

VEGETATIVE PROPAGATION IN AN EPIPHYTIC ORCHID OCCURRENCE AND ECOLOGICAL RELEVANCE

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INTRODUCTION

Many plants reproduce both sexually and vegetatively. The production of, e.g., runners, adventitious buds or secondary bulbs offers some obvious advantages over seeds: vegetative offspring will usually develop quicker and with lower mortality than a seed, owing to larger size or prolonged attachment to the mother plant (Harper 1978). However, only sexual reproduction is associated with genetic recombination. Among vascular epiphytes, vegetative propagation is a common feature, e.g., in the life cycle of bromeliads (Benzing 1980). In the Orchidaceae, by far the largest epiphytic taxon, this phenomenon seems to be rather rare, unless we define 'normal' sympodial growth as a form of vegetative propagation (Arditti 1992). Orchid growers are well aware of the existence of keikis, i.e., additional offshoots, which may develop on vegetative stems or flower stalks of several orchid genera. Initially considered an artefact of growing conditions in the greenhouse (convenient for the vegetative propagation of desirable genotypes, Brasch & Kocsis 1980) it has been shown that keikis also occur under natural conditions (De Vries 1953, Horich 1977). To date, however, neither a quantitative study on the occurrence of these additional offshoots *in situ* nor a hypothesis concerning a possible function are available.

Two explanations for their *in situ* formation are conceivable: (1) keikis are produced as a means of vegetative propagation on a more or less regular basis, (2) keikis result from "accidents", when the apical dominance of a plant is broken, e.g., after physical damage, disease, or because of other stress factors (Benzing 1978). Under these conditions,

other, dormant, meristems, such as those at the tip of older shoots, are reactivated and form small plantlets.

This report provides estimates for the *in situ* occurrence of keikis in an epiphytic orchid, *Dimerandra emarginata*, common in moist lowland forests in central Panama (Zotz 1998), describes their growth and development over several years, and discusses a possible adaptive function of these structures.

MATERIALS AND METHODS

The study was conducted on Barro Colorado Island (BCI) in the Republic of Panama. The forest of this biological reserve is classified as a tropical moist forest (Holdridge *et al.* 1971, Croat 1978). *Dimerandra emarginata* (G. Meyer) Hoehne (Orchidaceae) occurs from Mexico through Venezuela. On BCI it is mainly found high in the canopy and on exposed branches of *Annona glabra* and other tree species along the shore of Gatun Lake. The growth form of *D. emarginata* is sympodial. Each year in the late dry season (March–April) a new shoot is produced from the base of the previous shoot. This stem grows continuously for most of the wet season. The basal portions of successive shoots form the horizontal rhizome which is normally closely attached to the substrate. Detailed information on the demography of this species is provided by Zotz (1998).

The frequency of keikis was determined in 1995, on 30 randomly chosen *Annona glabra* trees with *D. emarginata* populations. In these trees, I measured the size of all individual epiphytes and noted the occurrence of additional offshoots. Plant size, i.e., the height of the most recent fully developed stem, and

