

Altitudinal changes in temperature responses of net photosynthesis and dark respiration in tropical bryophytes

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- **Background and Aims** There is a conspicuous increase of poikilohydric organisms (mosses, liverworts and macrolichens) with altitude in the tropics. This study addresses the hypothesis that the lack of bryophytes in the lowlands is due to high-temperature effects on the carbon balance. In particular, it is tested experimentally whether temperature responses of CO₂-exchange rates would lead to higher respiratory carbon losses at night, relative to potential daily gains, in lowland compared with lower montane forests.
- **Methods** Gas-exchange measurements were used to determine water-, light-, CO₂- and temperature-response curves of net photosynthesis and dark respiration of 18 tropical bryophyte species from three altitudes (sea level, 500 m and 1200 m) in Panama.
- **Key Results** Optimum temperatures of net photosynthesis were closely related to mean temperatures in the habitats in which the species grew at the different altitudes. The ratio of dark respiration to net photosynthesis at mean ambient night and day temperatures did not, as expected, decrease with altitude. Water-, light- and CO₂-responses varied between species but not systematically with altitude.
- **Conclusions** Drivers other than temperature-dependent metabolic rates must be more important in explaining the altitudinal gradient in bryophyte abundance. This does not discard near-zero carbon balances as a major problem for lowland species, but the main effect of temperature probably lies in increasing evaporation rates, thus restricting the time available for photosynthetic carbon gain, rather than in increasing nightly respiration rates. Since optimum temperatures for photosynthesis were so fine tuned to habitat temperatures we analysed published temperature responses of bryophyte species worldwide and found the same pattern on the large scale as we found along the tropical mountain slope we studied.

Key words: Altitudinal gradient, bryophytes, carbon balance, dark respiration, gas-exchange measurements, hepatics, liverworts, mosses, net photosynthesis, photosynthesis-response curves, temperature, tropical rain forest.

INTRODUCTION

In the wet tropics, bryophytes (mosses and liverworts) decrease strongly in abundance (Frahm, 1990; Wolf, 1993) and diversity (Seifriz, 1924; Pócs, 1980; Gradstein and Pócs, 1989) with decreasing altitude. The poor development of these plants in the lowlands contradicts the intuitive expectation of a prospering bryophyte flora all over the wet tropics, i.e. areas where precipitation rarely drops below 100 mm month⁻¹ (e.g. Richards, 1996). The reasons for this conspicuous altitudinal pattern are unknown, though several untested hypotheses have been put forward over the years (summarized in Wagner *et al.*, 2012).

A plausible, though untested, physiological explanation for the lack of bryophytes in the warm lowlands was put forward almost 30 years ago by Richards (1984 and see also Frahm, 1987; Zotz, 1999; Wagner *et al.*, 2012), and was later extended to macrolichens (Zotz and Winter, 1994). Both bryophytes and lichens are poikilohydric organisms, their moisture content rapidly equilibrating with environmental conditions and physiological activity varying with moisture content (Green and Lange, 1994). Substantial carbon losses due to respiration can occur when poikilohydric organisms

are wet in the dark (e.g. Proctor, 1982; Lange, 2003b). In the lowland tropics, afternoon rains are common and nights are warm, so that respiration rates are high and a large proportion of assimilated carbon may be lost at night. Conversely, during the day CO₂ uptake of poikilohydric organisms is restricted by low light intensities, especially in the understorey and after rainstorms, or by fast drying, especially at exposed sites (Zotz and Winter, 1994; Zotz *et al.*, 1997, 1998). Due to these high losses and low gains, poikilohydric organisms have difficulties obtaining a positive carbon balance. One of the implicit assumptions in this hypothesis is that temperature responses of dark respiration in lowland bryophyte species are comparable to those from montane regions, so that the ratio of dark respiration to potential net photosynthesis (R_D/NP) at ambient temperatures is highest in the lowlands and decreases with altitude. We intend to test this assumption in the present study.

An additional assumption, put forward by Zotz (1999), has been addressed experimentally in a separate study (S. Wagner, G. Zotz and M. Y. Bader, unpubl. res.): lower montane species cannot acclimatize their metabolic rates, dark respiration in particular, to warmer (lowland) conditions. This assumption is also essential because, according to a hypothesis centred

on the dark respiration rate, inherent acclimation of these rates in montane species could allow them to fill open niches in the lowlands and would thus allow a higher diversity in the lowlands than is actually observed.

If the altitudinal patterns described are indeed caused by temperature, climatic warming could be directly detrimental for tropical bryophytes, further excluding them from the lowlands and diminishing biomass and diversity in montane areas. However, there is very little information on the physiology of tropical bryophytes (Wagner *et al.*, 2012), which would allow us to test Richard's notion rigorously, and predictions are thus hardly possible. This motivated the present study. Here, we present temperature-response curves of net photosynthesis (NP) and dark respiration (R_D) of 18 species of mosses and hepatics from tropical lowland to lower-montane rainforest in Panama, including the first such curves published for lowland bryophytes. We also report light- and water-response curves for these species and CO_2 -response curves for a subset of three species. In the discussion we will put our findings in the context of global patterns of the temperature responses of bryophytes, presenting a meta-analysis of published temperature optima for photosynthesis.

MATERIALS AND METHODS

Study areas

Sampling took place along the Caribbean slope of the continental divide in Western Panama. The lower study area, Bocas del Toro (BT), was in the lowland rainforest of Isla Colon in the Bocas del Toro archipelago (08°47'N, 082°13'W, sea level). The middle area, Palo Seco (PS), was also situated in lowland rainforest, but at a higher altitude (approx. 500 m a.s.l.) in the Bosque Protector Palo Seco, Bocas Del Toro Province (08°48'N, 082°11'W). The highest study area was in the Reserva Forestal Fortuna (F), Chiriquí Province (08°43'N, 82°14'W, approx. 1200 m a.s.l.), which is covered

by lower montane rainforest. Mean annual rainfall ranged from 3300 mm year⁻¹ (2006–2009) in Bocas del Toro (STRI data for 2012) to 5400 mm year⁻¹ (1997–2009) in Fortuna (C. Espinosa, Panama, Smithsonian Tropical Research Institute, pers. comm.). Long-term rainfall data are not available for PS, hence precipitation was monitored with a rain gauge (HOBO Data logging rain gauge RG3) from 12 November 2009 to 17 May 2010 (2900 mm) and from 11 November 2010 to 5 May 2011 (2700 mm), yielding an estimated total of approx. 5700 mm year⁻¹ (not taking into account possible seasonal differences). Temperature was also monitored at the study sites with HOBO Pendant G Temperature/Lux data loggers and HOBO U23 Pro v2 Temperature/Relative Humidity data logger (Onset Computer Corporation). Measuring intervals lasted from November 2009 to May 2011 (BT and PS) and from June 2011 to December 2011 (F). Data loggers were installed inside the forest at about breast height. Mean daytime temperature decreased from 26.0 °C ($n = 4$) in BT over 22.6 °C ($n = 6$) in PS to 20.2 °C ($n = 3$) in Fortuna. Night-time temperature averaged 24.0 °C in BT, 21.4 °C in PS and 17.8 °C in Fortuna.

