BRIEF COMMUNICATION

Vivipary in coastal cacti: a potential reproductive strategy in halophytic environments[1]

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Vivipary, the germination of seeds within the fruit prior to abscission from the maternal plant, is an important event in plants. Two main types of vivipary are known in vascular plants: true vivipary and pseudovivipary. In crop grasses, pseudovivipary is an undesirable character as it results in lower yields. To date, vivipary in the Cactaceae has been reported for less than 20 species, most of which are cultivated. Here, we report viviparous (cryptoviviparous—a subcategory of true vivipary) cacti in nature in members of the tribes Cacteae and Pachycereeae (subfamily Cactoideae). We present four species inhabiting coastal plains in areas subject to periodic flooding, namely, *Ferocactus herrerae*, *Stenocereus alamosensis*, *S. thurberi*, and *Pachycereus schottii*. These species from localities in northwestern Mexico had viviparous fruits and offspring in different stages of development. A potential trend in the data indicates that the overall proportion of viviparous plants is higher in coastal flooding areas relative to halophytic, nonflooding areas. In our view, vivipary is a reproductive strategy that has evolved to provide a more efficient mechanism favoring germination and new avenues for survival by contributing to population maintenance and short-distance dispersal on halophytic substrates.

Key words: Cactaceae; *Ferocactus*; *Pachycereus*; precocious germination; *Stenocereus*; vivipary.

Vivipary, the germination of seeds within the fruit prior to abscission from the maternal plant, has been documented in alpine, arctic (Lee and Harmer, 1980; Elmqvist and Cox, 1996) and tropical (Farnsworth and Farrant, 1998; Cota-Sánchez, 2004) plants in arid and wet or flooded environments. In a viviparous organism, the embryo develops inside the maternal tissue from which it obtains nourishment, rather than inside an egg (ovipary), which nourishes and protects the embryo. Although vivipary is better known in placental mammals, it also occurs in many reptiles, some amphibians, insects, a few fish, and few plants, among others. At present, two main types of vivipary are known in flowering plants: true vivipary and pseudovivipary (Elmqvist and Cox, 1996), both of which occur in equal proportions in nature (Cota-Sánchez, 2004). True vivipary involves the production of sexual offspring, which are dispersed via the rupture of the pericarp wall as a result of embryo growth. Several mangrove species, such as *Bruguiera gymnorrhiza* (L.) Lamk., *Rhizophora mangle* L. (Tomlinson, 1986) and *Avicennia marina* (Forssk.) Vierh. (Farrant et al., 1993), among others, are some of the best-known angiosperms with true vivipary. Pseudovivipary, in turn, entails the formation of asexual propagules and is common in monocots, in particular the Poaceae (Beetle, 1980).

Vivipary, a phenomenon characterized by lack of dormancy, is important because in addition to being a relatively unusual event in nature, it has been interpreted as a specialized trait of evolutionary and biological significance providing new avenues for survival (Cota-Sánchez, 2004) and as a mechanism for protecting the embryo from high saline concentrations (Rabinowitz, 1978). This trait has only been reported in 78 families of vascular plants including 143 genera and 195 species (less than 0.1% of tracheophytes), of which 65 species are fully viviparous or cryptoviviparous (Farnsworth, 2000). Approximately 45 species are pseudoviviparous (Elmqvist and Cox, 1996). The most recent findings include cases of pseudovivipary in the seagrass *Posidonia oceanica* (L.) Delile (Ballesteros et al., 2005) and the cactus *Eriosyce aspillagae* (Sohrens.) Katt. (Lira, 2006).

Vivipary is also significant from an agricultural perspective. For instance, in some annual crops, such as rice, the lack of seed dormancy is undesirable because premature sprouting of grains creates a major challenge in maintaining food supplies, resulting in lower yields (Tsiantis, 2006). In addition, some aspects of vivipary and the ensuing desiccation intolerance are relevant to plant conservation. Because recalcitrant seeds generally lose viability upon drying, desiccation intolerance and vivipary can be detrimental because it affects species diversity in seed bank repositories. Thus, precocious germination and desiccation-sensitive seeds create a particularly serious issue in many rare tropical plant species, for which traditional methods of seed storage of nondormant (desiccation-intolerant) seeds are not effective (Tweddle et al., 2003). Consequently, these species tend to be absent from permanent seed bank collections (Thompson, 2000). The existence of nondormant seeds in the Cactaceae, a plant family with numerous endangered species, also affects germplasm collections. Thus, the pursuit of practical alternative approaches is required.

