Spine function in Cactaceae, a review

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ABSTRACT

Spines are one of the most conspicuous organs of cacti and are present even in the most basal species of the family. The aim of this review was to analyse the proven functions of spines, the number of species studied, their taxonomical (subfamily) and the geographic origin of studied species. Twenty-four studies that analyzed a total of five functions were found. A total of 39 species (around 2% of total diversity in the family) were studied. The most studied function was thermoregulation, where spines protect the stem from extreme temperatures, followed by anti-herbivory defense. Other functions are water collection, dispersion and antiparasitism defense. Most of the studied species belong to the Cactoideae subfamily, ten to Opuntioideae subfamily and only one, to the Pereskioideae. There is also a bias to the study of species from North America, particularly Mexico and United States of America (USA). The most studied species was *Carnegiea gigantea* that was the subject of 5 published papers. Surprisingly, there are few studies that analyzed species in environmental gradients or that analyzed the effect of spine removal. These results indicate the necessity of further investigation that include species with different spinescence patterns, and which rigorously test possible functions.

Keywords: Cactaceae; function; defense; thermoregulation.

INTRODUCTION

Spines are one of the most conspicuous organs of the Cactaceae. Spines are a primitive character in the family, since they are present in the most basal taxa (Arakaki *et al.*, 2011), but in some taxa had disappeared, or greatly reduced. In Cactaceae, spines are modified leaves (Boke, 1980) or modified bud scales (Mauseth, 2006) that have lost their photosynthetic function and acquired a primarily defensive one. Areoles are axillary buds without internodes, from which new branches, spines or flowers emerge (Rowley, 2003). Cactus axillary buds become active immediately and produce spine primordia.

The high richness of the family, around 1850 species (Nyffeler and Eggli, 2010), is also accompanied by a high diversity of spines forms. Spines are present with a high size variability (from few millimeters to 20 cm), almost always occur in clusters, a distinguish character of this

family (Fig. 1 A). A spine cluster creates a more effective defense than separate spines and the development of a corky covering on part of the areole may also decrease water losses (Gibson and Nobel, 1986). Most are needle-like and either round in cross-section and can be flattened on one side or hooked (Mauseth, 2017). Also, some species present more than one type of spines. For example, species of the Andean genus *Oreocereus* present normal defensive spines and hairy spines (Fig. 1 B). Spines often occur in many patterns within an areole, but two are the most extended and easy to recognize (Mauseth, 2017). The first one consists in a pectinate arrangement in which spines occur in two rows and all are the same size (Fig. 1 C). The other one is a differentiation into central, longer, and heavier, and radial spines. This high diversity in spines forms must be related to spines function. Besides the primary function of cacti, defense from predators, a number of other functions had been attributed to spines.
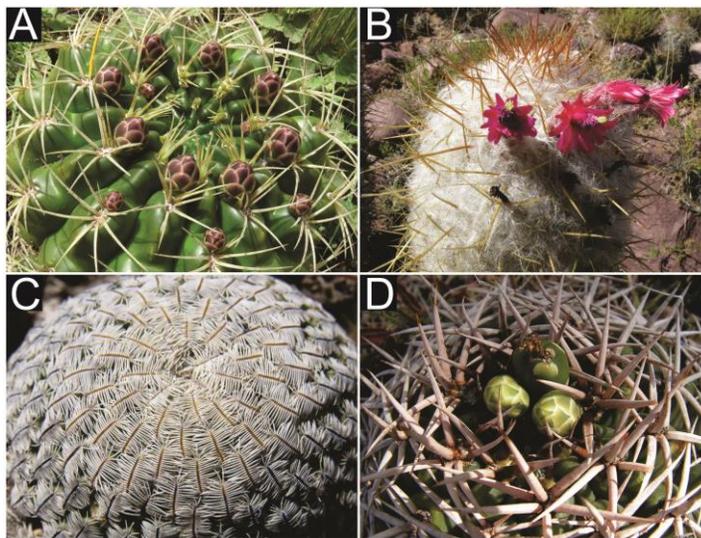
Figure 1. Photographs of: A) *Gymnocalycium monvillei*, B) *Oreocereus trolli*, C) *Mammillaria pectinifera*, D) *Gymnocalycium castellanosii*. Photos: Diego E. Gurvich.

