Tsivanga are covered by a mosaic of *Hagenia*-, *Podocarpus*- and *Arundinaria*-forests. At the collection site on Mount Kahuzi the tree line was formed by an elfin forest of *Erica rugegensis*, intermingled by *Senecio johnstoni* treelets. Diurnal courses of habitat microclimates were measured at Irangi during two days and at the Kasirusiru station during four consecutive days. The measurements were taken at both sites in the immediate vicinity of epiphytic moss wefts near the forest grounds. PAR was sensed by two SKYE 215 sensors, humidity by a Vaisala humidity sensor, air and soil temperatures by screened NTC sensors, all connected with two data logger (Squirrel 1209, Grant Instruments, GB). Measurements were logged every ten minutes as the mean of 10 point measurements between the logging intervals. (for reasons of instrument failure readings were taken manually at the Irangi station). At the Kasirusiru station *Pilotrichella* pendants were suspended from spring-balances (Pesola, CH, resolution 0.5 g), and time courses of their weight loss and gain depending upon ambient air humidity were registered.

The collected moss and liverwort species which were used for gas exchange measurements are listed in table 1. All mosses and hepatics collected during the expedition are listed and in part explicitly described in a previous volume of "Tropical Bryology" (Frahm 1993). The samples were either air dried or kept moist during the transport to Europe. Both treatments did not negatively affect the general vitality of the mosses and liverworts nor the specific photosynthetic activity: After rewetting and cultivation under controlled conditions O_2 gas exchange was not

Table 1: Names and collection sites of the investigated mosses and hepatics - The nomenclature follows the preliminary floristic enumeration of the collection numbers of the BRYOTROP III expedition and personal informations by specialists; it has been updated as far as possible according to Fischer (1993b) and Born et al.(1993).

Breutelia diffracta Mitt., BARTRAMIACEAE: Mt. Biega (2700 m)
Breutelia stuhlmannii Broth., BARTRAMIACEAE: Mt. Biega (2700 m)
Campylopus hildebrandtii (C.Müll.) Jaeg., DICRANACEAE: Kasirusiru (2200 m)
Dicranoloma billardieri (Brid.) Par., DICRANACEAE: Mt. Kahuzi (3200 m)
Dicranum johnstonii Mitt., DICRANACEAE: Mt. Kahuzi (2700 m)
Ectropothecium cf. perrotii Ren. & Card., HYPNACEAE: Irangi (800 m)
Frullania spec., FRULLANIACEAE: Irangi (800 m)
Leptodontium luteum (= *L.viticulosoides* (P.Beauv.) Wijk & Marg.), POTTIACEAE: Mt. Biega (2700 m)
Neckera spec., (presumably *N. madecassa* (Besch.) = *Neckeropsis madecassa* (Besch.)Fleisch.), NECKERACEAE: Irangi (800 m)
Neckera platyantha (C. Müll.) Par., NECKERACEAE: Mt. Biega (2300 m)
Pilotrichella ampullacea (C. Müll.) Jaeg., METEORIACEAE: Mt. Biega (2500 m)
Pilotrichella cuspidata, METEORIACEAE: Mt. Biega (2600 m)
Plagiochila barteri Mitt., PLAGIOCHILACEAE: Mt. Kahuzi (2700 m)
Plagiochila divergens Steph., PLAGIOCHILACEAE: Irangi (800 m), Kasirusiru (2200 m), Tsivanga (2200 m)
Plagiochila squamulosa Mitt., PLAGIOCHILACEAE: Irangi (800 m), Tsivanga (2200 m)
Porothamnium stipiatum (Mitt.) Touw ex De Sloover, NECKERACEAE: Irangi 800 m)
Porotrichum molliculum Broth., NECKERACEAE: Irangi (800 m)
Porotrichum elongatum (Welw. & Duby) Gepp, NECKERACEAE: Mt. Kahuzi (2700 m)
Racopilum tomentosum (Hedw.) Brid., RACOPILACEAE: Irangi (800 m)
Radula boryana (Web.) Nees ex Mont., RADULACEAE: Irangi (800 m)
Rhizogonium spiniforme (Hedw.) Br. (= *Pyrrhobryum s.* (Hedw.) Mitt.), RHIZOGONIACEAE: Irangi (800 m), Mt. Biega
(2700 m)
Sphagnum davidii Warnst., SPHAGNACEAE: Mt. Biega (2700 m)

different with samples kept dry or moist during the transport.

In the laboratory the moss cushions or mats were cultivated for maximally two months in open, large petri dishes in a climatized chamber at 15 °C and a photosynthetic active radiation of 5-30 µmol photons m^{-2} sec^{-1} under a 12 : 12 h dark/ light rhythm. Photosynthetic and respiratory gas exchange was measured as O$_2$ loss or gain by Warburg manometry (model V 166, Braun/ Melsungen) using 0.1 M Na$_2$CO$_3$-/NaHCO$_3$ (1:10 v/v) buffer solutions as C0$_2$ source. Measurements were done with samples of 20-40 mg dry weight which were cleaned from dead parts and rinsed with distilled water prior to insertion into the Warburg-vessels. Photosynthesis and respiration were measured in the temperature range between 15 and 35 °C at light intensities of 250 µmol photons m^{-2} sec^{-1}. Photosynthetic light responses were measured at 20 °C and 25 °C under different illumination intensities coming from the incandescent lamps of the Warburg apparatus and from additional halogene lamps. The exact quantum fluence rate was determined discontinuously with a Skye 215 PAR sensor (Skye instruments, GB) placed in a baker at the level of the Warburg reaction vessels, and during the measurements with an adequately calibrated

miniaturized GaAs sensor (Hamamatsu G1118) fixed at the fountain bottom of an empty reaction vessel. During 30 minutes every five minutes the O_2 consumption or production was read from the Warburg manometers. Two of the 14 measurement units of the Warburg apparatus served as thermobarometers. Readings of the dark respiration data were done using a low intensity green-light lamp. The reported values are means from measurements of 3 - 7 samples per species. The gas exchange rates were related to the sample dry weights.

The chlorophyll contents of the studied byrophytes were determined in aceton extracts according to Ziegler (1965) using the calculation formulas by Arnon (1948). The chlorophyll absorption was determined at the wavelengths 647, 664 and 750 nm using a Diode-array spectrophotometer (Hewlett-Packard HP8452a).

Results

Microclimatic situation of the habitats

The microclimates of the two stations Irangi (800 m) and Kasirusiru (2200 m) differ considerably (Fig. 1). Although at both sites, the *Uapaca* community of Irangi and the *Arundinaria alpina* community of Kasirusiru, the sensors were placed not higher than 80 cm above ground, peak values of PAR at the highland site was more than twice as high as in the lowland rainforest. There, PAR only seldom exceeded 100 µmol photons m^{-2} sec^{-1}, the lowest value measured during the daylight period at Kasirusiru. The daily integrals of PAR measured on 23. and 30.8.1991 are 2.5 mol photons m^{-2} d^{-1} and 18.3 mol photons m^{-2} d^{-1}, respectively. The available radiation for the bryophytes in the understory of the bamboo forest is therefore more than six times higher than that in the upper rainforest zone, it will be even higher at and above the treeline of the mountains. The temperature was quite constant in the Irangi rainforest never falling substantially below 20 °C. By contrast, cold nights and mornings prevailed in the mountains where highest air temperatures just reached the average lowland temperature. The air inside the rainforest was nearly always vapor-saturated. This probably is very often also the case in the elfin forest at tree line where clouds condense at the mountain slopes (continuous humidity measurements not available). Inside the bamboo forests, several hundered meters below the cloud layer, humidity falls to 60 - 70 % rel. hum. under sunshine conditions. There, epiphytic mosses dehydrate for several hours per day. They become rewetted during the night from high ambient humidities, when temperatures are low (Fig. 2). After vapor saturation deficit of the air has approximated zero, 8 to 9 hours are needed to regain full saturation. This occurs when dew fall is not yet an important microclimatic factor. Moisture loss under an increasing vapor saturation deficit of the air reduces, on the other hand, the pendant water content down to ca. 80 % of the saturation water content within 1 1/2 hours in the case of *Pilotrichella ampullacea*, within 3 hours in *Plagiochila divergens*.