Madison (1977) indicated that vivipary could be overrepresented in fleshy-fruited taxa of the Araceae, Cactaceae, and Gesneriaceae. Current data, however, show that this reproductive strategy is rather rare in the Cactaceae. To date, the reports of vivipary in the Cactaceae include less than 20 species and
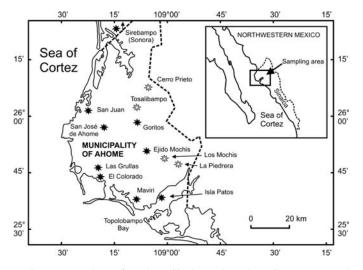
Fig. 1. Locations of northern Sinaloa and southern Sonora surveyed for viviparous fruits of native cacti in northwestern Mexico. Black asterisks indicate localities with cacti with viviparous seeds.

are based mainly on cultivated specimens. Several references, e.g., Mitich, 1964; Buxbaum, 1968; Conde, 1975; Lombardi, 1993; Cota-Sánchez, 2002; and Lira, 2006, have described examples of pseudovivipary in the family. The most extensive account of cactus vivipary is that of Cota-Sánchez (2004), who documented eight additional viviparous species (including one hybrid) for a total of 11 taxa encompassing four tribes of the subfamily Cactoideae. Based on embryonic development and characteristics of the viviparous fruits, the first author suggested the occurrence of cryptovivipary (a subcategory of true vivipary), a condition in which the zygote develops inside the fruit without protruding from the pericarp for dispersal purposes. Further, he predicted that "this trait may be more widespread in the family than originally thought and more attention should be given to the different stages of fruit development in wild and cultivated specimens … seeking evidence of its occurrence in nature" (Cota-Sánchez, 2004, p. 489).

Here, we confirm his hypothesis on the widespread condition of vivipary and provide reports of viviparous (cryptoviviparous) cacti in nature in members of the tribes Cacteae and Pachycereeae (subfamily Cactoideae). We present four species inhabiting coastal plains in areas subject to periodic flooding, namely *Ferocactus herrerae* J. G. Ortega, *Stenocereus alamosensis* (J. M. Coult.) A. C. Gibson & K. E. Horak, *S. thurberi* (Engelm.) Buxbaum, and *Pachycereus schottii* (Engelm.) D. R. Hunt. These taxa, distributed in several localities in northwestern Mexico (Fig. 1), displayed viviparous fruits and offspring in different stages of development. The first finding of viviparous plants occurred in populations of the barrel cactus *F. herrerae* near San Juan, northern Sinaloa (Fig. 1), in areas of sand dunes with halophytous vegetation (Fig. 2A). Seeds in several stages of germination, including seedlings of significant size, were found inside mature *F. herrerae* fruits (Fig. 2C, D) when these were dissected to harvest seeds. This initial finding triggered our curiosity, and we continued to sample nearby barrel cacti in search of additional viviparous plants.

An extensive search including adjacent areas with saline soils located in coastal plains and areas subject to cyclic flooding was conducted in the municipality of Ahome in the state of Sinaloa and in the southern part of the state of Sonora, Mexico (Fig. 1). In this survey, we investigated all the native cacti in the region, including five additional species inhabiting coastal plains and neighboring sand dunes [*Cylindropuntia fulgida* (Engelm.) F. M. Knuth, *Mammillaria mazatlanensis* K. Schum., *Pachycereus schottii*, *Stenocereus alamosensis*, and *S. thurberi*] and found that vivipary in this region is restricted to the columnar species (*P. schottii, S. alamosensis,* and *S. thurberi*) and to *F. herrerae*. Of these last four species, we sampled approximately 450 plants (50 to 200 plants per species, see Table 1) distributed throughout the study area. Viviparity is present in nine of the 13 investigated localities subject to flooding (see Fig. 1). Viviparous individuals are more common in *F. herrerae* (19 of 100 plants) and *S. thurberi* (25 of 200 plants) and less common in *S. alamosensis* (nine of 100 plants) and *P. schottii* (one of 50 plants) (Table 1), but we are uncertain whether these frequencies are consistent in each of the nine localities with viviparous plants. In none of these cases did the seedlings puncture or protrude from the pericarp, a characteristic of cryptovivipary.

