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Author: Gerhard Zotz Glenda Mendieta Katrin Wagner

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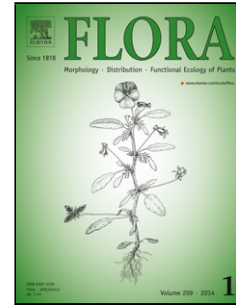
Vascular epiphytes at the treeline – composition of species assemblages and population biology

Gerhard Zotz [1,2], Glenda Mendieta[1], Katrin Wagner[1]

[1] Functional Ecology of Plants, Institute of Biology and Environmental Sciences, University of Oldenburg, P.O. Box 2503, D-26111 Oldenburg, Germany

[2] Smithsonian Tropical Research Institute, Apdo 08343-03092, Panama, Republic of Panama

Corresponding author: gerhard.zotz@uni-oldenburg.de

Highlights

► We studied key aspects of epiphyte demography and community structure at the tree line
► The epiphyte community at the tree line is less diverse than in comparable lowland
habitats ► Some species may only form sink populations, which depend on constant input
from lower elevations ► Many species, however, seem to form viable local populations

Abstract

Do epiphytes drop out above the treeline because of climatic reasons or due to lack of appropriate substrate? We set out to address this question by studying various key aspects of their biology at a natural treeline on a tropical mountain top in Panama: species composition of assemblages, host preferences, population structure and dynamics, individual growth and reproductive investment. Lack of relevant climate data caused us to monitor microclimatic conditions in tree crowns for 12 months. At our study site we found 15 epiphyte species, mostly ferns, although in terms of abundance orchids were highly dominant. Compared to lowland vegetation of similar stature, the epiphyte assemblages were less species-rich and abundances lower. Some species may only be present at this treeline because of continuous immigration from lower elevations (i.e. represent sink populations). Many species, however, were rather abundant with many reproductive individuals, arguably forming viable local populations. The results of a detailed demographic study with the orchid *Pachyphyllum hispidulum* over three years also support this notion, being comparable to studies from lowland habitats. Our descriptive study does not allow unambiguous conclusions on mechanisms, but the results suggest that lack of suitable substrate (=trees) rather than climatic reasons are responsible for the disappearance of epiphytes immediately above the treeline. This notion needs rigorous verification by experimental physiological studies.

Introduction

Vascular epiphytes grow non-parasitically on other plants, usually trees (Benzing 1990). Thus, this structurally dependent life form should inevitably fade out at the transition from tropical subalpine forest to alpine vegetation, which has few, if any, substrates for epiphyte establishment, such as treelets and shrubs. Although reports on large-scale altitudinal changes in vegetation generally support this expectation (Bussmann, 2001, 2003, Kluge et al., 2008), these studies also document a few species that occur as epiphytes in subalpine forest, but exist above the timberline as terrestrials or lithophytes (Kluge et al., 2008). Alternatively, ambient conditions may already limit epiphytic growth and survival of most species at or below the treeline, which is suggested by the generally

observed mid-elevation peak in species richness and abundance at 1000 – 1500 m a.s.l. (Cardelús et al., 2006, Krömer et al., 2005). Possibly, most epiphyte populations at the treeline may already be sink populations supported from source populations at lower elevations (cf. Bhattarai et al., 2004).

To date, there is very little quantitative information about the presence of vascular epiphytes on mountain peaks at or above the treeline in the tropics. Detailed studies on population biology or physiological ecology of some epiphytes found there are entirely missing. However, there is a clear need for such basic ecological data, not only for a better understanding of the processes behind current epiphyte distributional patterns. Observations from the temperate zone (cf. Pauli et al., 2012) suggest that such habitats may experience, or may already have experienced, quite dramatic changes in the composition of the vegetation. Currently, such changes would remain unnoticed.

