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Demography of the epiphytic orchid, *Dimerandra emarginata*

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ABSTRACT. Vegetative growth, reproductive effort, seedling establishment, and mortality of the bark epiphyte, *Dimerandra emarginata* (Orchidaceae), were studied over a 3-y period in the moist lowland tropical forest on Barro Colorado Island, Panama. The study included more than 350 individuals growing on 12 branches of five different host tree species. Mortality was highest among small individuals. Most deaths occurred during the dry season and were probably related to drought. Mortality among older individuals, on the other hand, was always related to the instability of the substrate, i.e. flaking bark, breaking branches or falling trees. Vegetative growth was slow. The average increase in size (= height of the most recent, fully developed shoot) was 2.7 cm over 3 y (not considering 'stemless' seedlings). This increase was negatively correlated with initial plant size. Growth was highly seasonal, with little variation between years. The reproductive effort increased strongly with plant size. Larger individuals produced fruits more frequently, in larger numbers and of larger size. After reproduction, plants showed reduced vegetative growth in the following year (in 1994). There was no negative effect on future reproduction. Compared to seed production, annual recruitment was very low and showed large year-to-year variation. Fewer than 50% of the seedlings survived the first dry season after germination. After 3 y, their average size was 0.5 cm. The results suggest that slow-growing epiphytes such as *D. emarginata* can attain considerable age and that their longevity – after an initial vulnerable juvenile stage – is almost exclusively limited by substrate durability.

KEY WORDS: Barro Colorado Island, demography, *Dimerandra emarginata*, epiphytes, Orchidaceae, Panama, reproductive effort, resource limitation, tropical forests.

INTRODUCTION

Tree crowns present extraordinary challenges to resident flora. Epiphytes occupy scattered 'host islands', i.e. discontinuous substrate with large gaps between individual branches or trunks. This substrate is also highly variable in time. It slowly increases due to the growth of the host tree or is suddenly destroyed when a branch breaks or a tree falls. Once dislodged, survival on the forest floor is usually brief (Matelson *et al.* 1993). Thus, epiphytes should ideally show high growth rates, mature rapidly and produce abundant, highly mobile propagules (Benzing 1978). Some species, such as the small twig epiphytes, approach such a strategy (Chase 1987). In most tropical forests, however, frequent drought or infertile substrates will not allow high growth rates, and maturity appears to require many years (Benzing 1981, 1990; Larson 1992, Zotz 1995).

Actual quantitative evidence for all of these statements is rare. This is particularly true for the estimated 14 000 species of epiphytic orchids (Benzing 1990). Researchers have therefore repeatedly stressed the need for long-term demographic studies (Benzing 1995, Zimmerman & Aide 1989). Recently, the breeding system of tropical orchids has received much attention (Ackerman 1989, Ackerman & Montalvo 1990, Montalvo & Ackerman 1987, Zimmerman & Aide 1989), and this in turn has stimulated the study of vegetative growth to distinguish pollinator *vs.* resource limitation of reproduction (Primack & Hall 1990). However, since only larger, mature individuals were included in these studies, information on the dynamics of natural populations and the vegetative and reproductive performance of individual plants over the entire size range of a species is not available for any epiphytic orchid.

A species that seemed ideally suited for such a demographic study is *Dimerandra emarginata*. This bark epiphyte is abundant in the lowland moist forests of central Panama (Croat 1978, Zotz 1995), and shows unbranched, linear sympodial growth, which greatly facilitates non-destructive, repeated measurements *in situ*. Furthermore, the water, carbon and nutrient relations of this species have already been studied (Zotz 1997, Zotz & Tyree 1996), allowing an ecophysiological interpretation of its demographic profile.

MATERIALS AND METHODS

Habitat and plant material

This study was conducted on Barro Colorado Island (BCI) and the adjacent mainland (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 *c.* 2600 mm with a pronounced dry season from late December to late April (Windsor 1990). During this 4-mo period intervals of no rain last for several weeks. Detailed descriptions of vegetation, climate and ecology are reported by Croat (1978) and Leigh *et al.* (1982). All species names follow Croat (1978).

Dimerandra emarginata (G. Meyer) Hoehne (Orchidaceae) occurs from Mexico to Venezuela (Siegerist 1986). On Barro Colorado Island it is mainly found high in the canopy, but also on exposed lower branches along the shore of Gatun Lake.

Census data

During April and May 1993, eight trees hosting *D. emarginata* were selected. On these trees I demarcated areas on the upper side of horizontal branches with populations of *D. emarginata*. In total, 12 plots were set up, which were 2–36 m above the ground. Consequently, most plots were only accessible by climbing the host trees using single-rope techniques. Plots were designed to include the population of a given branch entirely or at least in its majority. The area of an individual plot was between 720 and 12 500 cm^2. Sites were chosen to incorporate a representative range of different crown microhabitats and various typical host tree species. Some host tree species are evergreen (*Anacardium excelsum*, *Ficus obtusifolia*), while others are semi-evergreen (*Annona glabra*) or deciduous (*Ceiba pentandra*, *Pseudobombax septenatum*). Host trees were growing in the forest or along the shore of Gatun Lake. More than 350 individual epiphytes were marked in May 1993 using coloured telephone wire twisted around the youngest shoot. Small plants were marked with a nearby numbered pin. In addition, a map of each plot with the X- and Y-co-ordinates of the epiphytes was drawn to facilitate subsequent observations. For each plant, the number and height of shoots, and the number of leaves per shoot were determined. Censuses were conducted twice a year in December/January (end of the wet season) and April/May (end of the dry season) until May 1996. During each census I also noted the occurrence of disease and herbivory and the occurrence of flowers or fruits. The flowering season was mostly finished at the December census date. Therefore, only fruits were considered. When new plants germinated, they were also marked and mapped. Additional offshoots developed a few times at the tip of older, leafless shoots, but were ignored.