Study species

Six locally common species, including both mosses and hepatics, were chosen from each altitude. Different life-forms (*sensu* Mägdefrau, 1982) (Table 1) were chosen to cover a substantial portion of the variety of bryophytes in the study areas. In BT and PS all species were from the forest understorey, while in Fortuna five out of six species were from forest edges. The latter habitats were 1.2 °C warmer during the day, but had similar temperature during the night compared with Fortuna understorey plots (S. Wagner, G. Zotz and M. Y. Bader, unpubl. res.). This might result in upward shifts in temperature responses compared with understorey species, independent of altitudinal origin. Therefore, the

TABLE 1. *Bryophyte species from tropical Panama for which gas-exchange response curves were determined*

Location	Species	Family	Exposure	Life-form
BT	<i>Octoblepharum pulvinatum</i> (Dozy & Molke.) Mitt.	Leucobryaceae	Understorey	Cushion
BT	<i>Orthostichopsis tetragona</i> (Sw. ex Hedw.) Broth.	Pterobryaceae	Understorey	Pendant
BT	<i>Plagiochila</i> sp. 1	Plagiochilaceae	Understorey	Cover/fan
BT	<i>Stictolejeunea squamata</i> (Willd. ex F. Weber) Schiffn.	Lejeuneaceae	Understorey	Cover/fan
BT	<i>Symbiezidium</i> spp.	Lejeuneaceae	Understorey	Cover
BT	<i>Zelometeorium patulum</i> (Hedw.) Man.	Meteoriaceae	Understorey	Pendant
PS	<i>Bryopteris filicina</i> (Sw.) Nees	Lejeuneaceae	Understorey	Pendant/fan
PS	<i>Lepidopilum polytrichoides</i> (Hedw.) Brid.	Pilotrichaceae	Understorey	Cover/felt
PS	<i>Pilotrichum bipinnatum</i> (Schwä.) Brid.	Pilotrichaceae	Understorey	Pendant/fan
PS	<i>Plagiochila</i> sp. 2	Plagiochilaceae	Understorey	Cover/fan
PS	<i>Symbiezidium</i> spp.	Lejeuneaceae	Understorey	Cover
PS	<i>Syrrhopodon incompletus</i> Schwä.	Calympereaceae	Understorey	Cushion
F	<i>Durmortiera hirsuta</i> subsp. <i>hirsuta</i> (Sw.) Nees	Marchantiaceae	Understorey	thalloid
F	<i>Frullania mirabilis</i> Jack & Steph.	Frullaniaceae	Forest edge	Pendant
F	<i>Herbertus divergens</i> (Steph.) Herz.	Herbertaceae	Forest edge	Loose turf
F	<i>Leucobryum antillarum</i> Schimp. ex Besch.	Leucobryaceae	Forest edge	Cushion
F	<i>Phyllogonium fulgens</i> (Hedw.) Brid.	Phyllogoniaceae	Forest edge	Pendant
F	<i>Phyllogonium viscosum</i> (P. Beauv.) Mitt.	Phyllogoniaceae	Forest edge	Pendant

Locations: BT, Bocas del Toro, 0 m; PS, Palo Seco, 500 m; F, Fortuna, 1200 m.

Life-forms after Mägdefrau (1982). Note there are two very similar species of *Symbiezidium* in the study region which are very difficult to distinguish.

expected lower temperature optima in the Fortuna species might be masked to some extent by the exposure difference, and optima in undergrowth species are expected to be somewhat lower than those found in the exposed species.

Except for *Durmortiera hirsuta*, which is a terrestrial species, all bryophytes are epiphytes and were collected from branches, buttress roots (*Octoblepharum pulvinatum*) or tree trunks (*Syrrhopodon incompletus*) at heights up to approx. 3 m. Only specimens with no other species intermixed were sampled, although the *S. incompletus* samples were later found to contain a small proportion of *Cyclolejeunea luteola*. Voucher specimens of all the mosses and hepatics studied were deposited at the herbarium of the University of Panama (PMA), Republic of Panama.

Gas-exchange measurements

After collection, the bryophyte samples were brought to the field stations and stored outside in the shade for up to 1 week. One day prior to measurement they were wetted to ensure recovery of the vital metabolic processes. Dirt and dead biomass were removed, taking care to maintain the original shape and density of the samples as much as possible.

A portable open flow infrared gas analyser (GFS 3000, Walz, Effeltrich, Germany) with a special moss cuvette was used to determine light, water and temperature-response curves of net photosynthesis (NP) and dark respiration (R_D). At least five replicates per species and response type were used. The following conditions were used: CO_2 concentration at $380 \mu\text{mol mol}^{-1}$, relative humidity at 85 %, photosynthetic photon flux density (PPFD) near saturation for photosynthesis (Table 2; except for light-response curves), and temperature close to local ambient values (Table 2; except for temperature-response curves). Additionally, CO_2 -response curves were measured with a subset of three species in the laboratory in Oldenburg, Germany. These samples grew in glass jars at 20°C for approx. 9 months (*Herbertus divergens* and *Leucobryum antillarum*, two montane Fortuna species) or in the green house at approx. $26/20^\circ\text{C}$ (day/night) for >3 years (*Orthostichopsis tetragona*, a lowland species). These samples were then treated like those from the field and measured with the same gas-exchange equipment using the same settings (Table 2). After the measurements, all samples were dried for 3 d at 90°C to determine dry weight. All CO_2 -exchange rates are expressed relative to dry weight.

TABLE 2. Settings of temperature and light conditions during gas-exchange measurements at the three altitudes

Location	Altitude (m a.s.l.)	Measuring temperature ($^\circ\text{C}$)	Measuring light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	NP (% max)
Bocas del Toro	0	29	500	76 ± 5
Palo Seco	500	25	400	75 ± 3
Fortuna	1200	22	300	65 ± 9

Temperatures during measurements approximated ambient temperatures at the three locations.

Light intensity was near saturation for photosynthesis, based on the modelled maximum rate of photosynthesis of each species (means \pm s.d.).