Photosynthetic gas exchange: temperature responses

Maximal values of photosynthetic gas exchange ranged between 40 and 180 µmol 0_2 g^{-1} dw h^{-1} which is equivalent to values between 1.8 and 8.3 mg $C0_2$ g^{-1} dw h^{-1}. One must be aware comparing these values with data e.g. from IRGA measurements that the gradient of $C0_2$ from outside to the chloroplast was steeper during the measurements than in natural air due to the necessity to keep konstant the $C0_2$ partial pressure in the closed Warburg system by use of a carbonate buffer, while measuring the 0_2 turnover. This methodical circumstance could bring about a shift of the temperature-dependent maximal photosynthetic rates to higher values. Under the experimental conditions mosses from the *Uapaca*-forest of Irangi exhibited the highest 0_2 production mostly between 25 and 30°C (Fig. 3). Only a *Frullania* - the species could not be determined with certainity, probably it is *F. arecae* - reached the peak-value of photosynthesis already at 22°C. This species omitted, the mean optimum of temperature of the most conspicuous epiphytic mosses and hepatics from the upper zone of the Central African rainforest
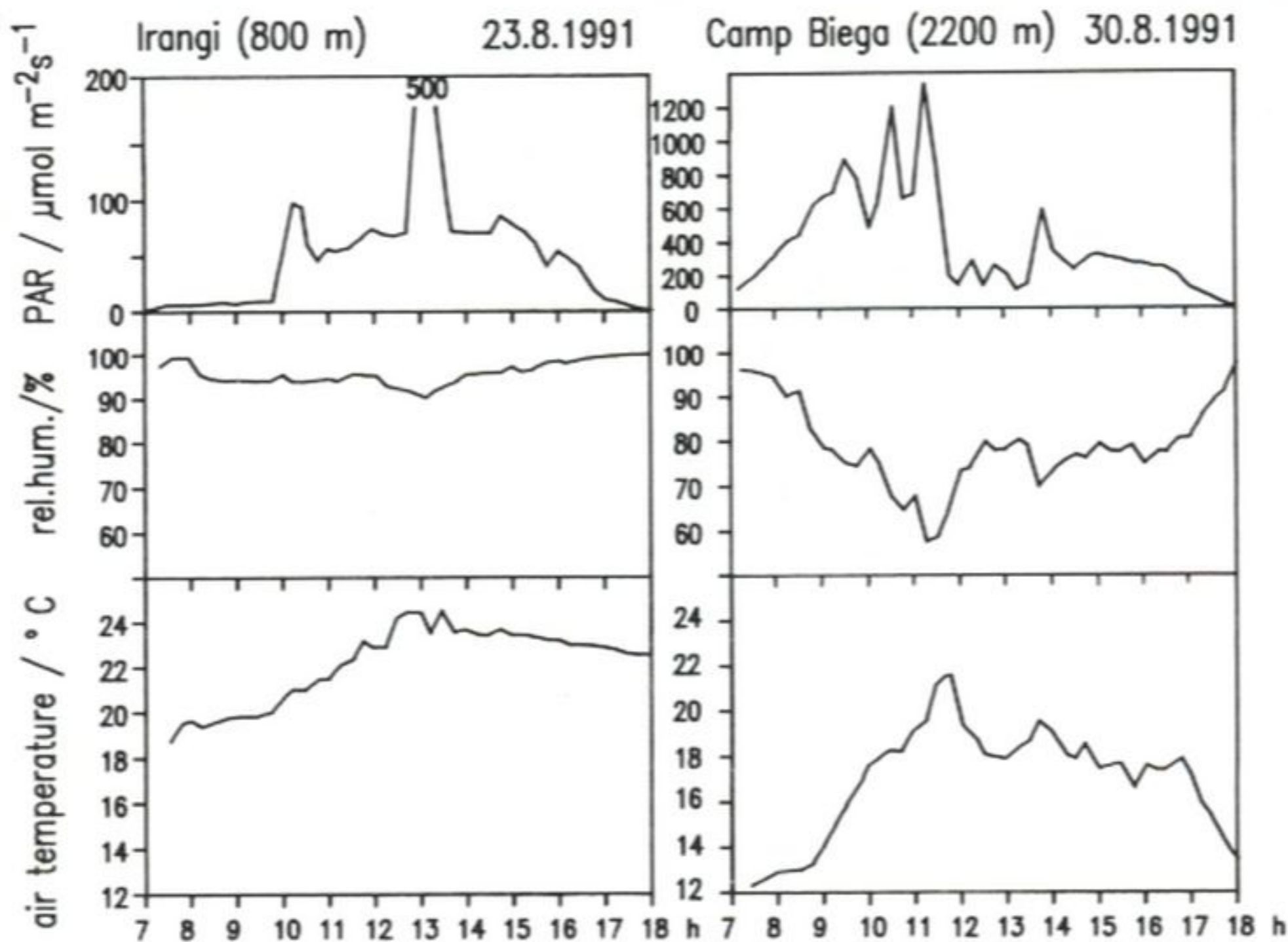
Fig. 1: Courses of daytime microclimate in the upper lowland rainforest near Irangi and the bamboo forest near Camp Biega/Kasirusiru, Kahuzi-Biega area, East Zaire .

comes to $27 \pm 2°C$. It must be noticed further that in these species the decrease of photosynthetic rates with further increasing temperatures is smaller than with decreasing temperatures below the peak values.

Such differences between the slopes of the temperature-depending photosynthesis above and below the optimum are not very evident with mosses from the mountain stations. Figure 4 presents three examples of epiphytic species, figure 5 the photosynthetic temperature curves of five preferably epigaeic species. Particularly the latter ones show a great homogeneity in their photosynthetic responses to temperature with increasing and decreasing average slopes of 2.6 $\mu mol\ O_2\ g^{-1}\ dw\ h^{-1}\ °C^{-1}$ and 4.3 $\mu mol\ O_2\ g^{-1}\ dw\ h^{-1}\ °C^{-1}$, respectively. Peak photosynthesis is reached in all the species shown in figure 5 at 25°C, their dark respiration rates are nearly identical.

The three by preference epiphytically living species (Fig. 4) are not as homogenous in their temperature responses of photosynthesis. But also these species display generally very flat temperature curves with only gently decreasing photosynthetic rates below or above the optimum temperature. Mean optimum temperature as calculated from all measurements with highland species averages at $24,7 \pm 2.4\ °C$.