The size of a plant was defined as the height of the most recent, fully developed shoot in cm (Figure 1). A few times, two shoots were produced in the same year. In those cases, the two shoots were treated as one and their heights were summed. To estimate leaf area I used a relationship between mean leaf area per leaf of a shoot and shoot height. This was determined by measuring the area of all the individual leaves of 31 shoots of different heights with a leaf-area meter, plotting mean leaf area per leaf against shoot height, and fitting a non-linear regression to the data set. Because shoot morphology varied with plant size, two different equations were used to estimate leaf area (cm^2) for smaller (<1.5 cm height) and for larger plants (1.5–50 cm): mean area per leaf = 0.54 shoot height$^{1.65}$ ($r^2 = 0.98$), and mean area per leaf $= -9.27 + 4.75 \ln(\text{shoot height} + 6.36)$ ($r^2 = 0.94$), respectively. In the field, it was thus only necessary to measure shoot height and count the number of attached leaves.

Reproduction

Mature fruits of 13 plants (size: 7–44 cm) were collected in March 1997. The dry weight was determined after 3 d at 60 °C. The seeds of four of these fruits (plant size 15–37 cm) were counted with a particle counter (Coulter Counter, Coulter Electronics, Luton, Beds, England).

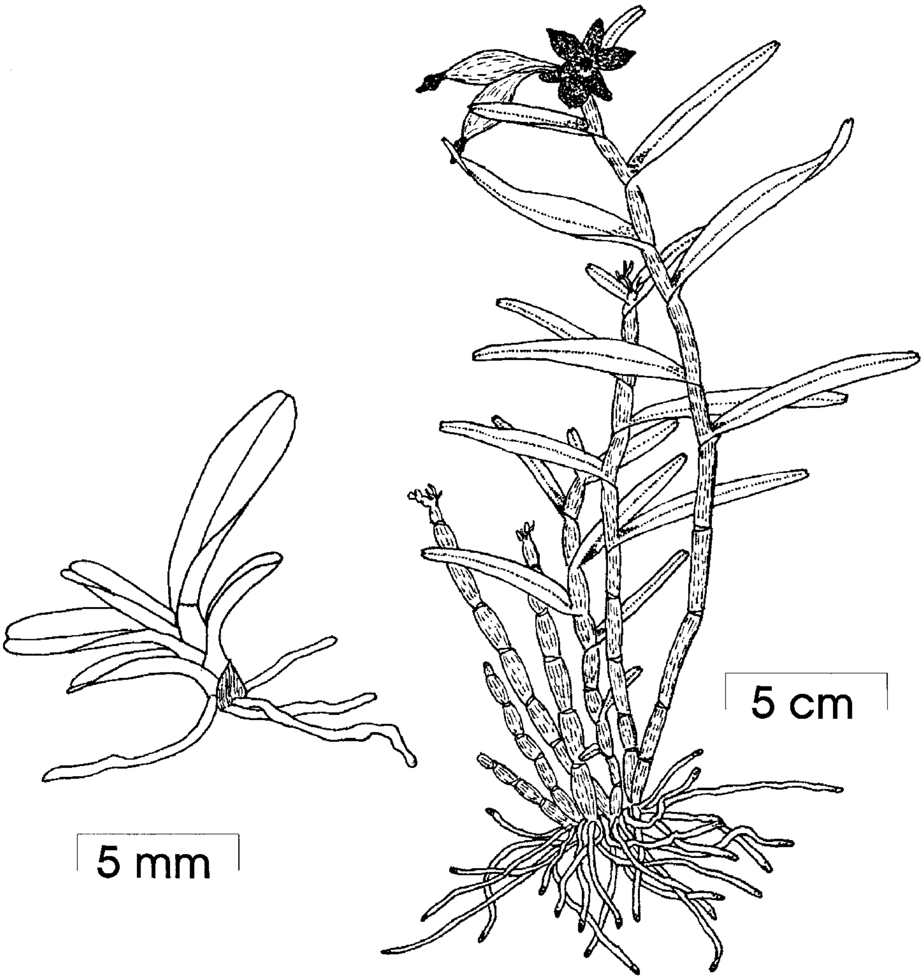

Figure 1. The form of habit of *Dimerandra emarginata*, showing a 'stemless' juvenile and a fruiting plant. Note the different scales.

Statistical analysis

In most cases the frequency distributions of the data were highly skewed to the right and had to be transformed before analysis (Sokal & Rohlf 1995): a square-root transformation yielded normally distributed data. After analysis regression lines and confidence limits were back-transformed to the linear scale.

RESULTS

Plant and leaf phenology

D. emarginata is sympodial (Figure 1). Each year in the late dry season (March–April) a new shoot emerges from the base of the previous shoot and grows through most of the wet season. The basal portions of successive shoots form the horizontal rhizome which is normally closely attached to the substrate. Censused plants consisted of up to eight shoots, one to four of which still bore leaves. Plant size and the number of shoots were correlated ($r = 0.80$, $n = 306$, $P < 0.05$; square-root transformed data of all plants ≥ 1 cm in May 1993). Shoot number changed with season. As shown in Table 1, most plants showed a net increase of shoots during the rainy season and no change or a net decrease during the dry season. Flowering occurred from late August to January. Developing fruits reached full size during the following dry season and usually dehisced at the beginning of the next wet season. This general scheme was different in seedlings and small plants (<1 cm). Seedlings were 'stemless' (i.e. without elongated internodes) for several years, although due to overlapping leaf bases the plants attained a height of up to 1 cm. In both seedlings and plants <1 cm, the production of a new shoot could be delayed for up to 3 y. Rarely, larger plants deviated from the above pattern by developing branching rhizomes or by growing additional offshoots at the tip of older shoots. These offshoots were generally small (<5 cm) and developed following the same annual pattern.

