

SIZE DEPENDENCE IN THE REPRODUCTIVE ALLOCATION OF *DIMERANDRA EMARGINATA*, AN EPIPHYTIC ORCHID

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Reproductive allocation is generally defined as the proportion of resources, for example biomass or nutrients, invested in reproductive organs or parts thereof (e.g., seeds) (Bazzaz 1996). Since most vascular epiphytes face both high abiotic stress and frequent disturbance (*sensu* Grime 1977), epiphytes are expected to use a large proportion of their resource pool to support fecundity (Benzing 1990). Indeed, the little information available for vascular epiphytes (i.e., for two species of orchids and one bromeliad, Benzing & Davidson 1979, Benzing & Ott 1981, Zotz 1999) reveals that, e.g., between 10 and 33% of total plant nitrogen and 16 to 29% of the plant phosphorous pool were invested in maturing fruits. This exceeds the reproductive investment in the majority of other, terrestrial perennials and reaches a level similar to many annuals (Hancock & Pritts 1987). A question of major interest in relation to life-history strategies is whether or not reproductive allocation varies with plant size (e.g., Schaffer 1974, Samson & Werk 1986). Such size dependency has been shown repeatedly in a large number of plants (e.g., Samson & Werk 1986). However, in spite of the fact that vascular epiphytes comprise c. 10% of all cormophytes (Benzing 1990), no study has addressed the size dependence of reproductive allocation in this group: the three studies mentioned above are of rather limited value in this context, because they either used only one size class (Zotz 1999) or did not even specify plant size (Benzing & Davidson 1979, Benzing & Ott 1981).

Considering this lack of information, the following study was initiated with the orchid *Dimerandra emarginata* (G. Meyer) Hoehne. This particular orchid

was chosen because it is one of the few tropical epiphyte species for which much physiological and ecological background information is already available (e.g., Zotz & Tyree 1996, Zotz 1998, Zotz 1999). For example, it is known that the species is at least facultatively autogamous (Zotz 1998). Size-dependent differences in pollinator limitation due to, e.g., larger display size in larger plants (compare Rodríguez-Robles *et al.* 1992) can therefore be excluded: reproductive effort is expected to be under complete control of the individual plant. At the study site, the moist tropical forest of Barro Colorado Island, Panama (for a description of the vegetation see Leigh *et al.* 1982), *D. emarginata* is quite common in the upper strata of the forest and at more exposed sites in smaller trees on the shore of Lake Gatun. The species features a sympodial growth form, with the production of one new vertical shoot per year arising from a horizontal rhizome attached to the substrate. Growth is quite slow: larger individuals are estimated to be several decades old (Zotz 1998). Flowering occurs mostly in the late rainy and early dry season from late August to January. Developing fruits mature during the dry season and usually dehisce at the beginning of the following wet season.

At the end of the 1999 dry season I collected 23 entire plants with nearly mature fruits, encompassing the entire adult size range (Zotz 1998), i.e., 4–35 cm length of the most recent shoot. Vegetative dry mass ranged from 1.1 to 12.1 g. The collection was made as follows. First, only specimens growing under similar environmental conditions in the central crown of a single host tree species, *Annona glabra* L., were considered. Secondly, irrespective of the number of fruits, I sampled only every third reproductive plant of a

given size which I encountered, in order to avoid a collecting bias. Because the quantitative removal of the entire root system from the bark of the host tree is very cumbersome, total root biomass was estimated using an already established allometric relationship between the root to shoot ratio (r/s) and shoot dry mass (s , in g) ($r/s = 0.812 - 0.544 (\log s) + 0.141 (\log s)^2 + 0.033 (\log s)^3 + 0.031 (\log s)^4 - 0.017 (\log s)^5$, $n = 36$ plants, range 0.5–35 cm shoot length, $r^2 = 0.78$; Zotz & Schmidt, unpublished). After collection, samples were separated into their component parts, i.e. leaves, stems, roots and capsules (including the short peduncle). After 2 weeks at 65°C, dry mass was measured. Mineral nutrient concentrations were determined subsequently at the University of Würzburg with an ICP spectrometer (JY 70 plus; ISA, Munich, Germany) and a CHN-O element analyser (Heraeus, Hanau, Germany). These measurements allowed reproductive allocation to be expressed not only in terms of biomass but also in terms of key nutrients such as nitrogen, phosphorus, or potassium. This approach is important in view of the ongoing debate on the correct currency of reproductive investment (e.g., Bazzaz & Ackerly 1992).

