

RESEARCH PAPER

Vivipary and offspring survival in the epiphytic cactus *Epiphyllum phyllanthus* (Cactaceae)

J. Hugo Cota-Sánchez^{1,*} and Deusa D. Abreu²

¹ University of Saskatchewan, Department of Biology, Saskatoon, SK S7N 5E2, Canada

² Universidade de São Paulo, Departamento de Botânica, São Paulo, Brazil

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Abstract

Vivipary, the germination of seeds before they are shed from the parent plant, is a rare event in angiosperms involving complex ecophysiological processes. Pseudovivipary and cryptovivipary occur in approximately 30 (2%) species of the cactus family. A remarkable case of vivipary in *Epiphyllum phyllanthus* is described here. Information is provided regarding the biology of viviparous fruits, morphology, mortality, survival rates of viviparous offspring, and some eco-evolutionary implications of this reproductive strategy in the Cactaceae. This epiphytic cactus has no host-specific relationship. A low proportion (33.3%) of individuals produced viviparous fruits. Seed number/fruit varied from 197 to 230 with percentage of viviparous germination from 97.5% to 99%. The viviparous seedlings exhibited normal development and were no different from non-viviparous offspring. Transplanting experiments showed that the first week is critical for seedling establishment, and high mortality occurred in the three treatments used: 69% on the phorophyte surface, 58.6% on the ground, and 44.8% under controlled conditions. The number of survivors gradually stabilized, and the contribution to establishment was comparable in each of the treatments after the acclimation phase. It is suggested that vivipary is associated with thermoregulation, parental care, conspecific nursing, and rapid seedling establishment. Germination is not a limiting factor in the perpetuation of this viviparous species, but seedling establishment is. In viviparous individuals of *E. phyllanthus*, seedling mortality during establishment rather than failure to germinate within the fruit is a limiting factor affecting local population density. Overall, viviparity is an intrinsic, genetic event involving high metabolic costs

favouring germination and dispersal of the fittest offspring regardless of substrate and environmental conditions.

Key words: Cactaceae, dispersal, *Epiphyllum phyllanthus*, epiphyte, nursing effect, precocious germination, seedling establishment, vivipary.

Introduction

The Cactaceae is an important phylogeographic element of the American deserts and the second largest plant family restricted to the New World (Anderson, 2001). The family exhibits an extensive habitat radiation accompanied by morphological and reproductive specialization. Several papers (Cota, 1993; Anderson, 2001; Pimienta-Barrios and Del Castillo, 2002; Cota-Sánchez and Crouch, 2007; Nassar *et al.*, 2007) have discussed the breeding systems and reproductive versatility of the Cactaceae. The striking floral shapes, designed to attract a wide range of pollinators, have also been discussed as a mechanism for cactus diversification by promoting genetic variability reinforced by outcrossing. However, out of the *c.* 1500 species of cacti (Anderson, 2001), the reproductive biology has been investigated in less than 10% of taxa. The limited amount of data impedes a better understanding of reproductive mechanisms in the family. In the same way, vivipary, a phenomenon characterized by lack of dormancy with subsequent germination of seeds within the fruit before they are shed from the parent plant, has been addressed in the Cactaceae in a few papers (Buxbaum, 1968; Conde, 1975; Lombardi, 1993; Cota-Sánchez, 2004; Cota-Sánchez *et al.*, 2007) as a notorious event.

Vivipary is, in effect, a remarkable condition not only because of its rarity in flowering plants (Elmqvist and

* To whom correspondence should be addressed. E-mail: hugo.cota@usask.ca

Cox, 1996; Cota-Sánchez, 2004), but also because of the complex ecophysiological process involved in seed germination and phytohormone production (Farnsworth and Farrant, 1998). To date, two types of vivipary are known in flowering plants: true vivipary (production of sexual offspring) and pseudovivipary (production of asexual propagules). This trait has significant consequences in the agricultural industry and plant conservation practices. For instance, pseudovivipary, the premature germination of seeds, is an undesirable trait in annual cereal crops because pre-harvest sprouting leads to lower yields and economic losses (Kermode, 2005). Also, non-dormant (desiccation-intolerant) seeds of many rare tropical species lose viability, which is a serious problem when seeds of rare and endangered tropical and subtropical cacti are stored in seed bank collections (Cota-Sánchez *et al.*, 2007).

In addition to being a sporadic event in plants, vivipary is a specialized trait of evolutionary and biological significance providing new avenues for survival (Cota-Sánchez, 2004) and a mechanism for protecting the embryo from extreme saline concentrations (Rabinowitz, 1978). Vivipary has been documented in *c.* 80 vascular plant families including 143 genera and 195 species (<0.1% of tracheophytes). Of these, 65 species are viviparous or cryptoviviparous (Farnsworth, 2000), and *c.* 45 are pseudoviviparous (Elmqvist and Cox, 1996, reviewed in Cota-Sánchez *et al.*, 2007). In the Cactaceae,

both pseudovivipary in *Coryphantha vivipara* (Nutt.) Britton & Rose (Elmqvist and Cox, 1996) and *Opuntia* L. spp (Palleiro *et al.*, 2006) and cryptovivipary (a subcategory of true vivipary in which the embryo does not protrude through the ovary wall) have been described (Cota-Sánchez, 2004; Cota-Sánchez *et al.*, 2007).

At present, vivipary is known to occur in approximately 30 (2%) species of the Cactaceae (JH Cota-Sánchez, unpublished data). Several reports have documented the occurrence of pseudovivipary in the family (Mitich, 1964; Buxbaum, 1968; Conde, 1975; Lombardi, 1993; Cota-Sánchez, 2002; Lira, 2006). On the other hand, Cota-Sánchez (2004) suggested the incidence of cryptovivipary in Cactaceae. Among the records of viviparity in the family, two exist for the epiphytic cactus *Epiphyllum* Haw., namely the hybrid *Epiphyllum* × *Fern la Borde* (Cota-Sánchez, 2004) and *E. phyllanthus* (L.) Haw. (Conde, 1975), the species which is the subject of this paper.

