

# 15 Population Structures of Two Understory Plant Species Along an Altitudinal Gradient in Costa Rican Montane Oak Forests

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## 15.1 Introduction

The altitudinal distribution of vascular plant species and communities has been intensively studied in neotropical montane forests (e.g., Cleef et al. 1984; Kappelle and Zamora 1995; Kappelle et al. 1995a; Lieberman et al. 1996; Chap. 4). However, still little is known about the population ecology of individual species and their responses to environmental factors along elevational gradients. Population structure studies of single species in relation to environmental factors have proven to be powerful in explaining ecological behavior in temperate regions (Wassen et al. 1990; Oostermeijer et al. 1994; Hegland et al. 2001), but such data are relatively scarce for tropical regions.

So far, the main emphasis in the tropics has been on population dynamics of lowland rainforest canopy trees (e.g., Arriaga et al. 1988; Martínez-Ramos et al. 1988; Álvarez-Buylla and Martínez-Ramos 1992; Olmsted and Alvarez-Buylla 1995), rather than on non-canopy species (Oyama 1990). Tropical studies directly relating population structure to environmental variables have not received much attention from scientists (Witkowski and Liston 1997; Hicks and Mauchamp 2000). To date, population dynamics of highland forest plant species are even rarer (but see Wesselingh et al. 1999, and Chaps. 14 and 18). In order to gain further insight into environmental factors (e.g., temperature, light availability) that may determine the population structure of vascular plant species on tropical mountains, we studied the relative proportions of different life stages of two tropical montane understory species in response to environmental changes occurring along an altitudinal gradient in Costa Rican montane oak forests.

## 15.2 Study Area

This study was conducted in undisturbed mature, old-growth *Quercus*-dominated tropical montane cloud forest along the Pacific slopes (2,000–3,000 m altitude) of the Costa Rican Cordillera de Talamanca. Two mountains were investigated: (1) the Cerro de la Muerte (CM; peak at 3,491 m; coordinates 09°34'N and 83°46'W), which borders the southern limit of the 58,495-ha Tapantí-Macizo de la Muerte National Park and the northeastern sector of the 62,000-ha Los Santos Forest Reserve; and (2) the Cerro Chirripó (CC; peak at 3,819 m; coordinates 09°30'N and 83°30'W), the highest mountain in southern Central America, located in the center of the 50,920-ha Chirripó National Park.

Both mountains are within the same, large forest tract, as the Los Santos Forest Reserve and Chirripó National Park are connected by the undisturbed Tapantí-Macizo de la Muerte National Park. The importance of this large forest tract for biodiversity conservation – including that of the La Amistad International Park to the east – is globally recognized, as it has been designated as a Biosphere Reserve, a World Heritage Site, an Endemic Bird Area, and a Center of Plant Diversity (Kappelle 1996; Chaps. 10 and 30).

Mean annual temperatures range from 15 °C at 2,000 m and 9.5 °C at 3,000 m, and mean annual vertical precipitation oscillates around 2,500 and 3,000 mm, respectively (Kappelle et al. 1996). The area's montane oak forests receive a considerable amount of additional horizontal precipitation in the form of fog or mist, which significantly increase the total amount of intercepted water (Zadroga 1981; Chap. 21). Vascular and non-vascular epiphytes are abundant. Forest soils are generally wet, acid, humus-rich and clayey, and are developed in volcanic ashes (andosols) originating from volcanoes to the north (Kappelle et al. 1995a; Chap. 4).

## 15.3 Field Sampling

Two altitudinal transects were established: one along the SW slope of Cerro de la Muerte (CM), parallel to the San Gerardo de Dota–Cerro de la Muerte (Cerro Buenavista) hiking trail, and one along the SW slope of Cerro Chirripó (CC), parallel to the San Gerardo de Rivas–Cerro Chirripó hiking trail (also known as the Termómetro–Fila Cementerio de la Máquina–Base Crestones trail). The CM transect covered an altitudinal belt at 2,200–2,900 m, the CC transect at 2,000–2,900 m. Forest disturbance made mature forest sampling impossible at 2,000–2,200 m elevation on the CM trail.

Along transects, plots were established at 50-m altitudinal intervals. Two replicate plots were established at each altitudinal interval along each tran-

sect, totaling 30 plots along the CM transect and 40 along the CC transect. Plot size was 0.03 ha (15×20 m). Individual plots consisted of three quadrants, each covering 0.01 ha (5×20 m), and separated by buffer strips of similar shape and size for quadrant sampling without destructive trampling. Each quadrant was subdivided into four 5×5 m subplots.