We initiated such a study on vascular epiphytes in the summit region of a tropical mountain, the Volcán Barú massif in the Republic of Panama. The summit is the highest point of this Central American country, reaching almost 3500 m asl. Apart from documented plant collections (e.g. in Correa A et al., 2004) we found no published information on the vegetation there in general, let alone the epiphytic component. There are a few detailed studies on the montane and alpine vegetation of Volcán Chirripó in neighbouring Costa Rica (Schneidt and Weberling, 1992, Stein and Weberling, 1992, Weber, 1958) but none of these papers deals with epiphytes in any detail either.

As a first step to understand the epiphyte ecology in the uppermost region of this tropical mountain, the present study sets out to study epiphytes at the treeline of Volcán Barú, with particular emphasis on two questions: 1) How diverse and abundant are vascular epiphyte assemblages at this treeline? 2) Are the local populations viable?

Methods

Study site

This study was performed close to the summit of Volcán Barú (Panama, Chiriquí Province, N8° 48.5' W82° 32.5', 3475 m asl) at an elevation of 3300–3400 m asl, between March 2010 and March 2013. We classify the local vegetation as páramo following the discussion of Weber (1958) for the Chirripó massif in neighbouring Costa Rica, where the treeline is also at c. 3300 m. This vegetation is characterized by a mosaic of patches of

stunted treelets dominated by *Comarostaphylis arbutoides* Lindl. subsp. *arbutoides* (Ericaceae) and herbaceous vegetation with grasses, ferns (mostly *Elaphoglossum* cf. *furfuraceum*), interspersed with subfruticose *Hypericum* sp., *Castilleja* sp. and others. Steeper slopes are covered by scree, and are almost devoid of plant cover, as are rock outcrops and the central crater area.

No climate data are available for this site, so we placed five HOBO Pendant Temperature/Light data loggers and one HOBO U23 Pro v2 Temperature/Relative Humidity data loggers (Onset Computer Corporation, Cape Cod, USA) in the open and within tree crowns next to the populations of the epiphytic orchid *Pachyphyllum hispidulum* (Rchb.f.) Garay & Dunst., to record basic climate variables (temperature, radiation, relative humidity) between early March 2011 and late February 2012. The "Light" dataloggers have a right skewed response curve for radiation from c. 200–1200 nm, but values are closely correlated with photosynthetic photon flux density ($r^2 = 0.88$, Wagner et al., 2014). Unfortunately, the dataloggers placed in the open were stolen, so only data for temperature and radiation in the centre of four *C. arbutoides* crowns can be shown. HOBO dataloggers were calibrated against ice water before and after the measuring campaign. The problem that the measurement of radiation and temperature with the same device inevitably leads to an increasing temperature deviation of device and air during periods of high radiation was addressed as follows: Independent measurements with a thermometer indicated that air temperature did not exceed 20°C even around noon. Thus, we inspected all individual data points > 20°C comparing them with the values of the three other loggers. Due to their location in the inner tree crown, it never happened that all four data loggers received high radiation loads at exactly the same time. Whenever a data logger received > 20000 lx with a temperature >20°C and/or a difference in temperature > 2°C to the average of the other sensors, the value was dropped from further analysis, which used the averages of two to four replicate measurements.

Composition of species assemblages

In March 2011, we selected 10 plots (5 x 5 m each) for a complete census of all woody plants (basal diameter > 1 cm) and all dependent vascular plants (epiphytes and mistletoes). Plots were chosen to capture a maximum of variation in slope (5°–45°), and vegetation height (average 2.2–4.2 m) and covered all cardinal directions in slope

orientation. In each plot, all trees were identified and all individual epiphytes identified and counted. Most specimens were not fertile at the time of our study, which did not allow unambiguous species identification of a couple of taxa. Vouchers are deposited at the Herbarium of the Universidad de Panamá.

Population biology of an epiphytic orchid

Plots for the demographic study with *Pachyphyllum hispidulum* (Orchidaceae) were established in early 2010. Each of the seven plots consisted of a trunk or branch section (0.7–2.20 m in length) not more than 1.80 m above the ground. The available surface area of a plot, which was estimated as the surface of a cylinder in more or less vertical plots and as a semi-cylinder in more or less horizontal plots, was 0.5–1.3 m^2. All plants were labeled with pins or colored wire. In each of the following 3 years, we recorded shoot length, number of fruits, and new epiphyte establishments within each plot. In total, 346 individuals were studied. Population densities were quantified for the year 2010.

