Selbyana 16(2): 150–154

HOW FAST DOES AN EPIPHYTE GROW?

GERHARD ZOTZ[1,2,3]

[1] SMITHSONIAN TROPICAL RESEARCH INSTITUTE, APDO. 2072, BALBOA, REPUBLIC OF PANAMA
[2] UNIVERSITY OF VERMONT, DEPARTMENT OF BOTANY, BURLINGTON, VERMONT, 05405, USA

ABSTRACT. Vegetative growth in the orchid *Dimerandra emarginata* was assessed in more than 300 individual plants growing on the host tree *Annona glabra.* For each growing season *D. emarginata* develops one vertical shoot which persists over several years. Past growth was quantified by comparing stem lengths of subsequent years. Average yearly stem height increments were estimated for different plant sizes and used to model long-term growth, which proved to be very slow. The implications of slow growth for age estimates, survival, and community processes are discussed.

INTRODUCTION

Epiphytes are generally viewed as very slow-growing plants (Benzing 1990). Frequent droughts and low nutrient availability are two of the main factors which potentially limit growth in the harsh environment where most epiphytes live. Considering the taxonomic diversity of vascular epiphytes with more than 20,000 species, our knowledge of the in situ growth patterns and other life history characteristics is extremely limited (Benzing 1987). Zimmerman and Aide (1989) and Ackerman and Montalvo (1990) found a significant negative correlation between the reproductive effort in one year and the vegetative growth in the following year in two orchids. Benzing (1981) studied the population structure of *Tillandsia circinnata* in Florida and states that this species requires 8–10 years to reach reproductive size.

No study has tried to reconstruct the entire growth history of an epiphyte. In part, this stems from the difficulty in delimiting epiphyte individuals. Bromeliads, for example, often form multiple rosettes and many orchids have ramified rhizomes. On the other hand, a given "stand" (Sanford 1968) of various rosettes or pseudobulbs may also consist of several individuals. If the development of an individual plant shall be followed over time, destructive harvesting of a dense stand of an epiphyte to distinguish between the different possibilities (individual or group) is not possible. Yet, there are species which lend themselves to growth analysis. The orchid *Dimerandra emarginata* is one such species. Vegetative growth in this bark epiphyte has two components (FIGURE 1). A linear, horizontal creeping rhizome grows without ramifications in one direction, and forms a new vertical stem once a year. Stems remain alive for many years. Each individual epiphyte thus documents many years of growth, sometimes more than a decade.

In this study, only plants growing on the same host tree species (*Annona glabra*) were included to avoid the possible influence of different substrates or microclimates on the growth of *D. emarginata.* This report presents the first results of a larger project on the growth, survival, and population dynamics of *D. emarginata* which is currently in progress.

MATERIALS AND METHODS

This study was conducted on Barro Colorado Island (9°10'N, 79°51'W) in the Republic of Panama. The forest of this biological reserve is classified as a tropical moist forest (Holdridge *et al.* 1971). Mean annual rainfall is approximately 2,600 mm with a pronounced dry season from late December to late April. During this time, rainless periods regularly extend for several weeks (Windsor 1990). Detailed descriptions of vegetation, climate and ecology are reported by Croat (1978) and Leigh *et al.* (1982).

Dimerandra emarginata (G. Meyer) Hoehne (Orchidaceae) occurs from Mexico through Venezuela (Siegerist 1986). On Barro Colorado Island it is mainly found high in the canopy and on exposed branches along the shore of Lake Gatun. It is very common on *Annona glabra L.* (Annonaceae), a freshwater mangrove growing in marshes along the shore. I located 305 epiphytes in 20 trees for this study. Only plants larger than 0.5 cm were included. (The "size" of a plant was defined by the height of the most recent stem) *D. emarginata* grows sympodially developing one new stem per season. This new stems begins to grow in the late dry season and continues to grow until the end of the wet season, when the larger individuals flower. Growth is reinitiated by a new stem in the next dry season. Each individual consists of several stems, but

---

[3] Address for correspondence: Gerhard Zotz, Julius-von-Sachs-Institut für Biowissenschaften, mit Botanischem Garten der Universität Würzburg, Lehrstuhl für Botanik II, Mittlerer Dallenbergweg 64, D-97082 Würzburg, Germany.