Table 1. Net changes in the number of shoots in *D. emarginata*. Included are all plants ≥ 1 cm (n = total number of individuals). For each season, the mean change in shoot numbers and the percentage of plants with a particular net change in shoot numbers are shown.

Year	Season	Net change in shoot number							
		mean	+2	+1	0	−1	−2	−3	n
1993	Rainy	+0.86	0	86	14	0	0	0	306
1994	Dry	−0.34	0	0	70	26	4	0	309
	Rainy	+0.78	1	78	19	2	0	0	306
1995	Dry	−0.62	0	0	55	32	12	2	299
	Rainy	+0.66	1	69	26	4	0	0	288
1996	Dry	−0.67	0	0	41	49	9	0	274

Because of the seasonal growth pattern, the relationship of plant size and plant leaf area (PLA) was different in the dry and the wet season (end of the 1993 dry season: $\log_{10}(\text{PLA}) = -0.020 + 1.385 \log_{10}(\text{size})$, $r^2 = 0.92$, $P < 0.001$, $n = 354$; end of the 1993 wet season: $\log_{10}(\text{PLA}) = 0.086 + 1.481 \log_{10}(\text{size})$, $r^2 = 0.96$, $P < 0.001$, $n = 387$). The leaves are arranged distichously on the youngest shoots (Figure 1). For a more detailed analysis of leaf phenology I followed the fate of all leaves present in the December 1993 census (Table 2). The half-life of a leaf was less than 2 y. Only *c.* 5% of all leaves survived 3 y and only 1 out of 1000 leaves reached an age of more than 4 y. Twice as many leaves were lost during the 4-mo dry season than during the 8-mo rainy season (Table 2).

Survival and establishment

The original size class distribution of the 354 individual plants is shown in Figure 2a. About 50% of all plants were < 5 cm, and the largest plant of this

Table 2. Leaf life-table of *D. emarginata*, using all leaves present in December 1993. New leaves developed during the rainy season. Any mortality in the months before the first census at the end of the rainy season is ignored (i.e. not determined, n.d.). Given are the numbers and age at the beginning of each period, the proportion of the initial cohort dying (mortality, d_x) and the mortality rate (q_x) during a given period.

Age (y)	Season	Number	Mortality (d_x)	Mortality rate (q_x)
0	rainy	n.d.	n.d.	n.d.
	dry	1000	0.241	0.241
1	rainy	759	0.171	0.226
	dry	588	0.267	0.455
2	rain	320	0.105	0.329
	dry	215	0.135	0.627
3	rainy	80	0.033	0.416
	dry	47	0.040	0.845
4	rainy	7	0.004	0.533
	dry	3	0.002	0.714
5	rainy	1	0.001	1.000

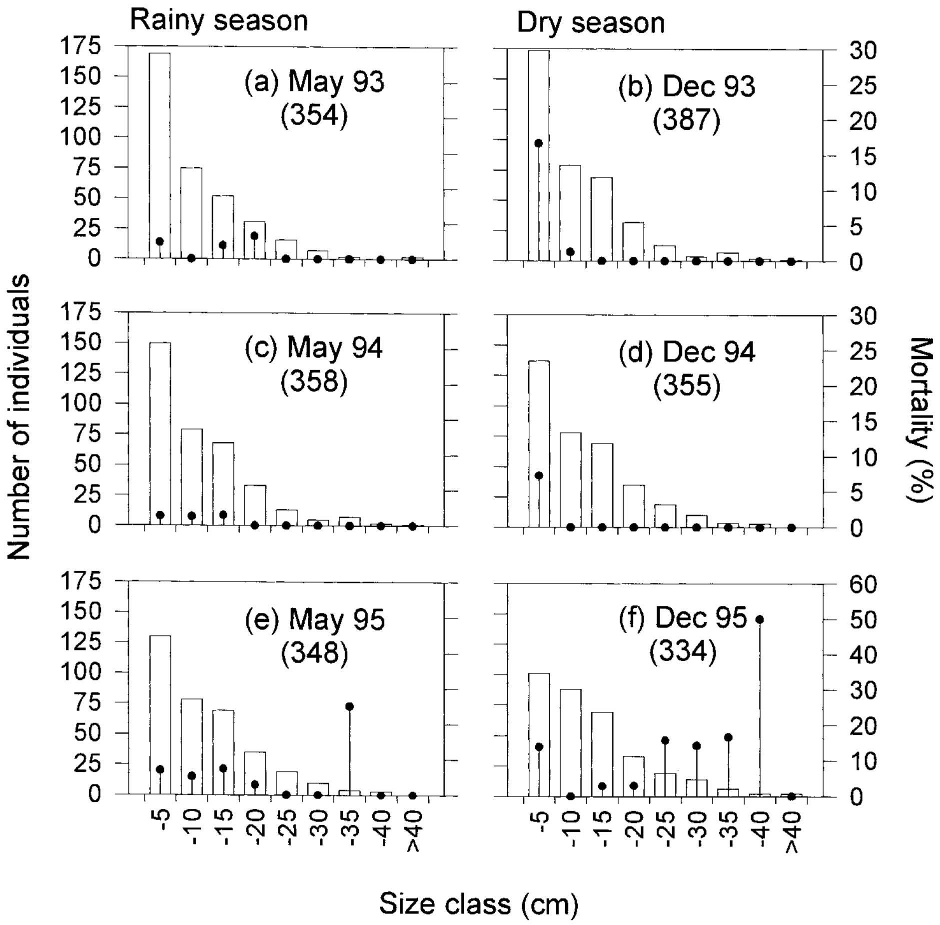

Figure 2. Population size class distribution and mortality in *D. emarginata*, showing histograms of the size class distributions in populations (open bars) at the beginning of the rainy and dry seasons from May 1993 to December 1995 and the seasonal mortality rates (in % of a size class, closed circles) during the following rainy and dry seasons, respectively. Note the different scales of the Y – axis (mortality) in 1993 and 1994 compared to 1995. Numbers in parenthesis are the population sizes.

