



Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Short Communication

Vivipary in the cactus family: A reply to Ortega-Baes' et al. evaluation of 25 species from northwestern Argentina

J.H. Cota-Sánchez^{a,*}, Á. Reyes-Olivas^b, D.D. Abreu^{a,c}^a Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada^b Universidad Autónoma de Sinaloa, Los Mochis, Sinaloa, CP 81220, Mexico^c Departamento de Botânica, Universidade de São Paulo, 05422-970 São Paulo, Brazil

ARTICLE INFO

Article history:

Received 4 August 2010

Received in revised form

22 February 2011

Accepted 7 April 2011

Available online xxx

Keywords:

Cactaceae

Fruit

Precocious germination

Seed

Seed development

Vivipary

ABSTRACT

This is a reply to Ortega-Baes' et al. (2010) survey of 25 Argentinean species of cacti evaluated for vivipary. We argue that the sample size and geographic area of the species investigated is insufficient to totally exclude the putative commonness of this condition in the Cactaceae. We indicate possible reasons why they did not find viviparous fruits in their survey. Failure to detect vivipary in cacti of NW Argentina may be correlated with limited taxonomic sampling and geographic region in addition to intrinsic and extrinsic plant factors, including different stages of fruit and seed development and genetic, ecological, and edaphic aspects, which, individually or in concert, control precocious germination. We uphold that viviparity is putatively frequent in this family and list 16 new cases for a total of 53 viviparous cacti, which make up ca. 4% incidence of viviparism in the Cactaceae, a substantially higher percentage than most angiosperm families exhibiting this condition. The Cactaceae ranks fourth in frequency of viviparity after the aquatic families of mangroves and seagrasses. We suggest the re-evaluation of cactus vivipary, primarily as a reproductive adaptation to changing environments and physiological stress with a secondary role as a reproductive strategy with limited offspring dispersal/survival and fitness advantages.

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Recently, Ortega-Baes et al. (2010) presented the results of a field survey of 25 Argentinean species of cacti evaluated for vivipary in this *Journal of Arid Environments*. Their study reports absence of viviparous plants among the species investigated, disagreeing with Cota-Sánchez's (2004) hypothesis that vivipary may be relatively common in the Cactaceae. The authors also disagree that vivipary is a trait conferring advantages for seedling establishment under stressed environmental conditions as proposed by Cota-Sánchez and Abreu (2007) and Cota-Sánchez et al. (2007). We feel obligated to reply to their note. Rather than responding to every point made, we address several issues regarding their study and their interpretation of our hypotheses on the putative frequency of precocious germinations in the Cactaceae and the association of this trait with harsh environments. Here we argue that (1) the sample size of the species investigated is insufficient to totally rule out vivipary in the Cactaceae, (2) vivipary, though reported in a relatively low number of cacti, is a putative common trait in this family, and (3) possible reasons exist why they did not find viviparous fruits during their survey.

Sample size of species investigated

Foremost, we believe that the study of vivipary in NW Argentina requires a more exhaustive taxonomic and geographic sampling. The limited number of species and restricted geography are not sufficient to rule out Cota-Sánchez's (2004) hypothesis about the putative frequency of vivipary in the Cactaceae. To argue this issue we need to consider first the Cactaceae of Argentina and the sampled area. According to the New Cactus Lexicon (Hunt et al., 2006), Argentina has approximately 170 species of cacti (out of an America-wide total of ca. 1430). Of these, 86 (over 50% of the country's cactus flora) occur in Jujuy and/or Salta (D. Hunt and R. Kiesling, pers. com.), which happens to include the region investigated by Ortega-Baes et al. (2010). Despite the large number of Argentinean cacti, the authors investigated a mere 25 species, that is, only 14.7% of Argentina's cactus diversity and 29% (less than one-third) of species of cacti in the Jujuy-Salta regions.