Some species occur and were collected over the whole altitudinal gradient from 800 m up to 3000 m, or at least closely related species belonging to the same genus were found at several of the investigated places. Thus the hepatic genus *Plagiochila* (Fig. 6) is represented by *P. squamulosa* from Irangi (800 m), by *P. divergens* from Tsivanga (2200 m), and by *P. barteri* from the tree-heath of Mount Kahuzi (2700 m). The altitudinal range of occurrence of all three spe-
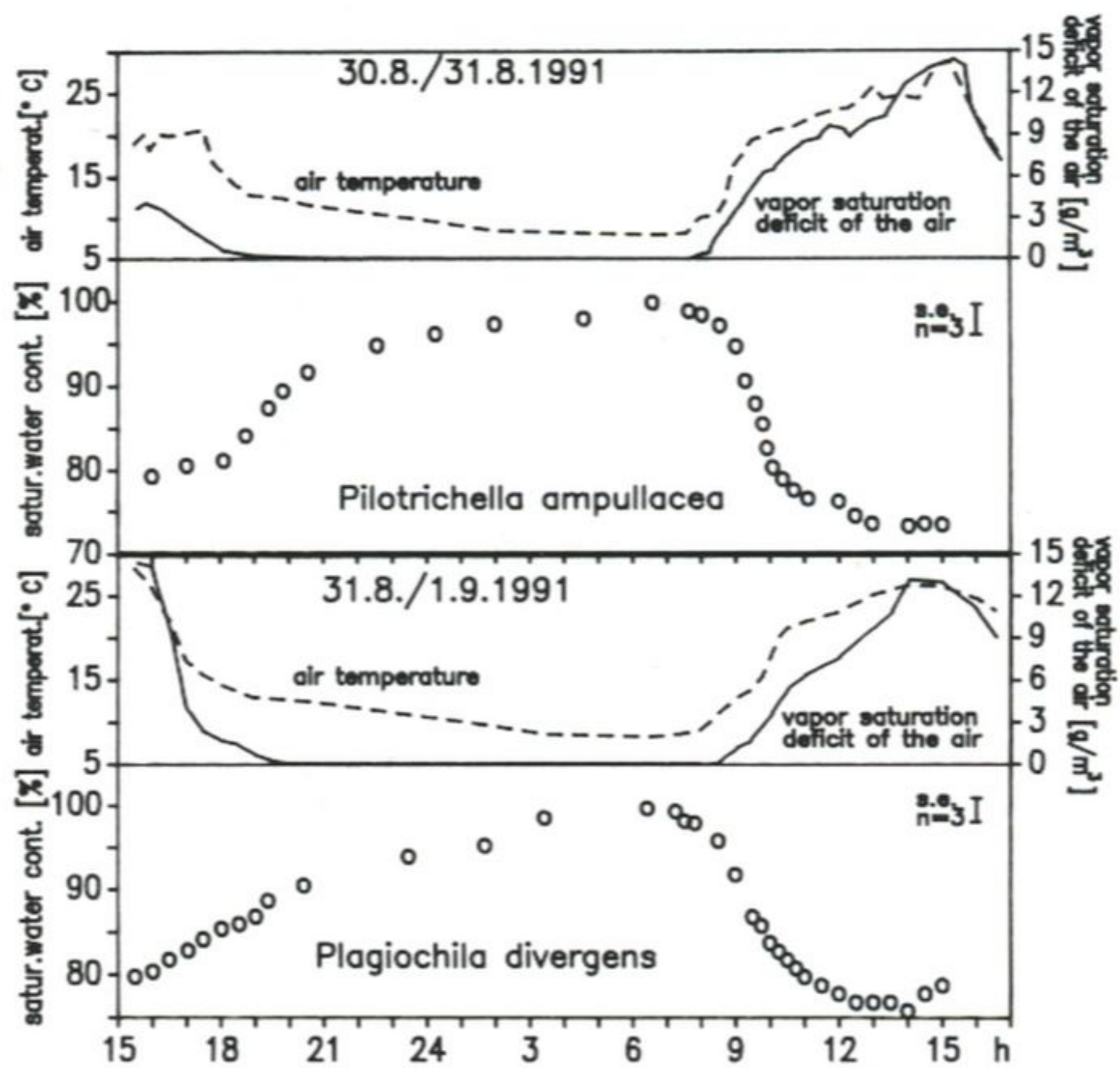
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Fig. 2: Diurnal courses of air temperature and vapor saturation deficit of the air in a Central African bamboo forest, and the water gain and loss of pendants of *Pilotrichella ampullacea* and *Plagiochila divergens* as determined gravimetrically.
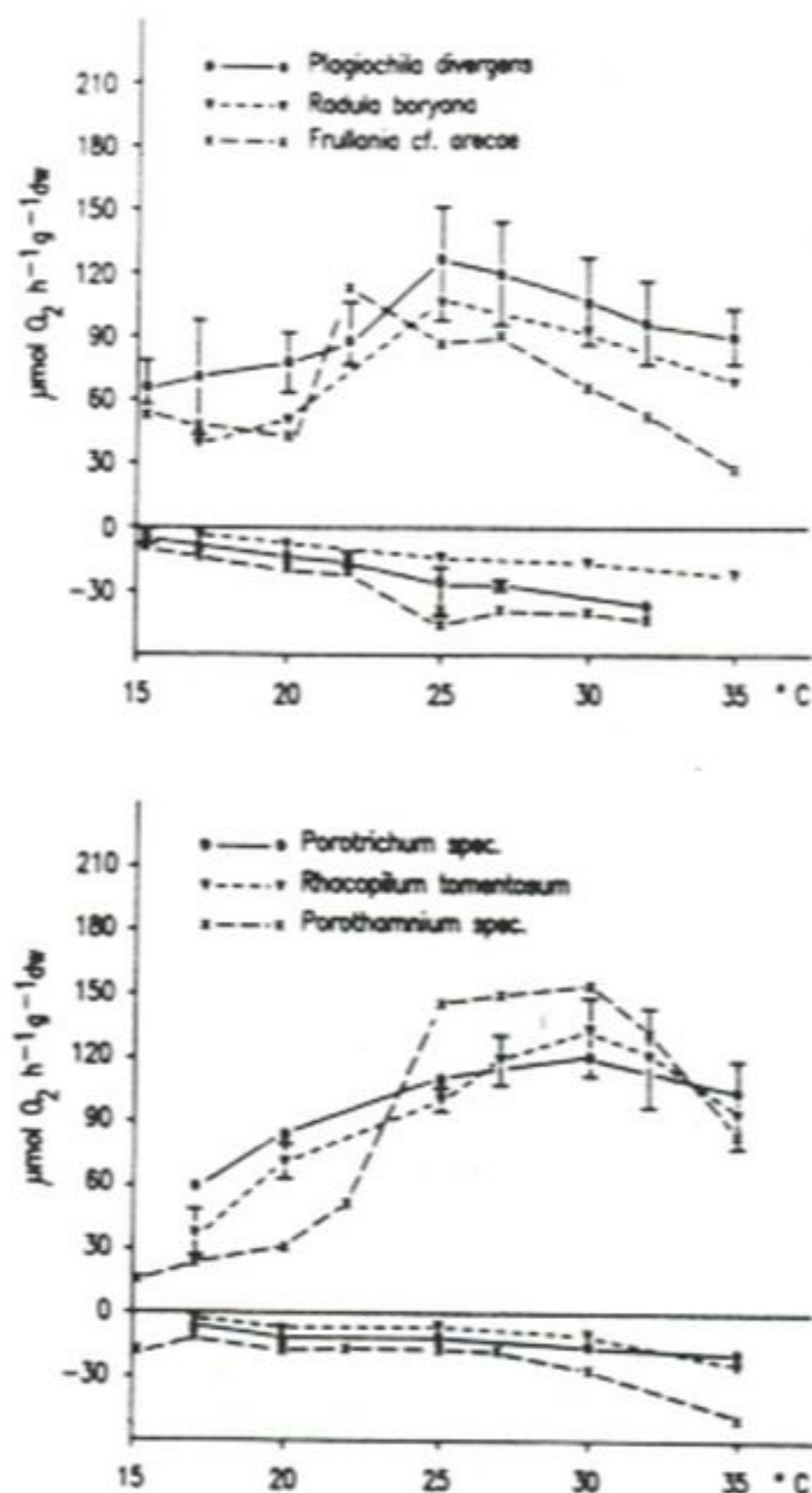
Fig. 3: Temperature response curves of oxygen gas exchange (Warburg manometry) of mosses and liverworts from the Central African upper lowland rainforest at Irangi.

on Mount Biega. All the various samples, in total nine different ones, did not differ in their temperature responses in photosynthesis, with maximal O_2 exchange rates at the high temperature of 35 °C. This moss documents most clearly the tendency found by most of the investigated species, regardless whether coming from the warm lowland or the temperate mountains, to perform best under relatively high temperatures but to photosynthesize still considerably under less favourable lower temperatures.