Epiphyllum phyllanthus (tribe Hylocereeae) is a widespread, epiphytic neotropical species. The plant has flat cladodes with crenate margins; solitary flowers; bright red or pink ridged pericarpel, with acute bract-scales; fruits ovoid to pear-shaped or pyriform (Fig. 1A, B), apiculate from 5–10 cm long and 2–3.5 cm wide, dehiscent by lateral slit or pore; deep-pink pericarp, smooth, with scattered fine, acute scales (Fig. 1A); white and mucilaginous funicular pulp (Taylor and Zappi, 2004); seeds

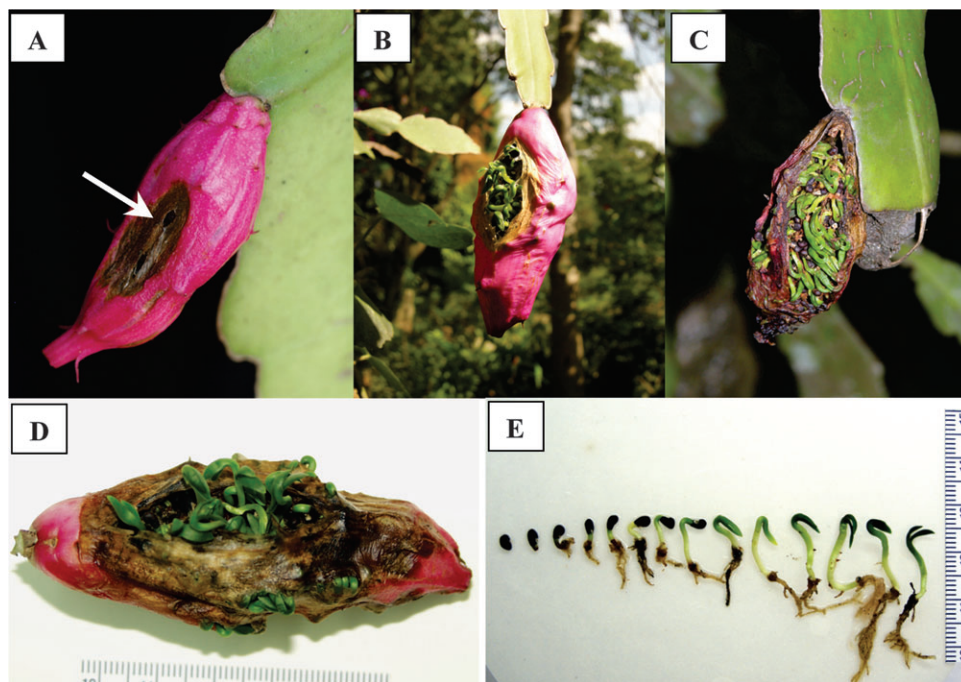


Fig. 1. Different stages of vivipary in fruits and offspring of *E. phyllanthus*. (A) Mature, 4-week-old fruit showing the area of dehiscence (arrow), region through which the viviparous seedlings emerge upon germination. (B) Six-week-old fruit on mother plant showing the emergence of viviparous seedlings through pericarp. (C) A 7-week-old fruit on mother plant with viviparous offspring. (D) Close-up of a 6-week-old viviparous fruit. (E) Developmental series of viviparous seedlings harvested from the fruit in the previous picture. Scale: 1 bar=1 mm.

4–4.5 mm, cochleariform with black seed coat (Barthlott and Hunt, 2000).

Although the establishment and survival of adult plants is well known in numerous species, seedling growth, establishment, and survival remain practically unexplored (Winkler *et al.*, 2005). Furthermore, the stages of germination, seedling mortality, and establishment are the most vulnerable stages of the plant life cycle (Benzing, 1990), yet these are poorly documented in nature. Indeed, little is known about the development and ecological requirements of orthodox, non-viviparous progeny, and much less is clear regarding establishment and survival rates of viviparous seedlings in cacti and other plant groups. In addition, there has been limited progress in understanding various relevant aspects regarding the biology of viviparous species, the offspring survival/mortality rates, and the ecological and evolutionary tradeoffs of this event. A remarkable case of vivipary is described here in *Epiphyllum phyllanthus*, a representative species of the Brazilian Mata Atlântica in Brazil and insights are provided into the biology of this event. For the first time, information is provided regarding the biology of viviparous fruits, morphology, mortality, and survival rates of viviparous offspring in this species, as well as some ecological and evolutionary implications of this reproductive strategy in the cactus family.

Materials and methods

Our observations are derived from a population of six individuals of *Epiphyllum phyllanthus* growing separately 15–50 m from each other in the small reserve of Mata Atlântica on the campus of the Universidade de São Paulo, Brazil. Among these six plants, three individuals bearing flowers (one with two flowers) were monitored weekly to document fruit ripening. The four fruits were collected in the month of March at different stages of ripeness (Fig. 1A–D), four, five, six, and seven weeks in order to document the total number of seeds/fruit, the presence or absence of vivipary, the number of seeds germinated, the general characteristics of viviparous seedlings, and the number of dead and surviving seedlings per fruit.