In each plot, we measured altitude (using a Thomme 5000 altimeter), slope direction, canopy and understory densities, stem density (number of tree stems with diameter at breast height (DBH) ≥ 25 cm), and percentage ground cover of living bryophytes, large litter (decaying trunks and branches), and uncovered forest floor (bare soil). Following Wolf's (1993) method, canopy coverage was estimated as the average percentage covered by black pixels (i.e., those that did not represent the sky) found on six scanned, computerized (Adobe Photoshop 5.5) vertical canopy photographs, which were taken in each plot using a 28-mm wide-angle lens on a 35-mm SLR camera at six fixed positions. Temperature (minimum and maximum values) was measured at 100-m intervals over 20-day periods.

## 15.4 Selected Study Species

Two indicator understory plant species were selected for this study: the dwarf palm *Geonoma orbignyana* Naud. (previously identified as *Geonoma hoffmanniana* H. Wendl. ex Spruce, in Kappelle et al. 1995a; Kappelle 1996; Chap. 4), and the aroid herb *Anthurium concinatum* Schott. These species can be used for feasible population structure analysis as they meet the following criteria: (1) high abundance along the entire altitudinal range, (2) easy identification of individuals during all life stages under harsh field conditions, (3) absence of clone reproduction, enabling identification of single individuals, and (4) easy age estimation based on growth of single-stemmed individuals, expressed in terms of stem length. For both species, representative specimens were collected, identified, and stored at the herbarium of INBio (INB) in Costa Rica.

*Geonoma orbignyana* (Arecaceae, Palmae), locally known as *súrtuba* or *súrtuba ratón*, is one of the most common and wide-spread palm species in Central American and Andean montane oak forests, and is the only palm that may reach elevations over 3,000 m (Henderson et al. 1995). This single-stemmed species may reach a maximum height of 4 m (Fig. 15.1). Adult individuals maintain up to 20 living leaves – though they generally have some 10–15 leaves – and can bear up to five inflorescences or infructescences at a time. Inflorescences are pollinated by a wide range of insects (Olesen and Balslev 1990; Listabarth 1993). Berries are dispersed mainly by birds (Zona and Henderson 1989).

*Anthurium concinatum* (Araceae) is found in montane rainforests ranging from Costa Rica to Colombia, and probably also in Ecuador (Croat and

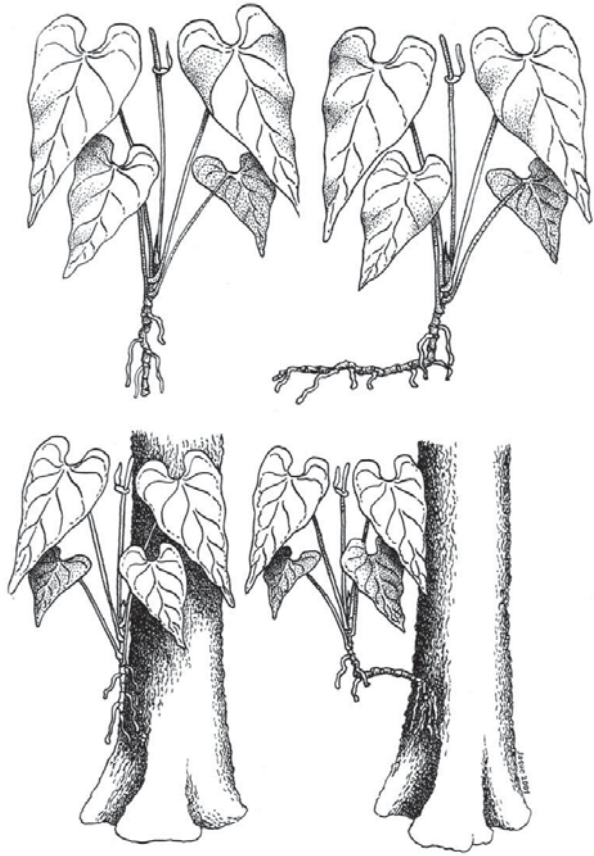


Fig. 15.1. Growth form of *Geonoma orbignyana*. Drawing by Francisco „Pancho“ Quesada (INBio, Costa Rica)