In an initial comparative survey, we assessed the distribution of viviparous fruits in flooding vs. nonflooding environments. Accordingly, approximately 1000 fruits from 267 plants of the four viviparous species (13 to 100 plants per species) were collected in two hilly localities away from the coast, 63 and 135 km north of Los Mochis, Sinaloa, in the municipality of El Fuerte (not shown in Fig. 1). With the exception of *S. thurberi* (21 of 100 viviparous plants sampled), the proportion of plants producing at least one viviparous fruit was lower in non-flooding than flooding localities, i.e., four plants of 54 in *S. alamosensis*, and 11 of 100 plants in *F. herrerae,* while vivipary was absent in all 13 of the *P. schottii* individuals sampled (Table 1). Similar to flooding localities, viviparous individuals were more common in *F. herrerae* (11%) and *S. thurberi* (21%) than in *S. alamosensis* (7.4%) and *P. schottii* (0%) (Table 1).

Finch-Savage and Leubner-Metzger (2006) indicated that species of the Cactaceae have both physiologically dormant and nondormant seeds with a peripheral embryo. In our survey, we found that some of the *Ferocactus herrerae, Stenocereus alamosensis*, and *S. thurberi* individuals sampled produced both viviparous and nonviviparous fruits. The latter type of fruit was more common in both estuarine flooding and inland environments. Although we do not have a conclusive explanation as to why the two fruit types are produced by the same plant, we hypothesize that various intrinsic and extrinsic factors of the plant may be involved, namely different stages of fruit and seed development, differential production levels and compartmentalization of phytohormones, particularly abscisic acid (ABA), cellular osmotic pressure, soil conditions, and temperature.

Overall, our data indicate that, in nonflooding and flooding sampled areas respectively, viviparous individuals vary from 11–19% in *Ferocactus herrerae,* 21–12.5% in *Stenocereus thurberi*, 7.4–9% in *S. alamosensis* (Fig. 3A–D), and 0–2% in *P. schottii* (Table 1). It should be noted that our field data and sample sizes limit the running of analytical tests, such as ANCOVA and chi-square, to test and interpret differences among habitats and species and determine whether the same plant has equal possibilities to produce both viviparous and nonviviparous fruits. Nonetheless, the data show a potential trend indicating that the overall proportion and distribution of
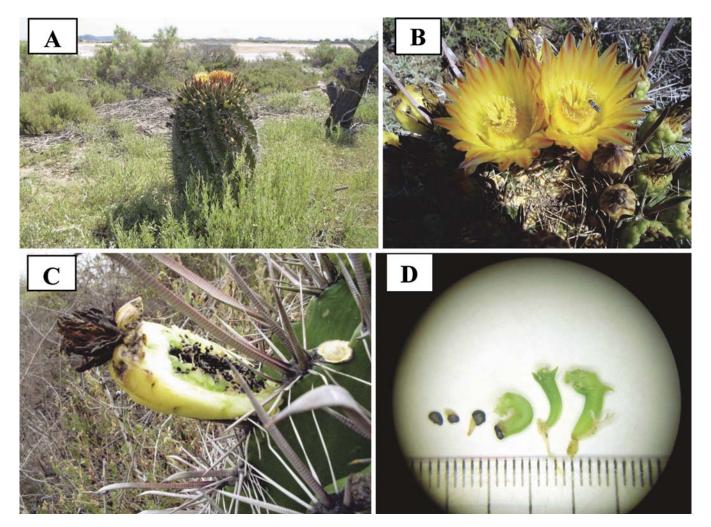
Fig. 2. General habitat, flowers, viviparous fruits and viviparous offspring of *Ferocactus herrerae*. (A) Habitat of viviparous plant growing with *Suaeda fruticosa* and *Atriplex polycarpa* between the beaches of San Juan and La Viznaga, in the state of Sinaloa. (B) A bee visiting *F. herrerae* flowers. (C) Longitudinal section of *F. herrerae* bearing a fruit with viviparous seeds attached to mother plant. (D) Different germination stages of viviparous seeds and offspring in *F. herrerae*. Scale in mm.

viviparous plants is higher in coastal flooding areas relative to halophytic, nonflooding environments (Table 1).

The four viviparous cacti discussed here have adapted to the arid climate and saline soils of the lower Sonoran Desert. Though these cacti grow well in various edaphic conditions,

the highest proportion of viviparous individuals is found on coastal plains with saline, sandy soils subjected to cyclic flooding, in particular during high tides. The same premise for the prevalence of vivipary in seashore flooding areas has been proposed by Joshi (1933, 1934) and Elmqvist and Cox (1996).

Table 1. Incidence of cactus vivipary in coastal flooding environments vs. inland nonflooding environments. Summarized data for 717 individuals from which 1–3 fruits/plant were randomly collected in nine flooding and two nonflooding localities. Note that fruits are not independent of one another (up to three fruits may come from one plant). Asterisks represent localities in which more than three fruits per plant were collected.