Photosynthetic gas exchange: light responses

Light-dependent photosynthesis comes to saturation at relatively low PAR rates (examples: Fig. 8). As a rule, half-saturation of photosynthesis is reached already at approx. 100 µmol photons m^{-2} sec^{-1}. With such saturation characteristics all the species can be classified as shade-adapted or at least shade-tolerant. This is underlined as well by low compensation points which are between 3 and 24 µmol photons m^{-2} sec^{-1}. Their analysis, however, separates clearly those species growing in the understory of the lowland rainforest from those which occur in the bamboo thickets and tree-heath shrublands of the mountains (Fig. 9). Only one *Neckera* species from Irangi exceeds considerably the compensation point value of 10 µmol m^{-2} sec^{-1}, wheras several of the important genera from the mountains (e.g. *Breutelia stuhlmannii, Sphagnum davidii, Dicranoloma billardieri, Plagiochila divergens*) come to O_2 release only at light intensities higher than 10 µmol m^{-2} sec^{-1}. Yet more important are the different slopes of the light response curves at light intensities around the compensation point. Those of the bryophytes from Irangi are much steeper than those of the probes collected at Tsivanga, Kasirusiru, Mount Biega or Mount Kahuzi. The average values of these slopes are 0.5 ± 0.2 µmol O_2 g^{-1} dw per mmol photons m^{-2} in the case of the lowland probes and 0.23 ± 0.09 µmol O_2 g^{-1} dw per mmol photons m^{-2} for those from 2000 m and above. With such light-response characteristics mosses and liverworts from the lowland rainforest evidently are extremely shade-adapted species. Those from the montane forests proved to be rather efficient utilizing low
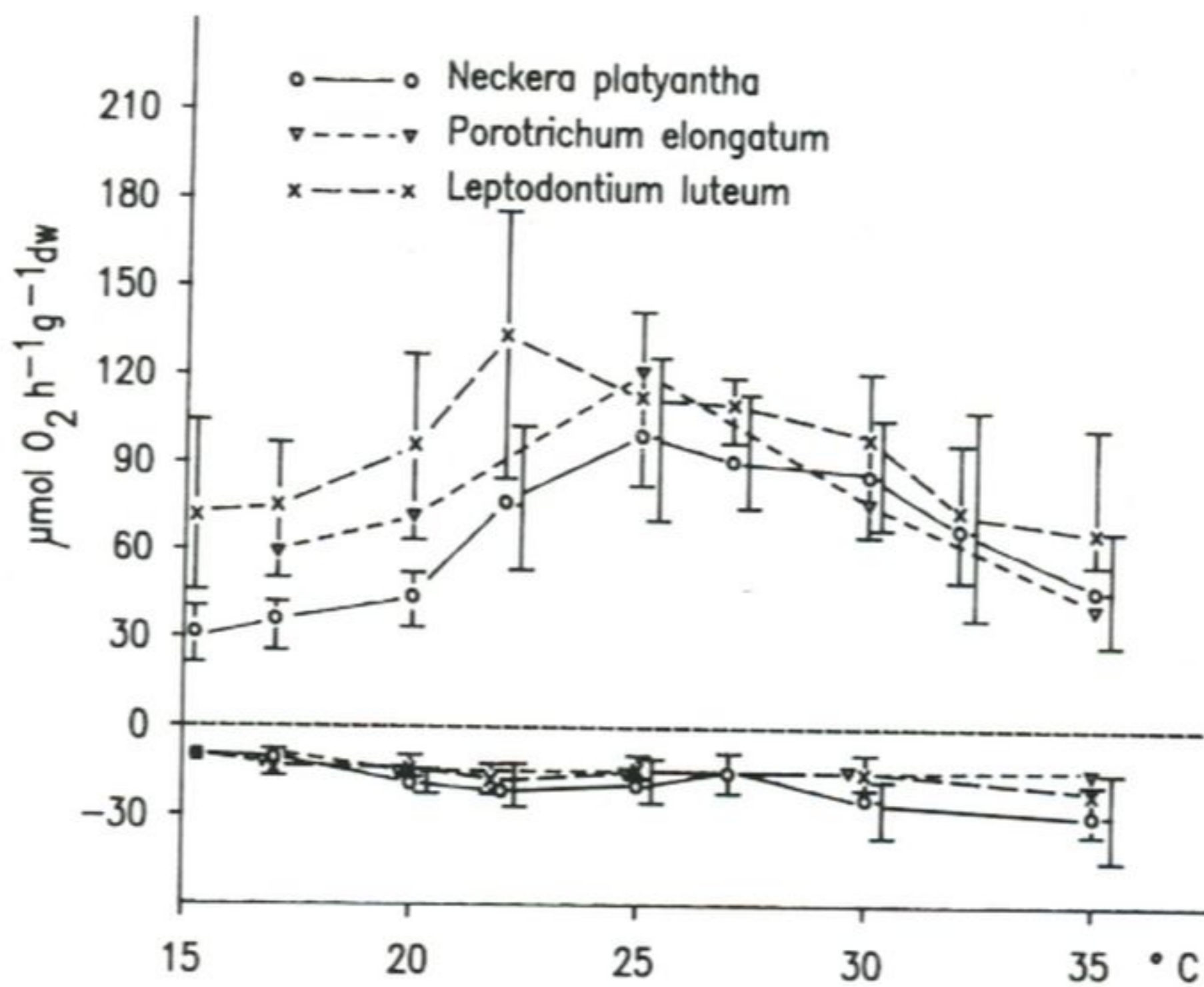
cies is rather broad (Pócs 1993). *Plagiochila barteri* has a flat and unspecific temperature response of photosynthesis, the other two species have nearly identical curves with highest gas exchange rates at 25 °C. Two closely related species of the hanging moss *Pilotrichella* were collected at the slopes near the summit of Mt. Biega. Both attain maximal photosynthetic rates between 25 and 30 °C, but that of *P. cuspidata* are with 150 µmol O_2 g^{-1} dw h^{-1} nearly twice as high as that of *P. ampullacea. Rhizogonium spiniforme* (Fig. 7) was collected at Irangi and
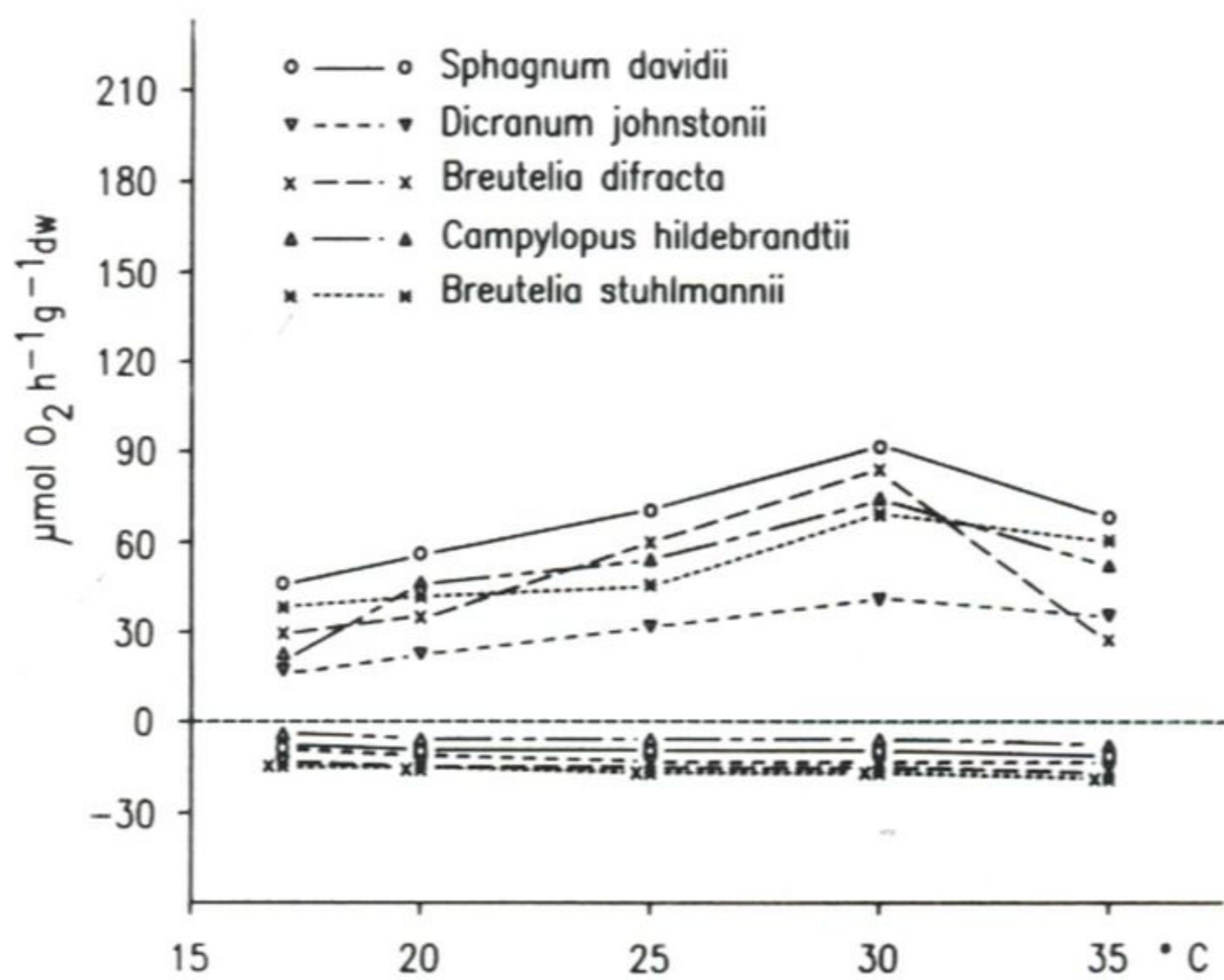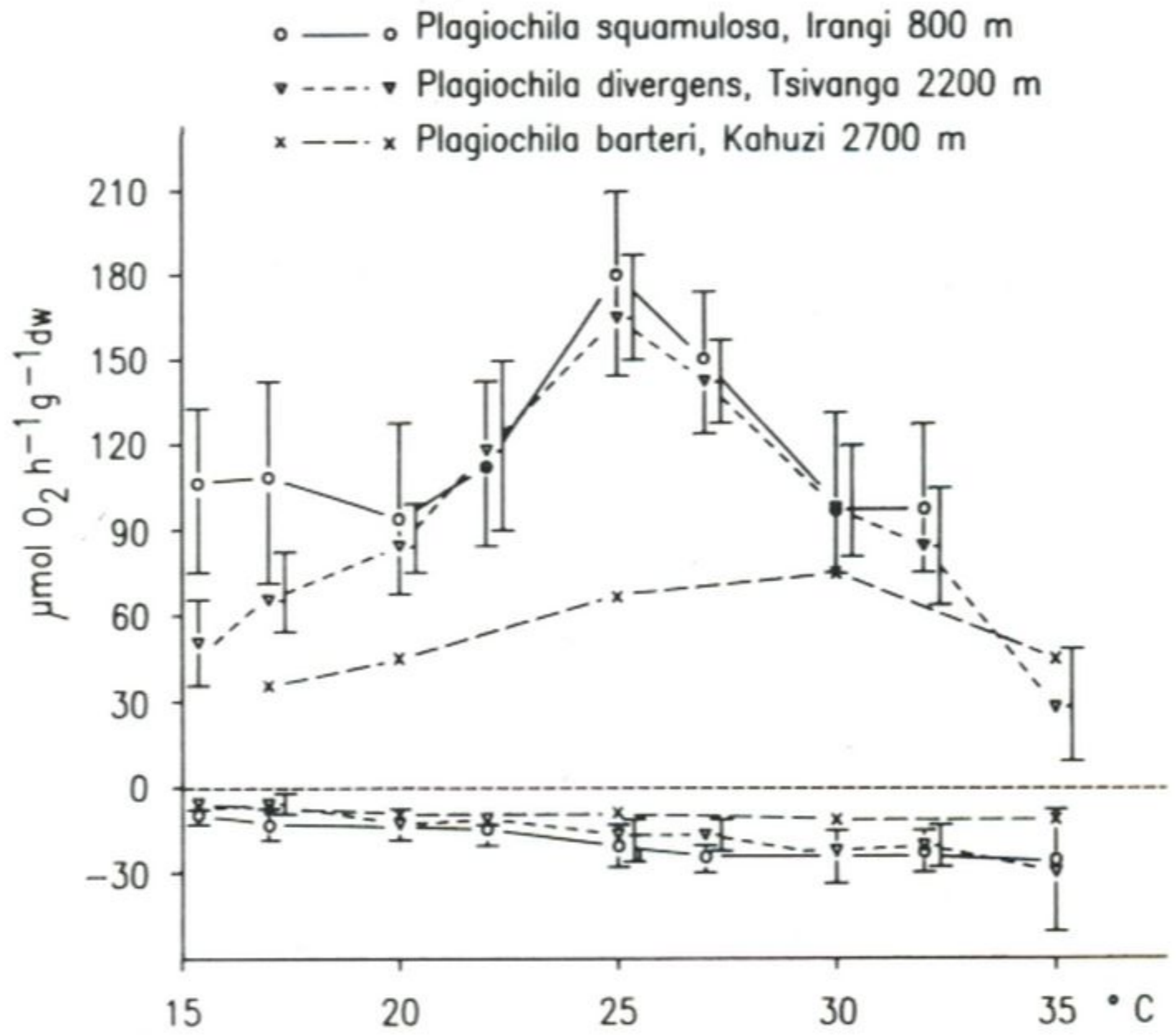
Fig. 4: Temperature response curves of oxygen gas exchange (Warburg manometry) of epiphytic mosses from the afromontane bamboo and tree heath forests of the Kahuzi-Biega area.