Foremost, two mature fruits, a 4-week-old fruit (fruit No. 1; Fig. 1A) and a 5-week-old fruit (fruit No. 2), were collected prior to the emergence of seedlings. A third 6-week-old fruit (fruit No. 3; Fig. 1B, D) was collected 1 week after the appearance of viviparous offspring. These seedlings were harvested, frozen, and stored for ongoing comparative studies of production levels of abscisic acid in embryonic and maternal tissues. Finally, the oldest, 7-week-old fruit (fruit No. 4; Fig. 1C) was collected 2 weeks after the germination and emergence of seedlings. The seedlings of this fruit were divided into three lots, each with 29 individuals, and transplanted in three different conditions: (i) on the surface of the phorophyte (host plant) near the mother plant, (ii) on the ground, near the phorophyte, and (iii) in sterile soil under controlled photoperiod (12/12 h light/dark at 28 °C) to evaluate the fitness advantages and abilities for survival and establishment of viviparous offspring. To date, these lots have been monitored on a daily basis for nearly 5 months to document the fate of surviving offspring in each of the three treatments. Monitoring of the remaining survivors is planned.

The 2004 Microsoft Graph package was used to display graphically the distribution of data in time versus the number of viviparous seedlings d^{-1} in each condition. A logarithmic regression analysis was performed and the coefficient of determination (R^2) was calculated for each of the conditions used to estimate the relationships between the two variables (survival versus time) and future trends for offspring survival in different substrates were predicted.

Results

The specimens of *E. phyllanthus* were growing on lower strata of different host trees, which supplied locations with distinct microhabitat conditions. Two individuals were found on *Caesalpinia pluviosa* DC in a rather exposed area and the third specimen on a species of *Ficus* L., in a more protected, shady site separated by a distance of about 50 m from conspecific plants. The other three plants were growing on *Jacaranda mimosifolia* D. Don and *Erythrina* aff. *speciosa* Andrews. The variety of phorophytes supporting *E. phyllanthus* suggests that this epiphytic cactus has no host-specific relationship. Lack of tree host specificity has also been observed in other vascular epiphytes (Laube and Zotz, 2006).

Within the *E. phyllanthus* population investigated, only 50% of the individuals (three out of six) produced fruits. However, there is a lower proportion (33.3%) of individuals producing at least one viviparous fruit, as only two plants produced viviparous offspring. The fruit gradually develops the characteristic fleshy pericarp (Fig. 1A–D) and the area of dehiscence, which is evident after ripening as a tiny portion of the fruit wall turning brown (Fig. 1A). The elapsed time for fruit maturation until it reaches the largest dimension ranges from 4–6 or 7 weeks. In the older fruits, the seeds and seedlings are visible through the dehiscence pores, which facilitate the emergence of viviparous propagules and progressively enlarge upon seed germination and subsequent seedling growth inside and outside the fruit (Fig. 1B–D).

Three *E. phyllanthus* individuals produced a total of four fruits. The younger fruits (Nos 1 and 2), though mature, did not show evidence of viviparity (Table 1), but about 40% of the seeds of these fruits germinated in Petri dishes 24 h after they were withdrawn from the fruit, indicating that the seeds were viable. The two older fruits (Nos 3 and 4; see Table 1) produced viviparous offspring. Our data indicate that the *E. phyllanthus* seeds are reniform to orbicular, medium-sized, ranging from 1.5–3 mm in length. The seed number produced by fruits is variable, ranging from 197 to 230. Seedling survival estimates in viviparous fruits vary from 45.4–100.0% (Table 1). This difference is probably associated with fruit age with concomitant seedling growth and depletion of the fruit pulp, maternal tissue from which the seedlings draw nutrients during the early developmental stages. This was particularly evident in the older fruit (No. 4), in

which higher incidence of mortality (105 dead seedlings) and dry pulp was observed.

From the morphological side, the viviparous seedlings exhibit normal development and are no different from non-viviparous, orthodox offspring. However, since germination times vary among the viviparous progeny, the seedlings exhibited differences in size and degree of organ development. For instance, the seedling root system varies from an incipient radicle to a well-differentiated, larger root (Fig. 1E). Depending on the age and propagule size, the cotyledons are evident once the seed testa falls off. The seedlings seem capable of photosynthesis, as the chlorophyll pigment is evident in the early stages of germination. In general, seedling size varies from 2–3 mm in the early germination stages to large propagules up to 3 cm (including root system) in the older stages (Fig. 1E). The same structures and degree of development has been observed in young viviparous offspring of *E. phyllanthus* (Conde, 1975) and the hybrid *Epiphyllum* × *Fern la Borde* (Cota-Sánchez, 2004).

Although seedling survival analyses are vital to understand the fate of the offspring (Winkler *et al.*, 2005), these studies are relatively uncommon in plant ecology. In this regard, our study is providing new information on the

survival of viviparous offspring. As indicated, the establishment stages of early viviparous propagules of *E. phyllanthus*, transplanted in three sites with different substrate and environmental conditions, have been monitored. Transplanting experiments showed that the first 7 d were critical for seedling establishment. During the first week there was an extremely high mortality in all three conditions: 69% on the phorophyte surface, 58.6% on the ground at the base of the host tree, and 44.8% under controlled photoperiod and temperature. The highest proportion of mortality occurred within the first 5 d, but after 1 week it gradually decreased as the progeny underwent a process of acclimation (Fig. 2).

One month after the transplant there was a trend in decreasing seedling mortality (establishment phase) in all conditions (Fig. 2). In addition, during the first 3 weeks after transplanting, the seedlings under controlled conditions and those on the ground substrate had relatively lower mortality rates, perhaps due to more favourable microhabitat conditions for establishment. In all, the number of surviving seedlings gradually stabilized over time so that the contribution to establishment, although in low proportion, was comparable in each of the conditions. Nearly 5 months after transplanting the proportion of

Table 1. Comparative data on seed number, germination, survival, and mortality of viviparous seedlings obtained from four fruits of *E. phyllanthus*

Asterisks indicate fruits with no viviparous offspring.