study measured 46 cm. Mortality showed a strong seasonality (Figure 2a,b). Of the 37 plants that died during the 12 mo after May 1993, 31 died during the dry season. Mortality was also highly size-dependent. It was highest in the size class <5 cm: 17% of these small plants died in the first year of this study (Figure 2a,b). The observed seasonal changes in the mortality of smaller plants make desiccation the most probable cause of death. No mortality was observed among larger plants (>25 cm). The two losses among intermediate-sized individuals (10–20 cm) occurred in the rainy season in the two populations growing on *Ficus obtusifolia*. A majority of the plants growing on this host tree species were loosely attached to the smooth, peeling bark by just a few roots. Thus it seems probable that the missing plants were dislodged during heavy rainstorms or by animals (Perry 1978).

While the mortality patterns in 1994 (Figure 2c,d) were comparable to those in 1993, there was a significant difference in 1995 (Figure 2e,f) caused by two accidents. The first accident occurred in late 1995 when a branch of *Anacardium excelsum* (plot 3) broke off, leaving only one epiphytic plant at the base of the branch. In the second case, an entire tree growing close to the shore of Gatun Lake (*Annona glabra*, plot 6) tipped over in early 1996, killing its epiphytes. Otherwise, seasonal and size-related patterns of mortality were similar in all of the 3 y (data not shown).

Between May 1993 and May 1996, 53 new seedlings were counted. Year-to-year variation was very large, with 41 seedlings in 1993, four in 1994, and eight in 1995. The survival of these plants is shown separately in Figure 3. Without exception, germination occurred in the rainy season. Most deaths, on the other hand, occurred in the first dry season after germination, when only 26 plants (<50%) survived. The mortality rates in the following wet and dry seasons were much lower, ranging from 10 to 20%. These figures are probably conservative because any losses prior to the first census at the end of a rainy season would have remained unnoticed.

Symptoms of diseases were only observed twice. A large plant (size: 26 cm) was defoliated by an unidentified fungus in the early 1993 rainy season. A new shoot emerged in May 1994. A second plant (size: 21 cm) growing on another tree developed a multitude of small shoots (<1 cm) during the 1994 rainy season. It failed to grow a normal shoot over the next 2 y and the large shoots had lost all but two leaves by May 1996. It was still alive in March 1997, but only three small green shoots remained.

Herbivory was only rarely observed. Signs of leaf herbivory were detected on no more than 1% of all plants during any census. Fruit herbivory was observed once in 3 y. The only herbivore which was found and identified was the caterpillar of *Cremna thasus* (Riodinidae), a species which also feeds on other orchids such as *Caularthron bilamellatum* (DeVries 1996).

Vegetative growth

Without destructive sampling, vegetative growth cannot be studied directly as biomass increment. Instead, growth was analysed by determining leaf area

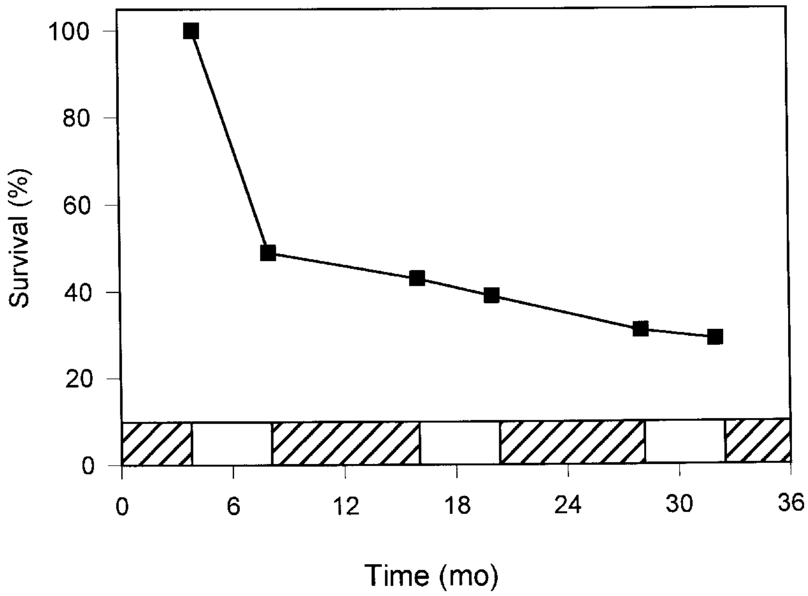

Figure 3. Survival of seedlings of *D. emarginata* over a 3-y period. The total number of new seedlings was 53 from May 1993 to May 1996. Germination was only observed in the rainy season. The rainy season (hatched bars) lasted twice as long as the dry season (open bars). Since censuses were conducted at the end of these periods, the mortality occurred during the preceding season.

changes over time or by comparing shoot heights of successive years, respectively. The seasonal net changes in plant leaf area (PLA) from May 1993 through May 1996 are depicted in Figure 4. On average, PLA increased by almost 100% during the rainy season (May–December). Virtually all of this increase in PLA was lost, however, in the following dry season, resulting in almost no net change in PLA over a 12-mo period. The average changes in plant size (= length of the most recent shoot) from year to year were also moderate. They were size-dependent, with considerable variation among individuals (Figure 5). On average, smaller individuals (<10 cm) increased >30% annually in size, while the largest plants (>30 cm) showed no increase or even a slight decrease.