First, the response of CO_2 exchange to changing plant water content (WC) was determined. After submerging samples in distilled water for up to 2 min, surface water was removed by vigorous shaking. Samples were then enclosed in the cuvette and CO_2 -exchange rates were recorded when steady state was reached. A typical measurement lasted from 2 to 5 min at most. Samples were then weighed to determine WC and left to dry until the next measurement approx. 30 min later. This procedure was repeated until the weight no longer changed.

Light-response and CO_2 -response curves were determined in samples with water contents slightly above the optimum because of inevitable water loss during the experiment. After enclosure in the cuvette, samples were light-induced at $300\text{--}500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $380 \mu\text{mol mol}^{-1} \text{CO}_2$ for 5 min. Light was then changed in 15 steps from 0 to $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, or CO_2 from $0\text{--}1500 \mu\text{mol mol}^{-1}$ in 11 steps, each step lasting approx. 3 min to reach steady state. Before and after the measurement, WC was determined to make sure that it was still near the optimum.

For the temperature-response curves the entire gas-exchange system had to be heated or cooled to prevent condensation in the tubing or cuvette. This was achieved by placing the system in a custom-built, temperature-controlled box. The moss samples were sprayed to reach near-optimal WC before being enclosed in the cuvette, where their CO_2 exchange was recorded at the adjusted temperature after approx. 3 min. The temperature was set to the next step and the sample was measured again after checking/adjusting its water content. Temperature ranges differed between altitudes: BT, $20\text{--}37.5^\circ\text{C}$; PS, $17.5\text{--}33^\circ\text{C}$ and F, $10\text{--}35^\circ\text{C}$. The temperatures of the moss samples were probably somewhat below those of the cuvette due to evaporative cooling.

No cold trap was used in the gas exchange measurement, so that the raw data was corrected for the effect of water vapour. A correction is already included in the equipment software, but we tested if additional corrections were necessary when measuring wet mosses by measuring 'CO₂ exchange' of tissue paper soaked in distilled water. This test revealed that net photosynthesis was underestimated (and dark respiration overestimated) by 0.13 ± 0.03 (mean \pm s.d., $n = 7$) $\mu\text{mol CO}_2$ (before taking dry weight into account). Thus, all data from light-, temperature- and water-response curves were corrected with this mean value. For water-response curves we assumed that the correction factor decreases linearly from the optimum towards lower water contents. In spite of this correction, the absolute rates of CO_2 exchange are still somewhat uncertain. The interpretation therefore stresses relative differences. The CO_2 -response curves were not corrected because the equipment had been serviced before these measurements and the wet tissue test no longer showed 'false' respiration.

Tissue chemistry

Nitrogen contents of moss samples, only including green parts as used in the gas-exchange measurements, were determined at the University of Oldenburg with a CHNS Analyzer (FLASHEA, 1112 Series; CE Elantech, Inc., Lakewood, USA). Chlorophyll *a* and *b* contents were determined at the Bocas del Toro field station, using methanol as

extractant. Fresh plant material (20–100 mg) was added to a vial and heated in a water bath for 10 min at 60 °C. The extract was decanted and the procedure was repeated. The gathered extracts were mixed well and measured in a photospectrometer (650 and 665 nm). The samples were then dried at 90 °C and the chlorophyll content was related to dry weight.

Data analysis

Using R version 2.14.0 (R Development Core Team, 2011) models were fitted to the response data and the main cardinal points (optimum, maximum, compensation point) were calculated from the modelled curves. Water-response curves were fitted to all measuring points, for several samples per species ($n \geq 5$). Respiration rates reaching values $>30\%$ of the general maximum at high water contents were considered artefacts and were excluded from the analysis (0–3 points per sample). Light-, CO_2 - and temperature-response curves were fitted to means of several samples per species ($n \geq 5$). Best-fit model types were chosen for the water and temperature-response curves and are only meaningful in the range of measurement.

$$\text{CO}_2 \text{ exchange} = \left(\frac{a \times \text{WC} \times (b \times \text{WC} + c)}{a \times \text{WC} + (b \times \text{WC} + c)} \right) - d \quad (1)$$

$$\text{CO}_2 \text{ exchange} = - \left(\frac{a \times \text{WC}}{b + \text{WC}} \right) \quad (2)$$

$$\text{CO}_2 \text{ exchange} = \frac{\alpha \times \text{PPFD}}{\sqrt{1 + \frac{(\alpha \times \text{PPFD})^2}{(\text{NP}_{\max} + R_D)^2}}} - R_D \quad (3)$$

$$\text{CO}_2 \text{ exchange} = \frac{\alpha \times \text{CO}_2}{\sqrt{1 + \frac{(\alpha \times \text{CO}_2)^2}{(\text{NP}_{\max} + R_D)^2}}} - R_D \quad (4)$$

$$\text{CO}_2 \text{ exchange} = a - b \times \text{Temp} \times (c - \text{Temp})^2 \quad (5)$$

$$\text{CO}_2 \text{ exchange} = -(a^{\text{Temp}} + b) \quad (6)$$

***Equations 1 (hyperbolic function) and 2 (Michaelis Menten) are models for the water-response curves in the presence of light and in dark, respectively. WC is the water content of the bryophyte samples. In the cases of the light- and CO_2 -response curves the modified ‘Smith-function’ (eqns 3 and 4) (Tenhunen *et al.*, 1976) was fitted, where α represents the initial slope of the curve, NP_{\max} the maximum rate of net photosynthesis and R_D the dark respiration rate. PPFD is the incident light in $\mu\text{mol m}^{-2} \text{s}^{-1}$ and CO_2 the CO_2 concentration in $\mu\text{mol mol}^{-1}$. Equations 5 and 6 were fitted to the temperature-response data, again in the light and in the dark. Temp is the temperature of the cuvette in °C. As the lower bounds of the optimal temperature ranges were frequently lower than the lowest experimental temperature, and since

the model used was not suitable for downward extrapolation, the lowest temperature measured in these cases is reported (Table 3). Additionally, based on the temperature-response curves, we calculated the ratio of R_D to NP at mean local night and day temperatures, respectively, as well as under three warming scenarios, assuming no acclimation (Table 4). Cardinal points of photosynthesis (Tables 3 and 4) were compared among altitudes using type I one-way ANOVA, followed, when appropriate, by Tukey HSD tests. Means are reported \pm s.d.