The main and likely more ancient function is defense against predators. Cactaceae originated about 30 million years ago associated with a global aridization process (Hernandez *et al.*, 2014). In these environments, succulent tissues were a year-round source of water (as occurs nowadays in many cacti dominated ecosystems). It is likely that in these context cacti developed spines as physical defenses (Peharec *et al.*, 2009). Present day diversity in spine morphology indicates that an increase in function occurred through the evolutionary radiation of the group. Gibson and Nobel (1986) proposed a number of present-day functions for spines, from defense to thermoregulation and protecting the stem from solar irradiation, such as ultraviolet radiation. They also produce indirect effects on photosynthetically active radiation (PAR) and net CO_2 uptake, and play a role structuring natural communities as they serve as home for a variety of animals. However, at the moment there is not a comprehensive review that addresses their functions. In the present study reviewed all published research on spine function. The main aims of the present article were, create a list of functions that contribute to

fitness, analyze the number of taxa studied, their geographic origin, their growth form and whether environmental gradients were considered. With this information we want to find gaps in the knowledge of spine function in Cactaceae to encourage future studies.

MATERIALS AND METHODS

We did a literature review of published papers that study any aspects of spines in Cactaceae. The search was done in Google Scholar and Scopus between May and July 2020. We analyzed each study searching for direct or indirect information about spine function in Cactaceae. We systematized the information considering the species studied, to which subfamily was each species, the function analyzed, if the study was made in laboratory or in the field, if species were studied through environmental gradients, their geographical distribution, and their growth form. We also searched for studies that did not directly analyze a function but provided data for a function (for example the analyses of some spine attributes trough and environmental gradient).

RESULTS

Twenty-four studies (Annex I) that analyzed a total of 39 species were found. With regards to subfamilies, 1 (6% - of total species belonging to the subfamily - Nyffeler and Eggli, 2010) Pereskioideae, 10 (3% - Nyffeler and Eggli, 2010) Opuntioideae and 28 (2% - Nyffeler and Eggli, 2010) Cactoideae species (Table 1). Studied species represent around the 2% of the whole family diversity (Nyffeler and Eggli, 2010).

Five functions were detected: anti herbivory defence (five studies [2, 14, 19, 20, 21]), antiparasitism defence (two studies [7, 12]), vegetative dispersion (three studies [1, 2, 5]), thermoregulation (eleven studies [3, 4, 6, 9, 13, 15, 16, 17, 18, 22, 24]) and water collection (four studies [8, 10, 11, 23]). Nine of the studies were performed just in the field, eight in laboratory conditions and seven both in the field and in laboratory conditions. Only five studies were performed using environmental gradients: altitudinal (Nobel and Bobich, 2002; Nobel, 1980a), latitudinal (Nobel, 1980a; Nobel, 1980b), and elevation, pH, and humidity (Drezner, 2017; Nobel, 1978).

With respect to the geographical origin of species, most of them are from North and Central America (México and USA), 31 species (16 studies), and South America, with only 8 species studied (7 studies [2, 7, 10, 11, 12, 17, 23]).

Globose cactus has been the most represented life form throughout the studies (twenty species), followed by opuntioids (ten species), then columnar (eight species) and finally only one shrubby species (*Pereskia grandiflora*).

Table 1. Number of species analysed for each function from each subfamily. Observe that there are two functions that were demonstrated only for species of a subfamily as antiparasitism defence (Cactoideae) and dispersion (Opuntioideae).

| Functions	Pereskioideae	Opuntioideae	Cactoideae
Anti-herbivory defence	1	6	1
Thermoregulation	-	5	19
Water collection	-	1	7
Antiparasitism defence	-	-	2
Dispersion	-	3	-

The species most studied were *Carnegiea gigantea* (five studies – thermoregulation [3, 4, 16, 18, 24]), followed by *Trichocereus chiloensis* (three studies – anti-herbivory defence [7, 12] and thermoregulation [17])*, Ferocactus wislizeni* (three studies – water collection [10, 11] and thermoregulation [17]) and *Ferocactus cylindraceus* (three studies – thermoregulation [9, 16, 17]) and then *Opuntia fragilis* (two studies – anti-herbivory defence [2] and vegetative dispersion [2, 5]), *Opuntia polyacantha* (two studies – anti-herbivory defence [2, 21]), *Opuntia acanthocarpa* (two studies – anti-herbivory defence [20] and thermoregulation [15]), *Opuntia bigelovii* (two studies – vegetative dispersion [1] and thermoregulation [6]), *Opuntia microdasys* (two studies– water collection [8] and thermoregulation [22]), *Copiapoa cinerea* var. *gigantea* (two studies – water collection [10, 11]), *Parodia mammulosa* (two studies – water collection [10, 11]) y *Mammillaria columbiana* subsp. *yucatanensis* (two studies – water collection [10, 11]). All other species were analysed in only one study. Only one study assessed more than a function for six species. Crofts and Anderson (2018) found that spines with ornaments are more easily anchored to animal tissue, deterring from herbivory, and facilitate dispersion by means of the same anchoring mechanism. This suggest that it is possible that spines in particular species or environments have more than one specific function. More studies that include an integral study of spines functions are necessary to understand their multiple roles.

