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POPULATION STRUCTURE OF THREE EPIPHYTIC ORCHIDS (*LYCASTE AROMATICA*, *JACQUINIELLA LEUCOMELANA*, AND *J. TERETIFOLIA*) IN A MEXICAN HUMID MONTANE FOREST

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ABSTRACT. The population structure of three epiphytic orchids (*Lycaste aromatica, Jacquiniella teretifolia,* and *J. leucomelana*) was studied in a Mexican humid montane forest. We measured all individuals on several trees and related plant size, number, and fertility to branch height and diameter. While *Lycaste* preferred thick branches, which are usually more shaded and stable, *Jacquiniella* spp. grew on thinner and more exposed branches with a higher rate of branchfall. The size-class distribution of *Lycaste* was relatively homogeneous, pointing to low recruitment and high survival. *Jacquiniella leucomelana* had a much higher proportion of juveniles, suggesting high recruitment and low survival. In *J. teretifolia,* recruitment appears irregular. The observed size classes and fertility rates are interpreted to reflect strategies of species adapted to different branches and, in part, as effects of individuals growing on branches of different sizes and stabilities. Using the regular production of pseudobulbs in *Lycaste,* we estimated the age when the first plants become fertile (10 years) and the time to reach full size (ca. 20 years).

Key words: epiphytes, growth, orchids, population structure

INTRODUCTION

The demography of epiphytic orchids contrasts in several ways with that of ground-rooted plants. Seeds of epiphytic orchids not only have to encounter a suitable fungal symbiont, as in terrestrial orchids, but also a branch with a fungus. Thus they depend on the tree's architecture. Apart from the physiological stress of living without soil contact, which may result in high mortality in periods of drought (Zotz 1998), epiphytic orchids are subject to plant mortality related to branch and tree mortality. In a study involving individuals of many epiphyte species, ca. 40% of total mortality resulted from branchfall (Hietz 1997). Thus the demography of an epiphyte is superimposed on the dynamics of its supporting branches.

To avoid extinction, an epiphyte must complete its population cycle at a rate faster than the turnover rate of suitable branches. The time available will mostly be shorter than the life of the branches themselves, since young branches may be too thin for epiphytes to hold onto or too exposed and dry. The oldest branches may be shadowed and overgrown by others, or an epiphyte can be replaced by more competitive epiphytic species. In general, small branches tend to break or be shed by self-pruning sooner than thick branches. Consequently the chance of dying with a falling branch is much higher for an epiphyte on a small branch. A species that prefers smaller branches thus experiences higher disturbance, and we expected to see this reflected in the population structure of our study species.

In contrast to other epiphytes, many epiphytic orchids are found growing in clusters of a few to many individuals in close vicinity. Often no conspecifics are found on nearby branches that appear equally suitable. Because orchid diaspores are highly mobile, this clustering may result from the low probability of finding a fungal partner on a branch not yet colonized (Hietz & Hietz-Seifert 1995a). This hypothesis has yet to be confirmed experimentally. A possible specificity between a fungus and the rare orchid *Lepanthes caritensis* also was reported by Tremblay et al. (1998), but the significance of this for orchid occurrence and establishment is unclear. Plants in such clusters on individual branches can be treated as sub-populations growing under more or less homogeneous conditions. If the branch affects survival and recruitment of a species, the population structure of sub-populations on branches also should depend on the branch type.

The size-class distribution of a species can be recorded based on a single observation of the individuals present. Recording age classes or growth rates normally requires repeated observations and measurements over a prolonged period. Such records are difficult to obtain for epiphytes, where trees have to be climbed repeat-

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edly without damaging the plants. As a result, such records are rare. The few results available suggest that orchids and bromeliads grow rather slowly and require 8–19 years to become fertile (Larson 1992, Hernández 1992, Zotz 1995, 1998). Twig epiphytes (mostly Pleurothalliinae) that mature within one or a few years are an exception (Chase 1987). To predict growth and age of the *Lycaste aromatica* plants measured, we used the regular production of pseudobulbs that are retained for several years.