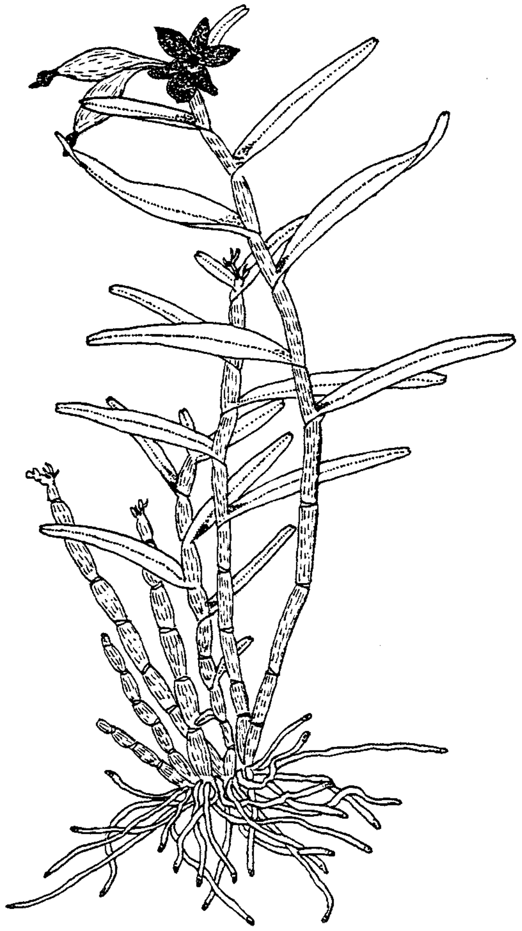

FIGURE 1. Habit sketch of *Dimerandra emarginata.*

only the stems of the last 2–4 yrs still bear leaves (G. Zotz, pers. obs.). In early 1995, I measured the height of the youngest 6 stems (1994–1989) to the nearest 0.2 cm, and counted the total number of living stems per plant.

I did not include a few plants where the creeping rhizome had ramified, giving rise to two growing points, or plants which had "kikies" (=additional offshoots; Horich 1977) at the tip of old stems. Only plants that showed no deviation from the normal linear growth pattern with one new stem per year were considered.

On an additional 233 stems which had developed in 1994, I counted the number of leaves. In most cases a few leaves had already been lost, but the insertion point at the stem was still clearly visible. The abscissed leaves were also included in the count to obtain the maximum number of leaves.

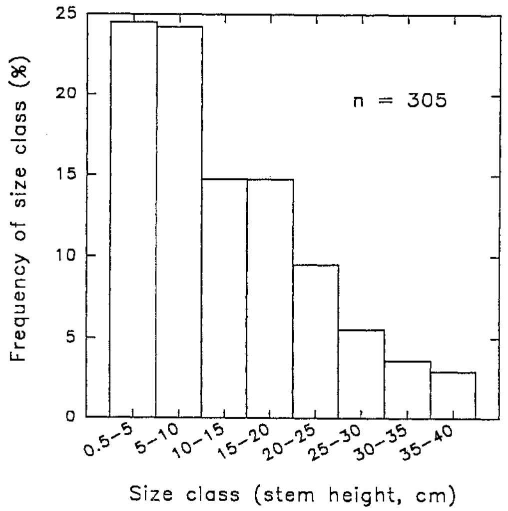

FIGURE 2. Size class distribution of *Dimerandra emarginata* on *Annona glabra.* Plants were exhaustively sampled on 20 *Annona* trees. Plant size is defined as the height of the most recent stem (= 1994). Plants shorter than 0.5 cm were rare and are not included. The largest plant measured 45 cm.

To estimate leaf area I collected 15 plants during the wet season of 1993, when the new stems still had all their leaves. Stems were between 2 and 43 cm tall. The area of each individual leaf was measured on a digitizing board.

The relationship of the height of stems of successive years was analyzed with a non-linear regression (Wilkinson 1990). The regression equation was then used to compute a model growth pattern. Starting with a 0.5 cm tall plant (year 1), the size of the stem in year 2 was computed. This size was then used to calculate the size of next year's stem. This process was reiterated until a final plant size was reached.

