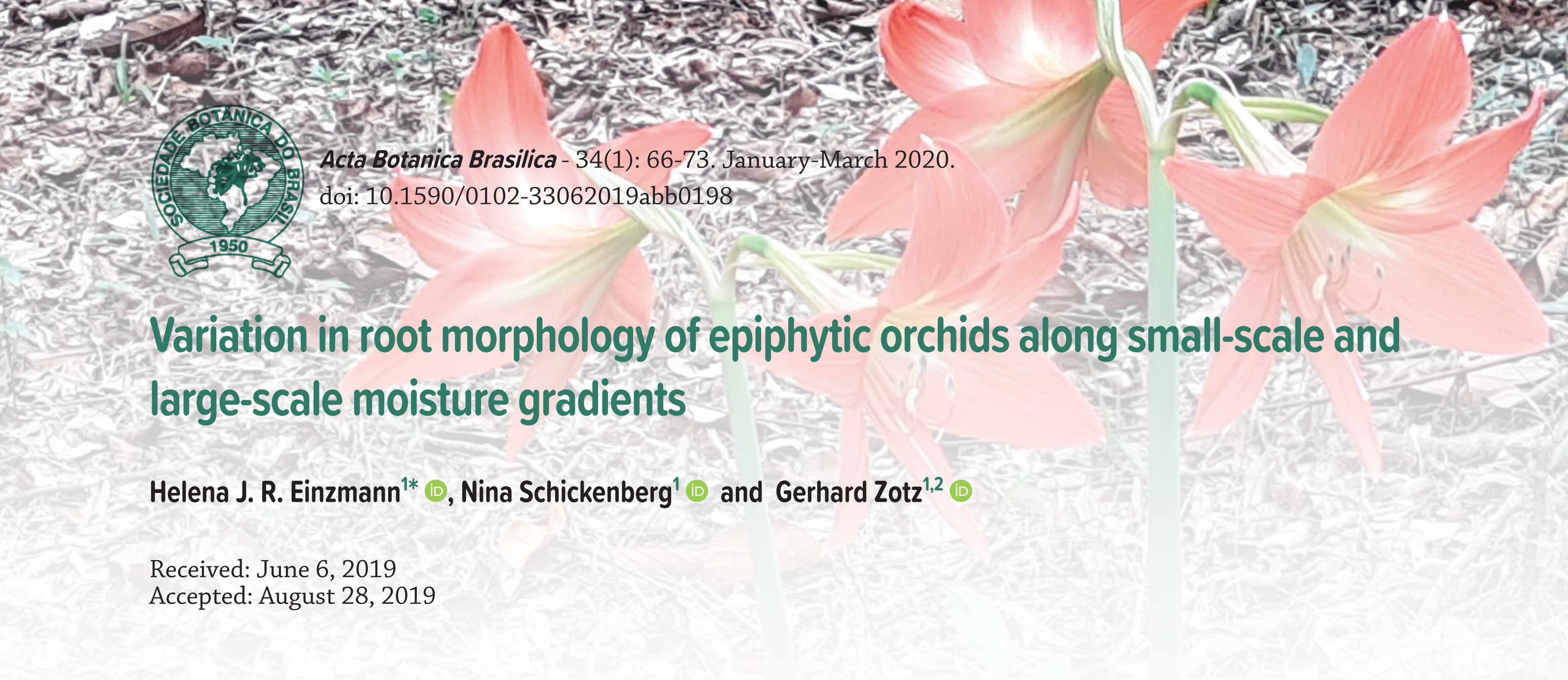

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Variation in root morphology of epiphytic orchids along small-scale and large-scale moisture gradients

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ABSTRACT

Root morphology is expected to respond to environmental conditions. Two earlier studies reported predictable changes in the structure of the velamen radicum (common in monocotyledons) along rainfall gradients, which was expected from its assumed role in plant-water-relations. The present study expanded on this idea by analysing nine root traits that can be linked to root function, including velamen structure, along two moisture gradients of different spatial scales: 1) along the vertical gradient of a lowland forest in central Panama and 2) along a strong regional rainfall gradient in western Panama. All studied traits (*e.g.* velamen width, number of xylem poles, lignification of the exodermis) of the 45 orchid species showed substantial intraspecific and interspecific variation, but none of this (within forest) or very little of this (regional gradient) was related to the gradients. Only the community weighted means of velamen width, stele width and xylem pole number varied significantly with rainfall, with substantial effect sizes only found in the latter two traits. Our results clearly disagree with those of earlier publications, which did not include species abundance and/or rigorous statistics in their analyses. This discrepancy highlights that our understanding of the link between velamen form and function is still rudimentary.