MATERIALS AND METHODS

Study Site

This study was conducted in a small reserve adjacent to the Instituto de Ecología, 2.5 km south of Xalapa, in central Veracruz, Mexico (19°31′N, 69°57′W) at 1350 m elevation. Average temperature is ca. 19°C, and annual precipitation in Xalapa is 1500 mm, 79% of which falls in the May–October wet season. The forest is at the transition between premontane moist forest and lower montane, according to the Holdridge life zone system (Holdridge 1967). According to Rzedowski (1986), this forest is commonly classified in Mexico as "bosque mesófilo de montaña" (mesophilous montane forest). Descriptions of the forest structure can be found in Williams-Linera (1997) and of the epiphyte community in Hietz and Hietz-Seifert (1995a).

Species Studied

Lycaste aromatica (Graham) Lindley produces thick pseudobulbs, up to 7 cm tall with 2–5 broad-lanceolate leaves up to 70 cm long. The pseudobulb is produced toward the end of the wet season. In the dry season, the leaves are shed, leaving the spiny leaf scars characteristic of the genus. Flowers are produced on short peduncles when the plant is leafless. Rarely are more than one shoot and pseudobulb produced in one season; but when this occurs, they originate from the old pseudobulb or in parallel, and the plant branches. Thus all pseudobulbs can be dated. Unless they are dying or become very dry, pseudobulbs do not shrink but retain their original sizes. Measuring size changes between subsequent pseudobulbs thus enabled us to measure growth.

Jacquiniella teretifolia (Sw.) Britton & Wilson is a caespitose, erect plant up to 30 cm tall with distichous, linear, 3–5 cm long fleshy leaves and single flowers produced at the apex of the stem. *Jacquiniella leucomelana* (Reichb. f.) Schltr. is vegetatively very similar to *J. teretifolia* but much smaller. Stems are usually less then 12 cm tall and leaves 1–2 cm long and at any given size shorter than those of *J. teretifolia.*

Data Collection

In August and September 1999, nearly 1200 plants of *Lycaste aromatica* (*N* = 254), *Jacquiniella leucomelana* (655) and *J. teretifolia* (258) on 47 branch sections of nine host trees (*Meliosma alba, Quercus xalapensis, Q. germana*) were marked and measured. All but one of the individual trees were oaks, reflecting in part their frequency in the forest (Williams-Linera et al. 1996) and perhaps also their suitability for epiphyte colonization (Hietz & Hietz-Seifert 1995b), but we did not deliberately select oaks. Branches 2.5–21 m above ground were climbed with single-rope technique. With the exception of a few individuals on inaccessible branches, all orchids on a tree were recorded. Branch circumference, inclination, distance to the trunk, and height above ground were measured. We estimated the proportion covered with moss and the canopy openness (percentage of visible sky in field of vision above the branch).

Orchid individuals were marked with numbered labels pinned into the bark, and the location of each on a branch was sketched. For *Lycaste,* height, width, and thickness of pseudobulbs and length of longest leaf were measured, and living and dead pseudobulbs were counted. If orchids branched, the pseudobulbs were sketched and numbered for dating. For *Jacquiniella* spp., we counted number of shoots per plant and measured length of longest stem. When orchids had become fertile (visible from flowers, fruits, or old pedicels), records were made on each individual.

In addition to the orchids measured directly, others were recorded and measured from photographs taken between 1992 and 1997 (Hietz 1997). As the sizes of plants measured from photographs are not easily comparable to direct measurements, we here use data from photos only for mortality and the size of the branch on which orchids grew.

A polynomial regression fitted to size increases of successive pseudobulbs (*N* = 583) was used to calculate the size increment depending on pseudobulb size. Starting with a pseudobulb size of 0.7 cm, which was the smallest observed in the field, we were then able to calculate the time a plant needed to obtain a given size. Pseudobulbs giving rise to two new ones were excluded. We thus estimated the age of the smallest plants becoming fertile and the average time required to reach full size.