Baker 1979). It grows at elevations of 2,000–3,000 m and is, within its genus, the species that occurs at the highest altitudes in Central America (Dortort 1980). *A. concinnatum* is a typical large-leaved, hemi-epiphytic understory species, rarely growing higher than 5 m above the forest floor. It produces a spadix 20–40 cm long, with up to 100 green oval fruits, each containing 1–3 seeds. Seeds are presumably dispersed by birds. It has multiple growth forms, ranging from terrestrial to epiphytic (Benzing 1990). Young plants commonly grow straight upward, but when they lack a suitable substrate to attach to, they eventually tend to fall down, after which they start to grow horizontally until they find a structure to climb on (Benzing 1990; Bown 2000). We identified four different types of growth forms (Fig. 15.2): (1) plants growing entirely upright and terrestrial (*standing terrestrial*); (2) plants growing (partly) horizontally and terrestrial (*lying terrestrial*); (3) plants growing entirely upright and epiphytic (*standing epiphytic*); (4) plants growing (partly) horizontally and epiphytic (*lying epiphytic*).

We estimated abundance values for both species, expressed in terms of their leaf ground cover proportions, applying conventional plant sociological

**Fig. 15.2.** Growth forms of *Anthurium concinatum*: standing terrestrial (upper left), lying terrestrial (upper right), standing epiphytic (lower left), and lying epiphytic (lower right) individuals. Drawing by Francisco „Pancho“ Quesada (INBio, Costa Rica)



procedures (Kappelle 1996). For each individual of both species we assessed: total plant height, height up to the first leaf, and phenological state (fertile vs. sterile). For *G. orbignyana*, we also counted the total number of green leaves, and for *A. concinatum* we additionally determined the type of growth form. Individuals of *G. orbignyana* less than 50 cm high and bearing less than five leaves were excluded from our analysis, as they could not be distinguished from other dwarf palm species present in this habitat.

In accordance with size and phenological state, each individual was assigned to one of the following criteria-based life stages, ranging from young to old:

- *G. orbignyana*: (1) sterile plant, total plant height < 50 cm, total stem height < 10 cm, and < 6 leaves; (2) sterile plant, total plant height 50–100 cm, total stem height 10–40 cm, or 6–12 leaves; (3) sterile plant, total plant height 100–150 cm, total stem height 40–100 cm; (4) sterile plant, total plant height  $\geq$  150 cm, or total stem height  $\geq$  100 cm, or  $\geq$  12 leaves; and (5) fertile plant;

- *A. concinatum*: (1) sterile plant, total plant height <30 cm, and length to first leaf <30 cm; (2) sterile plant, total plant height 30–80 cm, or length to first leaf 30–50 cm; (3) sterile plant, total plant height  $\geq$ 80 cm, or length to first leaf  $\geq$ 50 cm; and (4) fertile plant.

## 15.5 Data Analysis

We calculated Spearman's rank correlation coefficients to assess statistical relations existing among the environmental variables. We used a sequential Bonferroni procedure to correct for multiple tests (Holm 1979). We performed stepwise, linear and non-linear (unimodal) multiple regressions using SPSS v. 9.0 software for MacIntosh (SPSS Inc. 1990), to test which environmental variables best explained the variation in population structure of both species. The environmental variables investigated in each plot were treated as independent variables, whereas the relative proportions of the life stages in the plots were treated as dependent variables. As the fitting of linear regression models proved superior in all cases, only these are presented here (Tables 1 and 2). The structure of *A. concinatum* populations was also assessed independently for each of the four individual growth forms. Plots containing fewer than 40 individuals were excluded from the analysis, in order to eliminate sampling errors. Within-plot heterogeneity did not allow for statistical analysis of variations in absolute density for separate life stages.

## 15.6 Environmental Correlations

As we hypothesized and tested ( $P < 0.001$  after a Bonferroni correction for multiple tests), along both transects there was a strong positive correlation between minimum and maximum temperatures (CC: 0.886; CM: 0.679), and a clear negative correlation between both temperature measures and altitude (CC = -0.997, and CM = -0.704 for minimum temperature, and CC = -0.889 and CM = -0.991 for maximum temperature). Similarly, the percentage of uncovered forest floor and the percentage of large litter cover were highly inversely correlated in both transects (CC: -0.752; CM: -0.699). Along the CM transect, bryophyte ground cover was significantly positively correlated with altitude and, consequently, negatively with minimum and maximum temperatures (-0.849). Along the same transect, canopy cover was found to be positively correlated with the percentage uncovered forest floor (0.640). Hence, in plots with a dense canopy cover, the forest floor was relatively open.