RESULTS AND DISCUSSION

Due to the small stature of the host tree *Annona glabra* (mostly less than 4 m), I was able to measure almost all *Dimerandra* plants on the selected trees. The sample therefore provided a good representation of the population structure of *D. emarginata* in this tree species (FIGURE 2). Small plants (< 10 cm) made up about 50% of all individuals. Since tree ages and the time of establishment of individual epiphytes was not known, interpreting this pattern was difficult. However, since mortality of *Dimerandra* plants bigger than 5 cm was very rare over a two-year period (G. Zotz, unpublished data), the population probably consisted mostly of new arrivals (over the last 10–20 yrs) which were still growing.

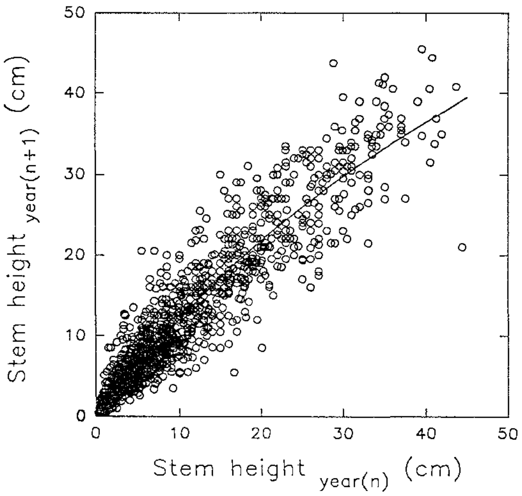

FIGURE 3. Relationship between stem heights in two consecutive years in *Dimerandra emarginata.* Data are from 305 plants over 5 years allowing 1,360 year to year comparisons. The regression line is: $\text{height}_{\text{year}(n+1)} = 1.35 \cdot \text{height}_{\text{year}(n)} / (1 + 0.012 \cdot \text{height}_{\text{year}(n)})$, ($R^2 = 0.89$, $p < 0.001$)

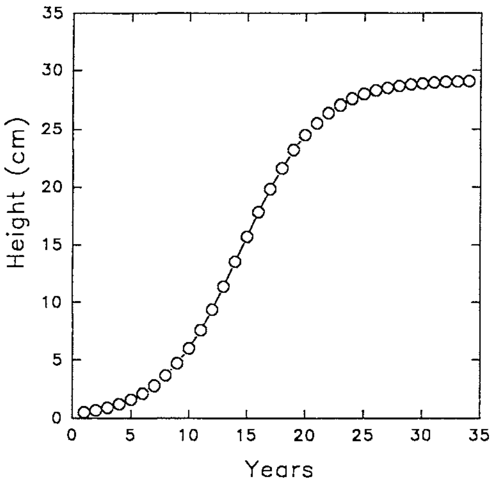

FIGURE 4. Model growth curve of *Dimerandra emarginata,* using the regression equation of FIGURE 3. Plant size at year 1 was set to 0.5 cm as this was the smallest size included in this study.

Vegetative growth of individual plants was analyzed by comparing the stem height of successive years (FIGURE 3). The plot included a total of 1,360 comparisons of pairs of stems from 1989 to 1994. In 75 % of all cases there was an increase in height between years. In ~ 25 %, new stems were as tall as the previous year or smaller. The non-linear regression fitted to the data is: $\text{height}_{\text{year}(n+1)} = 1.35 \cdot \text{height}_{\text{year}(n)} / (1 + 0.012 \cdot \text{height}_{\text{year}(n)})$, ($R^2 = 0.89$, $p < 0.001$). TABLE 1 compares the annual increase in stem height in three different size classes for the period of 1990 to 1994. There was no significant variation between years (repeated measures ANOVA, $p > 0.05$). The number of persistent stems per plant was highly variable. On average, a *Dimerandra* had 5.8 ± 1.4 stems (n = 305, range 3–11). There was a trend towards a larger number of stems in larger plants, but scatter was considerable ($R^2 = 0.11$, $p < 0.001$, $n = 305$). The number of leaves increased with stem size (leaf number = $1.824 \cdot \text{height} / (1 + 0.088 \cdot \text{height})$, $R^2 = 0.94$). For example, small stems (5–10 cm tall) had 6–9 leaves, whereas the largest stems (35–45 cm) ranged from 14–17 leaves per stem. Furthermore, the average leaf of larger plants was also bigger in size (mean area per leaf [cm^2] = $0.013 + 0.433 \cdot$ stem height [cm] $- 0.006 \cdot$ stem height^2 [cm]; $R^2 = 0.95$, $p < 0.001$, $n = 15$). Growth in stem height thus also corresponded to a strong increase of plant leaf area.