Fig. 5: Temperature response curves of oxygen gas exchange (Warburg manometry) of epigaeic mosses from the afro-montane tree heath forests of the Kahuzi-Biega area.

Fig. 6: Temperature response curves of oxygen gas exchange (Warburg manometry) of *Plagiochila* species from the upper lowland rainforest and the afromontane bamboo and tree heath forests of the Kahuzi-Biega area.

Table 2: Chlorophyll contents and chlorophyll a:b ratios of the investigated bryophytes.

Species name	Chlorophyll content [mg chl. g-1 dw]	chl. a:b ratio
LOWLAND		
Rhizogonium spiniforme	4.1 ± 0.2	1.88
Plagiochila divergens	3.8 ± 0.2	1.87
Porotrichum molliculum	3.8 ± 0.3	1.77
Racopilum africanum	2.7 ± 0.2	1.80
Radula boryana	2.6 ± 0.2	1.78
Porella spec.	2.5 ± 0.1	1.85
Ectropothecium perrottii	1.6 ± 0.1	1.90
MOUNTAIN SITES		
Plagiochila divergens	3.8 ± 0.2	1.80
Plagiochila squamulosa	3.4 ± 0.3	1.80
Rhizogonium spiniforme	3.3 ± 0.3	1.87
Pilotrichella cuspidata	3.3 ± 0.1	1.87
Neckera spec. (cf.madecassa)	3.0 ± 0.1	2.04
Porotrichum elongatum	2.7 ± 0.1	2.01
Plagiochila barteri	2.2 ± 0.1	2.00
Pilotrichella ampullacea	1.9 ± 0.1	1.80
Sphagnum davidii	1.9 ± 0.2	2.07
Breutelia stuhlmannii	1.4 ± 0.2	2.10
Dicranum johnstonii	1.1 ± 0.1	2.01
Leptodontium luteum	0.9 ± 0.1	2.04
Breutelia diffracta	0.9 ± 0.08	2.04
Campylopus hildebrandtii	0.5 ± 0.06	1.83

light intensities, but are obviously somehow more light-demanding.

