

ALTITUDINAL CHANGES IN DIVERSITY AND ABUNDANCE OF NON-VASCULAR EPIPHYTES IN THE TROPICS— AN ECOPHYSIOLOGICAL EXPLANATION

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ABSTRACT. It has long been noted that there is a pronounced increase in the abundance of non-vascular organisms, i.e., macrolichens, mosses, and liverworts with altitude in the tropics. In montane regions, these poikilohydric organisms may account for a considerable biomass in tree crowns, while being quite inconspicuous in the lowlands. Some 20 years ago, Richards suggested that the apparent unsuitability of lowland tropical forest for non-vascular organisms was due to a combination of continuous high temperature, high relative humidity, and low light intensities. Although we still do not have unequivocal evidence that this explanation is indeed true, the results of most studies make it a highly probable scenario. Here, results are presented from a number of field and laboratory studies with both bryophytes and lichens. These studies indicate, that on one hand these organisms are very likely to dry out during the day, which strongly reduces their carbon gain, and on the other hand are often hydrated at night, which at high temperatures leads to considerable respiratory losses. In combination, this results in frequent negative 24-h carbon balances in the lowlands, making growth and survival very difficult, if not impossible. Surprisingly, crustose lichens do not show the same altitudinal pattern, but to date no physiological data are available to address this puzzle.

INTRODUCTION

Plant ecophysiology seeks to describe the physiological mechanisms underlying ecological observations (Lambers, Chapin & Pons 1998). A biogeographical phenomenon, which has puzzled naturalists for more than a century, is the surprising difference in the abundance of lichens and bryophytes in tropical lowlands compared to montane forests: the non-vascular vegetation of mosses, liverworts, and macrolichens (i.e., foliose and fruticose lichens) is generally much poorer in the lowlands (Richards 1984, Sipman & Harris 1989). Most of these poikilohydric organisms are epiphytes and epiphylls on living substrate, while terrestrial forms or colonizers of dead material are rare. They share many characteristics in their physiology (Green & Lange 1994), making a common explanation likely. The following reviews the relevant ecophysiological literature and proposes directions for future research.

Hypotheses and Ecophysiological Measurements

During the last few decades, numerous theories have been put forward to explain the pattern described above (review in Frahm 1987). The

most recent one (Richards 1984), originally developed only for bryophytes but later extended to macrolichens by Zotz & Winter (1994), emphasized the importance of high nighttime temperatures in the lowlands. Richards argued that the associated high rates of dark respiration should lead to strong nocturnal CO₂ losses, which possibly could not be balanced by daytime photosynthesis due to limitations associated with their poikilohydric habit. Richards (1984) wrote: "Studies of photosynthesis, respiration and net assimilation rates in lowland and montane forest bryophytes might be of great interest in this connection." The first researcher to take up this challenge and to test Richards notion experimentally was Frahm (1987). In a laboratory study he subjected several species of bryophytes from a montane forest to montane (10°C) and lowland conditions (30°C), respectively. Neither of the three species was able to achieve positive rates of net CO₂ uptake under lowland conditions.

The first pertinent field study was conducted by Zotz and Winter (1994) with the foliose lichen, *Leptogium azureum*, in the lowland forest of Barro Colorado Island (BCI), Panama. There, *L. azureum* is comparatively common, but the results of this study suggest that BCI must be a marginal habitat for this species: diel (24h) carbon balances were negative in a majority of days, both at a canopy site in the crown of a