Matrix construction and further analyses

From the demographic data, stage transition matrices were constructed using five size classes: first year seedlings (*SC1*), other plants < 1 cm (*SC2*), plants ≥ 1 cm and < 2 cm (*SC3*), plant ≥ 2 cm and < 5 cm (*SC4*), and plants ≥ 5 cm (*SC5*). Average fecundity was estimated by dividing the number of new seedlings in year t+1 by the number of potentially reproductive adults in year t. A projection matrix (B = (*bij*), where *i, j* = 1, 2, . . , 5) contains the transition probabilities and contributions (i.e. fecundity) of an average individual at different stages of the life cycle over a unit time interval, in our case a year. The matrix operates over a vector (n*t*) containing the distribution of individuals in the size structure of the population at a particular time *t* (Caswell, 2001). The size of the population after one time interval is equal to the product of matrix B by vector n*t* or

$$N_{t+1} = B\ n_t.$$

The largest eigenvalue of matrix B(λ), is equivalent to the population's finite rate of increase, the right (w) and left (v) eigenvectors associated to λ are equivalent to the stable size distribution and the reproductive value distribution, respectively (Caswell, 2001).

We constructed both annual matrices, based on the data for each year, and a mean matrix based on the averages of the class-specific transition values for the three matrices

and analyzed them with RAMAS Ecolab 2.0 (Applied Biomathematics, Setauket, NY, USA). RAMAS was also used to explore population trajectories by running stochastic models, which included both demographic and environmental stochasticity: demographic stochasticity was modeled by sampling the number of survivors from a binomial distribution and the number of offspring from a Poisson distribution, while environmental stochasticity was approximated by sampling the elements of the transition matrix (survival rates and fecundities) at each time step from random distributions created from the mean matrices and the standard deviation matrix. Both matrices were derived from the annual matrices such that the mean and variance were the same as those observed in the past. For each population we ran 1000 replications of the model with durations of 20 y each.

The relative contribution of individual life-cycle transitions to population growth rate was analysed with elasticity analysis (Caswell, 2001). This tool quantifies the proportional change in λ resulting from an infinitesimal proportional change in a matrix transition a_{ij}:

$$e_{ij} = \delta (\log \lambda) / \delta (\log a_{ij}) = a_{ij} / \lambda \times \delta\lambda / \delta a_{ij}$$

All elasticities of a transitions matrix sum up to unity, and elasticities of transitions of similar type [e.g. survival = stasis and retrogression (L), growth (G), and reproduction (F)] may be added. These characteristics allow the comparison of the relative importance of different types of transitions between populations of the same or different species.

Reproduction was also studied with a functional perspective by analyzing the relative proportion of nitrogen and biomass allocated to fruits. Five plants ranging from 3.0–4.7 cm were sampled, dry weight of fruits, leaves, stems, and roots determined after 38 h in a drying oven at 80°C and nitrogen concentrations of each compartment were determined with a CHN-S element analyser (Flash EA, Thermo Electron, Milan, Italy).

Relative growth rates

To be able to estimate in situ growth rates we determined the relationship between plant dry weight (DW, after 48 h in a drying oven at 80°C) and shoot length of 13 non-reproductive individuals (SL = 0.5–8.0 cm). A polynomial regression of shoot length (SL, cm) and DW, which explained the highest amount of variance (DW = -0.0002 SL^3 + 0.020 SL^2 + 0.932 SL; r^2 = 0.92), allowed a non-destructive estimate of *in situ* relative growth rates (RGR) in g g^{-1} d^{-1} following Hunt (1982):

RGR = (ln DW$_{t+1}$ - ln DW$_t$) / Δt,

where DW$_{t+1}$ and DW$_t$ are plant dry weight estimates in subsequent years and Δt the time interval.