	Fruit age (weeks)	Total no. of seeds	No. of abnormal seeds	No. of germinated seeds	Germination in parent plant (%)	No. of surviving seedlings	No. of dead seedlings	Percentage survival (%)
Fruit 1*	4	230	4	0	0	N/A	N/A	NA
Fruit 2*	5	228	15	0	0	N/A	N/A	N/A
Fruit 3	6	205	2	203	99.0	203	0	100.0
Fruit 4	7	197	5	192	97.5	87	105	45.4

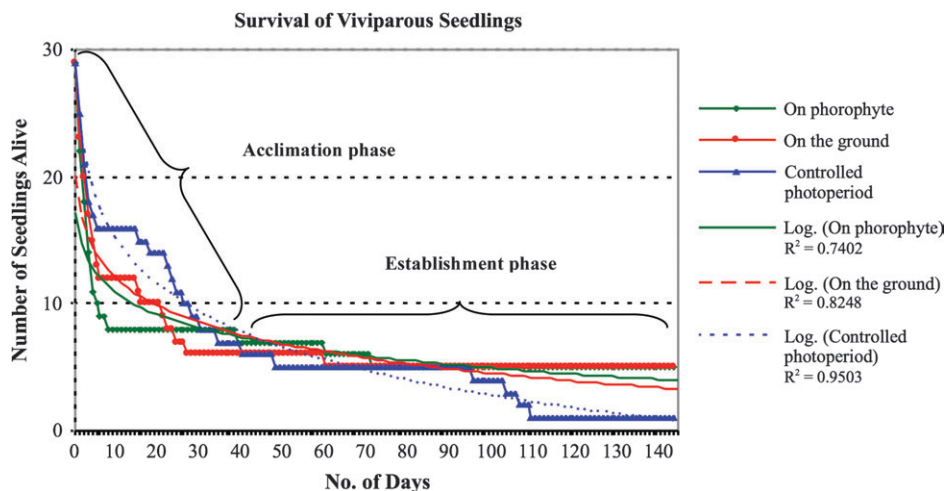


Fig. 2. Graphical representation of the trend for survival of viviparous seedlings of *E. phyllanthus* in different substrates, each with predicted future trend and R^2 values based on logarithmic regression analyses. Sample size in all three treatments: $n=29$ individuals.

surviving seedlings ranged from 3.6% to 17.2% in the three treatments, with specific values of 17.2% (five survivors) on the bark surface of the phorophyte and on the ground at the base of the host plant, and 3.6% (one survivor) under the controlled photoperiod conditions (Fig. 2).

The values of the coefficient of determination (R^2 , with $n=29$) obtained from the logarithmic regression analysis for seedling survival are as follows: $R^2=0.74$ on the phorophyte surface, $R^2=0.82$ on the ground, and $R^2=0.95$ under controlled conditions. The best fit for the data indicates that there is a closer relationship of seedling survival with the last two conditions than with the first. Our limited sample size restricts additional statistical tests. We were limited to examining the only two fruits showing vivipary in the population of *E. phyllanthus*, in which two out of six individuals produced one viviparous fruit each. In fact, our own observations and those of Cota-Sánchez *et al.* (2007) indicate that viviparous cacti produce a limited number of fruits making experimental replicates nearly impossible. As a result, aspects of vivipary are seldom documented. Our findings, nonetheless, provide new relevant information on this rare biological event in plants.

Discussion

The characteristics of the viviparous fruit and offspring of *E. phyllanthus* indicate that this as a case of cryptovivipary (subcategory of true vivipary) because there is no evidence of seedling growth protruding or rupturing the pericarp. Instead, the area of dehiscence of the fruit facilitates seedling emergence once germination occurs inside the fruit. Cryptovivipary has also been identified in various epiphytic cacti, including an *Epiphyllum* hybrid (Cota-Sánchez, 2004). In a general sense, Conde (1975) explained this phenomenon as vivipary in *E. phyllanthus*. The high seed viability and precocious *in situ* germination observed in fruits of this epiphytic cactus supports the idea of Benzing (1990) and Winkler *et al.* (2005) that epiphytic seeds do not form seed banks in nature.

We believe cryptovivipary represents a form of parental care with subsequent conspecific nursing. According to Hunter and Aarssen (1988), plants coexist in beneficial conspecific or heterospecific relationships to assist each other in establishment and colonization and to facilitate access to important extrinsic factors, such as light, nutrients, physical support, etc. There are various examples of nursing and parental care for offspring in plants, for example, Waser and Real (1979), Hunter and Aarssen (1988), and Weid and Galen (1998). In cacti, both conspecific (Nobel, 1980) and heterospecific (Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Suzan *et al.*, 1994; Mandujano *et al.*, 2002) nursing has been documented. Likewise, the beneficial effects of nurse

plants with concomitant reduced environmental pressures facilitate the establishment of cactus seedlings under extreme conditions of temperature and water availability in nature (Valiente-Banuet and Ezcurra, 1991).

Considering the cactus fruit anatomy, it is believed that through various means viviparous cacti provide a gradual series of opportunities for seedling establishment. For instance, the cactus ovary and fruit are exceptional in being surrounded by vegetative tissues, which in most species consist of many nodes, internodes, axillary buds, and even rather ordinary leaves (Cota-Sánchez, 2004). The combination of fruit characters (fleshy, mucilaginous, often with thin transparent pericarp) provides a suitably moist environment that promotes germination and incubation while embedding the seeds and young seedlings in an insulating barrier (particularly in medium- to large-sized fruits) that protects them from extreme environmental conditions, for example, drastic temperatures, desiccation, and exposure to direct sunlight, wind, and rain. It is hypothesized that the intrinsic characteristics of the cactus fruit parallels parental care and thermoregulation for young seedlings. The correlation between fruit characteristics and environmental conditions provide insight into the gradual process of establishment and the reciprocal relationships between viviparous cacti and their environment, a relationship that may be compared to endothermal parental care. Within this context, it makes sense to infer that precocious seed germination and seedling development is continually active under the uniform temperature conditions and availability of nourishment in the fruit, important steps for the development, establishment, and success of viviparous seedlings.