The regression of FIGURE 3 allowed the construction of a model growth pattern for *Dimerandra emarginata.* Since only plants > 0.5 cm were included in this study, the initial plant size was set to 0.5 cm. As shown in FIGURE 4, a plant of this size will on average need 30 years to reach a height of 30 cm. However, plants began to produce flowers and fruit much earlier. I observed fruiting in plants as small as 5 cm. A plant with an initial size of 0.5 cm needed less than 10 yrs to begin reproducing. Plants smaller than 0.5 cm were not very frequently found on *Annona glabra.* Since these small plants

TABLE 1. Comparison of mean annual increase in stem length (cm) in *Dimerandra emarginata* for three different size classes. There was no significant variation in annual increments among years (repeated measures ANOVA).

	Growth period						
Size class	1994	1993	1992	1991	1990	*P*-value	df
5–10 cm	2.0 ± 3.1	2.0 ± 2.5	1.6 ± 2.8	1.6 ± 2.9	1.9 ± 2.9	0.84	330
10–15 cm	1.2 ± 3.4	2.5 ± 4.3	2.0 ± 3.6	1.4 ± 3.8	2.6 ± 2.9	0.40	165
15–20 cm	2.1 ± 5.1	1.8 ± 4.2	1.8 ± 3.2	1.1 ± 4.0	2.4 ± 5.5	0.91	127

were stemless in the first years and afterwards did not produce a new shoot every year (G. Zotz, personal observation), a similar reconstruction of past growth by measuring a series of stems was not possible. However, observations of small plants on other host trees over the last two years (G. Zotz, pers. obs.) indicate that this stage lasts for several years.

The results presented here are consistent with the generally accepted view that epiphytes grow very slowly. Surprisingly, the photosynthetic capacity of *D. emarginata* was relatively high when well-watered (about 7 μmol m^{-2} s^{-1}, G. Zotz and M. T. Tyree, unpublished data). These rates were higher than those found in most other epiphytes (Zotz & Winter in press) and comparable to those in plants with higher growth rates (Larcher 1984). The observed low growth rates indicate that in situ favorable conditions for net CO_2 uptake probably occur only rarely or that a considerable proportion of the carbon gain is invested into reproduction. The investment in reproductive output was studied in other epiphytes and has been shown to be very large (Benzing & Davidson 1979).

Slow growth also means that the larger plants must be very old. Orchids are known to live for many decades in greenhouses (Pring 1944, Cooper 1946, Anonymus 1968), but information on longevity in a natural setting is scarce and mostly conjectural (Johansson 1974). As shown in FIGURE 4, a *Dimerandra* plant with several stems of ~ 30 cm can be estimated to be at least as old as 40 — 50 yrs, taking into account a seedling stage (< 0.5 cm) of several years and occasional decreases in stem length during some years (FIGURE 3).

Many epiphyte species seem to suffer high mortality as juveniles (Benzing 1981, Larson 1992, G. Zotz, unpublished data), which may be related to drought stress, because of higher surface to volume ratios in smaller plants. If mortality due to environmental stress is low in later life stages, then survival might be mostly limited by the longevity of the substrate. This is certainly true for epiphytes growing on short-lived twigs (Chase 1987), but larger branches of *Annona glabra* also die back and break off rather frequently (G. Zotz, personal observation). Even large limbs of forest trees might have a longevity that is lower than the life-expectancy of the epiphytes growing on them. Epiphytes on fallen branches of *Annona glabra* normally drown (G. Zotz, personal observation). Epiphytes fallen off forest trees also die rather quickly (Matelson *et al.* 1993).