In addition, size changes were also quantified for the entire 3-y period. The 290 plants of the original population that survived until May 1996 (excluding 'stemless' seedlings), were on average 2.7 ± 4.9 cm (mean ± SD) larger than in May 1993, and had also increased in leaf area by 8.1 ± 23.9 cm^2 (mean ± SD). As expected, this long-term increase (cm) was also size-dependent (size increase over 3 y = 4.0 – 0.55 (size May 1993)$^{0.5}$ ($r^2 = 0.03$; $P = 0.02$). For example, the average difference in shoot length for May 1996 *vs*. May 1993 was 3.4 cm for 1–10-cm tall plants, 1.2 cm for those 10–20 cm tall, and 1.1 cm for larger plants. These average figures conceal, however, that some plants showed much higher growth rates. For example, the largest absolute increase in size was observed in a plant growing on *Anacardium excelsum*, which increased from

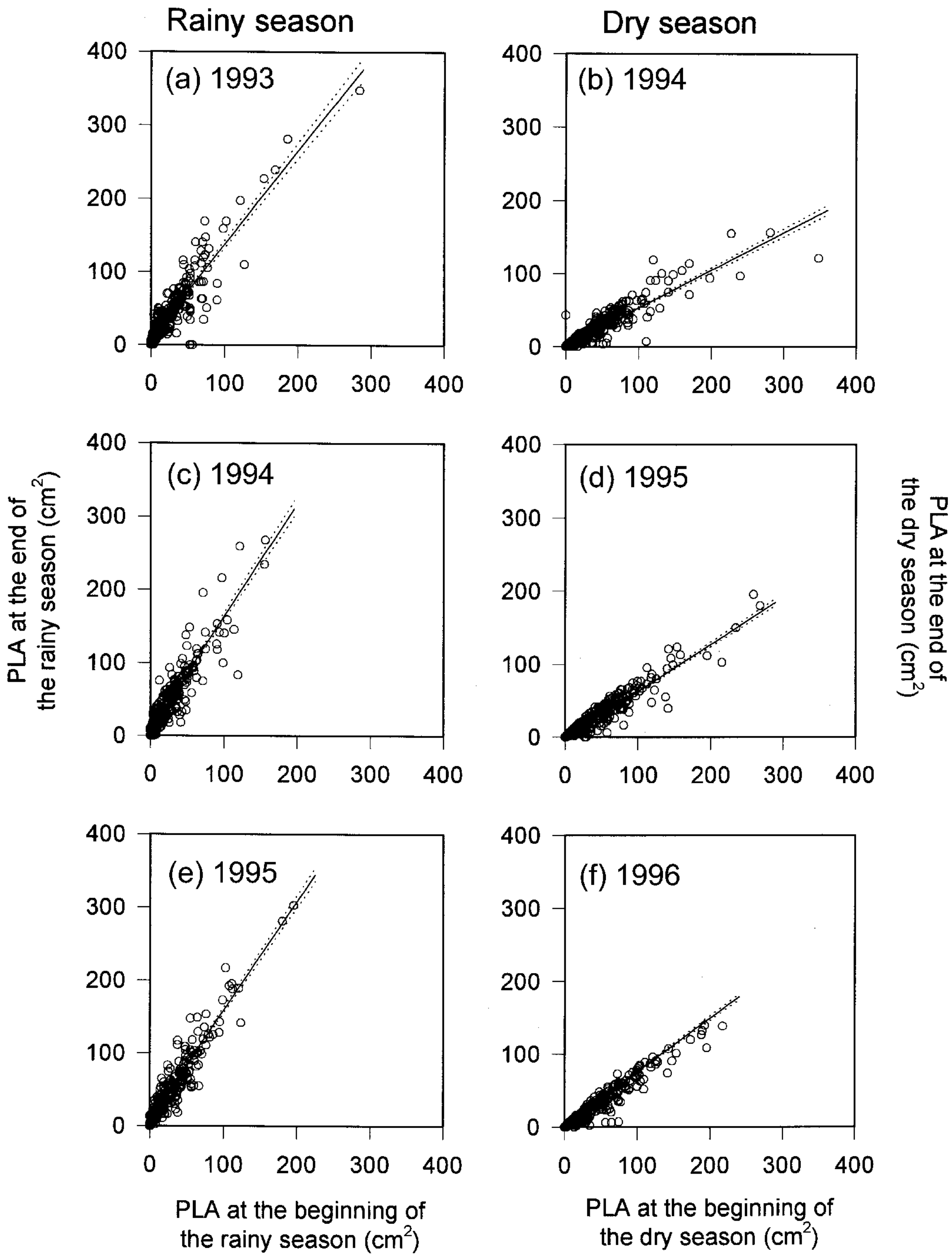

Figure 4. Vegetative growth in *D. emarginata*. Shown are the net changes in plant leaf area (PLA) during three rainy (a,c,e) and three dry seasons (b,d,f), respectively, from May 1993 to May 1996. The solid lines are linear regressions and the dotted ones the 95% confidence intervals of square-root transformed data. The correlation coefficients were between 0.84–0.93. The number of individual plants ranged from 354 (May 1993) to 312 (May 1996).