Keywords: epiphytic orchids, exodermis, interspecific variation, intraspecific variation, lignification, plant morphology, velamen radicum, water relations

Introduction

A generalized cross-section of a velamentous root features a typically multi-layered epidermis (the velamen radicum), which is dead at maturity; a living cortex with a morphologically distinct outermost layer (the exodermis); a similarly specialized innermost layer (the endodermis) and the central cylinder with vascular tissues (Pridgeon 1987). Although it has been repeatedly pointed out that a velamen can also be found in many terrestrial taxa (Goebel 1921; Pridgeon 1987; Zotz *et al.* 2017), current descriptions in textbooks still tend to depict this tissue as an idiosyncracy of many aerial roots (see discussion in Zotz *et al.* 2017). Although the functional implications of a velamen in terrestrial plants remain unresolved (Benzing 1996; Zotz *et al.* 2017), there have been many attempts to demonstrate its function among epiphytic plants, with an almost exclusive focus on the roots of epiphytic orchids (Capesius & Barthlott 1975; Haas 1975; Benzing 1996; Chomicki *et al.* 2015; Zotz *et al.* 2017). In his thorough review, Pridgeon (1987) provides a list of demonstrated or assumed functions, which include mechanical protection, rapid absorption of rain and dew, capture of nutrients, reduction of water loss and of heat load from the living cortex. More recently, Chomicki *et al.* (2015) discovered

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compounds in the velamen that are thought to provide UV-B protection.

Of all the aforementioned functions, the role of the velamen in the water relations of aerial roots has been studied most thoroughly. Particular attention has been given to the substantial variation in velamen thickness, which can vary from 1 to more than 20 cell layers (Pridgeon 1987; Arditti 1992). *Ex situ* experimental evidence suggests that water loss from roots is correlated to velamen thickness (Zotz & Winkler 2013), although other anatomical features such as pore size of velamen cell walls (Roth-Nebelsick *et al.* 2017) or the lignification of the exodermis (Sanford & Adanlawo 1973) are also functionally important. Correlative information from several studies support the notion of functional importance, both along the vertical gradient within a forest and along other, landscape-scale gradients of moisture availability. Went (1940) initially claimed that the most developed velamina are found among bark epiphytes, *i.e.* those most exposed to a drying atmosphere, although actual data were not provided. Later, Sanford & Adanlawo (1973) studied velamen characteristics of orchids along a rainfall gradient in West Africa. They reported an increase in velamina thickness of species in drier habitats. Unfortunately, their analysis depended only on species presence/absence data; no abundance data were given and no statistical analysis was attempted. A rather similar approach was used by Díaz & Ackerman (1990) with epiphytic orchids along a rainfall gradient in Puerto Rico, this time with statistical support. Their study, which also showed an inverse relationship of rainfall intensity and velamina thickness, left species abundance and intraspecific variation unconsidered.

Similar to plants in general, species abundances within a community of epiphytes typically vary strongly, with a few very common and many very rare species. For example, two *Scaphyglottis* species accounted for almost 50 % of all individuals of 48 species in a lowland forest plot of Panama, while the 19 rarest species made up < 0.1 % each (Zotz & Schultz 2008). Similarly, a single species (*Maxillaria parviflora*) represented > 50 % of all individuals of 16 epiphytic orchid species in a lowland forest in Ecuador, with 6 rare species occurring with only 1 individual each (Kreft *et al.* 2004). The quantification of community-weighted means of trait attributes and trait spread represents a much more appropriate way to investigate the variation of a particular trait attribute in a community than simple species averages (Laliberté & Legendre 2010; Garnier & Navas 2012; Kleyer *et al.* 2012). That previous studies did not include information on relative abundances may be related to the fact that obtaining this type of data can be very labour-intensive.

Intraspecific variability was also not considered in previous studies. This is interesting because root morphology may be found to differ among roots that are attached to the substrate and those that are truly aerial (Sanford & Adanlawo 1973). Additionally, authors frequently allured to the relation of intraspecific variation and environmental differences (*e.g.* Pridgeon 1987; Porembski & Barthlott 1988; Arditti 1992), but actual quantification is rare. One exception is a study by Rüter & Stern (1994). After identifying inconsistencies among the reported values of root traits in the literature for individual species, these authors conducted a detailed study on the intraindividual and intraspecific variation in the root anatomy of six nursery-grown epiphytic orchid species. The results were not conclusive as only half of the species showed variation in protoxylem pole numbers and number of velamen cell layers and standard deviations were mostly low even when differences were found. They concluded that sampling the middle part between tip and base of the root would give values closest to the average values for the two root characteristics.

In the present study, we assessed interspecific variation in root anatomy of epiphytic orchids along two environmental gradients, a) along the vertical gradient in the canopy of a lowland rain forest and b) along a regional rainfall gradient in pasture trees in lowland Panama. In both cases, we could take advantage of detailed earlier studies. In the first case, Zotz & Schultz (2008) had monitored 13,000 vascular epiphyte individuals in 0.4 ha, providing detailed information on their vertical distributions within the forest, in the second case, Einzmann & Zotz (2017) had recorded all epiphytes in 622 pasture trees. Finally, in order to assess how much intraspecific variation in root morphology may be hidden when species averages are used, we quantified differences in three species with a wide distributional range along the regional rainfall gradient.