Chlorophyll contents

Such a functional separation between the bryophytic floras of the lowland and the mountain forest is indicated also by the chlorophyll contents and chlorophyll a:b ratios (tab. 2). Chlorophyll contents of the investigated species were between 0.5 and 4 mg g^{-1} dw. Samples from the lowland site had an average chlorophyll content of 3.35 ± 0.4 mg g^{-1} dw, those from the highland stations reached only 2.09 ± 0.3 mg chlorophyll g^{-1} dw. Samples from species found in the two altitudinal zones, like *Plagiochila divergens* or *Rhizogonium spiniforme* did not differ significantly from each other. The chlorophyll a:b ratio of the lowland bryophytes was with 1.8 ± 0.06 somewhat lower than that of samples from the highlands, the average of which was 1.96 ± 0.1. Since higher chlorophyll contents per dry weight and lower chlorophyll a:b ratios both are characteristic for shade-plants, the chlorophyll contents of the studied bryophytes are in agreement with the functional characterization by the photosynthetic light responses. The species from the
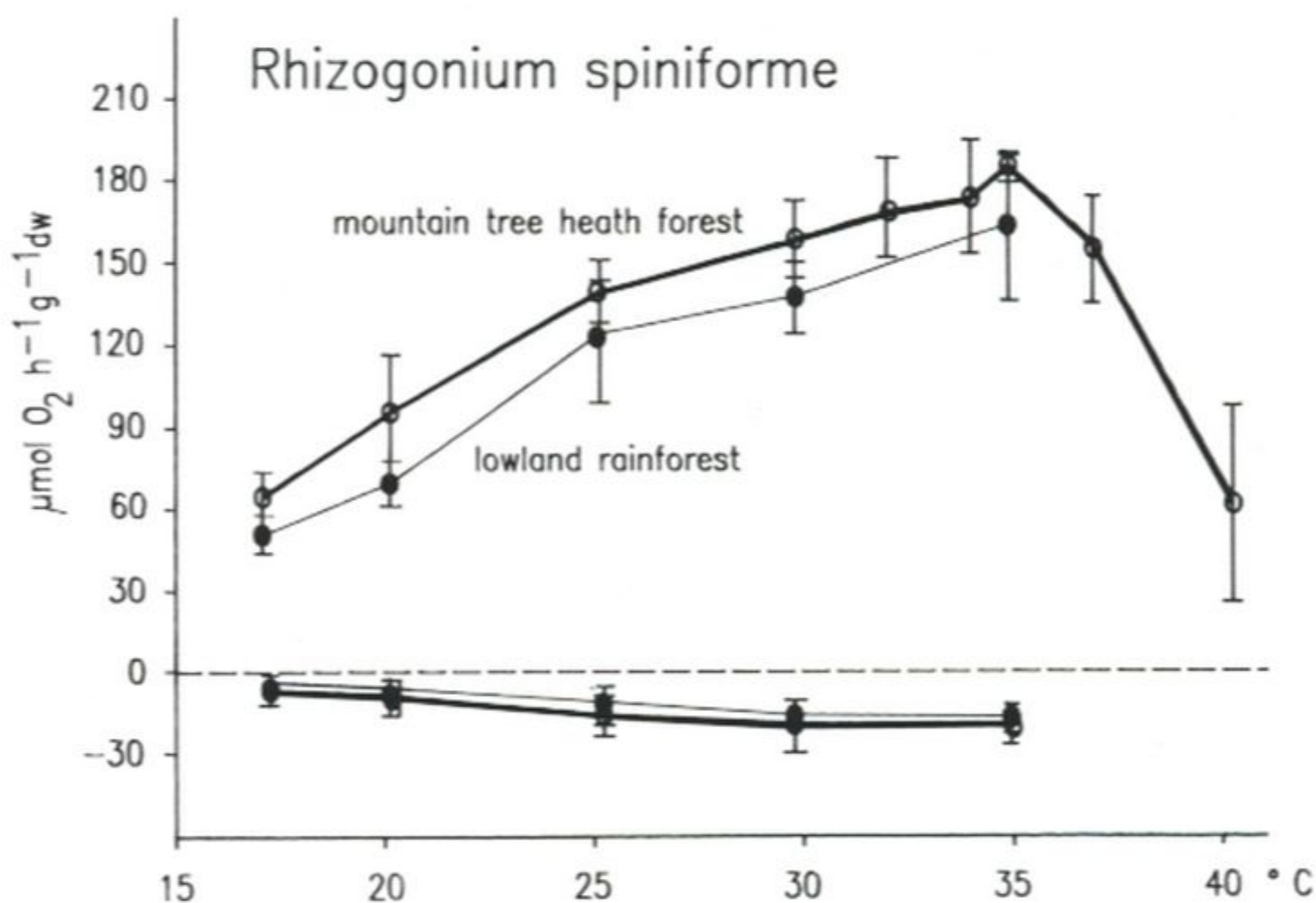
Fig. 7: Temperature response curves of oxygen gas exchange (Warburg manometry) of *Rhizogonium spiniforme* from the upper lowland rainforest and the afromontane bamboo and tree heath forests of the Kahuzi-Biega area.

lowland forest are extremely shade-adapted plants and those from the montane forests are more light-demanding.