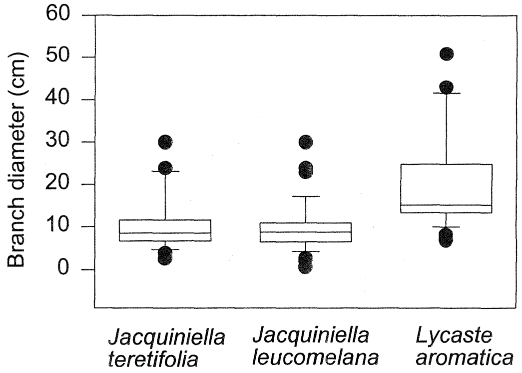

FIGURE 1. Distribution of colonies of three epiphytic orchid species on branches of different sizes. Boxplots show median, 25th, and 10th percentiles and outlying data points.

Statistical Analysis

Using non-parametric Kruskal-Wallis ANOVA, we tested whether the distribution of the three species differed in any branch parameter. Multiple linear regression was used to test if branch diameter or height had the stronger influence on the proportion of fertile plants on a branch carrying at least five individuals. Pearson correlation tested for relationships between branch height or diameter and either mean plant size of orchids on a branch or the proportion of fertiles on a branch with at least five plants. The influence of the branch on pseudobulb growth in *Lycaste* was tested with a normal one-way ANOVA (Sachs 1984). All statistical tests were calculated with SPSS 8.0 (SPSS Inc., Chicago, Il).

RESULTS

Plant Distribution

Of the branch parameters tested (circumference, height above ground, inclination, moss cover, and canopy openness), circumference and canopy openness significantly differed between species (Kruskal-Wallis test, circumference: $\chi^2 = 8.9$, $P = 0.011$, canopy openness: $\chi^2 = 10.9$, $P = 0.004$).

Mean branch diameter in *Lycaste* (20.7 cm) was almost twice that in *Jacquiniella teretifolia* (9.8 cm) and *J. leucomelana* (10.7 cm) (FIGURE 1). Branches with *J. leucomelana* and *J. teretifolia* also had a higher canopy openness than those hosting *Lycaste.*

Population Structure

The size-class distribution in percent of total number of individuals and percent of fertile individuals for each size class are shown in FIGURE 2. The size-class distribution in *Lycaste* was almost homogeneous, and only the largest classes were less common. The smallest classes were under-represented, because the first pseudobulbs frequently reached >1 cm. The proportion of juveniles in both species of *Jacquiniella* was much higher; however, *J. teretifolia* had very low numbers in the smallest stages, pointing to low recent recruitment. Plants of *Lycaste* became fertile with a leaf length >30 cm or a pseudobulb height of >3.5 cm; *J. teretifolia* with a shoot length >14 cm; and *J. leucomelana* with a shoot length >3 cm. In *Lycaste,* 13% of all individuals and 33% of those of fertile size had produced flowers; in *J. teretifolia,* 5.8% of all and 45% of fertile; and in *J. leucomelana,* 23% of all and 60% of fertile.

The proportion of fertile plants increased with plant size in *Jacquiniella* spp. In *Lycaste,* the proportion of fertiles was rather constant for all size classes with leaf lengths >30 cm but did increase with pseudobulb height (FIGURE 2). This appears reasonable, because flowers are produced from the pseudobulb and leaves de-

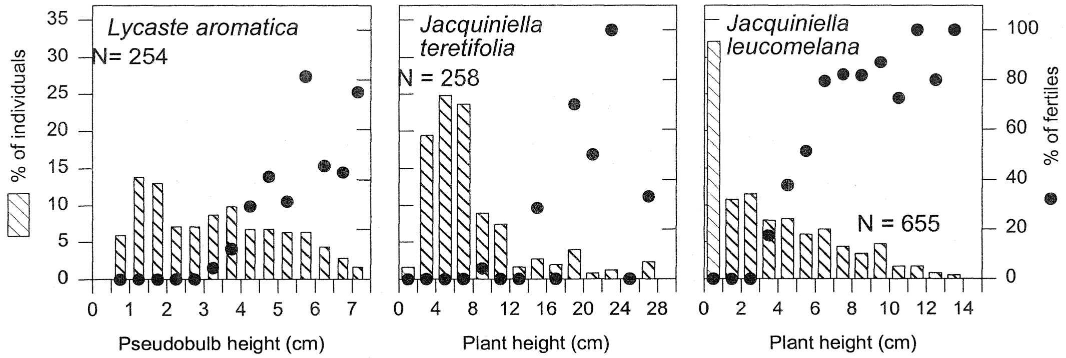

FIGURE 2. Plant size distribution of three epiphytic orchid species in a Mexican humid montane forest and the proportion of fertile plants in each size class.