Materials and methods

Study regions

Possible differences in root anatomy along a vertical gradient within a forest were studied at the San Lorenzo Canopy Crane. The average annual rainfall is estimated to be around 3500 mm with a mean annual temperature of 26 °C. Canopy height of this primary lowland rain forest is quite variable and reaches a maximum of c. 40 m (Wright *et al.* 2003). The use of a small gondola allowed access to all strata of the forest. Height of attachment was recorded for c. 13,000 epiphytes. There are more than 40 species of orchids in the plot (Zotz & Schultz 2008).

The second study region is located along the Pacific coast of western Panama on the peninsula of Azuero and the provinces of Chiriquí and Veraguas. Poltz & Zotz (2011) established >80 pasture plots for an epiphyte census that was repeated by Einzmann & Zotz (2017). The plots were located along a rainfall gradient of 1100-4200 mm per year (Poltz & Zotz 2011). After the deforestation to win agricultural land (Heckadon-Moreno 2009), the area's current vegetation resembles tropical dry and wet savannah. Some secondary forest stands do still exist in the region, but interspersed forest patches are rare (Poltz & Zotz 2011). The mean annual temperatures range from 27 °C along the coast to 25 °C further inland (Anonymous 2016). The second census yielded c. 60,000 vascular epiphytes of 86 species and eleven families. Orchids were the most species-rich family with 44 species (Einzmann & Zotz 2017).

Plant material and observations

Root morphology of epiphytic orchids typically differs between roots that are attached to bark substrate and free aerial roots (Sanford & Adanlawo 1973). Moreover, the lower and upper portions of attached roots also differ. In this work, all results refer to the upper portion of attached roots. The vast majority of the orchid roots in the lowlands of Panama grow attached to substrate (personal observations), and thus most samples for this study were attached roots. At San Lorenzo Canopy Crane, we collected 47 samples of 18 species. In the pasture trees, we collected roots of 35 species, missing nine (rare) species of those found in 2012/13 by Einzmann & Zotz (2017). Species names follow The Plant List (http://www.theplantlist.org/). Of most species, roots were collected from two-three individuals (see Tab. S1 in supplementary material). For three species with wide distributional ranges a larger number of replicates (*Brassavola nodosa* (L.) Lindl.: 43 samples, *Encyclia cordigera* (Kunth) Dressler: 16 samples, *Epidendrum difforme* Jacq.: 22 samples) was sampled, which allowed an assessment of intraspecific variation along the rainfall gradient.

After collection, samples were stored in 70 % ethanol. Freehand cuts were prepared at 1-3 cm from the tip with a disposable razor blade. In case of species with short roots (<4 cm length; *e.g. Phloeophila peperomioides* (Ames) Garay, *Trizeuxis falcata* Lindl.) the cuts were also made within the first cm from the tip, exempting the first third. The cuts were bleached for 20-45 minutes in a solution of c. 2 % NaClO to clear cell contents, rinsed three times in water and then stained. A double stain of astra blue (1 g in 100 ml deionized water) and safranin (0.1 g in 100 ml deionized water) at the ratio of 9:1 was used to stain cellulose (blue) and lignified/suberized cell walls (red). The double stain is a quick and simple staining method to highlight chemically differentiated cell walls (cp. Bukatsch 1972; Moreira & Isaias 2008). Cross sections were stained for 1-3 minutes, washed and soaked for 2-3 hours in 70 % ethanol to remove excess dye. Root sections were studied with a light microscope (Polyvar, Reichert-Jung, Austria). Pictures were taken with a digital camera (Olympus UC30, Olympus, Japan) and pictures analysed with the software CellSens Dimension 1.5. One cross section per individual was used to determine root diameter, the radius of the stele, the width and number of cell layers of cortex and velamen (Fig. 1), the number of xylem poles and the thickness of the exodermal lignification. Width and diameter were taken at three points of the cross section, at approximately 120° intervals. Lignification was also assessed at three points of the cross section. The ratio of velamen width to root radius was calculated as an additional variable. Measurements were averaged per species for the analysis of interspecific variation.