Further data analyses

Computation of expected species richness was done with EstimateS (Colwell, 2009). All other statistical analyses were done with R 2.15.0 (R Development Core Team, 2010). The relationship between plant size and maximum relative growth rate (RGR) in the field was explored by calculating the 95th percentiles of RGR for each of 11 classes of plant size (width 1 cm).

Results

Microclimate

Radiation data indicate a strong seasonality with daily mean illuminances in the light crowns of *Comarostaphylis arbutoides* of c. 2.8 klx during the drier months January–March compared to c. 1.4 klx in the wetter rest of the year (Fig. 1). Temperatures, with an annual mean of 9.1°C, also tended to be somewhat higher during these months, with average maxima of 17.5°C compared to 15.5°C during the wet season, whereas average minima tended to be slightly lower (5°C vs. 6°C, Fig. 1). The lowest absolute value was recorded around midnight on 23 October 2011 with 0.2°C.

<<< **Fig. 1** *(width of page)*

Composition of epiphyte assemblages

The ten plots contained between 12 and 55 treelets. Average treelet height per plot ranged from 2.2–4.2 m. A total of 14 woody species were recognized, most of them in the family Ericaceae, with *C. arbutoides* alone accounting for 40%–100% (average 62%) of all stems in individual plots. All other common host trees (~ 10 trees in total, or 3%–15% of all stems per plot) also belonged to this family. These were *Pernettya prostrata* (Cav.) DC.*, Disterigma* cf. *hammelii* Wilbur & Luteyn and *Macleania rupestris* (Kunth) A.C.Sm., the latter species also occurring as facultative epiphyte with conspicuous, massive lignotubers.

In total, we found > 5000 individual epiphyte individuals from 15 species and one species of mistletoe in 250 m^2 of vegetation. About 40% of all trees hosted at least one epiphyte. On average, trees with epiphytes had 28 epiphyte individuals belonging to two

different species (maximum 249 individuals and 7 species). The two orchids *Epidendrum repens* Cogn. and *Pachyphyllum hispidulum* were by far the most abundant taxa (Table 1). Other quite constant elements of the epiphyte flora were ferns, e.g. *Melpomene xiphopteroides* (Liebm.) A.R. Sm. & R.C. Moran and *Hymenophyllum polyanthos* Sw., and epiphytic individuals of *Macleania rupestris* (Ericaceae). Bromeliads, on the other hand, were rare and invariably juveniles. A few species, accounting for < 5% of all epiphytes, were not restricted to trees, most prominently *Elaphoglossum* cf. *furfuraceum*, which was abundantly growing terrestrially in open areas.

<<< Tab. 1

It is unlikely that we sampled the total species pool when doing the survey. Therefore we estimated the expected number of epiphyte species growing in these trees with the species richness estimators available in EstimateS (Colwell 2009). Values ranged from 16 (Michaelis Menten Means), which is hardly more than the number of species actually observed, to more than twice this value, 33.9 ± 15.6 (mean $\pm$ SD; Chao 2).

We found no evidence for preferential use of particular host tree species. First, the six tree species that embraced at least 8 individuals were used in similar proportions as host trees ($\chi^2 = 6.3$, df = 5, P = 0.28). Second, although the average number of individuals and species was highest in *C. arbutoides*, this species contributed also a high proportion of larger trees. Since larger trees had, on average, heavier epiphyte loads and more species (individuals and species number vs. basal area, Pearson Product Moment correlations, P < 0.001, $r^2 > 0.22$), tree size alone explained the seeming preference for this species. This conclusion is based on two ANCOVAs on the relationships of tree identity and tree size (= diameter at c. 10 cm) and epiphyte occurrence. This analysis confirmed the significant effect of tree size (P < 0.001), with no significant differences among tree species (P > 0.05; only *Disterigma* cf. *hammelii* was also common enough as host to be included).