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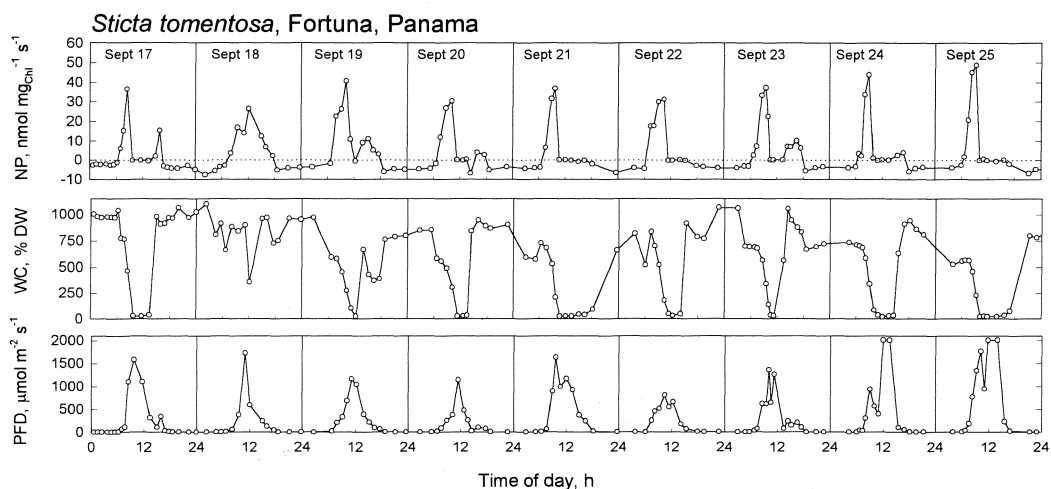


FIGURE 1. Diel courses of net photosynthesis (NP, $\text{nmol CO}_2 \text{ mg}_{\text{Chl}}^{-1} \text{ s}^{-1}$, upper panel), thallus water content (WC, % dry weight, center panel), and incident photon flux density (PFD, $\mu\text{mol m}^{-2} \text{ s}^{-1}$, bottom panel) for *Sticta tomentosa* from September 17 to 25, 1993. Sudden increases of WC indicate rain events (modified after Zotz et al. 1998).

large *Ceiba pentandra* and at an understory site. Consistent with Richard's hypothesis, nocturnal respiratory losses were very high (at average temperatures of 25°C), while daytime carbon gain was either restricted by low light (understory) or by frequent desiccation (canopy). A series of studies with several species of macrolichens and bryophytes in a lower montane forest in the Fortuna region, Panama, provided further

insight (Lange et al. 1994, Zotz et al. 1997, Zotz et al. 1998, Lange et al. in press). As shown in FIGURE 1, foliose lichens like *Sticta tomentosa* dried out around noon and were metabolically inactive on almost every day. This was a surprising finding considering the very wet conditions at this rain forest site with precipitation during the study month exceeding 500 mm (Zotz et al. 1998). Compared to the lowlands, the nighttime temperatures at Fortuna (1200 m a.s.l.) were considerably lower (average temperatures ca. 18°C), leading to much lower rates of dark respiration. However, an average of almost 60% of the diurnal carbon gain was still lost during the night. Similar or even higher losses were observed in other lichen species (*Dictyonema glabratum* and *Leptogium* spp.: Lange et al. 1994, in press) and in various moss and liverwort species (Zotz et al. 1997). The temperature response curves of, respectively, net assimilation and dark respiration of *S. tomentosa* (FIGURE 2), suggests that this species would be hardly able to thrive under lowland conditions. Assuming a temperature of 30°C (daytime) and 25°C (nighttime), the highest possible rate of net CO_2 uptake (NP_{max} : ca. $29 \text{ nmol mg}_{\text{Chl}}^{-1} \text{ s}^{-1}$) would exceed the rate of dark respiration (R_D : ca. $10 \text{ nmol mg}_{\text{Chl}}^{-1} \text{ s}^{-1}$) by less than a factor of three. Consequently, given the short duration of NP_{max} in the course of a day, the frequent states of diurnal metabolic rest, along with the respiratory activity at night (FIGURE 1), *S. tomentosa* is very unlikely to achieve a positive carbon balance, a first requirement for the establishment in any habitat (Alpert & Oechel 1985).