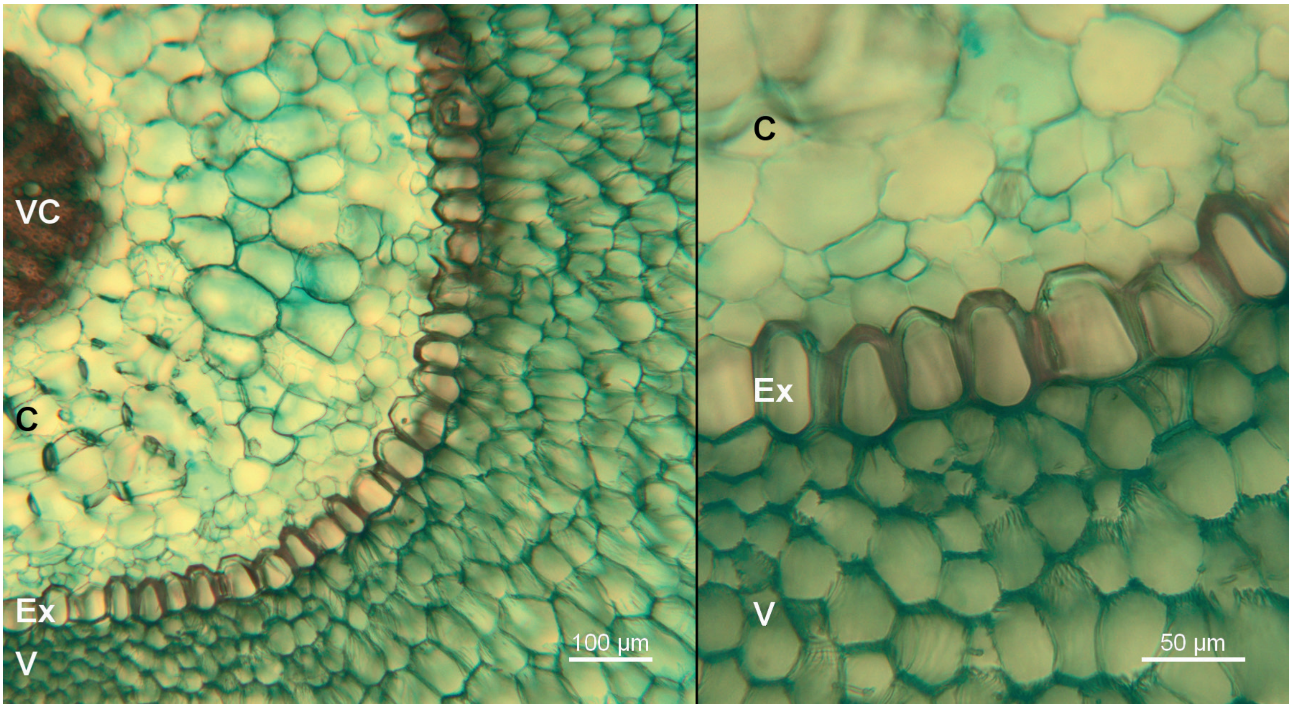

Figure 1. Transverse sections of a root of *Encyclia stellata*, showing different tissue types. Ex = exodermis; C = cortical parenchyma; V = velamen; VC = vascular cylinder.

Data analysis

Data analyses were conducted with R 3.5.1 (R Development Core Team 2019). For the San Lorenzo Canopy Crane we determined minimum, maximum and average height for each species based on data from Zotz & Schultz (2008). Regression analyses were conducted to determine the relationship of height (independent variable) and each of the nine studied anatomical traits (dependent variables; root diameter, stele radius, width and number of cell layers of cortex and velamen, number of xylem poles, thickness of the exodermal lignification and ratio of velamen width to root radius).

Poltz & Zotz (2011) interpolated annual rainfall for each pasture plot using a precipitation map of Panama. We divided the rainfall gradient in six classes ($<1500 < 2000 < 2500 < 3000 < 3500$ and ≥ 3500 mm y^{-1}) and pooled the data of all plots belonging to one class as one community. With increasing rainfall the number of occurring species increased in the first three rainfall classes, which led to a higher number of data for each root trait: 4 < 7-8 < 14-15 species were sampled in the respective class; in the three remaining rainfall classes (2500 mm y^{-1} and higher) data represented 25-26 species, depending on the root trait. For each species a mean value was calculated for each root trait, mostly of 1-3 individuals and for five species of up to ten individuals (Tab. S1 in supplementary material). Community-weighted means (CWM) were calculated for each trait using the package FD (Laliberté & Legendre 2010; Laliberté *et al.* 2014). Abundance data for CWM calculation were based on the data set collected by Einzmann & Zotz (2017) in 2012/13. As samples were collected for only a few individuals per species in the study region, the trait values used to calculate CWMs represent a "species mean" (Kleyer *et al.* 2012), avoiding the very labour-intensive sampling of trait values in each plot (Schellenberger-Costa *et al.* 2018). We regressed CWMs against the mean precipitation of the plots within each class. Due to the low power of our analysis, we used $p > 0.1$ as the cut-off for significance.

Trait spread, calculated as the difference between the maximum and minimum value of a trait, was analysed in a similar manner. In many cases, the relationship of the independent variable (rainfall gradient) and the root trait was clearly not linear. We therefore fitted three possible models to the data, a linear-, a saturation-, and a proportional growth using the nlsLM-function of the minpack.lm package (Elzhov *et al.* 2016). The saturation model used the common Michaelis-Menten equation:

$$y = \frac{a \times x}{b + x}$$

The proportional growth model used the following equation:

$$y = Y - \frac{V}{K}\left(1 - e^{-Kx}\right)$$

We used the Akaike's information criterion to decide which of the three models described the data best. After this, models with an $R^2 < 0.5$ were rejected.