Sources: Crofts and Anderson, 2018 (antiherbivory defence - Pereskioideae, Opuntioideae and Cactoideae), Nassar and Lev-Yadun, 2009, Oliveira *et al.*, 1999 Pickett and Clark, 1979, Rebollo *et al.*, 2002 (antiherbivory defence - Opuntioideae); Gibbs and Patten, 1970, Nobel and Bobich, 2002, Santini *et al.*, 2007 (thermoregulation – Opuntioideae), Drezner, 2011; 2017, Lewis and Nobel, 1977, Mosco, 2009, Nobel, 1978, Nobel, 1980a; 1980b, Santini *et al.*, 2007, Yeaton *et al.*, 1980 (thermoregulation – Cactoideae); Ju *et al.*, 2012 (water collection – Opuntioideae), Malik *et al.*, 2014; 2016, Schill and Barthlott, 1973 (water collection – Cactoideae); González *et al.*, 2007, Medel, 2000 (antiparasitism defence); Bobich and Nobel, 2001, Crofts and Anderson, 2018 and Frego and Staniforth, 1985 (vegetative dispersion).

DISCUSSION

Despite the importance of spines in the family only a tiny portion of its species (around 2 %) have been used as models for understanding spine function. Almost 80 % of the studied species are from North and Central America and only 20 % from South America. Even though species richness is higher in the Northern Hemisphere, there is a clear bias towards those species. This bias is mainly due that most research studies in the family are done in Mexico

and USA, likely because of historical reasons, and differences in the scientific communities of the different countries. South America bears an important richness of cacti species, which inhabit very extreme environments (from very arid deserts to rainforest, and from sea level to more than 4000 m.a.s.l.) that deserve more attention. Many studies address spines functions as thermoregulation or water collection but just a few analyzed anti-herbivory defense, antiparasitism defense or even vegetative dispersion.
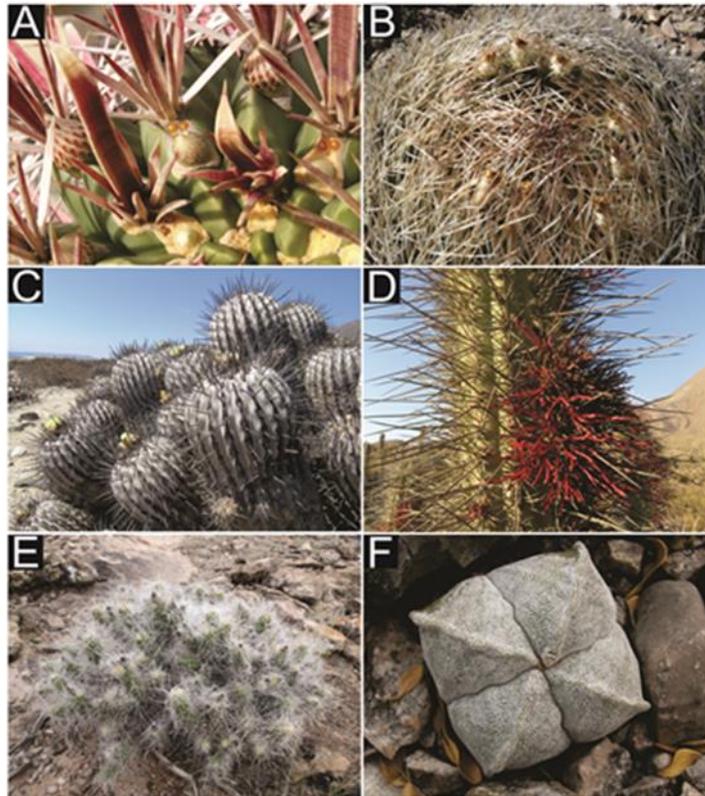
Figure 2.   Photographs of: A) *Ferocactus latispinus*, B) *Pyrrhocactus umadeave*, C) *Copiapoa cinerea*, D) *Echinopsis chilensis*, E) *Tephrocactus weberi,* F) *Astrophytum myriostigma*. Photos: Diego E. Gurvich.