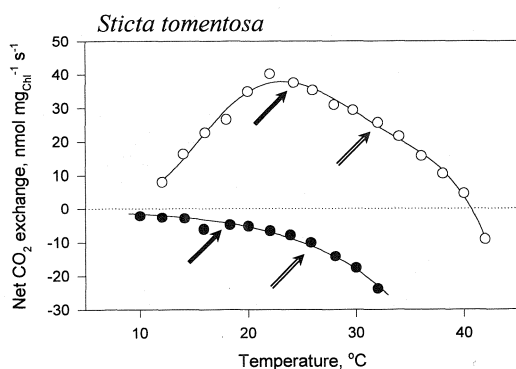


FIGURE 2. Relationship of, respectively, net photosynthesis (NP, open symbols) and dark respiration (R_D , closed symbols) and temperature. Values of NP are calculated after Zotz et al. (1998) for optimal thallus water content and saturating light intensity. Open arrows indicate typical lowland temperatures and closed arrows typical temperatures of the lower montane site (Zotz & Winter 1994, Zotz et al. 1998). A 5th degree polynome was fitted to the NP data ($r^2 = 0.98$) and an exponential function to the R_D data ($r^2 = 0.98$). The dotted line indicates zero gas exchange.

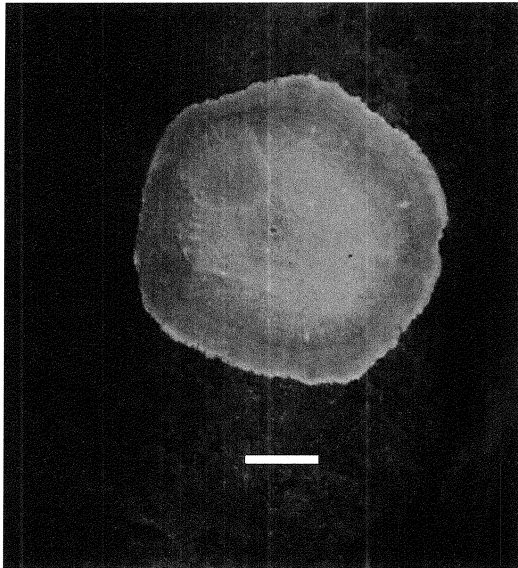


FIGURE 3. Medium sized thallus *Cryptothecia* sp. (Arthoniaceae). The length of the white bar is 1 cm.

While all the above studies found a strong dependency of dark respiration on temperature, i.e., were in accordance with the notion of Richards (1984), one gas exchange study is at variance: Löscher et al. (1994) could not find such a temperature response in a laboratory study with bryophytes from tropical Africa. Their different results were possibly due to pre-experimental treatment or the method used (i.e., Warburg manometry), which measures photosynthesis and respiration at elevated levels of CO_2 . To date, our data base is simply too limited for a final evaluation of these contrasting results.

There is a shortcoming in the argument above: our ignorance of a possible acclimation of dark respiration to lowland conditions, i.e., a relative reduction of R_d when growing under a high temperature regime. It has been demonstrated that at least some species of bryophytes and lichens may have a considerable potential for acclimation to changing temperature conditions (e.g., Hicklenton & Oechel 1976, Kershaw 1985). Conclusions drawn from FIGURE 2 should therefore be treated with caution. Before we can accept or disprove Richards' hypothesis, the question of acclimation has to be addressed experimentally. Laboratory studies, in which lichen or bryophyte samples are cultivated under a range of different temperature regimes are one possibility, but the author recommends experiments with in situ transplants. Using the latter approach in Panama by transferring several species of mosses and liverworts from 1200 m a.s.l.

(lower montane) to about 30 m a.s.l. (lowlands), Rottenberger and Zotz found almost no indication of acclimation after 10 days (unpubl. data). Acclimation over longer periods could not be studied, because most samples showed visible damage after this time. Hence, future studies should use a less drastic approach and transfer samples in a stepwise fashion, e.g., from 1200 m to 900 and 500 m a.s.l. to elucidate the acclimation potential.