Another concern has to do with the dry climate of the study area. In addition to extreme dry regions, NW Argentina is characterized by areas with dry winters and a wide range of altitudinal ranges, promoting diverse climatic types, phytogeographic provinces, and plant communities. It is not surprising that the authors

* Corresponding author. Tel.: +1 306 966 4405; fax: +1 306 966 4461.
E-mail address: hugo.cota@usask.ca (J.H. Cota-Sánchez).

failed to find viviparity because they sampled cacti characteristic of the driest areas rather than from the different phytogeographic regions of northern Argentina. Viviparity is associated with fluctuating levels of water stress, and germination is associated with water availability (Baskin and Baskin, 2001). Thus, the absence of viviparity in the areas of Salta and Jujuy is likely linked with prevailing dry environments and limited water availability. Dry conditions increase the abscisic acid (ABA) levels (Rodríguez-Gacio et al., 2009), a condition not favorable for viviparity, which is linked to low, not high, levels of ABA (Farnsworth and Farrant, 1998).

To better understand the ecological, geographic, and taxonomic distribution of viviparity in this family, an extensive sampling encompassing the taxonomic diversity of the cactus family and the wide array of growth forms and ecological environments in which the ca. 1430 species occur in the Americas is necessary. New reports (indicated below) are evidence that viviparity is a suspected common attribute in the Cactaceae.

New reports support that viviparity is a putative common trait in the cactus family

We marginally agree that viviparity in the Cactaceae may be an uncommon attribute. To understand this idea, it is necessary to keep in mind that viviparity is a rare condition in the plant kingdom (Elmqvist and Cox, 1996; Farnsworth, 2000; Cota-Sánchez et al., 2007). To date, this reproductive mode has been reported in less than 1% of tracheophytes (Cota-Sánchez, 2004). Among angiosperms, there is compelling evidence that the Cactaceae is one of the few plant families with a higher incidence of viviparity. We have data of 16 new cases of viviparous cacti, namely *Coryphantha radians* (DC) Britton & Rose, *Echinocactus platyacanthus* Link and Otto, *Epiphyllum guatemalense* Britton & Rose, *Ferocactus peninsulæ* (F.A.C. Weber) Britton & Rose, *Lepismium bolivianum* (Britton) Barthlott, *Leptocereus arboreus* Britton & Rose, *L. scopulophilus* Areces, *Leuchtenbergia principis* Hook., *Melocactus concinnus* Buining and Brederoo, *M. curvispinus* Pfeiff., *M. ernestii* Vaupel, *M. paucispinus* Heimen and Paul, *Pachycereus pecten-aboriginum* (Engelm. ex S. Watson) Britton & Rose, *Rhipsalis baccifera* (J.S. Mueller) Stearn. subsp. *baccifera*, *R. floccosa* Salm-Dyck ex Pfeiffer subsp. *pittieri* (Britton & Rose) Barthlott and N.P. Taylor, and *Weberocereus panamensis* Britton & Rose (Cota-Sánchez et al., unpub. data). Moreover, two recent wild cases of viviparous cacti [*Cephalocereus totalapensis* (Bravo and T. MacDoug.) Buxb. and *Pachycereus grandis* Rose] were described (Rojas-Aréchiga and Mandujano-Sánchez, 2009). The preceding data suggest that viviparism is becoming a more frequent event in the cactus family and is present in two forms (pseudoviviparity and cryptoviviparity) in at least 53 (3.7%) species (Cota-Sánchez et al., unpub. data).

For comparative purposes, we used data from Farnsworth (2000) to put in perspective the incidence of viviparity in the Cactaceae compared to other angiosperm families with viviparous species (Table 1). Remarkably, the Cactaceae, a mainly tropical and subtropical family with terrestrial and epiphytic lineages, ranks fourth in incidence of viviparity after the aquatic families of mangroves and seagrasses (Cymodoceaceae) (Table 1). Thus, we tend to concur, in part, that viviparity is rare in the Cactaceae, but only when considering the high number of species in the family. While the ca. 4% viviparous species in the Cactaceae might seem irrelevant, this number is rather significant bearing in mind the family's species diversity (1430) and considering that the number of viviparous species (53) is much higher than viviparous taxa in the Rhizophoraceae (18), Avicenniaceae (8), and Cymodoceaceae (4) (Table 1). These data substantiate that the Cactaceae is among the plant families with the highest incidence of viviparism.