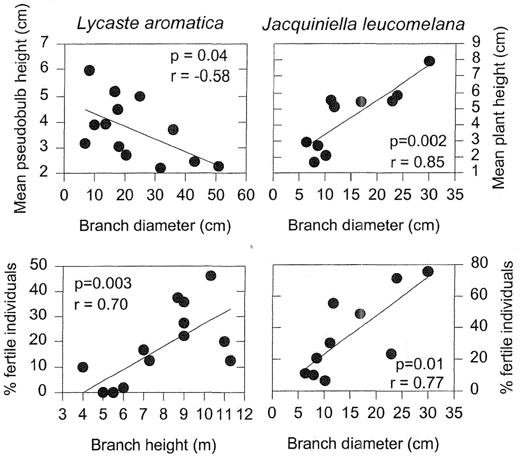

FIGURE 3. Relationship (Pearson correlation coefficient) between branch diameter and mean plant size of colonies with at least five individuals of epiphytic *Lycaste aromatica* (left) and *Jacquiniella leucomelana* (right) growing on a branch (top) and between branch height or size and the proportion of fertile plants on each branch (bottom).

velop only afterwards. In spite of the dominance of small size classes in *J. leucomelana,* the proportion of fertile plants was highest in this species. This resulted because the species tended to flower at small sizes, and because the proportion of fertiles in the larger size classes was highest.

Influences of Branch Parameters

In *Lycaste,* a significant correlation was found between the mean plant size in the sub-population on a branch and branch diameter (Pearson correlation: $P = 0.04$, FIGURE 3) or its height on the tree ($P = 0.04$). Average size did not depend on the number of individuals on a branch. In *Jacquiniella leucomelana,* the mean shoot height on ten branches carrying at least five plants also increased with branch diameter ($P = 0.002$, FIGURE 3). No correlations were found with other parameters such as height above ground, branch inclination, moss cover, distance to the trunk, or canopy openness. In *Lycaste,* the proportion of fertile plants increased with branch height ($P = 0.003$), but not with diameter; in *J. leucomelana* the reverse was the case, and the proportion of fertile plants increased with branch diameter (TABLE 1, FIGURE 3). For *J. teretifolia,* none of the relationships tested had significant results, which may be caused by the low number of branches found with more than a few individuals.

Growth in *Lycaste aromatica*

Though average pseudobulb growth differed significantly between branches (one-way ANOVA, $F_{11,162} = 2.6$, $P = 0.005$), this effect could not be attributed to any single branch parameter (diameter, height, inclination, canopy openness).

The mean height increment was 0.26 cm (±0.69 SD), declining slowly as plants reached full size and with substantial variation among individuals (FIGURE 4A). Some individuals had decreased in pseudobulb size over several years, especially when they had been overgrown by others. According to the growth curve predicted from a model of annual size increments, *Lycaste* takes 10 years to produce pseudobulbs of 4 cm height, the size when several fertile plants were observed, and 20 years to reach full size (6 cm, FIGURE 4B). Only two plants without pseudobulbs were found. These may be from the current year, as leaves are shed in the dry season, and plants without a pseudobulb presumably could not have survived. No protocorms were found, and we do not know how long *Lycaste* stays in this stage in the field. Using the growth curve (FIGURE 4B) to calculate the age of the oldest pseudobulb and adding the number of younger pseudobulbs, we estimated the age of each plant and thereby obtained an age-class distribution (FIGURE 5). This estimated age is probably inaccurate for the larger plants, but rather

TABLE 1. Influence of branch diameter and branch height on the proportion of fertile plants of *Lycaste aromatica* and *Jacquiniella leucomelana* tested by multiple linear regression. Only branches with at least five individuals were used.