Once the viviparous seedlings are shed from the parent fruit and become independent, they face the adverse environmental conditions. Indeed, drought, water availability, and high temperatures are limiting factors for seedling establishment (Benzing, 1990). If this is the case, then an important question is whether vivipary is, in effect, a successful trait allowing rapid seedling establishment in tropical and subtropical tree canopies and dry desert environments, where most cacti prevail. It is hypothesized that, under changing environmental factors, larger seedling size in *E. phyllanthus* (Fig. 1D, E) is an advantage for survival and an important trait to overcome selective pressures. The higher survival rates observed in large viviparous mangroves relative to smaller non-viviparous propagules (Rabinowitz, 1978) and the increase in survival rates with increasing seedling size in epiphytic bromeliads (Benzing, 1978; Winkler *et al.*, 2005) support this idea. Moreover, the increase in seed and propagule size in *Atriplex* L. has been indicated as a beneficial trait under conditions of competition and unfavourable circumstances (Salisbury, 1942). Thus, in viviparous cacti, larger, more vigorous seedlings produced from larger seeds, such as *E. phyllanthus*, will have

a higher probability of survival in adverse conditions as opposed to smaller seedlings produced from smaller seeds, such as *Rhipsalis baccifera* (J. S. Mueller) Stearn. subsp. *horrida* (Baker) Barthlott and *R. micrantha* (Kunth) DC (Cota-Sánchez, 2004). Our experimental transplanting tests conducted on and away from the host plant indicate that larger viviparous seedlings have a greater ability to establish under different conditions once they are 'shed' from the parent plant. This implies that the viviparous trait confers fitness advantages by disseminating offspring in time and space in new areas of the host plant and other ground substrates, which is in agreement with Cota-Sánchez *et al.* (2007), who suggested that vivipary evolved as a mechanism to provide a more efficient germination and survival means while contributing to population maintenance and short-distance dispersal. Accordingly, vivipary is an advantageous trait in tropical and subtropical environments because it is a reproductive strategy that allows perpetuation of species with low germination rates (Cota-Sánchez, 2004).

Winkler *et al.* (2005) have addressed the correlation of seedling size with subsequent successful establishment. Within the viviparous offspring of *E. phyllanthus*, larger seedlings with more developed structures, i.e. plantlets with differentiated cotyledons and roots, are able to establish sooner compared with conspecific seedlings, which germinated last. A similar pattern has been observed in other plants. For example, early germination and establishment in *Tillandsia circinnata* Schlecht. provide fitness advantages for early establishment and survival in different host areas and substrates (Benzing, 1978), early seedling emergence in the growing season favours the establishment of *Pinus sylvestris* L. plantlets in different microhabitats (Castro, 2006), and the anatomical features of viviparous mangroves with rapid root development assists seedling attachment with the subsequent ability to rise above fluctuating tides (Tomlinson and Cox, 2000). The post-germination root and cotyledon development observed in the viviparous offspring of *E. phyllanthus* suggests that the larger and more developed these structures are, the higher the chances for establishment will be. Hence, these organs are critical in the establishment of viviparous epiphytic plants by facilitating seedling attachment and the absorption of minerals with the simultaneous conversion of raw materials into chemical energy via photosynthesis in the fluctuating moisture, nutrient, and light environments in which they thrive.

High mortality rates are distinctive of the early establishment stages of viviparous *E. phyllanthus* seedlings. These data show that there was a dramatically high mortality percentage (from 44.8% to 69%) during the first week of the acclimation phase, followed by a gradual stabilization period in all three sites (Fig. 2). There was a temporary increase of seedling fitness and, eventually, the overall number of survivors converged in the three

trials. Higher mortality rates in the early juvenile stages are probably related to the seedling vulnerability and high metabolic costs involved in response to stressful habitats. Nobel (1988) and Zotz *et al.* (2001) have shown that high mortality in juvenile stages is related to low stem capacitance, which may be correlated to the characteristic lower photosynthetic capacity of small plants (Zotz, 1997). Likewise, a steady decrease in seedling mortality with a concomitant increase in seedling size and age has also been observed in epiphytic *Tillandsia* species (Benzing, 1978; Winkler *et al.*, 2005) and other vascular plants (Silvertown and Lovett-Doust, 1993), in addition to the *E. phyllanthus* seedlings monitored in this study.

It is also believed that seedling establishment during the young juvenile stages of *E. phyllanthus* depends on the surface area-to-volume (S/V) ratios of propagules. Surface-to-volume ratio and small size are important factors determining heat loss and gain. Several authors, for example, Benzing (1990), Mauseth (2000), Winkler *et al.* (2005), among others, have shown that this ratio is particularly important in epiphytic seedlings because they have smaller S/V ratios. In addition to the less efficient S/V ratio in juvenile stages of *E. phyllanthus*, the dry conditions prevailing in forest canopies are a major threat for seedlings as they desiccate much faster than adult siblings. In fact, tree canopies of wet tropical forests are generally characterized by recurrent drought periods and low nutrient input (Benzing, 1990); in addition, water stress and reduced photosynthetic ability are primary abiotic factors affecting epiphyte growth and establishment (Zotz and Hietz, 2001). Thus, the abilities of seedlings to establish may increase due to the increase in S/V ratios, which may also account for the increased ability to photosynthesize and respire above the potentially wet and anoxic mat of moss, lichens, ferns, and other plants or debris typically found on tropical tree branches.