RESULTS

Water response

The responses of CO_2 exchange to water content (WC) in the 18 studied species were quite variable quantitatively, but similar qualitatively, with strong depressions of both net photosynthesis (NP) and dark respiration (R_D) at low water contents, and a variable depression of NP (12–72 % of the max, mean = $52 \pm 17\%$, $n = 18$) and no depression of R_D at high water contents (Fig. 1 and Table 3). The fitted models for NP had r^2 values ranging from 0.49 to 0.81 and for R_D from 0.22 to 0.78. The optimum WC for NP (where NP exceeded 90 % of NP_{\max}) differed considerably amongst species, ranging from approx. 150 to 750 %. Species with high maximum water contents generally had greater optimum ranges as well ($r = 0.96$ for $\text{WC}_{\max} - \text{WC}_{\text{opt lower}}$ and $r = 0.93$ $\text{WC}_{\max} - \text{WC}_{\text{opt upper}}$). Optimum water contents for photosynthesis did not differ significantly between altitudes ($P = 0.39$).

Light and CO_2 response

The light responses of all 18 species were described well by the modified Smith function ($r^2 \geq 0.99$). Maximum rates of NP varied 6-fold from 4.8 $\text{nmol g}^{-1} \text{d. wt s}^{-1}$ in the turf *H. divergens* to 28.5 $\text{nmol g}^{-1} \text{d. wt s}^{-1}$ in the thallose terrestrial liverwort *D. hirsuta* (Table 3). Light compensation points were rather high relative to light conditions in the natural habitat in all species. The lowest light compensation point was found in the understorey species *S. incompletus* (20 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 2A) and the highest in the exposed-growing species *Frullania mirabilis* (159 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Altitude had no significant effect on any parameter of the light-response curve ($P = 0.13$ – 0.49). The ratio of NP to R_D was rather variable and ranged from 1.3 to 4.0.

A second modified Smith function appropriately described the response of NP to varying CO_2 concentrations ($r^2 = 0.62$ – 0.97 ; Fig. 2B). Carbon dioxide concentrations can be up to approx. 480 $\mu\text{mol mol}^{-1}$ in the moss phylloplane (Wagner *et al.*, 2012), but the effects of this small increase in CO_2 on NP are moderate when compared with atmospheric concentrations of approx. 380 $\mu\text{mol mol}^{-1}$: exchange rates rise from 3.1 to 3.5 $\text{nmol g}^{-1} \text{s}^{-1}$ in *H. divergens*, from 6.5 to 7.1 $\text{nmol g}^{-1} \text{s}^{-1}$ in *L. antillarum* and from 3.8 to 4.6 $\text{nmol g}^{-1} \text{s}^{-1}$ in *O. tetragona* (all $n = 5$). Actual rates of net photosynthesis in the natural habitat of the moss may thus be 9–20 % higher than rates determined at CO_2 concentrations in the air of 380 $\mu\text{mol mol}^{-1}$.

TABLE 3. Cardinal points of the photosynthesis response curves of 18 tropical bryophyte species from three locations in Panama

Location	Species	WC _{opt} (90%) (% of d. wt)	WC _{max} (% of d. wt)	Depression (% of max NP)	NP _{max} (nmol g ⁻¹ s ⁻¹)	LCP (μmol m ⁻² s ⁻¹)	R _D /NP _{max} (%)	T _{opt} (°C)	T _{opt} (90%) (°C)	T _{NP=RD} (°C)	T _{comp} (°C)	Q ₁₀
BT	<i>Octoblepharum pulvinatum</i>				10.8	22	23	27	21–32	33	>37.5	
BT	<i>Orthostichopsis tetragona</i>	210–808	1294	66	22.0	35	37	25	<20–30	36	>37.5	3.6
BT	<i>Plagiochila</i> sp. 1	256–597	768	68	14.5	42	53	24	<20–29	33	37	1.6
BT	<i>Stictolejeunea squamata</i>	152–479	967	36	12.5	69	63	25	21–29	30	36	2.1
BT	<i>Symbiezidium</i> spp.	262–523	814	12	16.0	47	48	27	24–31	32	37	2.1
BT	<i>Zelometeorium patulum</i>	244–1007	1558	70	18.6	48	53	25	19–30	35	>37.5	2.2
PS	<i>Bryopteris filicina</i>	184–418	663	40	16.0	43	50	25	19–29	30	>33	2.3
PS	<i>Lepidopilum polytrichoides</i>	281–669	1092	38	19.8	34	48	24	20–28	28	>33	2.8
PS	<i>Pilotrichum bipinnatum</i>	226–745	1065	70	16.1	27	38	23	<18–28	30	>33	2.5
PS	<i>Plagiochila</i> sp. 2	232–530	756	55	16.1	27	38	26	21–31	31	>33	2.4
PS	<i>Symbiezidium</i> spp.	217–519	869	34	19.1	38	42	25	20–30	31	>33	3.6
PS	<i>Syrrophodon incompletus</i>	187–404	617	41	16.1	20	29	27	22–31	30	>33	3.2
F	<i>Durmortiera hirsuta</i>	701–998	1082	67	28.5	29	38	20	<10–26	28	>35	1.9
F	<i>Frullania mirabilis</i>	127–289	464	36	12.5	159	63	16	<10–21	19	29	3.1
F	<i>Herbertus divergens</i>	177–334	426	57	4.8	77	77	21	14–26	26	35	3.8
F	<i>Leucobryum antillarum</i>	667–1286	1711	52	12.9	38	71	23	15–28	31	>35	3.5
F	<i>Phyllogonium fulgens</i>	201–466	645	63	9.3	79	77	17	<10–23	23	33	2.3
F	<i>Phyllogonium viscosum</i>	324–849	1110	72	12.8	30	37	23	16–28	29	>35	4.1
ANOVA for location		N/A	n.s.	n.s.	n.s.	n.s.	n.s.	***	N/A	**	N/A	n.s.

Locations: BT, Bocas del Toro (0 m); PS, Palo Seco (500 m); F, Fortuna (1200 m).

Parameters from left to right: WC_{opt} (90%) = range of water contents (WC) where net photosynthesis (NP) >90 % of the maximum NP rate; WC_{max} = maximum WC, i.e. WC at full saturation; Depression = % depression of maximum NP at the WC_{max}; NP_{max} = maximum rate of net photosynthesis (based on light-response curve); LCP = light compensation point; R_D/NP = ratio of R_D to NP_{max} (last two based on light-response curve, rates at standard measuring temperature; see Table 2); T_{opt} = temperature optimum of NP; T_{opt} (90%) = optimum temperature range where NP >90 % NP_{max}; T_{NP=RD} = temperature where NP = R_D; T_{comp} = high-temperature compensation point of NP; Q₁₀ = Q₁₀ of R_D, calculated at ± 3 °C of local mean night temperature (BT = 24 °C, PS = 21 °C, F = 18 °C).

Values are means of at least five samples per response curve and species.

Where appropriate and possible, a Type I one-way ANOVA was conducted (significance levels: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; n.s., not significant; N/A, ANOVA not done).