Discussion

Due to the poikilohydric structure and the comparatively low chlorophyll contents photosynthesis of bryophytes is generally lower than that of flowering plants (Vallane 1984). Maximal gas exchange rates of mosses range between 50 and 500 μmol O_2 g^{-1} dw h^{-1} (Rastorfer 1970, Dilks & Proctor 1975, Rütten 1991). The values measured with mosses and hepatics from Central Africa fit into these figures, but fall mostly into the lower range of values. This might indicate that the vitality of the experimental material could have been influenced negatively by the transport from Africa to Europe. There were different time-spans between collection and measurements - between five days and three weeks - and different storage treatments underway -transport in wet or dry state, storage in the
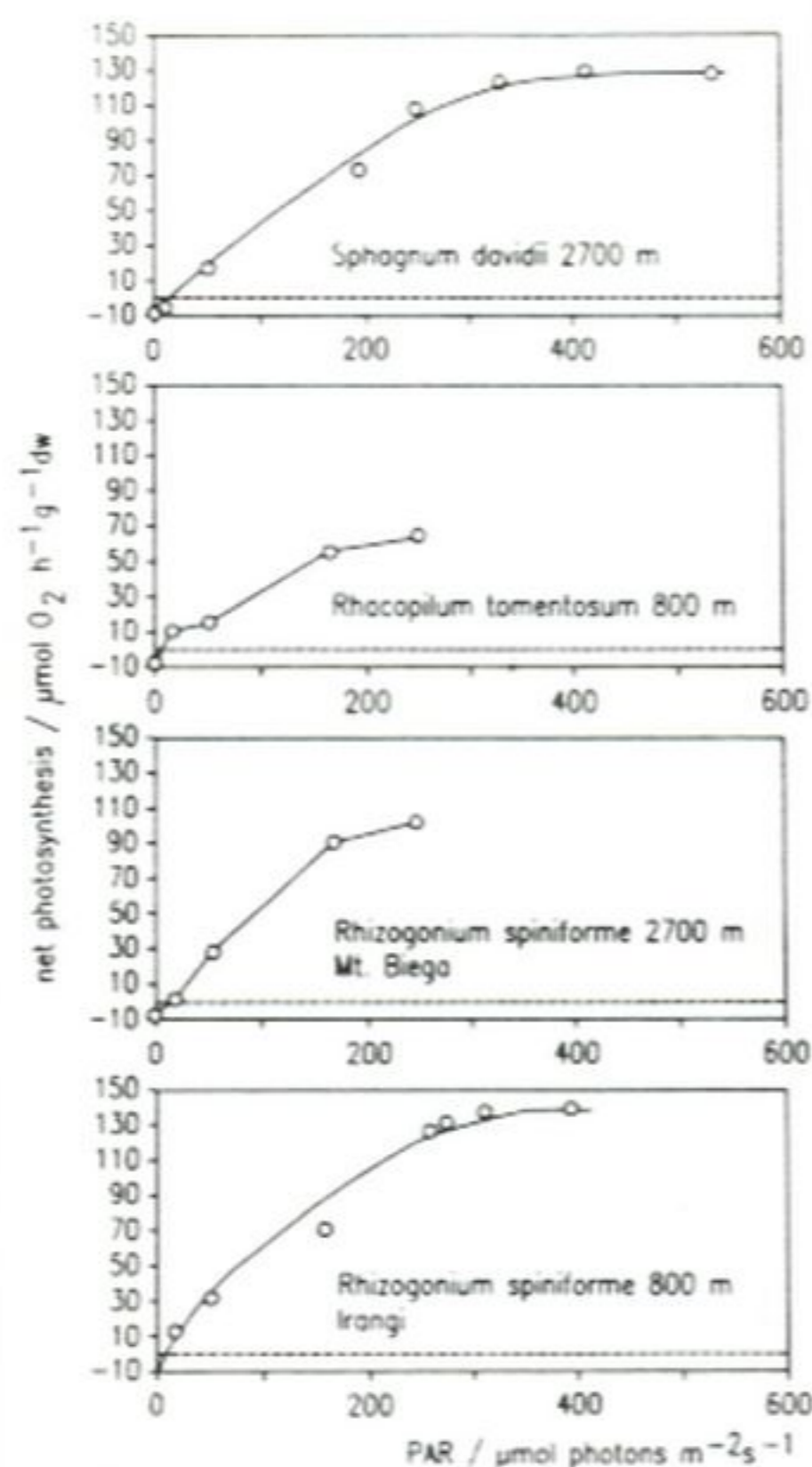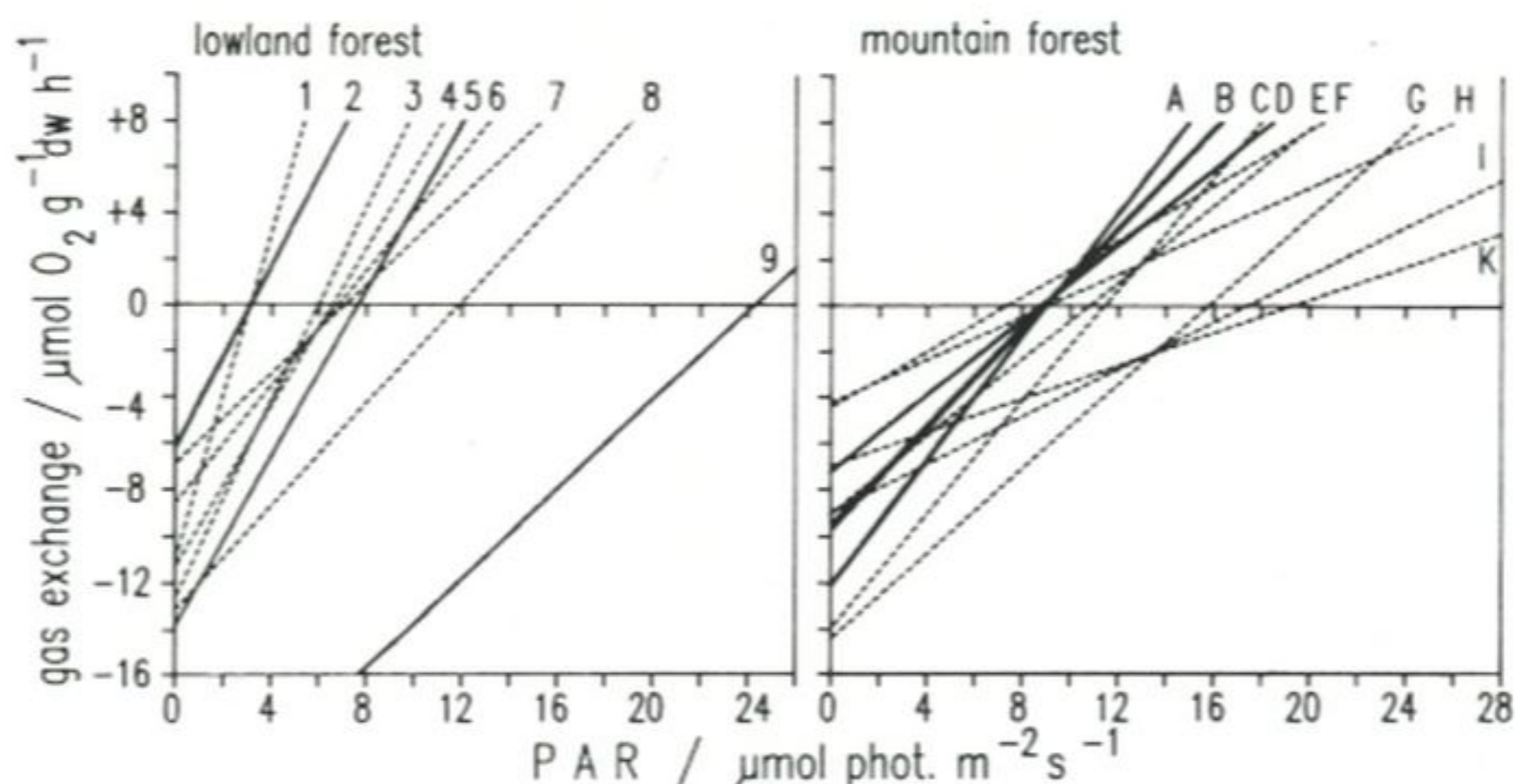
Fig. 8: Light response curves of oxygen gas exchange (Warburg manometry) of three mosses from the upper lowland rainforest and the afromontane tree-heath forest of the Kahuzi-Biega area, East Zaire.

the time-span of reliable experiments.