Jacquiniella leucomelana	$N = 10$	F = 6.093	Sign (F) = 0.029
Branch height		T = 0.956	Sign (T) = 0.371
Branch diameter		T = 3.407	Sign (T) = 0.011
Constant		T = −0.873	Sign (T) = 0.412
Lycaste aromatica	$N = 15$	F = 6.010	Sign (F) = 0.016
Branch height		T = 3.225	Sign (T) = 0.007
Branch diameter		T = −0.338	Sign (T) = 0.741
Constant		T = −1.144	Sign (T) = 0.275

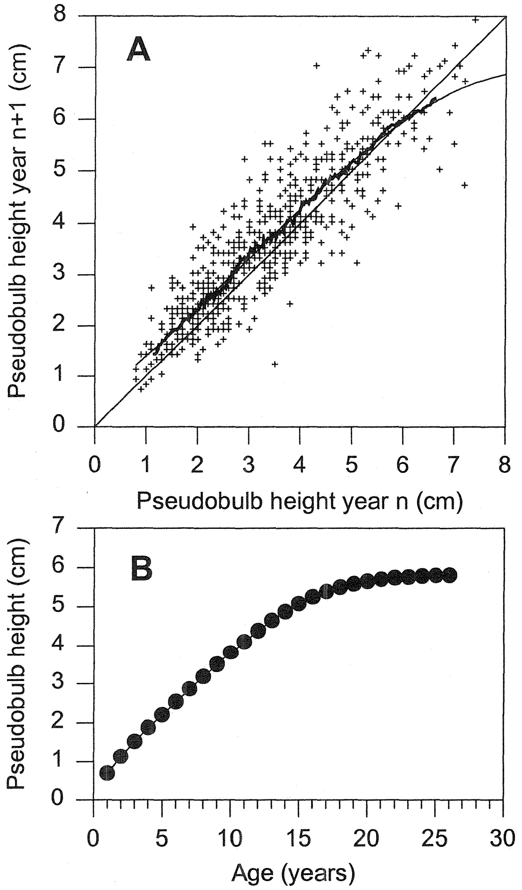

FIGURE 4. Pseudobulb height in *Lycaste aromatica.* **A.** One-year changes of pseudobulb height. The thick line is a moving average (over 30 data points), the thin line (mostly covered by the thick) is a fitted function ($h_{n+1} = 0.563 + 0.762*h_n + 0.081\ h_n^2 - 0.00976\ h_n^3$; $r^2 = 0.79$). The difference between the thick line and the straight 1:1 line is the average annual growth. **B.** Growth predicted from the function of annual size increments starting with the smallest observed pseudobulb height of 0.7 cm.

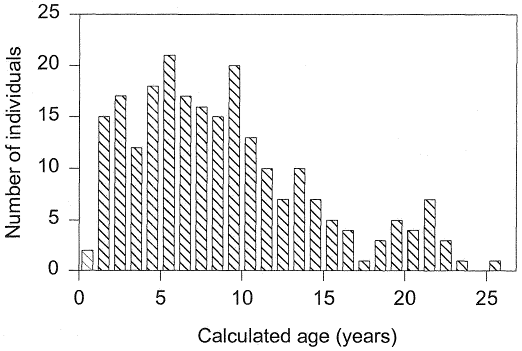

FIGURE 5. Age-class distribution of *Lycaste aromatica* calculated from the estimated age of the oldest pseudobulb and the number of younger pseudobulbs. The youngest class consists of individuals without pseudobulbs.

accurate for the smaller ones, which had most of their pseudobulbs still attached.

DISCUSSION

Many studies have shown patterns of epiphyte distribution within a host tree (Oliver 1930, Johansson 1974, Kelly 1985). Slow to emerge are data on which features predispose a plant to a certain tree zone and on how host tree characteristics affect the epiphytes (Kelly 1985, Griffiths & Smith 1983, Hietz 1997). The potential importance of population dynamics has not been considered in this respect. Population structures have previously been reported for a few epiphytic orchids and bromeliads. Benzing (1981) and Zotz (1997) found a strong dominance of the smallest plants, similar to the pattern found in *Jacquiniella leucomelana.* Data presented by Bennett (1991) show no clear trend, but in this case the size classes were very inhomogeneous. Also in the orchid *Dimerandra emarginata* the smallest size class (<5 cm) was the most frequent (Zotz 1998), but this included plants to the size of the smallest fertile individual, and fertile plants of *D. emarginata* keep growing in shoot length for a long time. If the first size class in *Lycaste aromatica* comprised all plants smaller than the smallest fertile individual, this category alone would include nearly half of all individuals. Tremblay (1997) also found a comparatively high proportion of potentially fertile individuals (32%) in the small epiphytic orchid *Lepanthes caritensis.* In general the proportion of fertile individuals appears to be higher in epiphytic orchids than in bromeliads.