Population biology of Pachyphyllum hispidulum

In the study area, *Pachyphyllum hispidulum* reached up to 8.5 cm in shoot length. Plant densities in the seven plots varied from 30 to 101 individuals m^{-2} bark surface. The smallest plant with fruits measured just 1.4 cm, although the number of fruits was related to plant size, more than tripling from an average of 0.8 ± 0.6 fruits per plant in SC 3 (mean $\pm$ SD, n = 164 plants) to 2.7 ± 2.5 fruits per plant in SC 5 (n = 68 plants).

About 40% of all seedlings did not survive their first year, while mortality among later stages was much lower, between 10–20% y^{-1} (Table 2). The reasons for this mortality are diverse, but available data are not unambiguous enough to allow quantitative analysis. For example, desiccated individuals suggest that these succumbed to drought stress, but desiccation may also be secondary. Less ambiguous are missing plants associated with broken branches and twigs, or with flaking bark. While such accidents affect the epiphyte irrespective of size, other factors of mortality are more specific: we repeatedly observed that lichens (e.g. *Hypotrachyna* sp.) had overgrown small seedlings.

Population growth rates (λ) for individual years ranged from 0.8 (2011–2012) to 0.99 (2012–2013) with an average λ of 0.9. Stochastic simulation models (not shown) based on two of the three individual years or the average matrix predict a strong decline in population size, with a very high probability of extinction in the next 20 years. In contrast, a model using the matrix based on the 2012–2013 interval suggests long-term persistence.

Overall, the analysis of the three annual transition matrices yielded small annual differences in the relative contributions of the three demographic processes 1) growth (G), 2) survival (L), and 3) sexual reproduction (F) to λ (Table 3). Summed elasticity values of L (mostly stasis, particularly in the largest individuals) ranged between 81%–85%, while G averaged 14% and F scores were invariably low (c. 3%).

Relative growth rates (RGR) were highest in the smallest individuals, with RGR of up to 0.006 d^{-1} (Fig. 2). A steady decline in RGR with size was balanced by an increasingly large investment into reproduction in larger individuals. We quantified this investment in five individuals (range = 30–47 mm shoot length): fruit biomass made up 19% ± 6% (mean ± SD, n = 5) of total plant biomass, the relative amount of N invested in fruits as a proportion of total plant N being slightly higher (22% ± 5%).

Discussion

Microclimate

Weber (1958) reports frost in the open from neighbouring Volcán Chirripó at elevations as low as 3100 m. However, in spite of personal experience that frost occurs in

the summit region of Volcán Barú as well (Zotz, pers. obs.), our annual data set did not indicate a single frost event. This probably reflects the fact that tree crowns buffer against radiation frost (Aussenac, 2000), and we measured air temperatures in the central crowns of four *Comarostaphylis arbutoides* trees. Although some frost tolerance has been documented for vascular epiphytes (Halbinger, 1941; Jenkins, 1999), potential protection of epiphytes against frost by host tree crowns may be relevant when discussing altitudinal and latitudinal limits to epiphyte occurrence, where frost is frequently invoked as a prime limiting factor (Kessler, 2002; Zotz, 2005).

Unfortunately, there are no data relevant in the context of plant water relations such as precipitation or relative humidity data. Reports from neighbouring Costa Rica (Villa Mills, Talamanca, 3000 m a.s.l.; Herrera, 2005) document substantial amounts of rainfall (c. 2800 mm). At our study site, there is a pronounced dry season from January to April, but it is unclear how much this affects epiphytic flora, since clouds and mist are frequent in the dry season as well.

Epiphyte assemblages

The number of species and individuals at our study site do not suggest that epiphytes could not exist at higher elevations if it were not for the absence of trees. (Naturally, such a statement does not apply for facultative epiphytes such as *Elaphoglossum* cf. *furfuraceum*). Meaningful quantitative and qualitative comparisons of the studied epiphyte assemblages are restricted to those on trees with a similar, small stature, such as the vascular epiphytes studied on small *Annona glabra* trees in the lowlands of Panama (Zotz et al. 1999). There, up to 15 species were found on a single tree, with up to 407 individuals. Thus, the epiphyte vegetation at the treeline on Volcán Barú is relatively species-poor even when the small stature of the host trees is taken into account. Another distinction between a comparable lowland site is a prevalence of small to tiny epiphyte species (generally < 10–15 cm shoot resp. leaf length) at the treeline, the only exception being the facultative epiphyte *Macleania rupestris* (Ericacae) with its massive tubers. Although we found at least a few fertile individuals in most cases, an unknown proportion of the epiphyte species found at the summit region of Volcán Barú may not form viable populations, but rather depend on input from source populations from lower elevations (Silvertown and Doust, 1993). For example, athough the first author explored the peak area