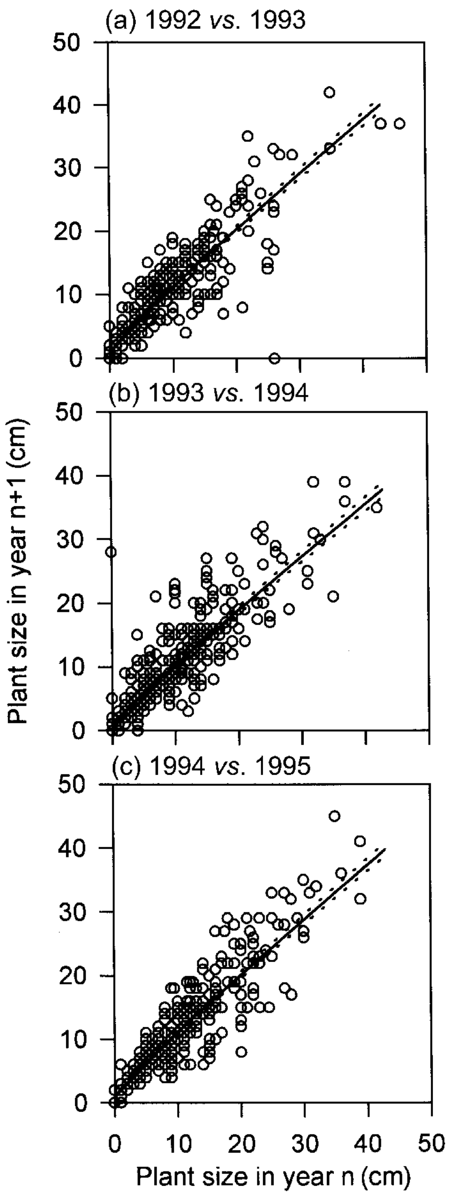

Figure 5. Vegetative growth in *D. emarginata*. Shown are the relationships of plant size (= length of the most recent shoot) of two consecutive years. The solid lines are linear regressions and the dotted ones the 95% confidence intervals of square-root transformed data. The correlation coefficients were between 0.76–0.84.

15 cm in May 1993 to 33 cm in May 1996. The largest relative increase in size was found in a smaller individual on another tree: it grew from 1 cm to a size of 7 cm in the same period.

Finally, growth was analysed separately using the 14 seedlings that had germinated during the 1993 rainy season and survived until May 1996. The average size after almost 3 y was 0.5 ± 0.3 cm (mean ± SD, range 0.2–1.2 cm).

Fruiting

The breeding system of *D. emarginata* is unknown. However, circumstantial evidence suggests at least facultative autogamy or apomixy: (1) in all cases when a flower was observed in the December census ($n = 12$), a fruit had developed by the time of the next census in April/May, (2) six plants kept in a greenhouse in Würzburg, repeatedly set fruit in the last years.

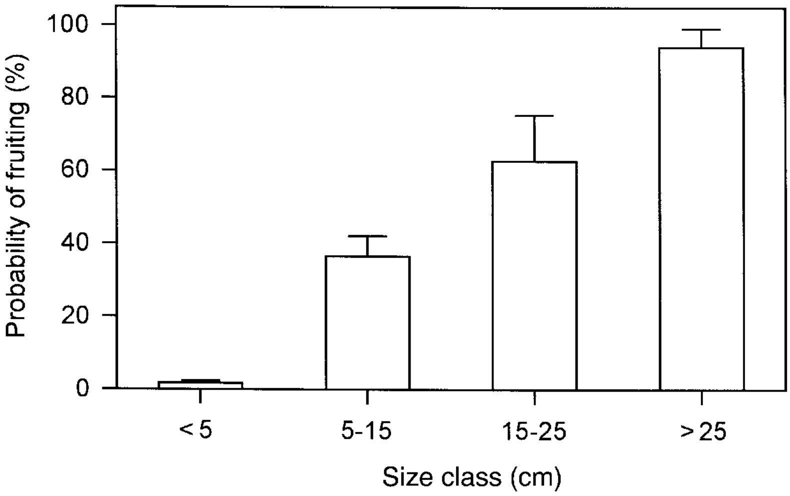

Figure 6. Relationship of plant size and the probability of a fruiting event in *D. emarginata*. Values are means ± SD ($n = 3$ y). Only plants surviving the entire study period were included ($n = 294$). For each individual, plant size was averaged over the 3 y. The correlation of plant size and fruiting was significant (Kendall's $\tau = 1.00$, $df = 2$, $P = 0.04$).

The probability of fruiting increased linearly with size (Figure 6). Plants <5 cm only flowered and fruited in rare cases, whereas almost all plants > 25 cm produced fruits in each of the three years. Larger plants not only fruited more frequently, but they also produced more (Figure 7) and heavier fruits (fruit dry weight [mg] = 110 + 3 plant size [cm]; $r^2 = 0.66$, $n = 13$, $P < 0.001$). Up to four fruits developed on a single shoot. Fruits were observed on shoots of almost all ages, but most frequently on those of the previous year (Table 3). The most recent shoot bore only about 20% of all fruits, comparable to the combined production of the leafless, 3- to 5-y old shoots.

Fruit-set in one year had no effect on reproduction in the next year. The following observations support this statement: of the 42 plants that fruited in all three years of this study, the number of fruits of consecutive years decreased in only one third of all cases. Usually, the number of fruits remained constant (35%) or even increased (31%). In the 43 plants which fruited only twice, but in consecutive years, a similar picture emerged with 30% of all plants with decreased, 47% with constant, and 23% with increased fruit set. Vegetative growth, on the other hand, was affected. Plants that had fruited tended to show decreased growth during the following wet season; the average height difference between successive shoots was zero or even negative (Figure 8).

