Genetic diversity in the Cactaceae

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From arid zones to dry forests, available evidence indicates that anthropogenic activities are causing major negative impacts on dry ecosystems around the world. Land conversion and desertification are causing considerable degradation of soils, reduction of population size of many xerophilous plants and population fragmentation. In many cases, these effects are accompanied with loss of genetic diversity and an increase in the risk of extinction of species at a local and regional level. Management and conservation programs aimed to recover threatened plant species under this scenario should include information on the levels of genetic diversity present in the remnant populations.

In general, plants from arid lands have been the subject of relatively few genetic diversity surveys. This is so despite the fact that many woody species associated with xeric lands can be considered key elements that sustain life in these environments. Estimates of genetic diversity obtained until present in this ecosystem type correspond to approximately 118 species, belonging to 13 families. Fabaceae, Cactaceae and Colchicaceae are the dominant groups, representing 81% of all species. For cacti, we have estimates of genetic diversity for 31 species. This number of taxa is considerably low for a family with more than 1800 species recognized; however, an analysis of the available estimates on genetic variability on this group can give us some preliminary trends for the family.

All species included in our review were analyzed using allozymes as genetic marker. Allozymes remain as the main genetic markers used to examine genetic diversity in cacti, and it is still frequently used in surveys of genetic diversity in plants in general. Parameters of genetic diversity reviewed included percentage of polymorphic loci (*P*), number of alleles per locus (*A*), number of alleles per polymorphic locus (*AP*), effective number of alleles per locus (*A*e), and Nei´s genetic diversity (equivalent to expected heterozygosity in the case of diploid taxa). Genetic structure parameters reviewed included the inbreeding coefficient (*FIS*) and several genetic differentiation coefficients (*FST*, *GST*, and θ).

Species reviewed included one leaf-bearing cactus (*Pereskia guamacho*), two segmented cacti (*Opuntia basilaris* and *O. caracassana*), six globose cacti (*Melocactus curvispinus*, *M. glaucescens*, *M. paucispinus*, *M. ernestii*, *M. ×albicephalus* and *M. concinnus*), 22 columnar cacti (*Carnegiea gigantea*, *Cereus repandus*, *Escontria chiotilla*, *Facheiroa squamosa*, *Pachycereus gatesii*, *P. pringlei*, *P. schottii*, *Pilosocereus aureispinus*, *P. lanuginosus*, *P. machrisii*, *P. tillianus*, *P. vilaboensis*, *Polaskia chende*, *P. chichipe*, *Praecereus euchlorus*, *Stenocereus eruca*, *S. griseus*, *S. gummosus*, *S. pruinosus*, *S. stellatus*, *S. thurberi* and *Weberbauerocereus weberbaueri*). In our review, four species are autotetraploid: *Pachycereus pringlei*, *Pilosocereus lanuginosus*, *P. tillianus* and *Weberbauerocereus weberbaueri.*

Cacti have on average equal or more genetic diversity than other families studied in xeric environments with the exception of the legumes, which seem to be in first place. The average *H* of allozymic variation for cacti was 0,256, a pretty high value compared with plants in general (*H*= 0,15) and woody (*H*= 0,17) species in particular. This result suggests that cacti in general have pretty high levels of genetic diversity among flowering plants. The species with the highest heterozygosity were the treelike cactus and columnar cacti (*H*= 0,129-0,443). Most of these species are predominantly xenogamous.

Regarding population genetic structure, cacti on average have a moderate level of population differentiation (F_{ST}= 0,142), this meaning that gene flow is not negligible among populations and in many species it is enough to counteract population genetic isolation. Compared to plants in general, cacti exchange much more genetic material among populations than many species. But compared with woody plants, cacti possess more genetic structure, a pattern in concordance with George L. Stebbin's and Daniel Axelrod's ideas of rapid speciation in arid landscapes. The lowest estimates of genetic structure were associated with columnar cacti (F_{ST}= 0,127; min= 0,028-max= 0,484). This result suggests that substantial historical gene flow has occurred among their populations. The melocacti as a group presented higher levels of population structure (F_{ST}= 0,190), probably due to limited gene flow among their populations. In relation with the inbreeding coefficient, the highest deficit of heterozygote individuals was associated with the melocacti, a group in which all species have mixed-mating.

We recognize that there is still a very limited number of cacti studied to detect patterns. Besides this, available data are not equally balanced between the different growth forms, mating systems and geographic origin of the taxa. Therefore, we are missing important aspects of the ecology and evolutionary history of cacti that need to be considered to construct a more representative database.

Despite these limitations, we can observe the following emerging trends:

1. As a group, the Cactaceae present high genetic diversity at both species and population levels. This family possesses more genetic diversity than other groups of higher vascular plants investigated.
2. They have population genetic structure above the average value reported for woody species.
3. Large cacti, including both leafy and columnar cacti, are the species with the highest levels of genetic variation in the family. This must be in part correlated with the predominance of xenogamy and limited clonality in this growth forms.
4. Mixed-mating increases the level of inbreeding in cacti.

We need to increase the number of species studied to continue walking the route towards defining the patterns of genetic diversity and structure in the Cactaceae. For this, we need to balance the number of species representative of the different categories of the relevant factors that we think have influence on the population genetics of cacti: more globose and opuntioid cacti, inclusion of epiphytic cacti, more mixed mating, autogamous and clonal species, and species with restricted geographic distribution.