of Volcán Barú for more than 10 years, there is not a single observation of a large, let alone blooming or fruiting bromeliad. Hence, it is conceivable that all observed bromeliad individuals result from dispersal from lower elevations, and may die before reaching reproductive size. Alternatively, the few juvenile bromeliads may be the first arrivals from lower elevations of previously excluded species due to change in temperature in recent decades (Colwell et al., 2008). Reports as the present one will allow us to detect such a possible change in the future.

Population biology

The detailed analysis of the structure and the dynamics of *Pachyphyllum hispidulum* populations provides stronger insight into the viability of an epiphyte population at the treeline. Although relative growth rates were quite low, they still were in the range of values reported by earlier studies from both lowland and montane habitats (e.g. Hietz et al., 2002, Schmidt and Zotz, 2002). Larger individuals hardly increased in size between censuses (Fig. 2), which is probably directly related to a very high investment of resources into reproduction: the average allocation of 22% of total N into fruits found in *P. hispidulum* is at the high end of known reproductive investments among epiphytic orchids (average of 11 species: 14%: Benzing and Ott, 1981; Zotz, 1999; Zotz, unpubl. data).

Population growth rates <1 are frequently found in lowland forests as well (e.g. Zotz and Schmidt 2006). One possible explanation for these low λs in epiphytes has been offered by Winkler et al. (2009). These authors suggested that a metapopulation approach may be more suitable for capturing the true dynamics at a regional scale. Again, long-term observations are needed. All plots have been photographed and are geo-referenced and can be visited again in the future to document population dynamics directly.

To conclude, we report on several key aspects of epiphyte biology from assemblages at the treeline at one of the highest mountain peaks in Central America. Taken together, the evidence suggests that the primary reason for epiphytes to fade out above the treeline is not directly related to climate, but rather to the lack of mechanical support. However, there is an important caveat. The treeline at Volcán Barú is relatively low compared to other tropical sites (Körner, 2012), and consequently, temperatures are relatively high. Moreover, since tree crowns provide shelter from radiation frosts, freezing damage cannot be excluded as ultimately limiting elevational distributions of epiphytes,

even at our relatively low treeline. Experimental autoecological studies are needed to establish unambiguously the link between treelines and epiphyte occurrence.

Acknowledgements

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Tables

Table 1. Epiphytic vascular plants in the peak region of Volcán Barú, Panama. Abundance refers to the total number of individuals in 10 plots (25 m^2 each). (f) = facultative epiphyte. A parasitic mistletoe included in this list is highlighted by " [*)] ".

Species	Family	Abundance
Guzmania sp1	Bromeliaceae	5
Guzmania sp2	Bromeliaceae	1
Macleania rupestris (Kunth) A.C. Sm. (f)	Ericaceae	46
Cochlidium serrulatum (Sw.) L.E. Bishop	Polypodiaceae	1
Lellingeria subsessilis (Baker) A.R. Sm. & R.C. Moran	Polypodiaceae	50
Melpomene moniliformis (Lag. ex Sw.) A.R. Sm. & R.C. Moran	Polypodiaceae	361
Melpomene xiphopterioides (Liebm.) A.R. Sm. & R.C. Moran	Polypodiaceae	411
Terpsichore alsopteris (C.V. Morton) A.R. Sm.	Polypodiaceae	1
Hymenophyllum polyanthos Sw.	Hymenophyllaceae	184
Elaphoglossum cf. *furfuraceum* (Mett. ex Kuhn) Christ (f)	Dryopteridaceae	17
Elaphoglossum hoffmannii (Mett. ex Kuhn) Christ	Dryopteridaceae	3
Elaphoglossum sp.	Dryopteridaceae	5
Epidendrum cf. *obliquifolium* Ames, F.T. Hubb. & C. Schweinf.	Orchidaceae	8
Epidendrum repens Cogn.	Orchidaceae	2549
Pachyphyllum hispidulum (Rchb. f.) Garay & Dunst.	Orchidaceae	1640
Dendrophthora sp. [*)]	Santalaceae	8