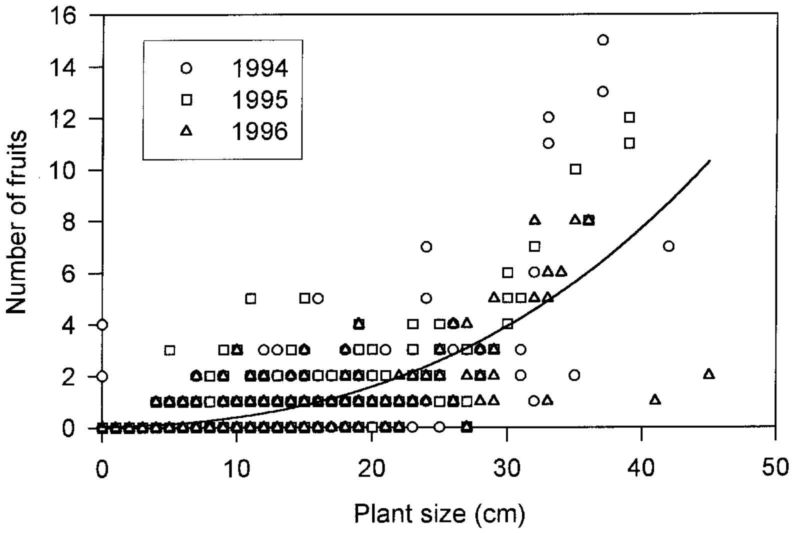

Figure 7. Relationship of plant size and number of fruits per plant and year from 1994 – 1996. The solid line is the best-fit polynomial regression: number of fruits = 0.039 + 5.91 10^{-3} (plant size) + 2.47 10^{-3} (plant size)^2 + 5.5 10^{-5} (plant size)^3 ($r^2 = 0.54$, n = 870).

On a population level, the total numbers of fruits (= 716 capsules/3 y) should be compared to the number of germinated plants (= 53 plants/3 y). There was no correlation of the number of fruits in a plot and the number of seedlings in the following rainy season (Table 4). For the estimation of the probability of successful germination of a seed the following assumptions were made: (1) germination occurs primarily in the vicinity of the mother plant, i.e. within the same plot (Benzing 1990), (2) seeds can only germinate in a few months after dispersal (Benzing 1990), (3) germination outside the plot is balanced by an equal number of germinants inside the plot from imported seeds. The number of seeds was determined for four fruits of four plants. Fruits contained 146 000 seeds (plant size 15 cm) to 273 000 seeds (plant size 37 cm), averaging 213 000 ± 67 200 seeds/fruit (mean ± SD). Using an estimate of $2 \cdot 10^5$ seeds per capsule, less than one out of two million seeds may have yielded a seedling. Even if the third assumption may be wrong by one order of magnitude, the basic conclusion would hold: successful germination is rare in *D. emarginata*.

Table 3. Distribution of fruit-bearing shoots in *D. emarginata*. Percentages of fruits produced on shoots of different ages were computed separately for 1994–1996. Shown are means ± SD for the three years. All included plants had at least five shoots. Total fruit production amounted to 262 (1994), 249 (1995), and 205 fruits (1996).

Age of shoot (y)	% fruits
Current year	19.8 ± 13.1
1	37.8 ± 7.8
2	24.5 ± 6.7
3	11.2 ± 2.7
4	5.6 ± 2.7
5	1.6 ± 1.3

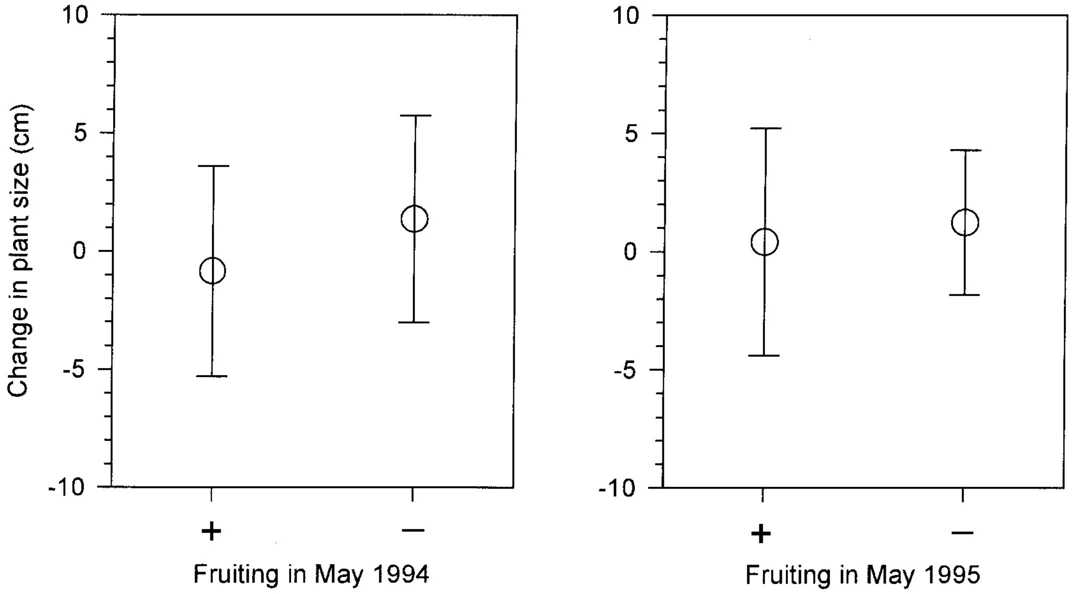

Figure 8. Effect of fruiting on vegetative growth. Compared are the size increases of plants (means ± SD) which had fruited the previous year *vs.* those plants which had not fruited. Differences were significant in 1994 (P = 0.002), but not in 1995 (P = 0.45, t-test for independent samples). All plants ≥ 5 cm (n = 211 for 1994; n = 208 for 1995) were included in the analysis (compare Figure 6).

Recruitment did not balance mortality. This is the case even when excluding the losses caused by the two catastrophes. There was a total of 321 individuals in May 1993 (without plots 3 and 6) and 312 in May 1996. During these three years the number of individuals decreased in six, stayed constant in two, and increased in two plots (Table 4).

Table 4. Comparison of fruit set in the dry season and successful germinations in the following rainy season in *D. emarginata*. Given are the total number of fruits in a plot and the number of seedlings in 1994 and 1995, respectively, for 12 plots. Also given are the changes in population size from May 1993 through May 1996.