**Table 15.1.** Multiple linear regression models for *G. orbignyana* and *A. concinnatum* along both transects. Only the significant models are presented (\*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\*  $P < 0.0005$ )

Life stage	Cerro Chirripó transect				Cerro de la Muerte transect			
	Variable	Beta	df	F	Variable	Beta	df	F
<i>G. orbignyana</i>								
1	Slope dir.	0.450*	19	0.041	Canopy cov.	-1.000***	2	<0.001
2	-	-	-	-	Bryoph. cov.	1.129**	1	0.005
3	-	-	-	-	Min. temp.	0.993*	2	0.007
4	Tree s. den.	-0.427*	18	<0.001	-	-	-	-
4	Max. temp.	0.957*	18	<0.001	-	-	-	-
5	Altitude	0.446*	18	0.004	-	-	-	-
5	Canopy cov.	-0.392*	18	0.004	-	-	-	-
<i>A. concinnatum</i>								
1	-	-	-	-	Bryoph. cov.	-0.697**	25	<0.001
1	-	-	-	-	Max. temp.	-0.839***	25	<0.001
2	Uncov.	0.668**	21	0.001	-	-	-	-
3	Trees	0.372*	20	0.009	Canopy cov.	0.396*	24	0.001
3	Uncov.	-0.529*	20	0.009	Uncov.	-0.517**	24	0.001
3	-	-	-	-	Max. temp.	0.582**	24	0.001
4	-	-	-	-	Canopy cov.	0.407*	25	<0.001
4	-	-	-	-	Underst. den.	0.659***	25	<0.001

**Table 15.2.** Multiple linear regression models for four separate growth form types of *A. concinnatum* along both transects. Only the significant models are presented (\*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\*  $P < 0.0005$ )

Life stage	Cerro Chirripó transect				Cerro de la Muerte transect			
	Variable	Beta	df	F	Variable	Beta	df	F
<b>Standing epiphytic plants</b>								
1	Uncov.	0.676**	17	0.002	Underst. den.	-0.459*	20	0.032
2	Canopy cov.	0.658**	15	<0.001	-	-	-	-
2	Slope dir.	-0.388*	15	<0.001	-	-	-	-
3	Altitude	-0.402**	15	<0.001	Underst. den.	0.424*	20	0.050
3	Canopy cov.	-0.450**	15	<0.001	-	-	-	-
3	Uncov.	-0.719***	15	<0.001	-	-	-	-
4	Uncov.	-0.491*	17	0.033	Altitude	0.463*	18	<0.001
4	-	-	-	-	Large litter	-0.385***	18	<0.001
4	-	-	-	-	Underst. den.	0.688***	18	<0.001
<b>Lying epiphytic plants</b>								
1	-	-	-	-	Bryoph. cov.	-0.781**	10	0.003
2	-	-	-	-	Underst. den.	-0.632*	10	0.028
3	Underst.den.	-0.656*	9	0.028	Canopy cov.	0.597*	9	0.014
3	-	-	-	-	Bryoph. cov.	0.952**	9	0.014
4	Uncov.	-0.794**	9	0.004	Altitude	0.316*	9	<0.001
4	-	-	-	-	Underst. den.	0.974***	9	<0.001
<b>Standing terrestrial plants</b>								
1	Canopy cov.	0.458*	17	0.048	Bryoph. cov.	-0.512*	18	0.003
1	-	-	-	-	Slope dir.	0.384*	18	0.003
1	-	-	-	-	Underst. den.	0.407*	18	0.003
2	Min. temp.	0.529*	17	0.020	-	-	-	-
3	-	-	-	-	Bryoph. cov.	0.541*	19	0.009
3	-	-	-	-	Slope dir.	-0.441	19	0.009