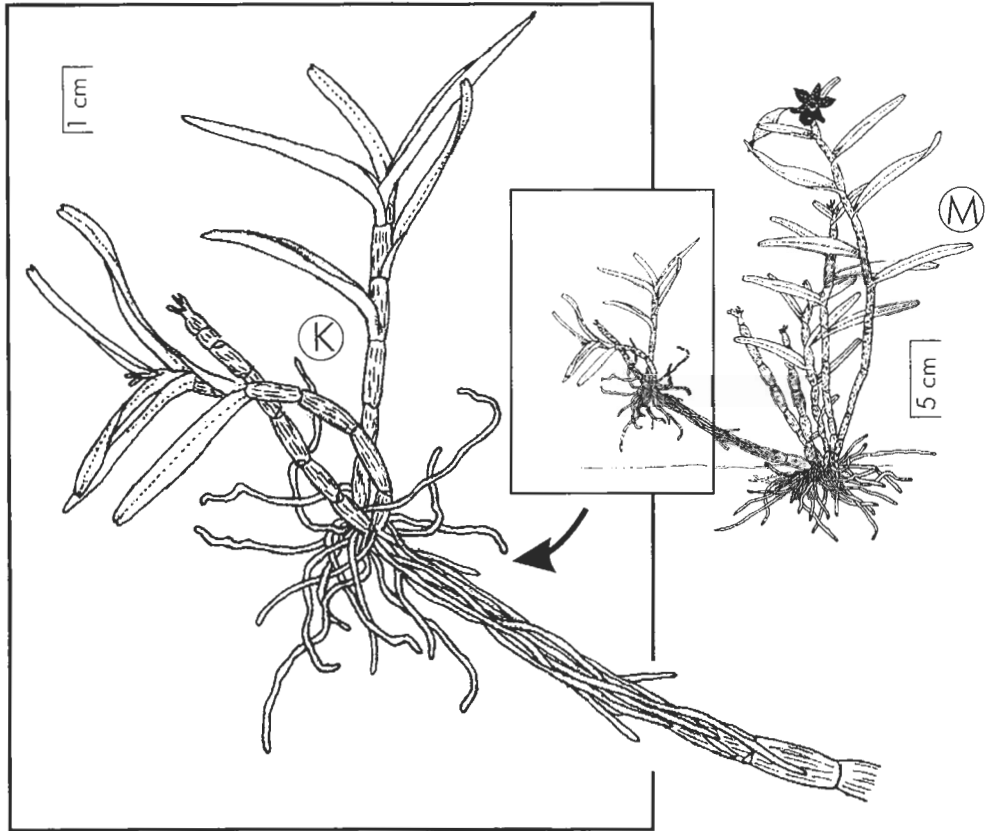


FIG. 1. Habit sketch of a *D. emarginata* with a keiki. The mother stem producing the keiki (with three stems) is enlarged. Note the different scales. K = keiki, M = mother plant.

the length of all stems of keikis were determined with a ruler (Fig. 1). Long-term observations on the development of keikis were made at regular intervals from May 1993 to April 1996 (at the end of each rainy and dry season) on a total of 313 individuals (size range: 1–46 cm) on 12 branches of five different tree species, i.e., *Anacardium excelsum*, *Annona glabra*, *Ceiba pentandra*, *Ficus obtusifolia*, *Pseudobombax septenatum*; names following Croat 1978).

RESULTS

Frequency. A total of 1469 individuals of *D. emarginata* ≥ 1 cm (i.e., all observed individuals except seedlings) were encountered on the 30 *Annona glabra* trees inspected for this study. The largest epiphyte measured 50 cm. Almost 2% of the sample (= 28

individuals) possessed additional offshoots (Fig. 2). Keikis were found significantly more often on larger plants (Kolmogorov-Smirnov test, $P < 0.001$). For example, of the 943 individuals < 10 cm only 3 (= 0.3%) had keikis, compared to 7 (= 12.7%) of the 55 plants > 30 cm.

Structure, growth and development. Keikis were found exclusively at the tips of stems, which could be of different ages. Morphologically, keikis were similar to small normal shoots (Fig. 1). Individual keikis consisted of up to 5 stems (average 2.7). These stems were almost always much smaller than the mother stems (5.3 ± 4.8 cm [means \pm SD], $n = 76$ vs 20.6 ± 8.9 cm [means \pm SD], $n = 28$, respectively). This average size of keikis should be compared with plants grown from seeds. These need between 6 and

10 years to reach 5 cm (i.e., the minimum size for flowering and fruiting, Zotz 1998).

Among the plants observed over three years, keikis proved to be as rare as in the larger census population (6 plants with keikis among 313 plants, i.e., about 2%, with two additional keikis developing on other plants during the study period). The long-term observations revealed the following growth pattern: after the initiation of an offshoot, a new stem developed annually at the tip of the mother stem. In two cases fruiting was observed in two of three years. Although successive stems of most keikis stayed small, they sometimes increased greatly in length (up to 17 cm). Normally, shoot-borne adventitious roots developed after one year. These roots grew in many directions, sometimes creeping down the mother stem (Fig. 1). In two cases, the mother stem drooped, the roots established contact with the bark and – after the senescence of the mother stem – yielded physically independent individuals (visually indistinguishable from plants originating from seeds). It is not clear whether the original bending of the mother stem was due to senescence or a consequence of active pulling of the roots of the keikis once they had reached the substrate (similar to aerial roots of hemiepiphytes, Zimmermann *et al.* 1968).

Physical damage and the development of keikis. Investigating the possibility that physical damage of the most recent stem could induce the formation of additional offshoots, the following experiment was conducted: in April 1996, the new shoots of 1996 which just started to grow (length < 1 cm) were removed by cutting them off at the base. This was done with all 74 individuals (size 2–32 cm) in a population growing on *A. glabra*. In another population of 90 plants (size 3–35 cm), the almost fully developed 1996 shoot was cut at the base in August 1996. In April 1997, I checked for vegetative growth and the occurrence of keikis. All the plants where the new shoot had been removed in April 1996 had regrown a shoot in the same year and had increased in size comparable to the long-term average of *D. emarginata* (compare Zotz 1995). None had developed a keiki. Almost all plants of the August experiment had also grown a new shoot (88 of 90 individuals), but with a considerably reduced length. Four of the 22 individuals > 20 cm of this second group had developed keikis. Although suggestive, these results do not provide evidence that physical damage induces additional offshoots: the frequency of keikis in the entire population of *D. emarginata* was not significantly lower (χ^2 test; $P = 0.35$).