The possible influence of precipitation on root traits within a species (intraspecific variation) was also assessed with regression analyses for *Brassavola nodosa*, *Encyclia cordigera* and *Epidendrum difforme*. For each collection site, the local annual precipitation was estimated as described above and root traits regressed against these values.

Results

Vertical gradient at the San Lorenzo Canopy Crane

Root radii varied about ninefold in the 18 species from 0.2-1.8 mm (Fig. 2, Tab. S2 in supplementary material). A similar degree of interspecific variation was found in other traits, *e.g.* the number of cell layers in the velamen (eightfold) or the diameter of the stele (sevenfold). Cortex thickness varied much more among species (fifteen-fold), while the number of xylem poles varied rather little (threefold). The ratio of velamen to total radius varied sevenfold. However, we did not find that this substantial variation was related to the height within the forest in any of these cases (Fig. 2).

Regional precipitation gradient in lowland Panama

The root radius varied more than eleven-fold in the 35 species, from 0.3-3.3 mm (Tab. S1 in supplementary material). Even higher interspecific variation was found in velamen width (37-fold), which varied from just 0.03 mm in *Trichosalpinx ciliaris* to 1.1 mm (in *Catasetum maculatum*). The ratio of velamen to total radius varied much less, about 10-fold. Only in three of the nine root traits (velamen width, stele radius and number of xylem poles) did community-weighted means show significant correlations with precipitation (Fig. 3). Velamen width tended to decrease with higher precipitation, although the effect size of c. 15 % reduction from the dry to wet end of the gradient was not very large. Two traits potentially related to long-distance water transport within the plant, *i.e.* stele size and the number of xylem poles, each increased by more than 50 % towards the wetter end of the rainfall gradient. In other traits, such as the degree of lignification of the exodermis (Fig. 3), there was the expected trend, but changes were not significant. Trait spread was clearly related to species diversity, which increased from 4 to 26 species from the drier to the wetter end of the gradient (Fig. S1 in supplementary material). Trait spread was typically low at the dry end of the gradient and increased substantially with increasing wetness (Fig. 4); however, the specific response was diverse. For example, the spread of cortex width increased linearly, while the trait spread of other traits (*e.g.* lignification of the exodermis) showed a steep initial increase with relative constant values at intermediate

