



Short Communication

Vivipary in the cactus family: An evaluation of 25 species from northwestern Argentina

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ABSTRACT

In this study, we evaluated the occurrence of vivipary in natural populations of 25 cactus species from the northwest of Argentina. The fruits of all species were dissected in order to analyze the presence of germinated seeds. In addition, we evaluated seed germination to determine whether seeds were dormant in the mature fruits. We did not record germinated seeds inside the fruits of any of the species, though 40% of the species had non-dormant seeds. Our results showed that vivipary is not a common phenomenon in the cactus family. In light of this, we believe that vivipary in cacti should be considered as a physiological response of the plants to their environmental conditions, rather than an adaptive strategy that maximizes their establishment.

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Vivipary is the phenomenon by which seeds germinate inside the fruits before dispersal. In flowering plants, vivipary is considered a rare reproductive strategy, which is proposed to confer advantages for survival and establishment in harsh environments (e.g. saline and alpine environments) and is associated with the presence of non-dormant seeds (Cota-Sánchez, 2004; Cota-Sánchez and Abreu, 2007; Cota-Sánchez et al., 2007; Farnsworth, 2000). In contrast, Elmquist and Cox (1996) have indicated that vivipary is a strategy associated to environments with physical and biotic homogeneity, where possible fitness gains, from seed dispersal in time and space, are reduced. This last condition would be essential for vivipary to be an evolutionarily stable strategy (Elmquist and Cox, 1996).

Recently, the occurrence of vivipary in the cactus family has been reported (Cota-Sánchez, 2004). It has been proposed that vivipary in cactus species has evolved as a mechanism to provide more efficient germination and seedling establishment, contributing to population maintenance and short distance dispersal (Cota-Sánchez and Abreu, 2007; Cota-Sánchez et al., 2007). However, this phenomenon has only been described for 16 cactus species (Cota-Sánchez, 2004; Cota-Sánchez and Abreu, 2007; Cota-Sánchez et al., 2007) and, in most of the cases, has been

documented for plants growing under greenhouse conditions (Cota-Sánchez, 2004).

Here, we evaluated the occurrence of vivipary in natural populations of 25 cactus species from the northwest of Argentina. Our first motivation was to determine if *Cleistocactus smaragdiflorus*, *Pfeiffera ianthothele*, *P. monacantha*, and *Rhipsalis baccifera*, four species cited by Cota-Sánchez (2004) as viviparous under greenhouse conditions, show vivipary in natural populations. Subsequently, we extended this study to a further 21 species growing in the same region, including some species belonging to the genera reported as being viviparous.

The evaluated species (named according to Hunt, 2006; Table 1) belong to four tribes (Cereeae, Notocactaceae, Rhipsalidae and Trichocereae). From January to March in 2007, 2008 and 2009, fruits of all species were collected in the Orán and San Martín counties and the Lerma and Calchaquí Valleys of the Salta province (Argentina). The locations of the collection sites are not mentioned to protect the populations. The number of populations, individuals and fruits evaluated varied among species due to the different availability recorded in the field (Table 1). Once collected, the fruits were dissected and all seeds were placed onto a sheet of paper and the number of germinated seeds evaluated under a stereoscopic microscope. Additionally, seeds from each population were germinated in the laboratory to determine whether seeds were dormant in the mature fruits. Germination was conducted during the month in which the seeds were collected, by sowing four

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Table 1
Cactus species of the Salta province (Argentina) in which the existence of vivipary was evaluated. Number of populations, individuals and fruits, and seed germination for each population (proportion, mean \pm standard deviation) were indicated. Vivipary was not registered in any of the species.