4	Uncov.	-0.686*	17	0.001	Canopy cov.	0.324	17	<0.001	
4	-	-	-	-	Slope dir.	-0.339*	17	<0.001	
4	-	-	-	-	Underst. den.	0.827***	17	<0.001	
4	-	-	-	-	Min. temp.	-0.548***	17	<0.001	
Lying terrestrial plants									
1	-	-	-	-	Canopy cov.	0.247*	7	<0.001	
1	-	-	-	-	Uncov.	0.576***	7	<0.001	
1	-	-	-	-	Slope dir.	0.677***	7	<0.001	
2	Canopy cov.	0.773**	12	0.001	Underst. den.	-0.842**	9	0.001	
3	-	-	-	-	Trees	0.298*	7	<0.001	
3	-	-	-	-	Uncov.	-0.675***	7	<0.001	
3	-	-	-	-	Slope dir.	-0.721***	7	<0.001	
4	Canopy cov.	-0.842***	12	<0.002	Underst. den.	0.916***	9	<0.001	

## 15.7 Abundance of Two Species

In all, 5,850 plant individuals of *G. orbignyana*, and 19,536 individuals of *A. concinatum* were recorded along the two transects. *G. orbignyana* reached peak abundance (20–50 % leaf ground cover) at 2,300–2,500 m elevation along the CC transect, and at 2,350–2,600 m along the CM transect (Fig. 15.3a). Maximum abundances for *G. orbignyana* were much higher at the CC than at the CM site. *A. concinatum* reached highest abundance values at 2,600–2,800 m along the CC transect, and at 2,350–2,850 m along the CM transect (Fig. 15.3b). Maximum abundances for *A. concinatum* were lower along the CC transect than along the CM transect.

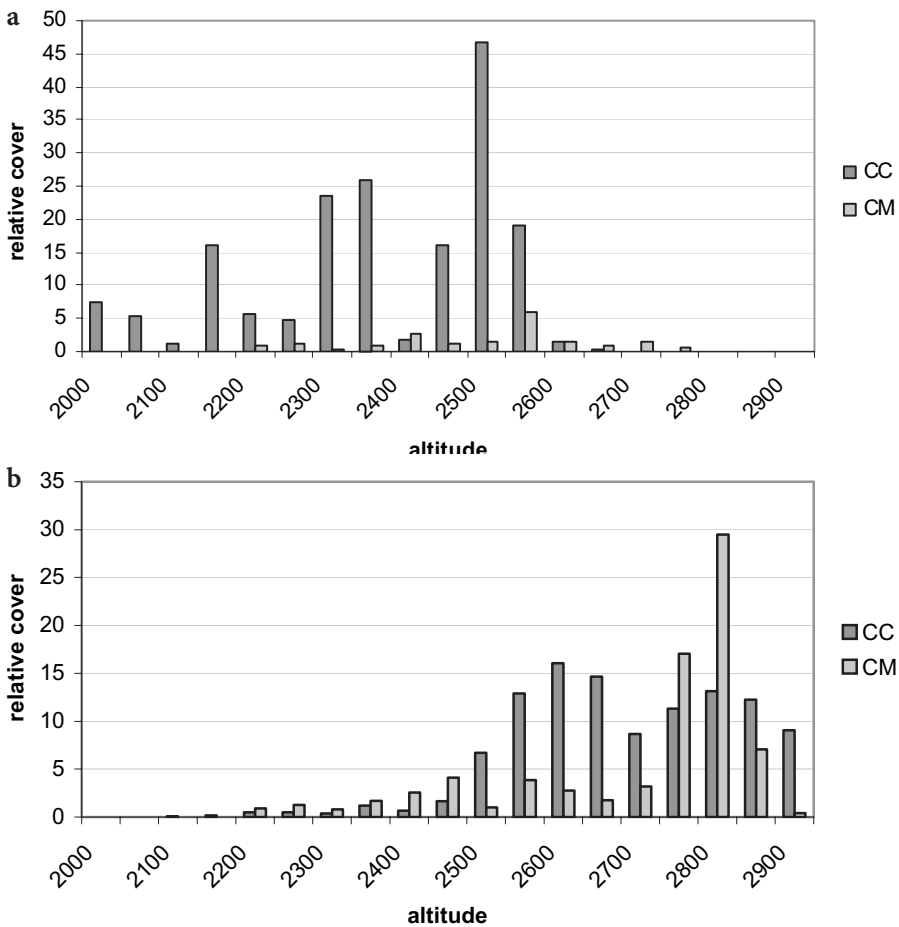


Fig. 15.3a, b. Relative ground leaf cover of a *Geonoma orbignyana*, and b *Anthurium concinatum* along both transects. CC Cerro Chirripó transect, CM Cerro de la Muerte transect