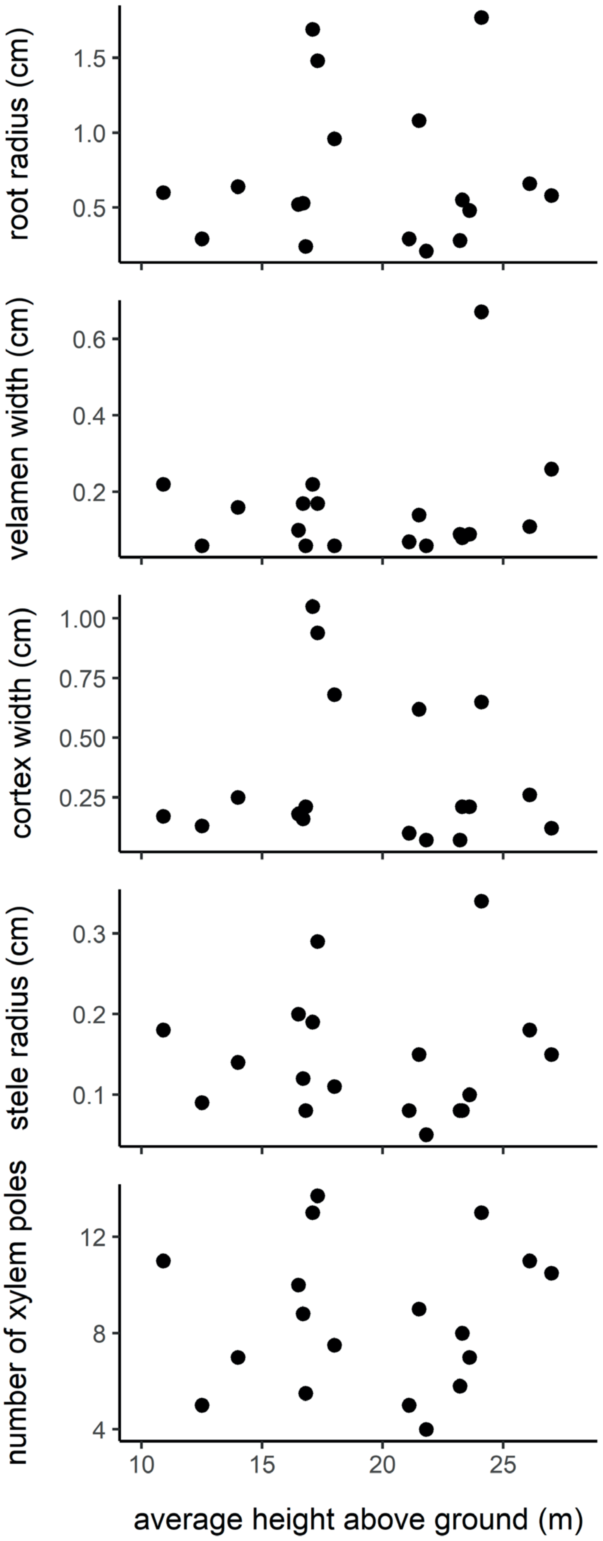

Figure 2. Relationships of root traits and average height of a species within the forest canopy of the San Lorenzo lowland forest. Using the minimum or maximum height as independent variable yielded similar results (not shown). A full list of the species values is given in Table S2 in supplementary material.

and wet parts of the gradient. To capture this diversity, we fitted three different models: linear, saturation and proportional growth.

In order to compare our results with earlier studies, we also analysed the relationships of simple species averages per community of the nine traits shown in Fig. 3 with annual rainfall. We found a single significant relationship: the degree of lignification of the exodermis increased by almost 30 % from the wet to the dry end of the gradient (data not shown).

Intraspecific variation

Brassavola nodosa occurs from the driest end of the regional gradient to the wettest end, making it an ideal candidate for the study of intraspecific variation. Somewhat smaller, but still considerable distributional ranges are observed in *Encyclia cordigera* and *Epidendrum difforme*. Intraspecific variation in root diameter, velamen thickness (absolute and relative) or exodermis lignification was substantial and none of the tested root traits changed significantly with precipitation (data not shown). Trends were also inconsistent: while root diameter increased in *Brassavola nodosa* and *Epidendrum difforme*, it decreased in *Encyclia cordigera*. Similarly, relative velamen thickness tended to decrease in *Brassavola nodosa* and *Epidendrum difforme*, but showed a tendency to increase in *Encyclia cordigera*. Overall, we found substantial intraspecific variation in morphological root traits but this variation was unrelated to precipitation.

Discussion

From our current understanding of the function of the velamen radicum in epiphytic orchids (Pridgeon 1987; Arditti 1992; Zotz & Winkler 2013), we would expect to find predictable changes in many root traits along gradients of water availability. Indeed, there are two published studies (Sanford & Adanlawo 1973; Díaz & Ackerman 1990) that addressed and supported this notion with data.

Our results, however, lend only moderate support to a close relationship of root structure and water availability in velamentous roots. This mostly negative result is not for lack of variation in traits like velamen thickness, lignification level of the exodermis or relative proportions of different tissues, which to the contrary is substantial. This was seen not only within a particular site, but also within conspecifics and among species along regional precipitation gradients. For one, differences in root structure among epiphyte species with substantial differences in vertical distribution within a forest canopy were completely unrelated to height above ground, although this would be expected following Went´s (1940) claims.

At least a few of the changes in the community-weighted means (CWM) of root traits along the regional gradient did fulfil expectations, but even the few significant relationships that we found did not unanimously suggest very strong effects. For example, the CWM of velamen width differed by only c. 15 % from 0.23 mm at the dry end to 0.2 mm at the wet extreme (Fig. 3). A corresponding, substantial trait spread in velamen width of up to 1.1 mm (Fig. 4) does not suggest either that the selection for particular velamen width is very strong, but rather that there may be a strong phylogenetic signal in roots traits (Porembski & Barthlott 1988), so that the differences between communities are more related to the particularities of the participating taxa and to a lesser degree due to a strong environmental filter. There were two traits, stele size and the number of xylem poles, which showed a strong effect (> 50 % over the entire gradient). Both have arguably a clear functional consequence: this increase in conducting tissue should allow larger quantities of water to be transported from the roots to the shoot (Arx *et al.* 2012). It would be highly instructive to study leaf gas exchange and other aspects of water relations of these species and relate the results to these root traits.

Although not statistically significant in the case of CWMs (Fig. 3), the observed differences in thickness of lignification of the exodermis, along with a significant relationship using species averages, are suggestive of possible biological relevance, which justifies further experimental scrutiny. Sanford & Adanlawo (1973) also studied the lignification at the contact zone of velamen and exodermis in orchid roots, but only used a semi-quantitative scoring scheme, which makes direct comparison impossible. The reduction of water loss is one of the major functions that Pridgeon (1987) proposed for the velamen; Sanford & Adanlawo (1973) even suggested that the lignification of the exodermis should be more important in that regard than velamen thickness.