Temperature response

Temperature optima differed predictably between altitudes (Figs 3 and 4 and Table 3). The fitted models for NP had r^2 values from 0.72 to 0.99, for R_D $r^2 = 0.79\text{--}0.99$. The optimum ranges for net photosynthesis (with NP > 90 % NP_{max}) usually spanned approx. 10 °C and included the mean daytime averages of temperature experienced at the respective altitudes.

Differences in optimum temperatures for NP (means of six species) were significant between the lower montane rainforest site (F; 20 °C) and the two lowland sites (BT and PS; 26 and 25 °C) (Fig. 4). The only species that was measured at two altitudes (*Symbiezidium* sp.) showed a trend to a somewhat higher optimum temperature in BT compared with PS (27 °C vs. 25 °C, $P = 0.26$), possibly suggesting either acclimation or divergence between populations (genetic variation).

The temperature at which NP equalled R_D was also significantly higher in BT compared with F ($P < 0.01$), while the differences between PS and F and between PS and BT were not significant ($P = 0.06$ and 0.14, respectively). The upper

temperature compensation points were beyond the range of measurements for most species. Q_{10} values for dark respiration, based on a temperature interval of ± 3 °C around the local mean night temperature, tended to increase with increasing altitude, but this trend was not significant (Fig. 4; $P = 0.23$). Also Q_{10} values were calculated using the same temperature range for all species (20–30 °C), which yielded smaller and non-significant differences (BT = 2.3 ± 0.7 , $n = 5$; PS = 2.6 ± 0.7 , $n = 6$ and $F = 2.5 \pm 0.3$, $n = 6$).

The ratio of R_D to NP at mean local night and day temperatures (Table 4) did not differ between altitudes ($P = 0.40$). NP was determined at lower PPFD for the Fortuna samples (Table 2). Correcting for this, the mean value of R_D /NP for Fortuna samples decreased from 46 % to 37 %, i.e. ratios are probably even more similar along the altitudinal gradient. Effects of warming on R_D /NP were smallest at sea level and tended to increase with altitude although these differences were also not significant. A warming of 6 °C, which is approximately equivalent to a transfer from Fortuna to Bocas del Toro, would more-or-less double respiration for all species, with little reduction in photosynthesis.

TABLE 4. Ratio of dark respiration (R_D) to net photosynthesis (NP) of tropical bryophytes calculated for the mean local night/day temperature based on temperature-response curves

Location	R_D /NP (%) at mean T	R_D /NP (%) + 1 °C	R_D /NP (%) + 3 °C	R_D /NP (%) + 6 °C
Bocas del Toro	31 ± 16	35 ± 17	44 ± 19	72 ± 34
Palo Seco	40 ± 5	44 ± 5	52 ± 6	75 ± 11
Fortuna	46 ± 26	52 ± 31	68 ± 45	118 ± 110

Data are means ± s.d. of six species.

Tissue chemistry

The average nitrogen content for all species was 12.1 ± 3.5 mg g⁻¹ d. wt, with up to 3-fold differences between species (Table 5). Chlorophyll contents (chlorophyll *a* + *b*) varied more than 20-fold (Table 5). None of the parameters (N, total Chl or Chl *a/b*) differed significantly between altitudes (one-way ANOVA, $P = 0.10$, 0.16 and 0.09, respectively). Linear regressions of NP_{max} as a function of N and total chlorophyll content showed only a very weak positive relationship ($r^2 = 0.18$ for both N and Chl).

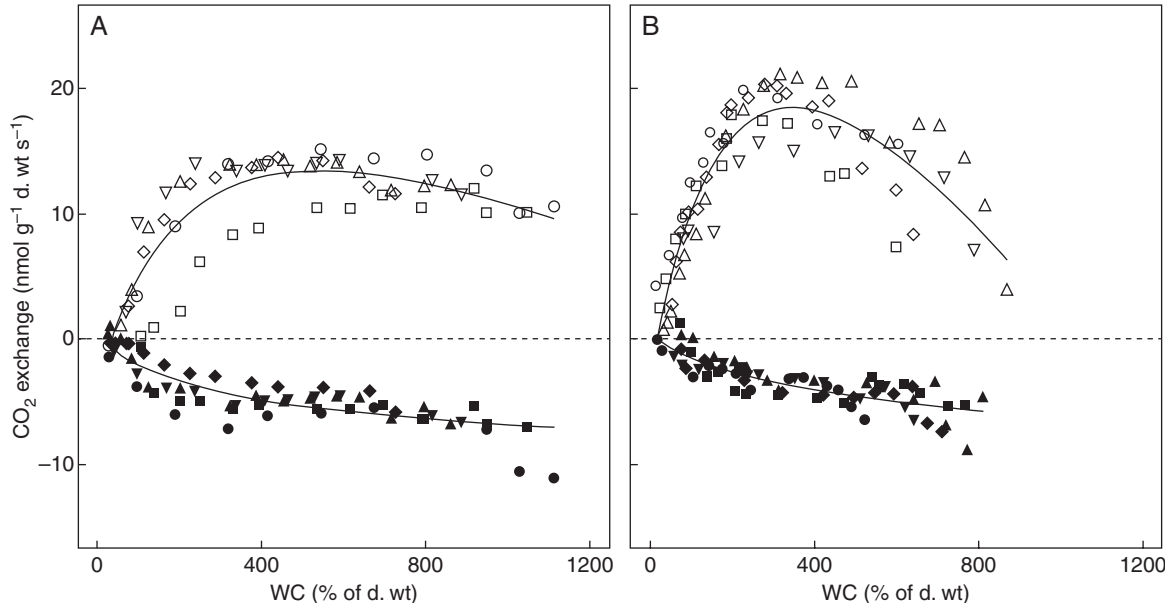


FIG. 1. Changes in net photosynthesis (NP) and dark respiration (R_D) as a function of thallus water content in (A) *Phyllogonium viscosum* (Fortuna) and (B) *Symbiezidium* spp. (Palo Seco). The open symbols denote NP, closed symbols are R_D . The different symbol shapes refer to different samples. Dashed lines indicate zero net gas exchange.