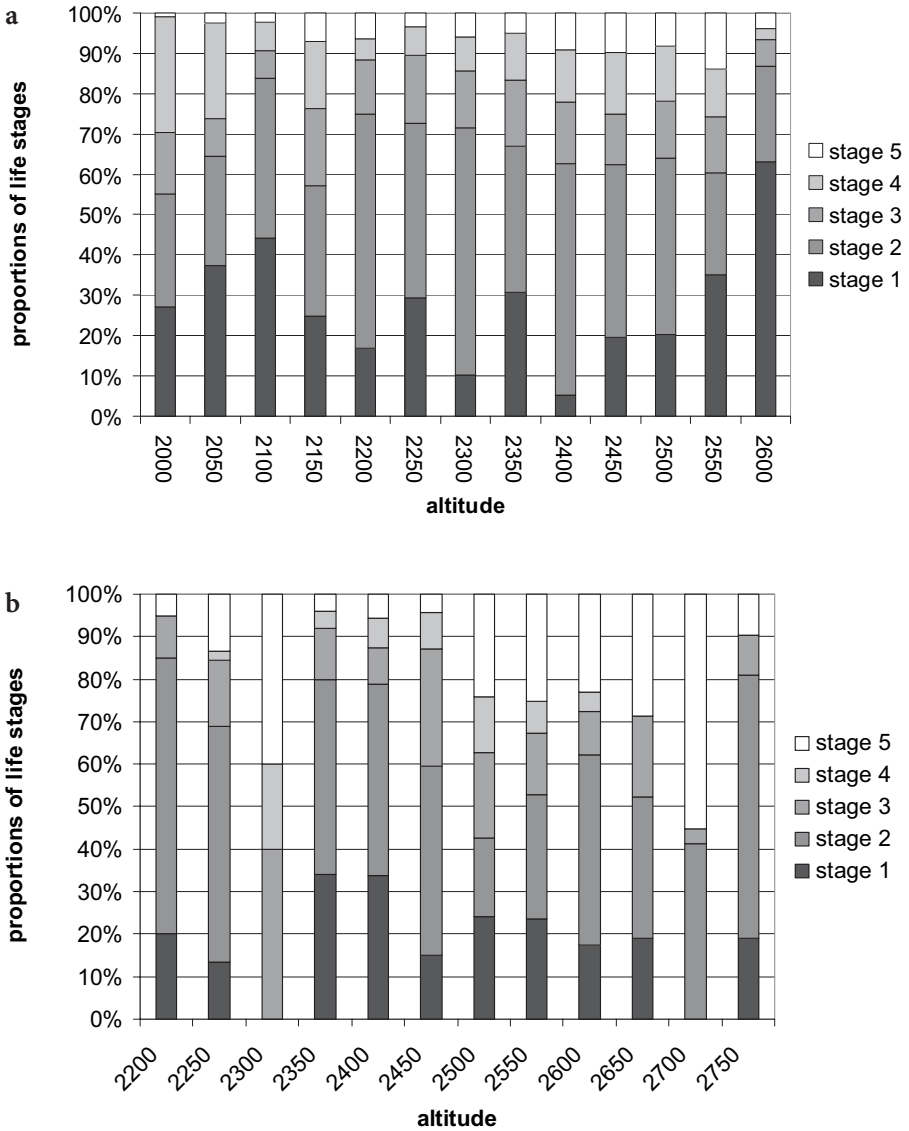


Fig. 15.4a, b. Proportions of five life stages of *Geonoma orbignyana* along the elevational gradient for the a CC transect (Cerro Chirripó), and b CM transect (Cerro de la Muerte)