In nature, germination, dispersal, and establishment of epiphytic offspring depend on plantlets landing in optimal and more sheltered microsites with fewer fluctuations in temperature, humidity, and light conditions than on the phorophyte (Benzing, 1990; Winkler *et al.*, 2005). Our observations indicate that there is a relationship of higher seedling survival in less stressed, more protected microsites of the host plant. It was also observed that torrential rains and compacted substrate are adverse factors for seedling establishment because they cause seedling uprooting and obstruct rooting, respectively, further suggesting that the chances of survival are directly related to landing in a protected microhabitat with favourable physical and chemical environments. Furthermore, it is believed that vivipary involves an adaptation to local dispersal. Thus, the greater the dispersal distance is, the higher the risk and the lower the probability of optimal dispersion as a result of acclimation to local landscape

conditions. That is to say that the optimal habitat conditions for epiphytic plants include bark surface with abundant debris from the host plant, resulting in dispersal capabilities limited to a characteristic landscape, which is in agreement with the idea of local adaptation proposed by Gros *et al.* (2006).

In our opinion, the *E. phyllanthus* seedlings are more likely to be dispersed locally, close to the mother plant, in areas with similar microhabitat conditions. In addition, we hypothesize that the heterospecific nursing effect provided by the host plant is beneficial during the more vulnerable stages of establishment of *E. phyllanthus* propagules. This, together with the putative advantages from conspecific nursing, is also important in successful establishment because it promotes the acclimation of seedlings to different environmental gradients. Nonetheless, competition is another critical factor to consider. There is evidence that intra- and interspecific competition for nutrients, water (Franco and Nobel, 1989) and light (Valiente-Banuet and Ezcurra, 1991) affects seedling growth in the saguaro cactus. Quite possibly, these factors also affect subsequent stages of the life cycle of viviparous progeny.

There is some controversy regarding the dispersal agents of *Epiphyllum* seeds involving chireptophyly (Greenhall, 1956) and ornithophyllous (van der Pijl, 1957; Anderson, 2001). Bregman (1988) suggested that the fleshy pulp in which the seeds are embedded entices bird-feeding habits thereby favouring internal (endozoochory) and external (epizoochory) dispersal when pulp and seeds attach to the animal body parts. Because *E. phyllanthus* seeds do not require scarification to germinate, it is assumed that it is more likely that seeds, not seedlings, are dispersed via epizoochory. However, animals normally do not disperse viviparous fruits, as they may not be palatable. Consequently, it is feasible that the fruits and seedlings fall primarily near the mother plant and the host plant. This leads us to another relevant enigma, i.e. whether the fruit itself is the unit of dispersal once the seeds have germinated or whether the viviparous offspring are eventually dispersed from the fruit, and if so, are the seedlings spread individually or in clusters.

Based on our observations, once the seeds germinate and the seedlings start developing the radicles, their root system gets tangled so that the separation of individuals is difficult, even when the seedlings are harvested manually. Comparable observations of tightly bound roots in viviparous seedlings in species of *Neoporteria* Britton & Rose were made by Buxbaum (1968), who interpreted the incidence of endogenous vivipary as a strategy for rapid rooting and establishment. Substantial seedling growth accompanied by knotted roots also occurs in viviparous fruits of *Ferocactus herrerae* J. G. Ortega and some columnar cactus (JH Cota-Sánchez, personal observation). It is predicted that post-germination dispersal of viviparous seedlings in *E. phyllanthus* occurs in clusters

upon the abscission of the fruit with the pericarp and pulp providing nutrients for growth and early seedling establishment. Therefore, dispersal of viviparous offspring occurs in masses close to the host plant. It is anticipated that distribution in space, however, is local and limited to nearby areas and the characteristic landscape of conspecific and heterospecific nursing, so that seedling dispersal has constraints unless stochastic distribution by animals, wind or rain occurs.

The origin of vivipary in plants is, in general, unknown, but the trait does have multiple evolutionary origins in angiosperms and involves the loss of seed dormancy even in unrelated lineages of the same plant family, such as in Rhizophoraceae (Farnsworth and Farrant, 1998) and the Cactaceae (Cota-Sánchez, 2004). Similarly, the current knowledge regarding the characteristics of viviparous species, fruits and seedlings, ecophysiological requirements, fitness advantages, and evolutionary consequences of this condition in the cactus family is, to date, modest. The most extensive discussions on cactus vivipary (Cota-Sánchez, 2004; Cota-Sánchez *et al.*, 2007) have proposed that it is an independent, convergent character occurring in phylogenetically distant lineages of the subfamily Cactoideae, in tribes Cacteeae, Hylocereeae, Pachycereeae, Rhipsalideae, and Trichocereae. Further, there is no single unifying character associated with vivipary. For instance, vivipary occurs in epiphytic lineages in cultivated (Cota-Sánchez, 2004) as well as terrestrial columnar and cylindrical cacti distributed in flooding and non-flooding halophytic environments, respectively (Cota-Sánchez *et al.*, 2007). The fruit, and hence ovary wall, across viviparous cacti varies in size, thickness of the pericarp, number and size of seeds, and amount of pulp. There are fruits with thick and leathery pericarp in *Ferocactus herrerae*, to intermediate thickness in *Stenocereus alamosensis* (J. M. Coult.) A. C. Gibson & K. E. Horak, and *S. thurberii* (Engelm.) Buxbaum (Cota-Sánchez *et al.*, 2007) to relatively thin and semi- or transparent in *Disocactus martianus* (Zucc.) Barthlott, *Lepismium ianthothele* (Monv.) Barthlott, and *L. monacanthum* (Griseb.) Barthlott (Cota-Sánchez, 2004). Finally, there is also considerable variation in size of viviparous propagules among species, from the minuscule seedlings of *Rhipsalis baccifera* subsp. *horrida* to the large seedlings with well-developed cotyledons of *Epiphyllum* × *Fern la Borde* (Cota-Sánchez, 2004) and *E. phyllanthus* (Fig. 1E).