During a 3-year study by Zotz (1998), the proportion of the smallest size class decreased substantially because mortality was highest for small plants and recruitment was very low. Similarly a population of *Encyclia tampensis* in Florida, initially dominated by plants in the prebulb stage, became successively rarer; until, after 5 years, the whole population was killed by a frost (Larson 1992). These reported changes in population structure show that recruitment and/or survival can differ between years, and a stable population structure is unlikely. The very low number of plants in the prebulb stage suggests that the most recent recruitment in *Lycaste aromatica* largely failed, though the rather homogeneous age-class distribution shows that once pseudobulbs have been formed, subsequent survival is high.

Lycaste took at least 10 years and often substantially longer to become fertile, which is in the range found in other epiphytic orchids and bromeliads (Larson 1992, Zotz 1998, Benzing 1981).

The preferential growth on thicker branches may have several reasons. Thick branches are usually located in the shadier and more humid parts of the crown. Evidence indicates that microclimate does not limit the distribution of *Lycaste* on thin branches; the species is fairly common in the much drier and more open premontane forests of the area (Hietz & Hietz-Seifert 1995b). Thicker branches offer a better hold, which may be a factor in the distribution of large epiphytes such as *Lycaste.* Thicker branches also are more stable, which may be crucial for slowly maturing and long-living plants that might fall with a thin branch before reproducing. With average plant size larger on thin branches (relatively fewer juveniles) and with only thick branches having higher numbers of individuals, the data suggest higher recruitment and/or juvenile survival on thick branches.

Jacquiniella leucomelana had a higher number of small plants, suggesting higher recruitment and much lower survival than *Lycaste.* In spite of the low proportion of large plants, the proportion of fertile plants was the highest of the three species, because *J. leucomelana* reached fertility at a relatively small size and presumably earlier, and almost all of its larger plants were fertile. High recruitment and early fertility are valuable adaptations for a plant colonizing unstable substrates, such as thin branches. While mean plant size in *J. leucomelana* was higher on thick branches, the number of individuals per branch was not. If branch diameter is taken as a measure of age and thus the time the host substrate has been stable, then smaller branches would be more suitable for recruitment. Instability of small branches, however, appears to pose a limit to the reproduction of epiphytic orchids. If the proportion of fertile plants increases with branch size, it appears to be a result of the time available to become fertile.

In *Lycaste,* fertility did not correlate with the size of the branches, which were comparatively large and sufficiently stable. Here branchfall was not a significant constraint to reaching fertility. Analysis of survival rates from photographs (P. Hietz unpubl. data) showed that ca. 1/3 of total mortality in *Jacquiniella* spp. was a result of branchfall, but no death from branchfall was observed in *Lycaste.* Fertility in *Lycaste* did increase with branch height, which is a coarse measure of light penetrating through the canopy. For a plant growing on thick and mostly shady branches, light may become limiting, particularly for reproduction.

The size-class distribution of *Jacquiniella teretifolia* was similar to *J. leucomelana,* but the smallest class was almost lacking, pointing to a generally high but recently rather low recruitment. As plants only become fertile at shoot length > 14 cm and as large plants are comparatively rare, the proportion of fertile plants was low. Insecure recruitment also was apparent where several large, multi-stemmed, and fertile plants had no or very few juveniles surrounding them.

Certainly the complexities of the canopy cannot be reduced to branch size and position, nor will an epiphyte's characteristics all be reflected in its demography. Bark type, moss and humus cover, or interactions with other epiphytes may all affect an epiphyte's distribution (Benzing 1990), and physiological adaptations may help explain the survival and growth of each species. The data presented do show, however, that even limited studies on epiphyte demography can reveal major features of canopy dynamics and differences in life strategies of epiphytes.

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