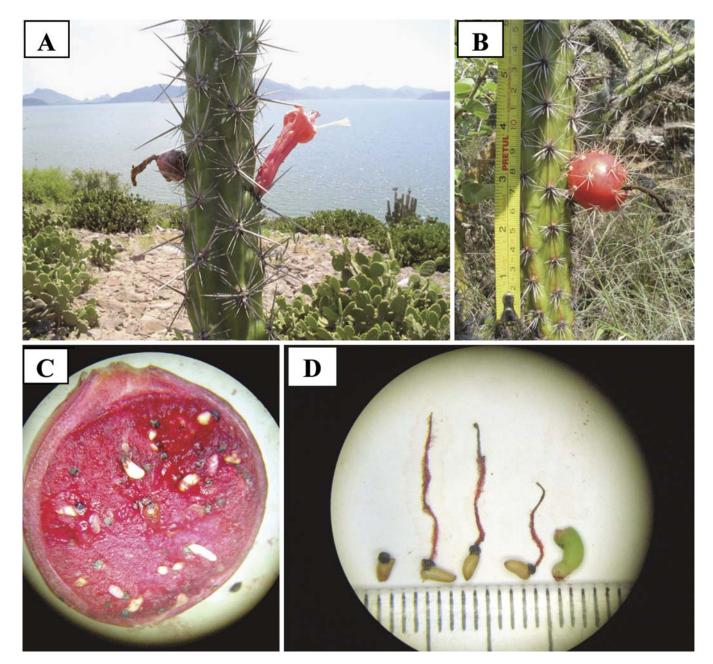| Taxon	Habitat	No. plants sampled/ No. viviparous plants	Viviparous plants (%)	No. viviparous fruits	No. nonviviparous fruits	Total fruits	Viviparous fruits (%)
Ferocactus herrerae	Coastal, flooding	100/19	19.0	28	93	121	23.1
	Inland, nonflooding*	100/11	11.0	33	424	457	7.2
Pachycereus schottii	Coastal, flooding	50/1	2.0	1	50	51	2.0
	Inland, nonflooding	13/0	0	0	13	13	0
Stenocereus alamosensis	Coastal, flooding	100/9	9.0	9	95	104	8.6
	Inland, nonflooding	54/4	7.4	7	122	129	5.4
S. thurberi	Coastal, flooding	200/25	12.5	48	272	320	15.0
	Inland, nonflooding*	100/21	21.0	89	312	401	22.2
Totals		717/90	n/a	215	1381	1596	13.5

Fig. 3. General habitat, fruit and viviparous seedlings of *Stenocereus alamosensis*. (A) General habitat with shallow, rocky substrate in Patos Island (Bahía de Ohuira), state of Sinaloa. *Opuntia* sp. can be seen in the background. (B) Stem with viviparous fruit growing with *Distichlis spicata* near El Maviri beach. (C) Longitudinal section of a fruit from Patos Island showing viviparous seeds. (D) Detail of viviparous seeds showing seed testa and funiculus. Scale in mm.

However, the disparate occurrence of viviparous individuals of these species in both flooding coastal environments and inland nonflooding halophytic areas with gravelly or rocky substrates suggests that this condition may be more widespread and not necessarily restricted to flooding regions as suggested by several authors, e.g., Joshi (1933, 1934), Elmqvist and Cox (1996), Farnsworth (2000), and Farnsworth and Farrant (1998), among others. It is possible that the high salt concentrations and temperatures prevailing in nonflooding halophytic soils also affect the production levels of phytohormones in these plants.

Previous to these reports, vivipary in the Cactaceae was restricted to tribes Cacteae, Hylocereeae, Rhipsalideae, and Trichocereeae, subfamily Cactoideae (Cota-Sánchez, 2004); the columnar viviparous cacti discussed here belong to the tribe Pachycereeae. Thus, the reports now extend to five tribes of the Cactoideae, suggesting the multiple origin of this trait in the cactus family and presumably the loss of dormancy in distantly related viviparous lines. We believe that cactus vivipary represents a shift toward a more efficient mechanism favoring germination and seedling establishment. Tomlinson and Cox (2000) also suggested that vivipary in mangroves facilitates establishment. Conceivably, this trait provides new avenues for

survival and contributes to cactus short-distance dispersal and population maintenance in halophytic substrates.

In conclusion, vivipary is an unconventional reproductive means deserving more attention in the laboratory and the field. These and other recent findings indicate that ample opportunity to investigate this trait from the ecophysiological and evolutionary perspectives exists. Future studies involving native cacti distributed in coastal regions, especially areas subject to estuarine influence would likely be instructive in improving our understanding of the relationship of cactus vivipary with saline/marine environments.

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