Slow growth also has important consequences for community processes since a slow-growing epiphyte will not be able to preemptively colonize a dynamic substrate. Co-existence of many physiologically similar species (Zotz & Winter 1994) in a similar micro-habitat is then possible, because densities leading to competition are not reached (Connell 1978). In other words, if new substrate, i.e. growing or newly emerging branches or limbs are formed at a rate similar to or greater than the growth of epiphytes, unused space will always be available for new arrivals (Benzing 1989).

This is the first attempt to quantify in situ growth rates in an epiphytic orchid over several years. Currently a long-term study is underway which will address many further questions, e.g. whether the occasional decrease of stem length from one year to another is related to the reproductive effort of the preceding year as in other species, how much mortality there is in different size-classes, the frequency of recruitment of seedlings, and how many years are needed from the first appearance as a small stemless seedling to reach the minimum size considered in this study.

LITERATURE CITED

ACKERMAN J. D. AND A. M. MONTALVO. 1990. Short- and long-term limitations to fruit production in a tropical orchid. Ecology 71: 263–272.

ANONYMUS 1968. How old is an orchid plant? Amer. Orch. Soc. Bull. 37: 405.

BENZING D. H. 1981. The population dynamics of *Tillandsia circinnata* (Bromeliaceae): cypress crown colonies in Southern Florida. Selbyana 5: 256–263.

——— 1987. Vascular epiphytism: taxonomic participation and adaptive diversity. Ann. Miss. Bot. Gardens 74: 183–204.

——— 1989. Vascular epiphytism in America. In: LIETH, H., AND WERGER, M. J. A. (eds.): Tropical Rain Forest Ecosystems. Amsterdam, p. 133–154.

——— 1990. Vascular epiphytes. General biology and related biota. Cambridge.

——— AND E. A. DAVIDSON. 1979. Oligotrophic *Tillandsia circinnata* Schlecht (Bromeliaceae): an assessment of its patterns of mineral allocation and reproduction. Am. J. Bot. 66: 386–397.

CHASE M. W. 1987. Obligate twig epiphytism in the Oncidiinae and other neotropical orchids. Selbyana 10: 24–30.

CONNELL J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

COOPER E. 1946. Duration of life in Orchids. Orchid Rev. 54: 93–96.

CROAT T. 1978. Flora of Barro Colorado Island. Stanford.

HOLDRIDGE L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI, JR. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, Oxford.

HORICH C. K. 1977. Los kikis y la multiplicación vegetativa de orquídeas por hijos adventicios. Orquideologia 12: 81–93.

JOHANSSON D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr. Suecica 59: 1–136.

LARCHER W. 1984. Ökologie der Pflanzen. 4th Ed., Ulmer, Stuttgart.

LARSON R. J. 1992. Population dynamics of *Encyclia tampensis* in Florida. Selbyana 13: 50–56.

LEIGH E. G., JR., A. S. RAND, AND D. M. WINDSOR, eds. 1982. The Ecology of a Tropical Forest. Seasonal rhythms and long-term changes. Washington, D.C. 468 pp.

MATELSON T. J., N. M. NADKARNI, AND J. T. LONGINO. 1993. Longevity of fallen epiphytes in a neotropical montane forest. Ecology 74: 265–269.

PRING G. H. 1944. The life of an orchid plant. Mo. Bot. Gard. Bull. 32: 111–112.

SANFORD W. W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria. J. Ecol. 56: 697–705.

SIEGERIST E. S. 1986. The genus *Dimerandra.* Bot. Mus. Leafl. Harv. Univ. 30: 199–222.

WILKINSON L. 1990. SYSTAT: the system for statistics. Evanston, SYSTAT Inc.

WINDSOR D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá. Washington.

ZIMMERMAN J. K. AND T. M. AIDE. 1989. Patterns of fruit production in a neotropical orchid: pollinator vs. resource limitation. Am. J. Bot. 76: 67–73.

ZOTZ G. AND K. WINTER. 1994. Annual carbon balance and nitrogen use efficiency in tropical C_3 and CAM epiphytes. New Phytol. 126: 481–492.

——— (in press). Diel pattern of CO_2 exchange in rainforest canopy plants. *In:* A. P. SMITH, S. S. MULKEY, AND R. L. CHAZDON, eds., Tropical Forest Plant Ecophysiology, New York, Chapman & Hall.