Defense against herbivores is likely the first function of spines in the evolution of the family (Fig. 1 D). However, only a few studies analyzed this as a function (Rebollo *et al.*, 2009). Crofts and Anderson (2018) found that spines help to puncture the tissues of mammal predators. As a result, herbivores prefer to bite new branches where spines are less abundant. Nassar and Lev-Yadun (2009) found that spine density is higher on the upper range in an Opuntioideae species, where herbivores have more access. Spines could act as defenses against a high diversity of herbivores, from mammals, reptiles or even insects or mollusks. Many studies assess vertebrates, mainly mammals, as herbivores. It is well known that both evolutionary and ecologically, number of spines increase in spiny plants after a long exposure to herbivory by large animals (Stenberg *et al.*, 2000). However, a few studies analyzed invertebrates as predators or even reptiles or birds. Some spines had modified into extrafloral nectaries in some Opuntioideae species, but also in the subfamily Cactoideae, as *Ferocactus* species (Mauseth,

2006) (Fig. 2 A). They attract protective ants, which defended the stem from cactus-feeding insects (Pickett and Clark, 1979; Oliveira *et al.*, 1999).

Many studies address thermoregulation as a spines function (Drezner, 2011; Gibson and Nobel, 1986; Lewis and Nobel, 1977; Mosco, 2009; Nobel, 1978; Nobel, 1980a; Nobel, 1980b; Santini *et al.*, 2007; Yeaton *et al.*, 1980). Gibbs and Patten (1970) found that spines protect the stem from extreme temperatures and, also, reflect and absorb much of the environmental energy load, protecting the stems from overheating (Fig. 2 B). Drezner (2017) showed that spines length increased with temperature and in xerophyte environments. A study which considered an altitudinal gradient found that spine density increases at high altitudes showing that they protect the stem from low temperatures (Nobel and Bobich, 2002). Overall, spines regulate temperatures to prevent both overheating and low temperatures (chilling and freezing).

Because of the xerophyte environments where many cacti grow, they have developed an efficient fog collection system and spines are the main element of this process (Fig. 2 C). Water condenses at the tip of the spine; it is directed to the base and it enters the stem where it will be stored. Some studies demonstrated that there could be a hydraulic connection between spines and the xylem system (Ju *et al.*, 2012), which indicates that water can ingress the stem trough spines. However, there are species that have hydrophobic spines, so water never condenses on their surface (Malik *et al.*, 2014; 2016). Malik *et al.* (2016) showed that dew can formed on the stem of individuals whose spines were removed in arid areas, but this can also inhibit the dew harvesting ability in some species, so spines are important to dew formation and therefore, water harvesting. These studies were done in lab conditions, so field studies are necessary to check this process in more realistic conditions.

The spines have an interesting function as antiparasitism. To our knowledge there is only one plant that parasitizes cacti, *Tristerix aphyllus*, a mistletoe, which inhabits Central Chile and parasites *Trichocereus chiloensis* and *Eulychnia acida* (Fig. 2 D)*. The parasite is dispersed by birds that use cacti as perch. *Trichocereus chiloensis* has developed large spines to avoid the activity of seed dispersing birds (González *et al.*, 2007; Medel, 2000). They prevent birds from perching on the stem and, as a result, reduce droppings. This function was demonstrated only in the species mentioned above for a particular specie of mistletoe that is extremely specific. To our knowledge there is no other mistletoe that parasitizes other cacti species.

Three studies analyzed vegetative dispersion, in which spines play an important role; however, was evaluated in opuntioid species only (Bobich and Nobel, 2001; Crofts and Anderson, 2018; Frego and Staniforth, 1985). The spines help the cladodes hook onto the skin of animals, who can move them over long distances (Fig. 2 E). Once they are detached, they can be established and generate a new individual. Although none of these studies evaluated the dispersion itself, this would indicate the dispersal capacity of spines.