The Crustose Lichen Enigma

Even if future experimental work will indeed confirm the ecophysiological explanation outlined above, we are still ignorant of the physiological mechanisms behind the divergent pattern in crustose forms. In contrast to foliose and fruticose forms, crustose lichens may be extremely diverse and common in the lowlands, often completely covering the bark of many trees (e.g., Aptroot & Sipman 1997). Quantitative evidence for their vigor in lowland habitats is provided by a recent growth study with the lichen, *Cryptothecia* sp. (Arthoniaceae) (FIGURES 3, 4). The average annual increment in radius of the mostly circular thalli of this species growing on a number of different host trees in a gap on BCI was 5.1 mm. Such growth rates exceed most known values for crustose lichens from alpine (Frey 1959), temperate (Hale 1959), or subtropical desert habitats (Lange 1990) by about an order of magnitude. Relative growth rates of *Cryptothecia* sp. decreased strongly with thallus size (FIGURE 4a), resulting in a rather constant radial increment irrespective of initial thallus size (FIGURE 4b). The smallest thallus of the study (initial area: 50 mm²) reached 305 mm² after one year, i.e., increased by ca. 500%. Similar to other crustose species (Lange 1990), growth was supported by a marginal annulus of a few mm width. Removal of the central part, which was lighter and contained much less chlorophyll than the darker annulus ($24 \pm 6\%$, $N = 4$; Zotz, unpubl. results), yielded even slightly increased radial increments (5.9 mm yr^{-1} ; FIGURE 4b). To date, there are no ecophysiological or micrometeorological data for tropical crustose lichens that could explain this performance or identify possible differences in microhabitat and/or physiology of the different lichen forms.

CONCLUSIONS

Excluding crustose lichens, the results of ecophysiological studies with tropical non-vascular epiphytes, conducted during the last ten years, are mostly consistent with Richards' (1984) hypothesis. However, the available evidence is still

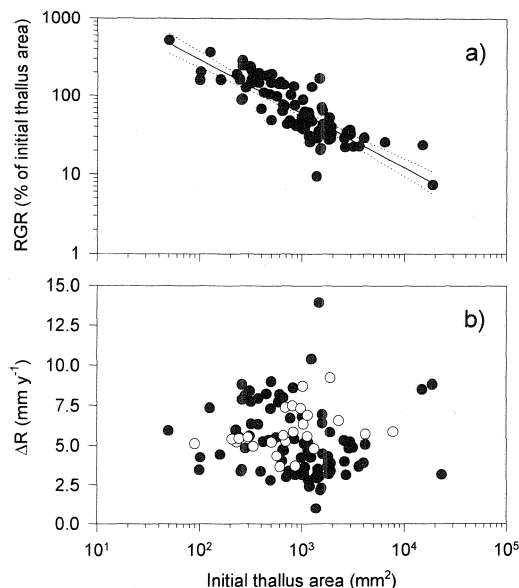


FIGURE 4. Growth in a crustose lichen (*Cryptothelia* sp.). Panel a shows the correlation of RGR (Relative growth rate in % of the initial thallus area) with the initial thallus area (TA) of 86 intact thalli. Lines are linear regression and 95% confidence intervals, respectively. The regression equation is: $\log \text{RGR} = 3.84 - 0.69 \log \text{TA}$ ($r^2 = 0.70$, $P < 0.001$). Panel b shows the relationship of annual radial increment (ΔR) of 86 intact thalli (closed symbols) and 25 thalli, where the central part was removed (open symbols) with TA. The correlation between initial thallus area and radial increment was not significant in either case ($P > 0.1$). The average ΔR was slightly higher in the manipulated thalli (5.9 ± 1.4 mm vs. 5.1 ± 2.2 mm; means \pm SD). Measurements were from April 1996–April 1997 (G. Zotz & R. Wirth, previously unpubl. data, for methods compare Hale 1959). Voucher specimens are deposited at the herbarium of BCI and at the Universidad de Panama.

circumstantial and an experimental approach is clearly needed. First results of this type of study seem to confirm our present view, and future, more refined transplant experiments should finally provide unequivocal evidence. Even if this biogeographical puzzle may be solved soon, we are still at the very beginning of an understanding of the ecophysiology of crustose lichens in the tropics—their distribution pattern does not match that of macrolichens and bryophytes, clearly demanding a different explanation.

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