There was much variation in capsule numbers (range 1–8 per plant) and capsule mass (0.08–0.35 g per capsule), and both the number of fruits ($r = 0.56$, $P < 0.01$) and total fruit mass ($r = 0.52$, $P < 0.001$) increased significantly with plant size. However, this increase in reproductive output was simply proportional to the increase in plant size. As shown in Fig. 1, neither measure of reproductive allocation, i.e., the relative allocations of plant biomass, macronutrients like nitrogen, phosphorus, and potassium, or other nutrients (Table 1) in reproduction, showed a significant size dependence ($P > 0.74$). Irrespective of plant size, a fruiting *D. emarginata* plant invested on average c. 13% of its biomass, c. 12% of its nitrogen, c. 18% of its phosphorus, and c. 31% of its potassium pool in mature fruits. These averages conceal a considerable scatter. For example, the relative proportion of plant K found in mature fruits ranged from 12 to 58%, and the relative proportion of plant biomass in fruits varied even more, i.e., between 4 and 25%, or by a factor of six (Fig. 1). While single fruiting events do therefore not scale with plant size, the frequency of fruiting does. In a three-year demographic study with *D. emarginata*, Zotz (1998) found that almost all plants > 25 cm reproduced every year, while smaller individuals showed a successively lower probability of fruiting: plants 15–25 cm in size fruited in

TABLE 1. Average nutrient concentrations in mature capsules of *D. emarginata* and reproductive allocation (RA = fruit nutrient content/vegetative plant nutrient content \times 100). Data are means \pm SD ($n = 23$). Neither measure of RA correlates with plant size ($P > 0.7$).

Nutrient element	Concentration ($\mu\text{g g}^{-1}$)	RA (%)
K	19987 \pm 1535	30.7 \pm 12.4
P	769 \pm 157	17.6 \pm 7.0
Mg	1542 \pm 257	12.0 \pm 6.3
Zn	12 \pm 5	12.0 \pm 6.8
N	7320 \pm 101	11.7 \pm 5.3
S	515 \pm 59	8.3 \pm 4.7
Mn	17 \pm 11	6.8 \pm 3.1
Ca	4243 \pm 910	5.8 \pm 2.8
Fe	23 \pm 9	2.4 \pm 1.5

two of three years, plants of 5–15 cm reproduced every third year, while smaller plants fruited only in exceptional cases. In consequence, there is a strong size effect when the production of fruits is expressed as the average annual reproductive investment (Table 2). The average annual proportion of plant biomass allocated to reproduction increases continuously from less than 1% in plants just surpassing the minimum threshold of plant size for reproduction (i.e., c. 5 cm, Zotz 1998) to c. 12% in the largest plants (Table 2). Trends in other resources were even more impressive, e.g., from c. 2% to c. 29% in the case of potassium.

TABLE 2. Size-related differences in reproductive allocation (RA) expressed as estimated annual proportion of plant dry mass invested in fruits. Similar qualitative results emerged when RA was expressed on the basis of N, P, or K investment. The table integrates annual probabilities of fruiting (Zotz 1998) and data from Fig. 1.

Size class	Annual RA (% vegetative DM)
< 5 cm	0.2
5–15 cm	4.7
15–25 cm	8.0
> 25 cm	12.1