| Species | Populations | Individuals | Fruits | Seed germination |
|--------------------------------------|-------------|-------------|--------|---|
| Cereaceae | | | | |
| <i>Cereus aetiops</i> | 1 | 5 | 7 | 0.20 \pm 0.07 |
| <i>Cereus hankeanus</i> | 2 | 15 | 30 | 0.40 \pm 0.06; 0.32 \pm 0.13 |
| Notocactaceae | | | | |
| <i>Parodia aureicentra</i> | 2 | 23 | 40 | 0.78 \pm 0.11; 0.73 \pm 0.11 |
| <i>Parodia microsperma</i> | 3 | 29 | 45 | 0.92 \pm 0.03; 0.88 \pm 0.03; 0.84 \pm 0.03 |
| Rhipsalidaceae | | | | |
| <i>Pfeiffera ianthothele</i> | 3 | 10 | 20 | 0.77 \pm 0.10; 0.72 \pm 0.09; 0.10 \pm 0.07 |
| <i>P. monacantha</i> | 3 | 8 | 21 | 0.37 \pm 0.09; 0.33 \pm 0.09; 0.29 \pm 0.07 |
| <i>Rhipsalis baccifera</i> | 3 | 8 | 25 | 0.85 \pm 0.04; 0.80 \pm 0.10; 0.78 \pm 0.05 |
| <i>R. floccosa</i> | 2 | 6 | 15 | 0.29 \pm 0.06; 0.19 \pm 0.05 |
| Trichocereaceae | | | | |
| <i>Cleistocactus baumannii</i> | 1 | 15 | 20 | 0.93 \pm 0.02 |
| <i>Cleistocactus smaragdiflorus</i> | 3 | 30 | 65 | 0.94 \pm 0.05; 0.91 \pm 0.04; 0.87 \pm 0.04 |
| <i>Echinopsis albispinosa</i> | 1 | 18 | 23 | 0.38 \pm 0.05 |
| <i>Echinopsis ancistrophora</i> | 1 | 35 | 41 | 0.37 \pm 0.08 |
| <i>Echinopsis angelesiae</i> | 1 | 15 | 15 | 0.56 \pm 0.07 |
| <i>Echinopsis atacamensis</i> | 5 | 30 | 80 | 0.96 \pm 0.03; 0.93 \pm 0.04; 0.91 \pm 0.04; 0.88 \pm 0.03; 0.87 \pm 0.07 |
| <i>Echinopsis haematantha</i> | 1 | 14 | 15 | 0.27 \pm 0.07 |
| <i>Echinopsis leucantha</i> | 1 | 6 | 15 | 0.14 \pm 0.05 |
| <i>Echinopsis schickendantzii</i> | 1 | 20 | 60 | 0.86 \pm 0.05 |
| <i>Echinopsis terscheckii</i> | 2 | 30 | 70 | 0.92 \pm 0.03; 0.86 \pm 0.07 |
| <i>Echinopsis thelegona</i> | 1 | 9 | 10 | 0.94 \pm 0.05 |
| <i>Echinopsis thionantha</i> | 2 | 18 | 25 | 0.49 \pm 0.04; 0.42 \pm 0.05 |
| <i>Echinopsis walterii</i> | 1 | 5 | 5 | 0.64 \pm 0.07 |
| <i>Gymnocalycium saglionis</i> | 1 | 30 | 45 | 0.39 \pm 0.04 |
| <i>Gymnocalycium schickendantzii</i> | 2 | 16 | 18 | 0.11 \pm 0.07; 0.17 \pm 0.09 |
| <i>Gymnocalycium spegazzinii</i> | 2 | 15 | 15 | 0.50 \pm 0.05; 0.59 \pm 0.07 |
| <i>Harrisia pomanensis</i> | 2 | 12 | 15 | 0.21 \pm 0.07; 0.24 \pm 0.06 |

replicates of 25 seeds onto the surface of 1% agar in Petri dishes and incubating at 25 °C with a 12 h-light/12 h-dark photoperiod. Seed germination was recorded for 30 days, where germination was considered to have occurred once the radicle had emerged. At the end of the germination assays, non-germinated seeds were cut longitudinally and embryos were observed under a stereoscopic microscope to assess viability. Seeds were considered viable if their embryos were white and turgid. According to this analysis, all seeds in this study were viable. We adopted $\geq 70\%$ germination as a criterion for a lack of dormancy (Flores et al., 2006). Germination proportions for each population are shown in Table 1.

None of the species or populations studied had germinated seeds inside the fruits. Forty percent of the species showed non-dormant seeds (Table 1). The four species listed as viviparous by Cota-Sánchez (2004) showed different germination behaviors. *P. ianthothele* registered a dual behavior showing dormant and non-dormant seeds according to the populations studied (Table 1). On the other hand, *P. monacantha* showed dormant seeds, while *C. smaragdiflorus* and *R. baccifera* presented non-dormant seeds (Table 1).