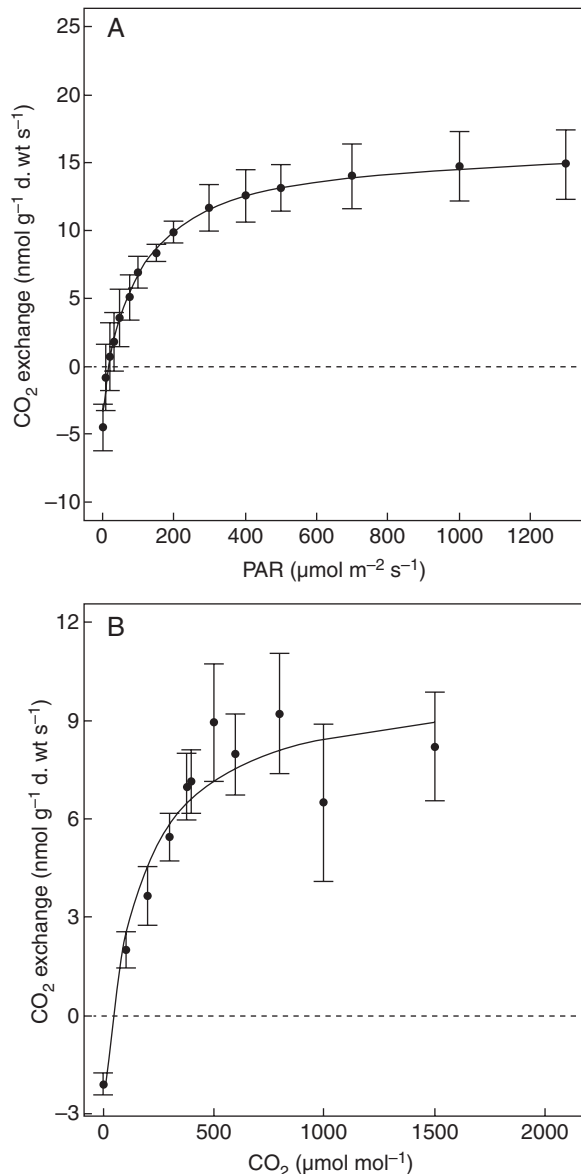


FIG. 2. (A) Net photosynthesis (NP) as a function of light in the moss *Syrrhopodon incompletus* (Palo Seco, Panama, 500 m). (B) NP as a function of ambient CO₂ concentration in *Leucobryum antillarum* (Fortuna, Panama, 1200 m). Data are means \pm s.d., $n = 5$. Dashed lines indicate zero net gas exchange.

DISCUSSION

The response of net CO₂ uptake to varying temperatures in the tropical mosses and liverworts studied shows a clear adaptation, or acclimatization, to mean habitat temperatures, while light responses and water responses show no such relationship with altitude and are more species specific. The change in optimum temperatures for photosynthesis (26, 25, 20 °C) closely matches ambient temperatures between sea level and 1200 m a.s.l. (26, 23, 20 °C), and also approximates the moist adiabatic lapse rate of the atmosphere (approx. 0.6 °C/100 m; Richards, 1996). In spite of this appealing coincidence, we cannot completely exclude that the lower optimum

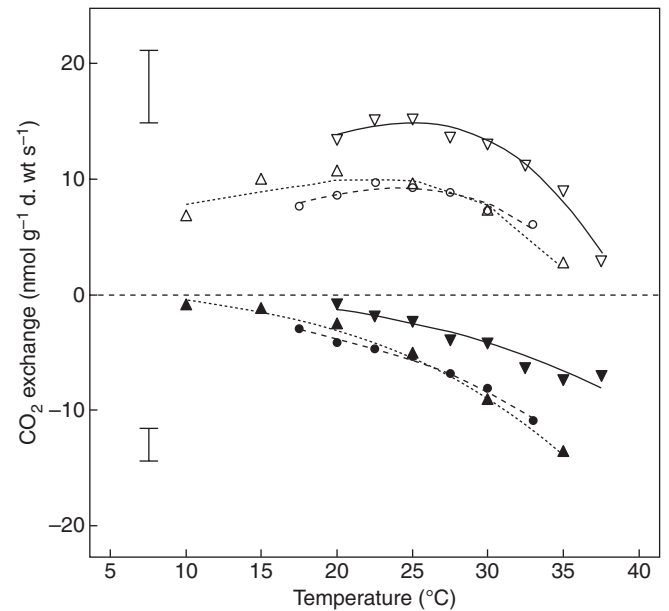


FIG. 3. Net photosynthesis (NP; open symbols) and dark respiration (R_D ; closed symbols) as a function of temperature of three pendant bryophyte species from three altitudes in Panama: *Orthostichopsis tetragona*, continuous lines, downward-pointing triangles (0 m, Bocas del Toro); *Bryopteris filicina*, dashed lines, downward-pointing triangles (500 m, Palo Seco); *Phyllogonium viscosum*, dotted lines, upward-pointing triangles (1200 m, Fortuna). $n = 5$ for each species, error bars indicate mean standard deviations of NP and R_D for the three species.

temperature in the Fortuna species is due to their more exposed growing sites. However, the higher temperature and brighter light here would usually result in higher rather than lower temperature optima (Niinemets *et al.*, 1999) so that including understory species or samples for Fortuna might, arguably, have yielded an even stronger gradient.

The Q_{10} of dark respiration declines with increasing temperatures in a range of plant species from ecosystems worldwide, probably due to a shift from enzyme-limitation at lower temperatures to substrate or energy-demand limitation at higher temperatures (Atkin and Tjoelker, 2003). This pattern seems to hold true for tropical bryophytes, where dark respiration tended to respond more strongly to temperature (higher Q_{10}) in the lower montane species, i.e. at lower measuring temperatures, than in the lowland species, though differences in our study were not significant. This altitudinal trend disappeared when the Q_{10} of all species was calculated for the same temperature range, suggesting no special adaptation or acclimation of Q_{10} to altitude (i.e. ambient temperatures).

In contrast to our expectation, the ratio between dark respiration and net photosynthesis rates at ambient temperatures did not differ between altitudes (Table 4). High respiration rates due to warm nights thus do not appear to be a distinguishing feature of the tropical lowland species compared with species from more bryophyte-rich lower montane areas. In fact, lowland species appear to be, if anything, better acclimatized or adapted to their ambient temperatures in terms of potential metabolic rates than montane species. However, these instantaneous rates are affected also by factors other than