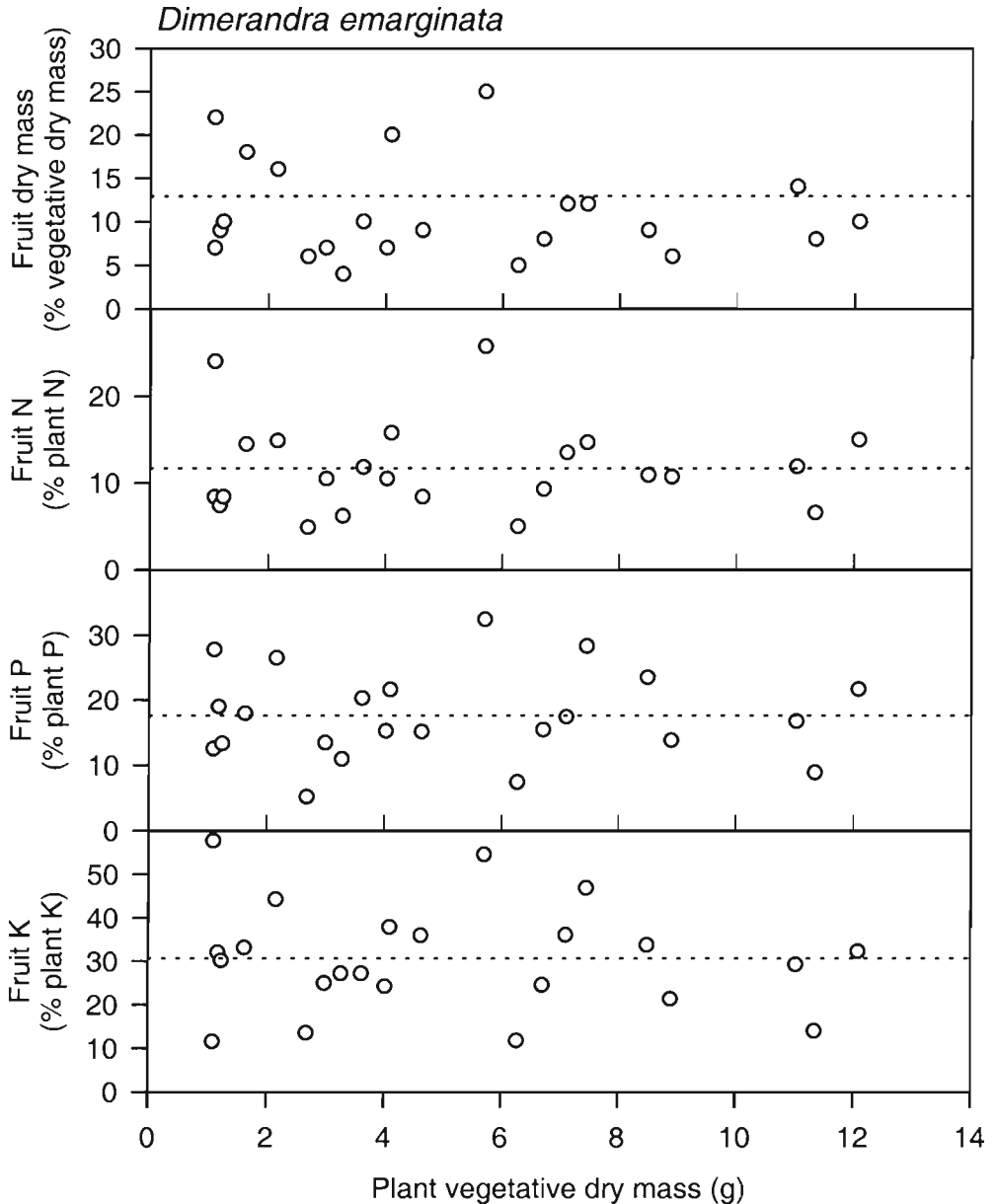


FIG. 1 Relationship between plant size (in g vegetative dry mass; DM) and reproductive allocation in *D. emarginata*. Reproductive allocation is expressed as the ratio of fruit DM or fruit nutrient content to plant vegetative DM and plant nutrient content. Average values are indicated by dotted lines, e.g., 12.9% for dry mass (for other values see Table 1).

This observation can be interpreted in the context of resource allocation and resource availability (Bazzaz *et al.* 1987). Partitioning of resources within a plant should lead to a trade-off between reproduction and vegetative growth. If smaller individuals grow at a more rapid rate, fewer resources are allocated to storage (and subsequent reproduction) and more to current growth. Indeed, in *D. emarginata* relative growth rates decrease with plant size in reproductive plants (Zotz 1998). Assuming a threshold of stored resources for the initiation of flowering, longer intervals between reproductive events in smaller plants are the consequence. Alternatively, resource availability may scale non-linearly with plant size. The habitat of vascular epiphytes is generally described as nutrient-poor, and availability of nutrients is both patchy in time and space (Benzing 1990). Under these circumstances the more extensive root system of larger individuals may be much more efficient at procuring water and nutrients. Although the r/s ratio decreases with size (see above), the absolute root mass increases more than 10-fold from the smallest adults, i.e., 4-cm-tall plants (roots: c. 0.4 g) to individuals of 33 cm (roots: c. 5.5 g). Similarly, total root length increases from c. 200 cm to > 1200 cm. It is conceivable that the larger area covered by the root system of larger individuals may increase the probability of accessing more nutrient-rich patches in the heterogeneous epiphytic habitat more than proportionately (Benzing 1990). However, this scenario is still speculative and needs rigorous testing. At present, short-term laboratory and long-term field experiments are underway to elucidate the proposed size-related differences in resource availability and their influence on the frequency of reproduction *in situ*.

In conclusion, there is no size dependency of reproductive allocation in the epiphytic orchid, *Dimerandra emarginata*, as far as individual fruiting events are concerned, but differences in fruiting frequencies lead to substantial differences in the average annual allocation to reproduction.

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