Our results did not confirm the idea that vivipary is a common phenomenon in the cactus family. Furthermore, the natural populations of the species mentioned as viviparous under greenhouse conditions (*C. smaragdiflorus*, *P. ianthothele*, *P. monacantha*, and *R. baccifera*), did not show germinated seeds inside the fruits. This suggests that vivipary in cacti should be considered as a physiological response of plants to their environmental conditions, rather than an adaptative strategy to maximize their establishment. It has been indicated that vivipary is related to low levels of ABA (abscisic acid; a phytohormone that inhibits seed germination) in seeds or fruits (Farnsworth, 2000), and that ABA formation, accumulation, lateral transport within the roots, and long-distance translocation depend on external factors (Jiang and Hartung, 2008). Future

studies should evaluate experimentally, whether cactus species produce seedlings by vivipary under certain environmental conditions (e.g. water stress, high salinity) and if the ABA concentration can be correlated to this.

Our results agreed with the idea that cactus species can have dormant or non-dormant seeds (Rojas-Aréchiga and Vázquez-Yanes, 2000) and showed that cactus species with non-dormant seeds did not necessarily produce viviparous seedlings. The production of non-dormant seeds is probably related to seed germination process in the soil rather than to the capacity of producing viviparous offspring. Many cactus species bloom during the dry season, so seed dispersal occurs at the beginning of the ensuing rainy season allowing the immediate germination of non-dormant seeds (Bustamante and Búrquez, 2008). An interesting result of our study was the dual germination behavior in *P. ianthothele*. This species is an epiphytic cactus, which occupies environments ranging from humid to semiarid that differ in vertical vegetation structure. These environmental differences could explain our finding. Variation of seed dormancy could be either the result of local adaptation to particular environmental conditions (Yang et al., 1999) or a maternal effect on seed dormancy (Schütz and Milberg, 1997).

Some morphological, physiological and ecological seed traits such as small size, light requirement and dormancy have been linked to the ability of a species to form persistent seed banks (Bowers, 2000; Flores et al., 2006; Rojas-Aréchiga and Batis, 2001). It has been assumed that cactus species do not produce seed banks; however, this has not been adequately evaluated. Seed dormancy in 60% of the species evaluated in this work suggests that they could form persistent seed banks. These species are positively photoblastic and have small seeds (Ortega-Baes et al. unpublished data). Preliminary studies have shown that *Echinopsis acistrophora* and *Echinopsis albispinosa*, two cactus species with dormant, positively

photoblastic and small seeds, have at least a short-term persistent seed bank (Ortega-Baes, unpublished data).

Cota-Sánchez and Abreu (2007) have strongly advocated that vivipary in the cactus family must be interpreted as a reproductive strategy, which increases the seedling survival and is thus an adaptation for the persistence of the population in stressful environments. However, we consider that the ecological and evolutionary implications of vivipary in the cactus family are not as clear; therefore, the interpretation of this phenomenon must be carried out with caution. We considered that the low proportion of viviparous fruits per individual and the low proportion of viviparous individuals per population registered in previous studies (see Cota-Sánchez and Abreu, 2007) do not prove vivipary as a strategy selected in stressful environments. Cota-Sánchez et al. (2007) has mentioned that the strongest environmental filter in the establishment of viviparous cactus plants is associated with seedling survival; however, this pattern is common for all cactus species (Godínez-Alvarez et al., 2003). We considered that one of the aspects that has not been taken into account in previous discussions of vivipary is that the fleshy fruits of cactus species are widely eaten by frugivorous animals (seeds dispersers and seed predators; Godínez-Alvarez et al., 2002). This represents another environmental filter against the survival of seedlings that develop inside the fruit, since they would die in the digestive tracts of frugivorous animals.

Finally, we believe that the evaluation of the recurrence of vivipary in the Cactaceae should be continued. However, we consider that further research must also focus on the comparative studies of the recruitment patterns of viviparous and non-viviparous seedlings. If vivipary is an adaptative strategy that maximizes cactus survival in harsh environments, then it should be demonstrated that viviparous seedling performance is higher than the performance of seedlings from seeds that germinate outside of the fruits (Elmqvist and Cox, 1996).

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