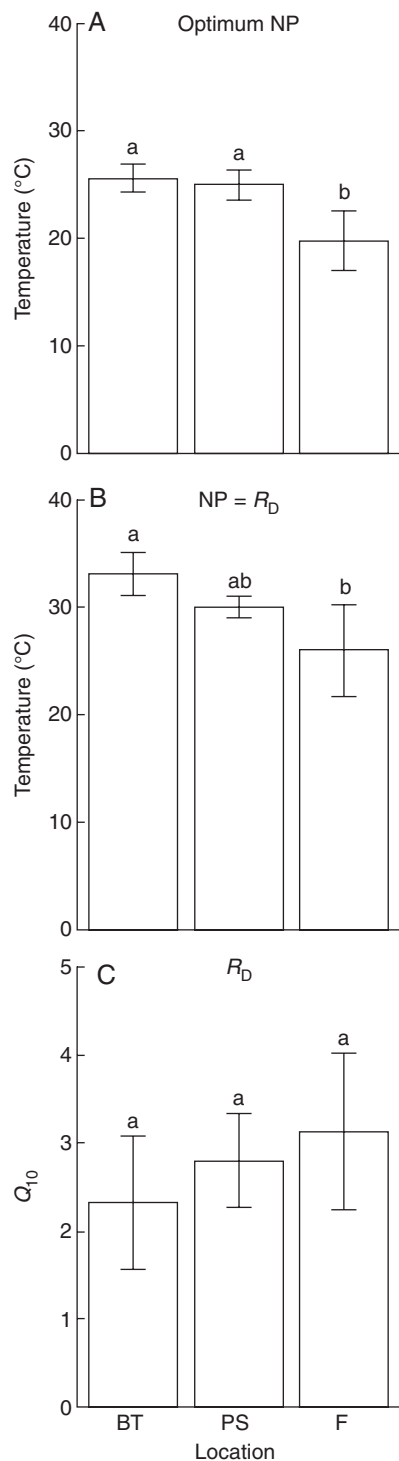


FIG. 4. Metabolic temperature-response parameters for bryophyte species from sea level (BT), 500 m (PS) and 1200 m (F) in Panama: (A) temperature optima of net photosynthesis (NP; $n = 6$ species); (B) temperature where NP equals dark respiration rates (R_D ; $n = 6$ species); (C) Q_{10} of R_D ($n = 6$ species, except BT, where $n = 5$ species, calculated at $\pm 3^\circ\text{C}$ of mean night temperature, BT = 24°C , PS = 21°C , F = 18°C). Error bars indicate s.d. Letters indicate significant differences between altitudes ($P < 0.001$ for optimum temperature and $P < 0.01$ for NP = R_D , one-way ANOVA followed by Tukey HSD-test).

temperature, so that integrated daily carbon gains cannot be predicted from temperature responses alone.

Respiratory carbon losses are not restricted to the night, but net losses can also occur during the day in times of suboptimal water contents and low light or during resaturation bursts following rewetting, all of which could lower the integrated carbon gain (Lange *et al.*, 2000, 2004). The major limitation of bryophyte net carbon gain is the availability of moisture. Drought tolerance *per se* does not appear to limit altitudinal distributions, because tolerances of both lowland and montane species in our study area far exceed the maximum duration of dry periods in most lowland forests (Bader *et al.*, 2012; Pardow and Lakatos, 2012) and is also high in tropical bryophytes from other regions (Proctor, 2002; León-Vargas *et al.*, 2006). However, the timing and duration of moisture availability determines physiological activity and, consequently, carbon gains and losses (Norris, 1990). Actual carbon gains and losses will be much lower than suggested by instantaneous rates derived from response curves (see Table 4) due to sub-optimal moisture conditions during most of the day. Based on integrated daily courses of *in situ* gas exchange, Zotz *et al.* (1997) estimated that montane bryophytes in Fortuna lost, on average, 60 % of daily gains to nightly respiration. This is comparable to values for the European lichen *Lecanora muralis* (lost 57 % on average) measured over the course of 1 year (Lange, 2003a). For the lowland lichen *Parmotrema endosulphureum*, however, nightly losses averaged 90 % with very frequent negative diel carbon balances (Zotz *et al.*, 2003). For this lichen the temperature optimum for photosynthesis was also low, at 22°C , and similar to that of the montane lichens *Dictyonema glabratum* (Lange *et al.*, 1994) and *Pseudocyphellaria aurata* (Lange *et al.*, 2004). The bryophytes we studied appear to be somewhat better-adapted physiologically to the high lowland temperatures than *P. endosulphureum*. They do, however, face the same challenges regarding the timing and duration of their physiological activity, which would be intensified by warmer temperatures (Bates, 1998; Kürschner *et al.*, 1999).

At higher temperatures, evaporation rates increase through higher vapour pressure deficits, causing faster drying and shorter activity times in poikilohydric organisms, such as many epiphytic bryophytes which do not have an effective boundary layer (Jonsson *et al.*, 2008). In contrast to mosses and liverworts in many montane areas, bryophytes growing in the lowlands generally cannot benefit from the frequent passage of clouds and fog (Cavelier *et al.*, 1996). Such lateral precipitation is especially beneficial when it occurs during the morning, as it often does, allowing activity at times of high light. As a case in point, a prospering bryophyte flora occurs in those rare lowland forests where morning fog is common (Gradstein *et al.*, 2010). Especially for loose life forms like wefts and pendants, where activity is already limited to 2 or 3 h after wetting (Zotz *et al.*, 1997; Proctor, 2002; Romero *et al.*, 2006; Wagner *et al.*, 2012), a reduced period of activity would severely limit carbon gain. Faster drying could also lead to more frequent rewetting causing carbon losses through carbohydrate leaching (Coxson *et al.*, 1992). Whether bursts of respiration at rewetting are really

TABLE 5. Nitrogen and chlorophyll content of green biomass of tropical bryophytes from three different altitudes (0 m, BT; 500 m PS; 1200 m, Fortuna) in Panama

Location	Species	N (mg g ⁻¹ d. wt)	Total Chl (mg chloro g ⁻¹ d. wt)	Chl <i>a/b</i>
BT	<i>Octoblepharum pulvinatum</i>	15.7 ± 1.0	7.7 ± 1.3	1.4 ± 0.1
BT	<i>Orthostichopsis tetragona</i>	12.4 ± 1.3	4.0 ± 0.5	1.7 ± 0.1
BT	<i>Plagiochila</i> sp. 1	9.9 ± 1.9	1.2 ± 0.5	0.9 ± 0.3
BT	<i>Stictolejeunea squamata</i>	12.1 ± 1.0	2.1 ± 0.4	1.4 ± 0.1
BT	<i>Symbiezidium</i> sp. 1	9.5 ± 0.4	1.6 ± 0.7	1.1 ± 0.3
BT	<i>Zelometeorium patulum</i>	11.0 ± 0.9	4.3 ± 0.9	1.5 ± 0.1
PS	<i>Bryopteris filicina</i>	12.9 ± 3.7	1.1 ± 1.0	1.1 ± 0.6
PS	<i>Lepidopilum polytrichoides</i>	21.0 ± 2.2	9.9 ± 2.0	1.1 ± 0.1
PS	<i>Pilotrichum bipinnatum</i>	16.2 ± 2.1	8.4 ± 2.6	1.1 ± 0.1
PS	<i>Plagiochila</i> sp. 2	14.3 ± 0.9	3.9 ± 0.4	1.1 ± 0.4
PS	<i>Symbiezidium</i> sp. 2	11.9 ± 1.0	3.7 ± 2.0	1.3 ± 0.5
PS	<i>Syrrhopodon incompletus</i>	9.8 ± 0.8	N/A	N/A
F	<i>Durmortiera hirsuta</i>	12.8 ± 0.9	5.2 ± 1.9	1.3 ± 0.3
F	<i>Frullania mirabilis</i>	14.3 ± 0.5	0.5 ± 0.4	1.9 ± 0.5
F	<i>Herbertus divergens</i>	5.8 ± 0.8	0.4 ± 0.1	1.5 ± 0.1
F	<i>Leucobryum antillarum</i>	10.9 ± 0.7	2.6 ± 1.8	1.2 ± 0.2
F	<i>Phyllogonium fulgens</i>	8.4 ± 0.8	1.6 ± 0.3	1.9 ± 1.3
F	<i>Phyllogonium viscosum</i>	8.4 ± 0.2	2.4 ± 0.2	1.3 ± 0.1