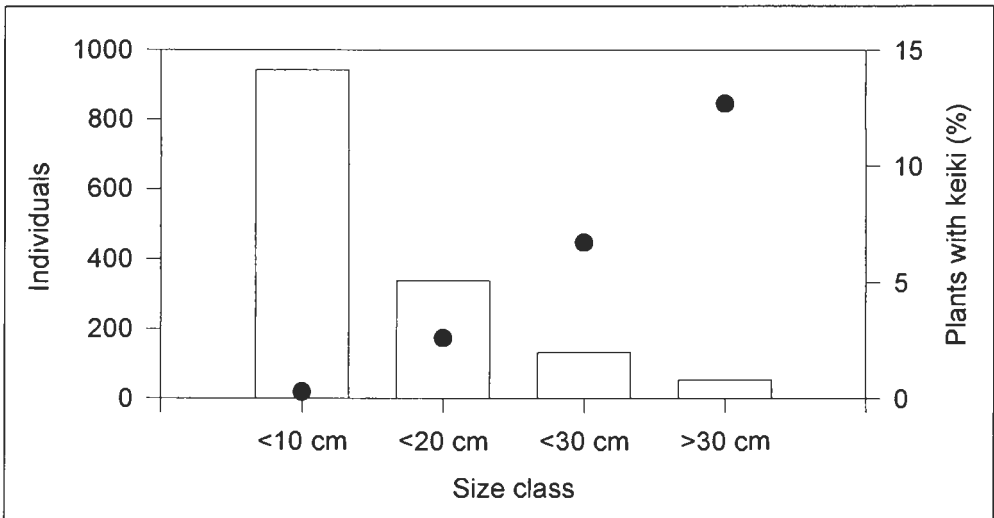


FIG. 2. Size class distribution of *D. emarginata* (bars) and relative proportion of plants with keikis (filled circles). Included were 1469 individuals ≥ 1 cm growing in the host tree *A. glabra*. The largest epiphyte measured 50 cm.

DISCUSSION

Dimerandra emarginata possesses the potential for *in situ* vegetative propagation. However, the ecological importance of this alternative to seed dispersal seems rather limited in view of the rare *in situ* occurrence of keikis (Fig. 2). Furthermore, few keikis may actually gain physical independence. Finally, even if independence is achieved, the distance between independent keiki and mother plant can hardly exceed 50 cm (the length of the largest stem in this species, Zotz 1998). Consequently, the new ramet will almost always root on the same branch. Assuming the validity of the frequently expressed opinion that low substrate durability, which severely limits long-term survival at a given microsite, is a main constraint of the epiphytic habitat (e.g., Benzing 1990, Zotz 1998), vegetative propagation on such a small scale may provide little advantage: only long-distance dispersal and establishment on other branches or on other trees may allow the long-term subsistence of this epiphytic species.

I tested an alternative explanation for the production of keikis in *D. emarginata*, i.e., offshoots being the results of "accidents". Although I was able to find some indication that physical damage induces additional offshoots, the overall result was not significantly different from the untreated population. Of course, the limited data-set does not allow me to fully exclude the possibility that disease, climatic stress or a combination thereof induce keikis. The horticultural literature indeed reports that stress or "poor care" can lead to the formation of keikis in a large number of orchid species (Horich 1977, Arango T. 1979).

We should not jump to conclusions and completely dismiss the notion of keikis as adaptive structures in this and other species. After independence, keikis reduce the risk of dislodgement of the entire genet (e.g., by arboreal animals, Perry 1978) and allow the utilization of additional resources in the patchy tree crown environment (e.g., light, water, nutrients: Benzing 1990, Percy 1990), possibly resulting in an increased seed production of the whole genet. Indeed, Abrahamson (1980) argues that a mixed strategy of sexual and asexual reproduction optimizes plant fitness in extreme habitats.

In summary, the production of keikis, even though providing the potential for vegetative propagation, seems ecologically rather unimportant in *D. emarginata*. Whether this assessment can be extended to other epiphytic orchids remains to be

shown. As outlined above, the epiphytic habitat may simply not be conducive to small-scale clonal reproduction. It should be emphasized, however, that other modes of vegetative reproduction, with larger distances between individual modules, e.g., branching, long-creeping rhizomes, are more likely to be relevant in this context. Unfortunately, as yet no study has been conducted to evaluate their adaptive significance.

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