The bewildering set of morphological characters and the assorted environmental conditions associated with cactus vivipary suggest that several selective forces have been involved in the evolution of this condition in the Cactaceae. In mangroves, the most studied group including viviparous plants, several ideas have been proposed. Tomlinson and Cox (2000) suggested that vivipary is a successful strategy in estuarine flooding

environments. Likewise, independent origins and specialized traits, such as photosynthetic acclimation and the ability to secrete salt, have been used to explain the occurrence of vivipary in unrelated species (Farnsworth, 2004; Shi *et al.*, 2005). Despite the fact that the origin of vivipary remains a mystery, true vivipary in mangroves has been regarded as a mechanism conferring the ability to survive in stress environments subject to flooding and high saline conditions (Rabinowitz, 1978; Tomlinson, 1986; Farnsworth and Farrant, 1998; Tomlinson and Cox, 2000). In our view, vivipary is an important character that has allowed evolutionary diversification in phylogenetically derived taxa of the Cactoideae. Although we believe that vivipary is a derived trait, the possibility that it is a plesiomorphic condition that has been retained in a few disparate species should not be excluded. We hypothesize that vivipary in cacti is a reproductive strategy that increases potential survival and adaptation for the perpetuation of species in the stressed and driest conditions of the tree canopies of tropical forests and subtropical deserts by promoting the formation of viable offspring and facilitating germination, rapid rooting, and early seedling establishment, features that are relevant in changing environmental conditions. Further, it is agreed that precocious germination provides adaptive advantages associated with local dispersal and degree of habitat specialization as proposed by Cota-Sánchez *et al.* (2007). Obeso (2002) indicated that plants invest in costly reproductive strategies, which in concert with more efficient competition and defence mechanisms provide them with fitness advantages to perpetuate the species. Vivipary in the cactus family is a risky and expensive process involving a combination of these factors, in which the mother plant invests high metabolic energy to produce, often in stressed environments, fit, viable offspring able to establish under different selective pressures. Further investigations of this complex biological attribute are warranted due to the scarcity of viviparous examples in the plant kingdom and the putative conspecific altruism involved.

Our data suggest that vivipary is an intrinsic reproductive mechanism favouring the germination and dispersal of the fittest offspring regardless of substrate and environmental conditions. Even with the expensive metabolic costs involved in viviparous reproduction, the proportion of the fittest individuals able to establish successfully during the early stages, though relatively low, is equivalent in the two lots under natural conditions. Therefore, germination is not a limiting factor in the perpetuation of viviparous species, but seedling establishment is. In viviparous individuals of *E. phyllanthus* seedling mortality during the acclimation and establishment phases rather than failure to germinate within the fruit appears to be one of the limiting factors affecting local population density.

In conclusion, the incidence of vivipary in phylogenetically distinct lineages of the cactus family is evidence of a parallel directional change towards a more practical reproductive mechanism. In other words, it is a reproductive advantage that, in addition to allowing propagules to root and grow almost immediately, favours quick establishment whenever seedlings land on suitable substrates. While some progress has been made towards the understanding of viviparous offspring in the Cactaceae, a wide range of issues remains unanswered. Vivipary itself is a remarkable, biologically complex process deserving investigation to fill key knowledge gaps to unveil the ecological tradeoffs, evolutionary consequences, as well as the plant-intrinsic genetic factors controlling this event. Future work involving the investigation of the ecophysiological basis governing this process and the central role of phytohormone signalling in developing seeds and its putative compartmentalized synthesis in embryonic and maternal tissues should be instrumental in understanding vivipary in plants.

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References

- Anderson EF. 2001. *The Cactus family*. Portland, OR: Timber Press.
- Barthlott W, Hunt D. 2000. Seed diversity in the Cactaceae subfam. Cactoideae. *Succulent Plant Research* **5**, 1–173.
- Benzing DH. 1978. Germination and early establishment of *Tillandsia circinnata* Schlecht. (Bromeliaceae) on some of its hosts and other supports in Southern Florida. *Selbyana* **5**, 95–106.
- Benzing DH. 1990. *Vascular epiphytes. General biology and related biota*. Cambridge, MA: Cambridge University Press.
- Bregman R. 1988. Forms of seed dispersal in Cactaceae. *Acta Botanica Neerlandica* **37**, 395–402.
- Buxbaum F. 1968. Endogene Viviparie bei *Neoporteria*-Arten. *Kakteen und andere Sukkulente* **19**, 2–3.
- Castro J. 2006. Short delay in timing of emergence determines establishment success in *Pinus sylvestris* across microhabitats. *Annals of Botany* **98**, 1233–1240.
- Conde FL. 1975. Vivipary in *Epiphyllum*. *Cactus and Succulent Journal (U.S.)* **47**, 38–39.
- Cota JH. 1993. Pollination syndromes in the genus *Echinocereus*: a review. *Cactus and Succulent Journal (U.S.)* **65**, 19–26.
- Cota-Sánchez JH. 2002. Taxonomy, distribution, rarity status and uses of Canadian cacti. *Haseltonia* **9**, 17–25.