Means means ± s.d., *n* = 3, except for chlorophyll content of *Herbertus divergens*, where *n* = 2.

irrelevant ecologically, as suggested by Zotz *et al.* (1998) for the tropical lichen *Sticta tomentosa*, needs to be tested for other mosses and lichens.

Our study showed a clear relationship between mean temperatures experienced and temperature responses of net photosynthesis. The positive relationship between ambient temperature and temperature response can also be extended to bryophytes worldwide: the temperature optima of net photosynthesis of 61 bryophyte species scale significantly with the mean temperatures during the growing season (Fig. 5). One species, *Rhacomitrium lanuginosum*, did not follow this trend and has a somewhat strange behaviour. A study by Kallio and Heinonen (1975) showed that the temperature optimum of net photosynthesis in this boreal species was always 5 °C, irrespective of latitude (latitudinal range: 47–79 °N and 53 °S). This is a very low temperature compared with the optima of other species, even from the arctic, and the homogeneity suggests virtually no acclimatization or adaptation potential. On the other hand, the optimum temperature of the same species measured in south-west England (approx. 50 °N) was nearly threefold higher (see Supplementary Data Table S1 and Tallis, 1959). In spite of uncertainties in the temperature estimations (exact locations and harvesting times were not reported in all sources, even though the latter seems especially important in seasonal climates; Hicklenton and Oechel, 1977; Larigauderie and Körner, 1995), and methodological differences between data sources (although we only included measurements under ambient CO₂ concentrations), the relationship is clear. Temperature responses of net photosynthesis, and of respiration rates, commonly closely match climatic conditions.

Such an adaption could also restrict species to certain climatic ranges (e.g. montane tropics), though this restriction

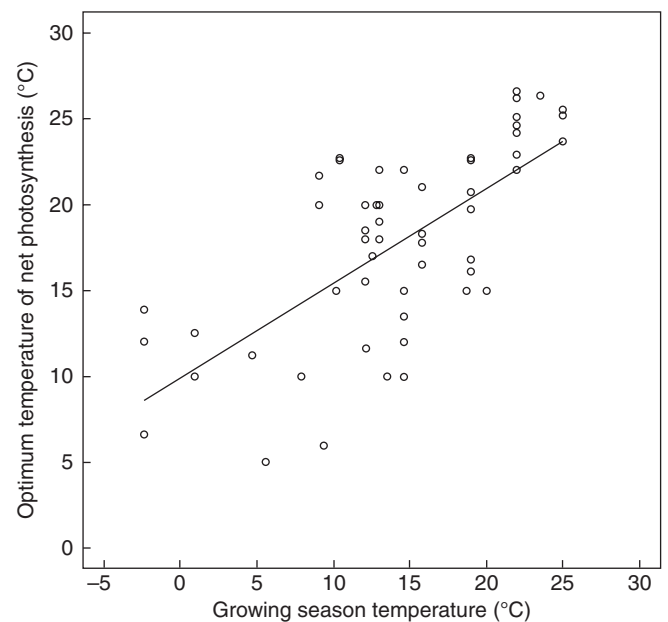


FIG. 5. Temperature optima of net photosynthesis of 61 bryophyte species in relation to mean temperature of the habitat during the growing season, based on 19 studies from a wide range of ecosystems: polar, alpine, temperate, desert and tropical regions. Each data point represents one species. Growing-season temperatures are based on data from the nearest climate station (monthly averages from 1970–2009 or less). Mean temperatures of the study sites were adjusted according to altitude (moist adiabatic lapse rate: 0.6 °C 100 m⁻¹). Where ranges were reported the arithmetic mean of the range was used for the analysis. Optimum temperatures were averaged where species showed seasonal acclimation or came from different altitudes. The line represents a linear regression model ($r^2 = 0.46$, $P < 0.001$). All studies included net photosynthesis measured at normal atmospheric CO₂ concentrations and at close to saturating irradiances. For details and references see Supplementary Data Table S1 online.

would be lifted if rates can acclimatize to ambient temperatures. A recent study found no metabolic acclimation to higher temperatures in a range of tropical bryophytes from 500 and 1200 m a.s.l., although some samples survived nearly 2 years at higher temperatures and recovered growth rates after initial dieback during this time (S. Wagner, G. Zotz and M. Y. Bader, unpubl. res.). The lack of warmer areas to which samples could be transplanted precluded the inclusion of lowland species in that study. The question of the acclimation potential of tropical bryophytes is thus still not resolved. If lowland species were already at their physiological limit, predicted temperature increases could severely threaten bryophytes in the tropical lowlands.

In conclusion, this study showed that tropical bryophytes, in contrast to lichens, are well adapted physiologically to the prevalent temperatures of their habitat. This refutes a common explanation for the observed altitudinal gradient in the tropics. An alternative explanation for altitudinal sorting, differences in desiccation tolerance, has been dismissed recently because the tolerance of montane species to prolonged desiccation is fully sufficient for them to survive even under lowland conditions (Bader *et al.*, 2012). We suggest that the timing and duration of hydration, more than metabolic rates, are most likely the main drivers for the precarious carbon balance and, consequently, the low biomass of lowland bryophytes. Restricted photosynthetic activity may also be the main limitation for montane bryophytes to establish at lower altitudes. Thus, future research on the causes of bryophyte abundance patterns in the tropics should focus on activity times during day and night.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of Table S1: data used for the regression analysis of temperature optima of net photosynthesis in relation to mean habitat temperature of the respective growing season.

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