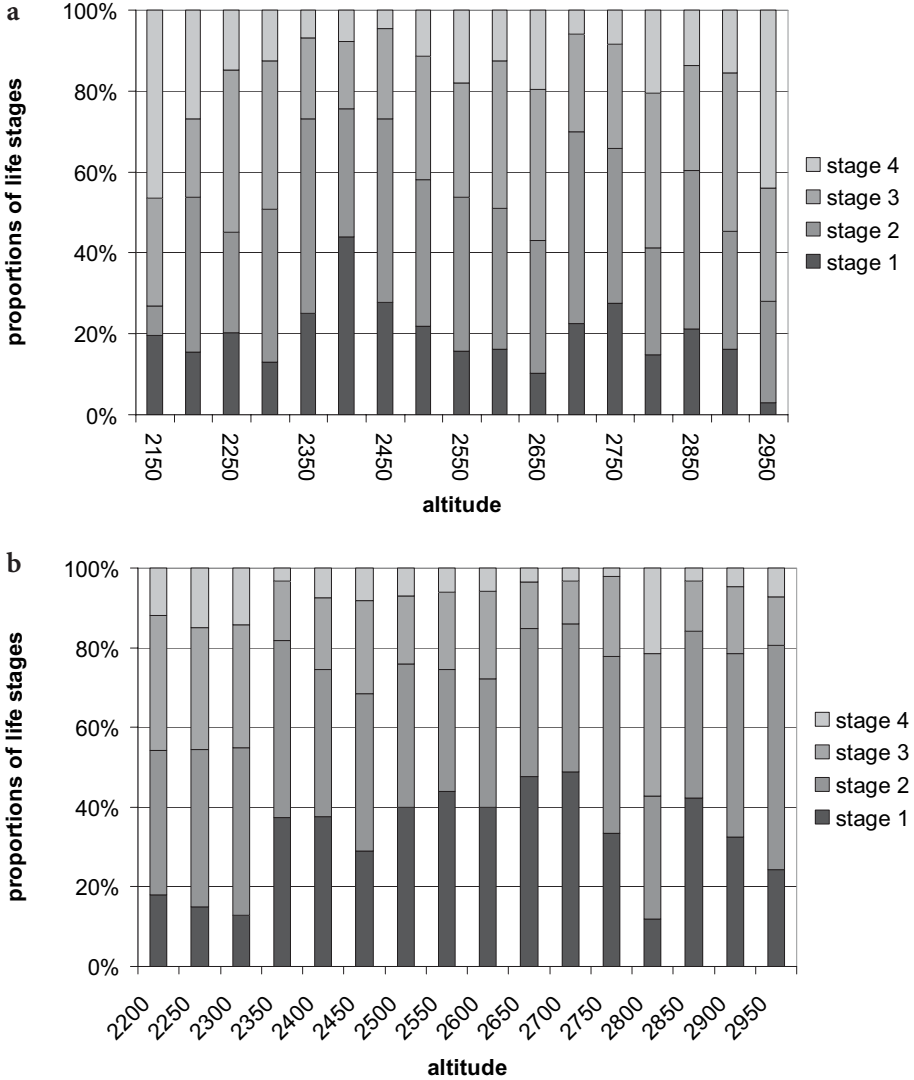


Fig. 15.5a, b. Proportions of four life stages of *Anthurium concinatum* along the elevational gradient for the a CC transect (Cerro Chirripó), and b CM transect (Cerro de la Muerte). All plant individuals are included, regardless their specific growth form

The proportions of the different life stages of both *G. orbignyana* and *A. concinatum* did not show any relationship with altitude (Figs. 15.4 and 15.5). Although the multiple regressions showed some significant correlations for *G. orbignyana*, none of these reflected a response in the structure of the population as a whole.

## 15.8 Life Stages and Growth Forms of *A. concinatum*

Multiple regressions on life stages of *A. concinatum*, irrespective of growth form, showed that along the CC transect, the percentage of uncovered forest floor was positively related to the proportion of life stage 2 (younger plants), whereas it was negatively related to life stage 3 (older plants). Along the CM transect, maximum temperature was negatively correlated to the proportion of *A. concinatum*'s life stage 1. This phenomenon was reconfirmed by the positive correlation of maximum temperature to life stage 3. This result implies that more small individuals were observed in plots with a lower temperature (i.e., at higher altitude).

Multiple linear regression analyses of data collected along the CC transect for *A. concinatum*'s standing epiphytic growth form showed that the percentage of uncovered forest floor was positively related to the proportion of life stage 1, whereas it was negatively related to the proportions of life stages 3 and 4. Likewise, along the CM transect the proportion of life stage 1 decreased with increasing undergrowth density, whereas the proportions of life stages 3 and 4 increased. The percentage uncovered forest floor and the density of the undergrowth are both measures of the structure of the understory vegetation. An open understory thus appears to promote the recruitment of standing epiphytes.

Along the CC transect, canopy cover was additionally positively correlated with the proportion of life stage 2, and negatively with the proportion of life stage 3. Here, multiple regressions on the lying epiphytic growth form showed no significant population responses. Along the CM transect, however, a denser understory was negatively correlated to the proportion of life stage 2, and positively correlated to the proportion of life stage 4. Along the same transect, the proportion of life stage 1 was negatively related to the percentage cover of bryophytes, the reverse being the case for the proportion of life stage 3.