Table 2. Mean transition probability matrix for *Pachyphyllum hispidulum* at the treeline of Volcán Barú, Panama. Size classes are: *SC1*: first year seedlings, *SC2*: other plants < 1 cm, *SC3*: plants ≥ 1 cm and < 2 cm, *SC4:* plant ≥ 2 cm and < 5 cm, *SC5:* plants ≥ 5 cm. Data are mean ± SD of three annual transition matrices. Also given is size-class specific mortality.

Size class in year n+1	Size class in year n				
	1	2	3	4	5
1	0	0	0.03 ± 0.01	0.1 ± 0.01	0.1 ± 0.04
2	0.57 ± 0.2	0.5 ± 0.1	0 ± 0	0	0
3	0.02 ± 0.01	0.3 ± 0.2	0.7 ± 0.02	0.1 ± 0.01	0
4	0	0.01 ± 0.01	0.1 ± 0.03	0.7 ± 0.2	0.1 ± 0.1
5	0	0	0.01 ± 0.01	0.1 ± 0.02	0.7 ± 0.2
Mortality	0.4 ± 0.2	0.3 ± 0.1	0.2 ± 0	0.1 ± 0.1	0.2 ± 0.1

Table 3. Mean elasticity matrix for *Pachyphyllum hispidulum* at the treeline of Volcán Barú, Panama. Data are means ± SD of three annual elasticity matrices. Size classes are given in Table 2.

Size class in year n+1	Size class in year n+1				
	1	2	3	4	5
1	0	0	0.4 ± 0.3	1.2 ± 0.4	1.6 ± 0.6
2	3 ± 0.1	6.4 ± 7.4	0.8 ± 1.2	0	0
3	0.3 ± 0.1	3.7 ± 1	17.9 ± 15.5	0.8 ± 0.7	0
4	0	0.1 ± 0.2	3.5 ± 0.5	30.5 ± 19.6	1.8 ± 2
5	0	0	0.1 ± 0.1	3.4 ± 1.5	24.6 ± 19.9

FIGURE LEGENDS

Fig. 1. Mean microclimatic conditions in four *Comarostaphylis arbutoides* (Ericaceae) trees that hosted substantial populations of *Pachyphyllum hispidulum* at the treeline of Volcán Barú, Panama. Shown are integrated daily illuminance (means ± SD) and mean monthly temperature minima and maxima for 12 mo from March 2011 – Feb 2012.