- Cota-Sánchez JH.** 2004. Vivipary in the Cactaceae: its taxonomic occurrence and biological significance. *Flora* **199**, 481–490.
- Cota-Sánchez JH, Crutch DS.** 2007. Notes on the floral biology of *Pracereus euchlorus* subsp. *euchlorus* (Cactaceae). *Schumannia* **5**, 1–5.
- Cota-Sánchez JH, Reyes-Olivas A, Sánchez-Soto B.** 2007. Vivipary in coastal cacti: a potential reproductive strategy in halophytic environments. *American Journal of Botany* **94**, 1577–1581.
- Elmqvist T, Cox PA.** 1996. The evolution of vivipary in flowering plants. *Oikos* **77**, 3–9.
- Farnsworth E.** 2000. The ecology and physiology of viviparous and recalcitrant seeds. *Annual Review of Ecology and Systematics* **31**, 107–138.
- Farnsworth E.** 2004. Hormones and shifting ecology throughout plant development. *Ecology* **85**, 5–15.
- Farnsworth E, Farrant JM.** 1998. Reductions in abscisic acid are linked with viviparous reproduction in mangroves. *American Journal of Botany* **85**, 760–769.
- Franco AC, Nobel PS.** 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* **77**, 870–886.
- Greenhall AM.** 1956. The food of some Trinidad fruit bats (*Artibeus* and *Carollia*). *Journal of the Agricultural Society of Trinidad Supplement*, 3–26.
- Gros A, Poethke HJ, Hovestadt T.** 2006. Evolution of local adaptations in dispersal strategies. *Oikos* **114**, 544–552.
- Hunter AF, Aarssen LW.** 1988. Plants helping plants. *Bioscience* **38**, 34–39.
- Kermode AR.** 2005. Role of abscisic acid in seed dormancy. *Journal of Plant Growth Regulation* **24**, 319–344.
- Laube S, Zotz G.** 2006. Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* **97**, 1103–1114.
- Lira F.** 2006. Estado de conservación de las subpoblaciones de *Eriosyce aspillagae* (Sohrens.) Katt. en su localidad tipo: un enfoque exploratorio. *Revista Chilena de Flora y Vegetación*. Año 9. No. 1. Website <http://www.chlorischile.cl> [Accessed 10 February 2007].
- Lombardi JA.** 1993. Viviparity in *Rhipsalis pilocarpa* Löfgren (Cactaceae). *Ciência e Cultura* **45**, 407.
- Mandujano MC, Flores-Martínez A, Golubov J, Ezcurra E.** 2002. Spatial distribution of three globose cacti in relation to different nurse-plant canopies and bare areas. *Southwestern Naturalist* **47**, 162–168.
- Mauseth JD.** 2000. Theoretical aspects of surface-to-volume ratios and water-storage capacities of succulent shoots. *American Journal of Botany* **87**, 1107–1115.
- Mitch LW.** 1964. North Dakota native cacti. *Cactus and Succulent Journal (U.S.)* **36**, 42–44.
- Nassar JM, Ramírez N, Lampo M, González JA, Casado R, Nava F.** 2007. Reproductive biology and mating systems of two Andean melocacti, *Melocactus schatzlii* and *M. andinus* (Cactaceae). *Annals of Botany* **99**, 29–38.
- Nobel PS.** 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegie gigantea*. *Botanical Gazette* **141**, 188–191.
- Nobel PS.** 1988. *Environmental biology of agaves and cacti*. Cambridge, MA: Cambridge University Press.
- Obeso JR.** 2002. The cost of reproduction in plants. *New Phytologist* **155**, 321–348.
- Palleiro N, Mandujano MC, Golubov J.** 2006. Aborted fruits of *Opuntia microdasys* (Cactaceae): insurance against reproductive failure. *American Journal of Botany* **93**, 505–511.
- Pimienta-Barrios E, Del Castillo RF.** 2002. Reproductive biology. In: Nobel PS, ed. *Cacti: biology and uses*. Los Angeles, CA: University of California Press, 75–90.
- Rabinowitz D.** 1978. Dispersal properties of mangrove propagules. *Biotropica* **10**, 47–57.
- Salisbury EJ.** 1942. *The reproductive capacity of plants*. London: G. Bell & Sons.
- Shi S, Huang Y, Zeng K, Tan F, He H, Huang J, Fu Y.** 2005. Molecular phylogenetic analysis of mangroves: independent evolutionary origins of vivipary and salt secretion. *Molecular Biology and Evolution* **34**, 159–166.
- Silvertown JW, Lovett-Doust J.** 1993. *Introduction to plant population biology*. Oxford: Blackwell Science Ltd.
- Suzan H, Nabhan GP, Patten DT.** 1994. Nurse plant and floral biology of a rare night-blooming cereus, *Peniocereus striatus* (Brandegee) F. Buxbaum. *Conservation Biology* **8**, 461–470.
- Taylor NP, Zappi D.** 2004. *Cacti of Eastern Brazil*. Surrey, UK: The Royal Botanic Garden, Kew.
- Tomlinson PB.** 1986. *The botany of mangroves*. Cambridge, UK: Cambridge University Press.
- Tomlinson PB, Cox PA.** 2000. Systematic and functional anatomy of seedlings in mangrove Rhizophoraceae: vivipary explained? *Botanical Journal of the Linnean Society* **134**, 215–231.
- Valiente-Banuet A, Ezcurra E.** 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and nurse plant *Mimosa luisana* in the Tehuacan valley, Mexico. *Journal of Ecology* **79**, 961–971.
- Van der Pijl L.** 1957. The dispersal of plants by bats (Chiropterachory). *Acta Botanica Neerlandica* **6**, 291–315.
- Waser NM, Real LA.** 1979. Effective mutualism between sequentially flowering plant species. *Nature* **281**, 670–672.
- Weid A, Galen C.** 1998. Plant parental care: conspecific nurse effects in *Frasera speciosa* and *Cirsium scopulorum*. *Ecology* **79**, 1657–1668.
- Winkler M, Hülber K, Hietz P.** 2005. Effect of canopy on germination and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. *Annals of Botany* **95**, 1039–1045.
- Zotz G.** 1997. Photosynthetic capacity increases with plant size. *Botanica Acta* **110**, 306–308.
- Zotz G, Hietz P.** 2001. The ecophysiology of vascular epiphytes: current knowledge, open questions. *Journal of Experimental Botany* **52**, 2067–2078.
- Zotz G, Hietz P, Schmidt G.** 2001. Small plants, large plants: the importance of plant size for the physiological ecology of vascular epiphytes. *Journal of Experimental Botany* **52**, 2051–2056.