For *A. concinatum*'s standing terrestrial growth form, no significant population response was observed along the CC transect. Along the CM transect, by contrast, the percentage cover of bryophytes was negatively related to the proportion of life stage 1, and positively to the proportion of life stage 3. Along the latter transect, a more northern exposition was associated with a higher proportion of life stage 1, whereas at more southern expositions higher proportions of the old life stages 3 and 4 were observed.

Finally, understory density was negatively correlated with life stage 1, and positively with life stage 4. For *A. concinatum*'s lying terrestrial growth form along the CC transect, canopy density was positively related to the proportion of life stage 2, and negatively to life stage 4. Along the CM transect, the proportion of life stage 1 increased both at higher percentages of uncovered forest floor and at more northern expositions, the reverse being the case for life stage 3. The density of the understory also seemed to play a role here: it was

negatively correlated to the proportion of life stage 2, and positively to the proportion of life stage 4.

## 15.9 Conclusions

The variation in population structure of *G. orbignyana* was not explained by any of the environmental variables that we measured. We conclude that the population structure of *G. orbignyana* is controlled either by other environmental variables (e.g., thickness of humus layer, M. Kappelle, personal observations), or by factors that are not related to the environment (e.g., seed dispersal and seedling recruitment). A large number of palms that occur in the understory of tropical forests have been shown to respond strongly to the structure of the forest. Light availability has the effect that it largely enhances recruitment in those species (Oyama 1990). The genus *Geonoma* seems to be an exception, as it is reported to occur in undisturbed or late secondary forests only (Kappelle et al. 1995a, b). *Geonoma* species are often dominant in the understory (Chazdon 1986; Olesen and Balslev 1990; Listabarth 1993); they are shade-tolerant specialists that are highly adapted to the relative darkness of the understory (Chazdon 1986), and therefore may show at least some level of recruitment at any given light availability. Since our results show that a higher light availability does not seem to enhance recruitment, we may conclude that *G. orbignyana* is an understory specialist, too.

By contrast, *A. concinatum* has been observed in forests of all successional stages (Kappelle et al. 1995b). Recruitment of this species is thus expected to take place under completely open as well as partially open canopies, e.g., within newly formed gaps after a tree fall. Its young life stages were associated with an open understory, with little competition for space and light, and old life stages with a relatively open canopy and a high bryophyte cover. It has been observed in tropical forests that bryophyte cover is positively correlated with air humidity (Pócs 1982). Assuming that the same is true for the forests we studied, we suggest that the higher proportion of large individuals in bryophyte-rich patches is explained by higher moisture availability. This implies that drought stress prevents plants from becoming large in patches with fewer bryophytes. Such drought stress was also reported for the epiphytic species of *Anthurium bredemeyeri* (Rada and Jaimez 1992). Since bryophyte ground cover was negatively correlated with maximum temperature along the CM transect, the drought sensitivity of adults might also explain the higher proportions of large individuals observed at lower maximum temperatures, as seen in the general data analysis for this transect.

The low proportion of large standing epiphytes under a denser canopy along the CC transect can be explained by a reduction in growth of adult plants under low light availability. This finding is at odds with our initial

assumption of equal growth rates throughout transects. Nevertheless, observations on the distances between leaf scars on the stem suggest that in most plots size was indeed closely related to age (unpublished data).

Finally, competition for light and moisture availability seems important in determining the population structure of *A. concinnatum*. Higher levels of recruitment of this species appear to occur in more open understory. Within the context of tropical montane oak forest dynamics, we may conclude that *A. concinnatum* exhibits a pioneer strategy sensu Alvarez-Buylla and Martínez-Ramos (1992), being able to colonize relatively open patches in the understory, and requiring a relatively open canopy for optimal growth.

*Acknowledgements* We thank IBED staff for support during the research design and data analysis phases. L. Köhler and I. Holz, University of Göttingen, and INBio staff in Costa Rica are gratefully acknowledged for assistance during fieldwork. We are very grateful to Francisco Quesada (INBio) for preparing the two drawings. The Martínez family is thanked for their generous hospitality. This project was funded by the Alberta Mennega Foundation, FONA at IBN-DLO (now WURC), Shell Netherlands BV, the Pro-Natura Foundation, and the University of Amsterdam.

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