Plot number	1994 Number of		1995 Number of		Changes in population size (n)
	Fruits	Seedlings	Fruits	Seedlings	
1	18	0	57	0	−1
2	11	0	15	0	0
3	5	0	2	0	destroyed
4	4	1	8	0	−1
5	3	0	11	4	+2
6	35	2	35	1	destroyed
7	66	0	61	0	0
8	16	0	22	0	−1
9	12	0	18	0	+3
10	30	0	24	0	−2
11	22	1	27	0	−3
12	21	0	8	3	−6

DISCUSSION

D. emarginata grows slowly. After 3 y, seedlings were usually without a visible stem, and averaged only 0.5 cm in height. Growth rates increased in intermediate-sized plants, but were still moderate. For plants between 1 and 10 cm in size, the average size increase (= 1995 shoot length – 1992 shoot length) was about 3 cm in 3 y. In still larger plants vegetative growth decreased again. These results are largely consistent with an earlier report on growth in this species (Zotz 1995). *Dimerandra emarginata* does not flower until plants reach a size of 5 cm (Figure 6). Consequently, between 6 and 10 y are required to mature, which is comparable to estimates for other vascular epiphytes such as *Tillandsia paucifolia* (Benzing 1981). Thereafter, the relative investment in vegetative growth decreases (Figure 5), as reproductive effort rises (Figures 6, 7). Quite likely these two phenomena are causally related, considering that the relative investment of both carbon and nutrients in fruits is quite substantial in the epiphyte species studied to date (Benzing & Davidson 1979, Benzing & Ott 1981; G. Zotz, unpubl. data). A negative effect of reproductive effort on vegetative growth in the next year as shown in Figure 8 seems typical for orchids (Ackerman 1989, Ackerman & Montalvo 1990, Montalvo & Ackerman 1987, Primack & Hall 1990, Zimmerman & Aide 1989; but see Calvo 1990) and for many other plants (Bazzaz 1996). Most pertinent studies also report a negative effect on future reproduction (Ackerman 1989, Ackerman & Montalvo 1990, Montalvo & Ackerman 1987, Primack & Hall 1990, Zimmerman & Aide 1989). In *D. emarginata*, however, there is no indication of such an effect. This might be related to the breeding system of this species. Since *D. emarginata* is probably selfing, the investment in fruits should be under complete control of the plant. Reproduction should be only resource-limited, which is consistent with the observed tight correlation among fruit numbers, fruiting probability, and average fruit dry weight with size (Figures 6, 7).

Vegetative growth was strongly influenced by climatic conditions, in particular water supply. In all but the smallest individuals, plant leaf area increased considerably during the rainy season (Figure 4), accompanied by a net increase in the number of shoots (Table 1). During the dry season, on the other hand, plants lost much leaf area (Figure 4, Table 2) and older back shoots dried out (Table 1). This seasonal pattern is at least in part controlled directly by precipitation because leaf shedding starts a few days after severe drought begins and ceases immediately after re-irrigation (Zotz & Tyree 1996).

Slow growth is often associated with longevity. Zotz (1995) estimated the largest individuals of *D. emarginata* to be at least 40–50 y old. Scattered reports about other species growing in the greenhouse give similar or even higher values (Anonymous 1968, Cooper 1946, Pring 1944). Great age is not exclusive to epiphytic herbs. Many terrestrial herbs such as *Hepatica nobilis* or *Sanicula europaea* are known to live for many decades (Inghe & Tamm 1985, 1988). An important difference between terrestrial and epiphytic plants becomes obvious when the longevity of plants and substrate are compared. Branch-falls and tree-falls are frequent in tropical forests (van der Meer & Bongers 1996). In such a dynamic system, the longevity of the substrate might often limit the longevity of epiphytes more than any other biotic or abiotic factor (e.g. drought), once the plants have survived the precarious juvenile stage (Benzing 1990). Substrate instability may have consequences on a small scale when smooth bark like that of *Ficus obtusifolia* does not allow plants to secure themselves to the tree. It may have consequences on a larger scale, when, for example, a tree-fall destroys an entire population of epiphytes. Two such catastrophes occurred during this study when a total of 37 orchids were killed as the result of a tree-fall and a branch-fall (Figure 2e,f). Other authors also documented high density- and size-independent mortality: almost 90% of all deaths of mature *Aspasia principissa* (Orchidaceae) resulted from plants falling from or with their substrate (Zimmerman & Aide 1989).

Such accidents will affect epiphytes irrespective of plant size. Drought, however, has quite different effects on smaller and larger individuals. Because a substantial number of small plants on intact branches died during the dry season, desiccation is assumed to be the leading cause of death. Small, i.e. young, plants of *D. emarginata* possess less favourable surface/volume (S/V) ratios than larger ones (Zotz & Tyree 1996). Since bark-dwelling plants lack access to soil which may act as an external water reservoir during rainless periods, S/V ratios may be especially crucial for persistence during drought and may explain the increased vulnerability of smaller individuals to desiccation. This is analogous to plants in desert habitats (Nobel 1988). Plant size *per se* also seems to be important because under stress larger epiphytes can sacrifice 'expendable' parts such as leaves (Figure 4, Table 2) or older shoots (Table 1), thus achieving a more favourable S/V ratio. Small plants, in particular seedlings, do not have this option. Mortality caused by herbivores and pathogens appeared to be rare. Other epiphytic species seem to suffer much higher losses related to herbivory (Ackerman 1989, Ackerman & Montalvo 1990).

In conclusion, seasonal and size-related patterns of mortality suggest that the only major cause of mortality in small individuals of the bark epiphyte, *D. emarginata*, is desiccation. Once plants have passed this vulnerable stage, their longevity is limited almost exclusively by the durability of the substrate. As mature plants become larger, the balance of vegetative and reproductive investment shifts towards the latter. In spite of high seed production, successful recruitment is very low.

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