By comparison with IRGA measurements of photosynthesis in open systems, Warburg manometry is more artificial and might, by this way, influence the results. This could be true with respect to absolute rates of gas-exchange and to absolute values of temperature for which the photosynthetic optima were determined. Silvola (1985) measured a shift by 10°C to higher optimum temperatures of photosynthesis when *Sphagnum fuscum*, *S. angustifolium*, and *Dicranum majus* were supplied with 1000 ppm CO_2 instead with 320 ppm. Likewise, Proctor (1982) reports on shifts of photosynthetic optima towards higher temperatures, combined with considerable increases of CO_2 exchange rates of *Hylocomium splendens* and *Porella platyphylla* when CO_2 supply was increased from 300 to 2000 and 10000 vpm. According to Dilks & Proctor (1975) this results from a reduced photorespiratory CO_2 liberation and shifts of the activities of rate-limiting fixation processes of the Calvin cycle. True temperature optima of photosynthesis under natural conditions of the investigated tropical bryophytes could be lower, therefore. This might be the case particularly with species from the mountain sites which are more exposed to convective exchanges with the atmosphere. Even then, CO_2 concentrations around the moss layers near ground exceed considerably the average atmospheric levels, as it was measured, e.g. by Sonesson et al. (1992) for *Hylocomium splendens* in a subarctic habitat. These plants received during short periods CO_2 concentrations as high as 1143 ppm. In the damp interior of rainforests ambient CO_2 concentrations near the moist, litter-covered soil surface will by far exceed such amounts due to the intensive catabolic activity of microbes and soil invertebrates. Wanner (1970) and Wanner et al. (1973) measured an average soil respiration of 260 mg CO_2 m^{-2} h^{-1} in several East Asian rainforests, Whitemore (1984) quotes that three times as high values have been already measured. Therefore, the CO_2 saturation within the Warburg vessels may be no so far away from the situation in nature, and the photosynthetic rates and the high photosynthetic temperature optima of the Irangi samples, between 25 and 29 °C, are probably realistic. If the species from the moun-

open for some days under an East African Savanna climate or in a warm and humid greenhouse for a week before measurements or immediate transfer into the temperate, climatized cultivation chamber -. All these differences did not result in significantly different gas-exchange behavior of the samples, and therefore it is concluded that transport and storage conditions did not change seriously subsequent photosynthesis and respiration of the investigated plants. Decreases of the gas exchange responses were, on the other hand, obvious approximately two months after collection thus indicating clearly

Fig.9: Slopes of light curves of oxygen gas exchange (Warburg manometry) in the low light range and light compensation points of mosses and liverworts from the upper lowland rainforest and the afromontane bamboo and tree heath forests of the Kahuzi-Biega area, East Zaire.
Bryophyte species: 1 = *Ectropothecium perrotii*, 2= *Rhizogonium spiniforme*, 3 = *Porothamnium stipitatum*, 4 = *Porotrichum molliculum*, 5= *Plagiochila squamulosa*, 6 = *Radula boryana*, 7 = *Racopilum tomentosum*, 8 = *Frullania cf. arecae*, 9 = *Neckera cf. madecassa*, A = *Rhizogonium spiniforme*, B = *Plagiochila squamulosa*, C = *Pilotrichella cuspidata*, D = *Neckera cf. platyantha*, E = *Plagiochila divergens*, F = *Campylopus hildebrandtii*, G = *Dicranoloma billardieri*, H = *Dicranum johnstonii*, I = *Breutelia stuhlmannii*, K = *Sphagnum davidii*.

tain sites have lower optima of photosynthesis at their growing sites, the small measured difference of the optimum temperatures for gas exchange between highland and lowland samples becomes even more pronounced.

Higher gas exchange rates of bryophytes under a higher local CO_2 supply could explain also the occurrence of mosses and liverworts mostly on logs, buttresses, roots and other, preferably damp, sheltered places in the lowland rainforests and their decreased abundance higher up on the stems and in the higher canopy layers notwithstanding the high humidity prevailing also there. Exceptionally high respiration rates could not be measured so that even montane species would not suffer from detrimental respiration losses of carbon under lowland temperatures. This is obviously different from the gas exchange behaviour of boreal and arctic bryophytes the respiration of which increases exponentially with higher temperatures. With snowbed bryophytes dark respiration equals net photosynthesis alrea-

dy between 20 and 25 °C (IRGA-measurements; Lösch et al. 1983); with the antarctic *Bryum sandbergii* this situation occurs at approximately 30 °C (Warburg-measurements; Rasdorfer & Higinbotham 1970). More comparable with the respiration rates of the Central African bryophytes are those of mosses and liverworts from temperate regions (Dilks & Proctor 1975; Rütten 1991).

The physiological optima of the photosynthetic temperature response of the two groups, the lowland and the mountain bryophytes, coincide rather well with the prevailing temperatures at their respective natural environments. A similarity of optimal temperatures for photosynthesis and mean daytime temperatures of the habitats has been found also with mosses from temperate and subarctic regions (e.g. Stålfelt 1938; Hikklenton & Oechel 1977; Lösch et al. 1983). But, as common with bryophytes (Longton 1988), temperature curves of photosynthesis of the investigated tropical species are rather flat.

Sufficient photosynthesis can occur also over a broad range of temperatures below and above the optimum, and the probability is low that the Central African rainforest and mountain forest bryophytes ever will experience compensation point temperatures in their natural habitats. By extrapolation from the experimentally tested temperature range these will occur below 10 °C and above 40 °C. Longton (1988) mentions as general limits for net carbon gain of polar bryophytes temperatures below -10 to 0 °C and above 30 to 40 °C. This range probably is shifted in tropical species by 10 C to higher values. Longton (1988) summarizes the existing knowledge that "many of the features that permit bryophytes and lichens to maintain favourable carbon and energy budgets in severe Arctic and Antarctic environments are characteristic of these groups as a whole, rather than specific adaptations to polar conditions" (l.c. p.209/210). The broad temperature response curves of photosynthesis measured with tropical species underline that this holds true, in general, also for bryophytes from the warm regions of the earth.

A more distinct separation exists between lowland and afromontane bryophytes with respect to light requirements of photosynthesis. Like most bryophytes (Tuba 1987) also those from Central Africa possess a photosynthesis typical for shade plants. This holds true with respect to compensation points, steepness of the light-response curves of gas exchange, chlorophyll contents and chlorophyll a:b ratios. But within this general characterization those bryophytes from the rainforest are to be ranked as sciophilic, those from the mountains as heliophilic (Masarovicova & Elias 1987). The highest light requirements were found in mosses from the tree line of Mt. Kahuzi and the summit of Mt. Biega. The light-dependent photosynthesis of taxa growing alongside the whole altitudinal gradient, like *Rhizogonium* or *Plagiochila* are intermediate between a scio- and a heliophilic behaviour, but do not adapt to the particular local situation. Obviously, species-specific light responses of photosynthesis of the studied species are by and large genetically fixed. Afromontane species would suffer, therefore, considerably from the low radiation availability in the rainforest understory. At the montane sites, however, particular-

ly in the bamboo forests below the cloud layer, the favourable light climate during the day very often cannot be used for biomass production due to desiccation of the mosses into a non-saturated surrounding air. According to the weighings, *Pilotrichella* or *Plagiochila* probably will use only four to five morning hours for photosynthesis, thereafter gas exchange should cease due to stronger desiccation. But the pendants are able to resaturate overnight from a vapour-saturated atmosphere as it was documented also for several Europaean epiphytic mosses and hepatics (Lange 1969).

A rough estimate of the productivity of an average mosses from the rainforest understory, the bamboo forest, and the tree-heath elfin forest can be made taking into account light limitation in the former habitat, plant desiccation in the bamboo forest and sub-optimal temperatures at treeline. Than, the order of magnitude of net carbon gain in the rainforest and the bamboo thickets will come,to approximately 50 mg C kg^{-1} dw, in the elfin forest it might be at least twice as high. This might be one explanation for a ten times increase of standing epiphytic bryomass from lowland rainforests to montane cloud forests as reported from transects in South America and Borneo (Frahm 1987a, 1990b) and expected for the Zaire transect as well (Frahm, in prep.). In each of the three habitats the respective ecological constraint for productivity is offset, partially, by different favourable conditions. Thus, very high CO_2 concentrations near the forest floor combined with permanently optimal temperature and humidity conditions permit the growth of bryophytes in the lowland forest. Saturating light conditions and near optimum temperatures will be advantageously to the bryophytes in the bamboo forests. A most often perhumid situation and the diffuse light inside the cloud cover of the vegetation, high enough for an efficient photosynthesis, will be the essential prerequisites for the luxuriant growth of bryophytes in the heath-forests. The local combination of the beneficial and the adverse environmental parameters will offer a plenty of different niches where the individual species will gain competitive superiority, even if they would not be excluded for reasons of physiological capacities from other localities either.

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