We also assessed intraspecific variation, which has rarely been studied in orchid roots (but see Rüter & Stern 1994). They tested the variation of two root traits, *i.e.* the number of velamen cell layers and protoxylem pole number, along the longitudinal axis of different roots of individual plants and among plants of the same species of six greenhouse grown epiphytic orchids. Significant variation was only detected in half of the species. We also found substantial variation in all studied traits, but differences among conspecific individuals were unrelated to the regional gradient in precipitation and non-significant trends were inconsistent.

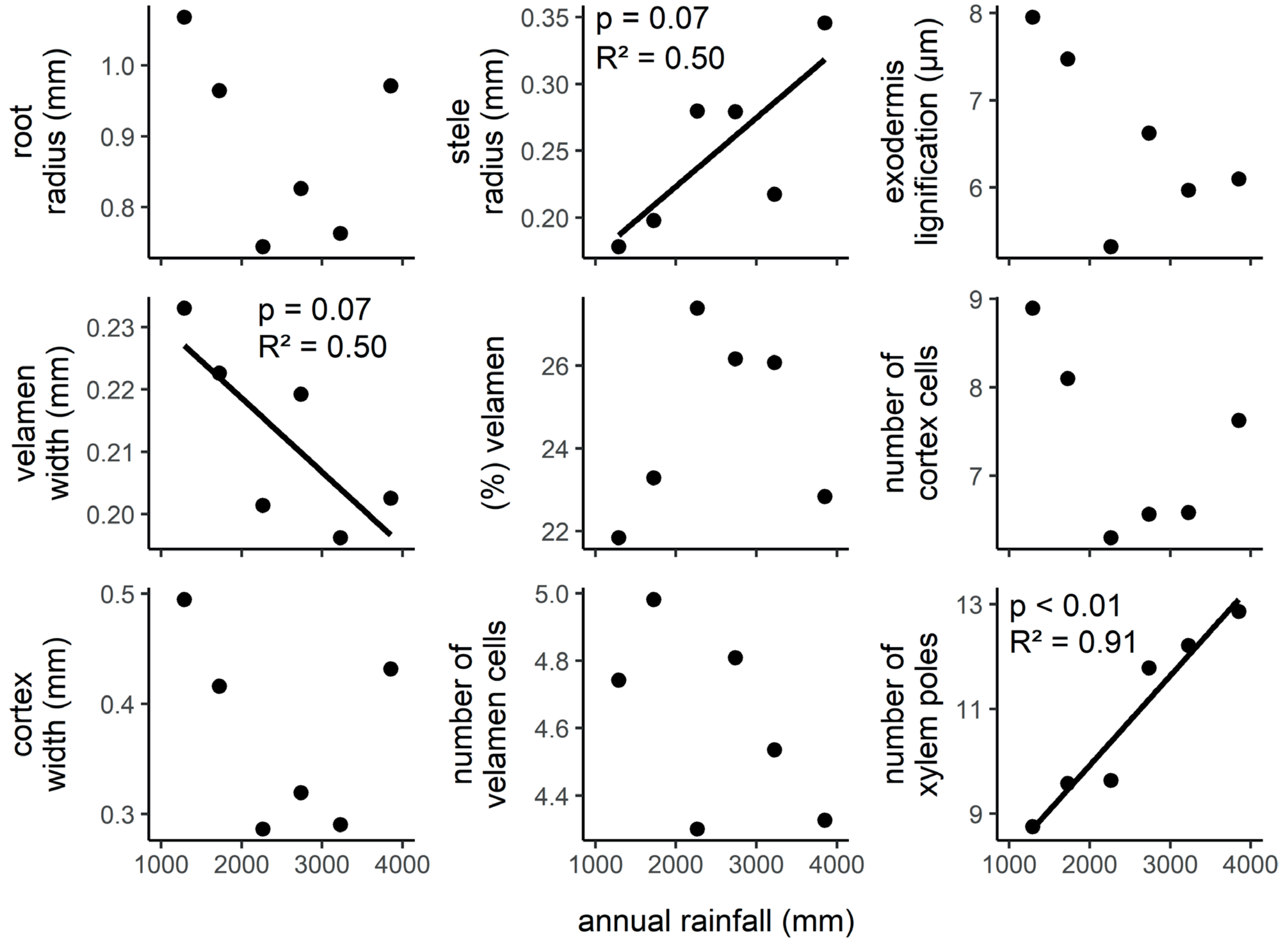

Figure 3. Changes in community weighted means (CWMs) of root traits along a rainfall gradient in lowland Panama. Solid lines indicate significant correlations. A full list of species values is given in Table S1 in supplementary material.