Table 1

A list of plant families with higher frequency of viviparous species. With the exception of the cactus family, the number of viviparous species is based on data provided by Farnsworth (2000). The number of species in each family is based on Judd et al. (2008).

Family	No. Species/No. viviparous species	Percentage of viviparity (%)
Avicenniaceae	11/8	72.7
Cymodoceaceae	16/4	25.0
Rhizophoraceae	87/18	20.7
Cactaceae	1430/53	3.7
Liliaceae	225/5	2.2
Cornaceae	110/2	1.8
Poaceae	9700/23	0.3
Myrsinaceae	1435/2	0.14
Arecaeae	2780/2	0.07
Fabaceae	18000/4	0.02

Other possible factors affecting the incidence of cactus viviparity in the wild

The occurrence of viviparity is concomitant with certain environmental, edaphic, climatic, and physiological factors (Cota-Sánchez and Abreu, 2007; Cota-Sánchez et al., 2007). Studies of viviparous cacti in NW Sinaloa, Mexico, suggest that the ecological requirements for precocious germination, including halophytic substrate and flooding environments, vary among species (Reyes-Olivas et al., unpub. data). Different production levels and compartmentalization of phytohormones (particularly ABA) as well as different physiological, genetic and ecological factors, individually or in concert, also play a major role in the rate of precocious germination. Failure to detect viviparity in cacti of NW Argentina may be correlated with the plants' intrinsic and extrinsic factors.

Other factors accounting for the absence of viviparity are seed development and fruit maturity. The completion of these two processes is necessary for embryo development and for seeds to enter the dormant phase (Baskin and Baskin, 2001). Embryo development in seed plants involves the morphogenesis and maturation phases. Thus, fruit maturity is determined by age and complete physiological development of seed and embryo. In orthodox and viviparous seeds, germination is timed to occur after fruit and seed development when favorable conditions are suitable for seedling establishment (Baskin and Baskin, 2001; Siobhan and Harada, 2008). It might be the case that 1) the fruits and seeds screened for viviparity in NW Argentina were not physiologically mature and/or the seeds were not fully developed and/or 2) the fruits lacked the appropriate conditions for germination to occur.

With cautious judgment and considering the overall limited data regarding number of species screened for viviparity to determine the taxonomic and ecological distribution of this trait in the Cactaceae, we believe that it is premature to rule out its presumed commonness in the family. In addition, in view of the scanty information regarding seedling establishment and survival, it is necessary to re-evaluate cactus viviparity, primarily as a reproductive adaptation to changing environments and physiological stress with a secondary role as a reproductive strategy with limited offspring dispersal/survival and fitness advantages.

In conclusion, although we are unable to provide a strong link between cactus viviparity and harsh conditions, most wild examples have been documented in stressful environments. Also, whether viviparity is indeed a reproductive strategy remains a disputed issue. Viviparity is a reproductive mode that has evolved in parallel in numerous angiosperm families (Cota-Sánchez and Abreu, 2007). It involves a high degree of ecophysiological specialization and complex phytohormone signaling (Farnsworth, 2000; Batygina and Bragina, 2009) and is detrimental in crop cereals (Tsiantis, 2006).

In-depth genetic, physiological, developmental and ecological studies will be instrumental in gaining a better understanding of the evolutionary and fitness advantages of this complex condition in angiosperms. The Cactaceae, a diverse monophyletic family of long-lived xerophytes and one of the few angiosperm lineages successfully radiating into different habitats, lends itself as a model group to study viviparism and unveil ecophysiological and evolutionary mechanisms that led to its reproductive specialization.

Acknowledgments

We thank H. J. Choi, A. Davis, and D. Litwiller, and two reviewers for their comments. To D. Hunt and R. Kiesling for validating the information on the cactus flora of Argentina and J. Flores for sharing data of *C. radians*, *E. platyacanthus*, and *L. principis*. This study was funded by the University of Saskatchewan Bridge Fund, Global Partners II, and the National Geographic Society (Grant No. 7382-02) to JHCS and the Universidad Autónoma de Sinaloa (Grant PROFAPI 2007-217) to ARO.

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