Fig. 2. Relative growth rates of *Pachyphyllum hispidulum* in the peak region of Volcán Barú during three consecutive years as a function of plant size (shoot length in cm). For each of eleven classes of plant size (width 1 cm) the upper 95th percentiles of RGR were calculated and connected with a solid line.
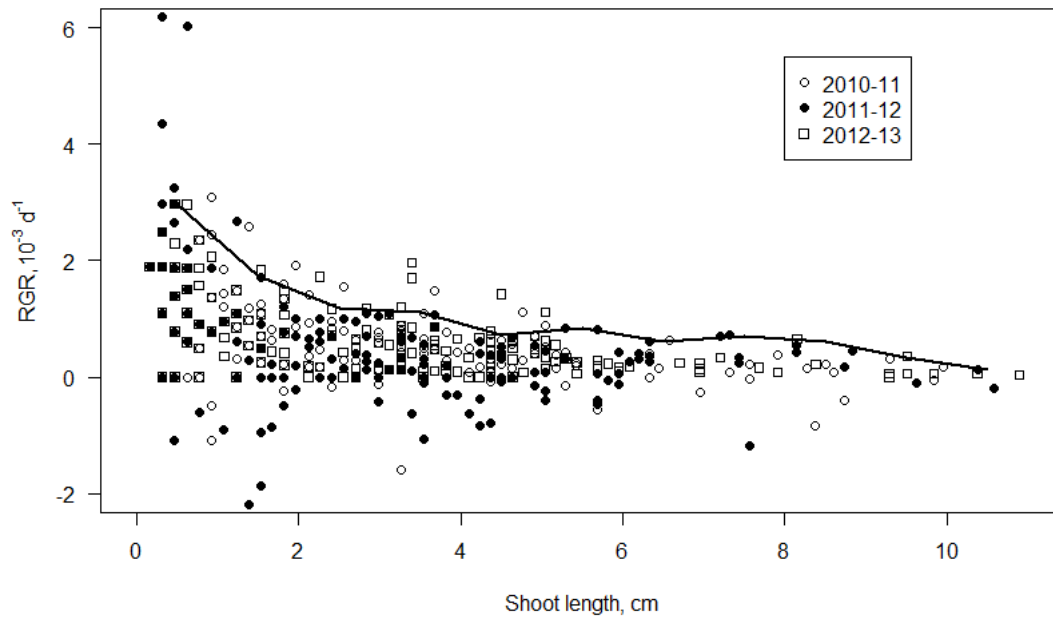
Fig 2 revised .

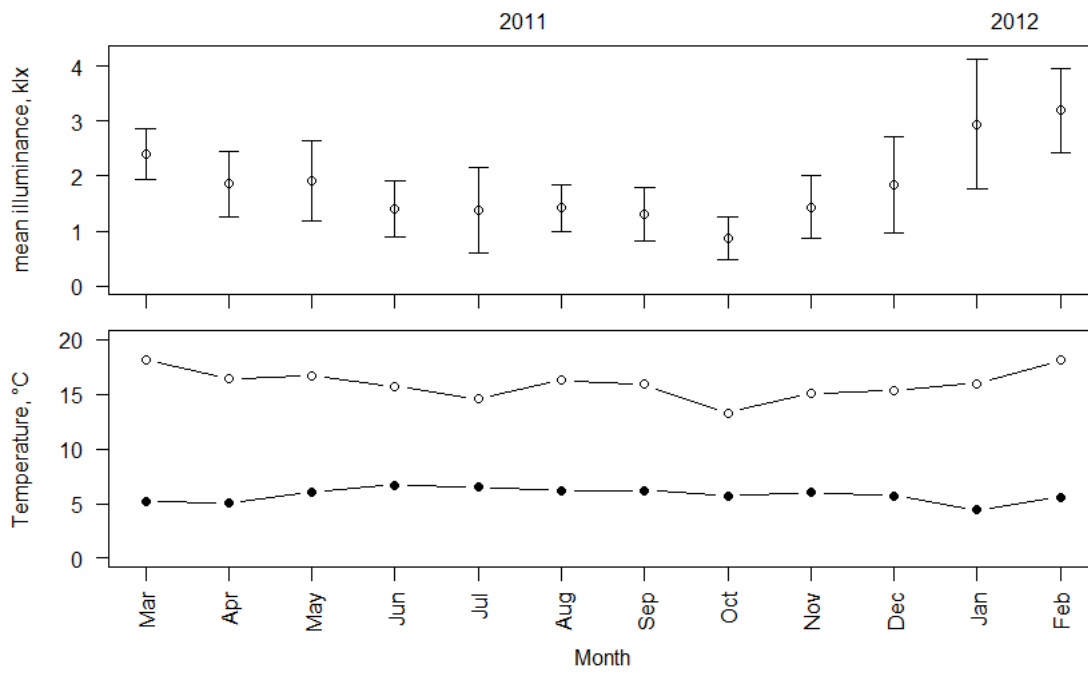Figure 1 revised .