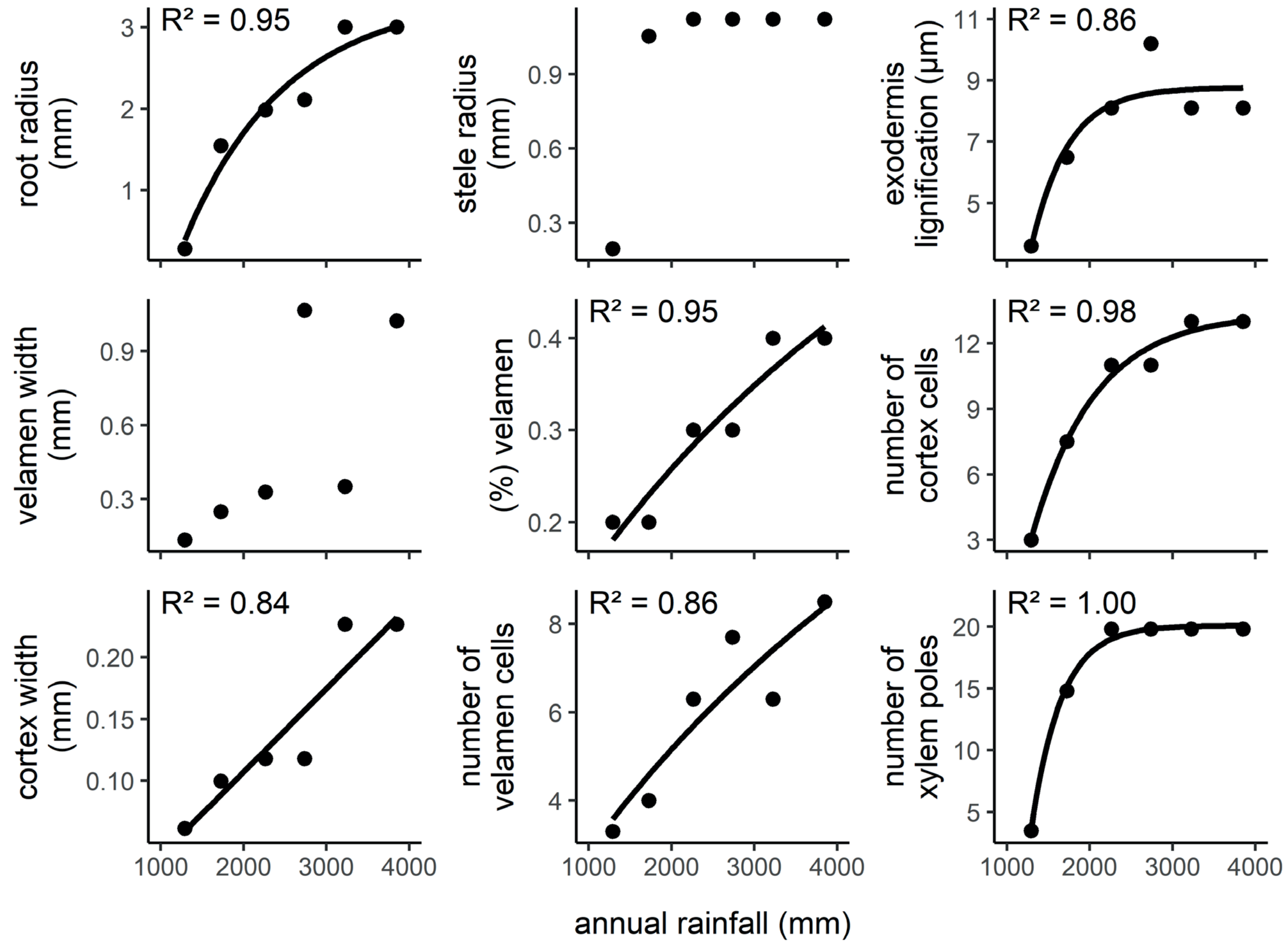

Figure 4. Trait spread in epiphyte communities along a rainfall gradient in lowland Panama. Cortex width data is described with a linear model, velamen-root ratio and number of velamen cells are described with saturation models, and all others with exponential models.

Taken together, the results of our study do not agree with the current understanding that the root structure of epiphytic orchids is strongly correlated with water availability (Pridgeon 1987). With the exception of two traits related to water conduction with a strong effect size along a regional precipitation gradient, differences were small and/or non-significant. Conceivably, this discrepancy could stem from the fact that the only other studies providing actual data on root traits and gradients in water availability (Sanford & Adanlawo 1973; Díaz & Ackerman 1990) used different types of analyses, although the results of our additional analysis with simple species averages contradicts this explanation. Other possible reasons are differing rainfall gradients, with a much shorter gradient in the first study (1100-2200 mm) and a mixture of a rainfall gradient *sensu strictu* and an elevational gradient in the second (900-4100 mm). Apart from these, we cannot offer a satisfying reason for the conspicuous discrepancies in the overall findings of the three studies. It is clear, however, that the function of the velamen radicum is still far from understood. Lack of functional understanding is also given at a much more fundamental level: we have recently highlighted that the velamen is not at all restricted to epiphytes and is much more common among terrestrial taxa than previously thought (Zotz *et al*. 2017). There, the question of the function of a velamen radicum remains completely unexplored.

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