Five functions have been tested, from the total analyzed studies. However, some authors mentioned functions that have not been demonstrated (Table 2). Anderson (2001) proposed that the spines serve as camouflage and thus protect the plant from predators. They also mentioned that spines can be easily recognized by pollinators increasing the probability of

pollination and also dispersion. Gibson and Nobel (1986) introduce the idea that the presence of spines reduce air movement forming a layer around the stem and thus, evapotranspiration. Although this is related to thermoregulation, there are no studies that analyzed or tests evapotranspiration as a function.

Table 2. Tested and untested functions among the studies.

Authors	Tested functions	Untested functions
Crofts and Anderson, 2018; Nassar and Lev-Yadun, 2009; Oliveira *et al.*, 1999, Pickett and Clark, 1979; Rebollo *et al.*, 2002.	Anti-herbivory defence	Camouflage against herbivores
Drezner, 2011 and 2017; Gibbs and Patten, 1970; Lewis and Nobel, 1977; Mosco, 2009; Nobel and Bobich, 2002; Nobel, 1978; 1980a and 1980b; Santini *et al.*, 2007; Yeaton *et al.*, 1980.	Thermoregulation	Pollinators attraction
Ju *et al.*, 2012; Malik *et al.*, 2014 and 2016; Schill and Barthlott, 1973.	Water collection	Reduce evapotranspiration
González *et al.*, 2007; Medel, 2000.	Antiparasitism defence	
Bobich and Nobel, 2001; Crofts and Anderson, 2018; Frego and Staniforth, 1985.	Dispersion	

Surprisingly very few studies (five) analyzed aspects of spines trough environmental gradients, as aridity, elevation, or even herbivory. The study comparing species, or populations, through gradients would increase the understanding of spines function. In this sense, both interspecific and intraspecific studies should be performed for a better understanding of spine function. Also, only four studies made spine removal experiments (Lewis and Nobel, 1977; Malik *et al.*, 2014; Nobel and Bobich, 2002; Nobel, 1978). We consider this experimental approach is much necessary to assess their real function and to avoid attribute functions that are not carried out by the spines alone or functions that are not typical of them.

A very few studies that analyzed spines in a growth resource allocation context were found (Loik, 2008). The spines are not a photosynthetic tissue, so they are costly for plants (Gibson and Nobel, 1986). The spines not only use carbon resources from the plant, but also diminish photosynthetic capacity by shadowing the stem (Nobel, 1983; Nobel *et al.*, 1991; Loik, 2008; Drezner, 2011). In some species this shadowing is important by decreasing solar radiation, becoming a function. De la Rosa-Manzano *et al.* (2016) analysed the effect of spine removal on three species whose spine-shading of stems varies. They found that spine removal increased the CAM activity and the effective quantum yield of Photosystem II in species having the higher spine shading. These studies indicate that there are important trade-offs operating in cactus species that integrate defence, thermoregulation, and photosynthesis, that should be investigated. Particularly, it would be interesting to perform studies that integrates spine function and costs.

We did not find studies that analyzed spineless species, or species with reduced spines. For example, species of *Lophophora* or *Astrophytum* shows a reduced number of spines (Fig. 2 F). The study of these species could give clues about the function of spines. For example, it is well knowing that *Lophophora* species produce high quantities of alkaloids (Cassels, 2019). These would indicate a trade-off between physical and chemical defenses. The combined studies of spines and chemical defenses could give clues about the tradeoffs behind the production of these defenses.

We also found some studies that noticed indirect functions of spines. For example, the stems of Opuntioideae species are easily detached and accumulate under the mother plant. In addition, to creating a favourable micro-habit for their development, their long spines protect the seedlings of other plant species from the predators (McAuliffe, 1984). Other studies found that some birds use spines as a tool to remove arthropods from tree holes. Tebbich *et al.* (2002) discovered that woodpecker finches use spines as a tool in arid zones, where food is limited and hard to access.

CONCLUSIONS

The present study is the first comprehensive review of spine function in Cactaceae. The main knowledge in relation to this topic and hope to find the main gaps was reviewed. Relatively few species had been studied, many in the Northern hemisphere, and that few studies were made in the field and particularly through environmental gradients. Also, most of them analyzed thermoregulation as a function and very few stops to evaluate the relationship between spines and herbivores. This is surprising given the evolutionary history of spines as a defense. In this way, we encourage future studies in order to fill the gaps in knowledge. In a rapidly changing world, where biodiversity is in crisis, the more information we have, the better we can manage our options.

ETHICS STATEMENT
"Not applicable"

CONSENT FOR PUBLICATION
"Not applicable"

AVAILABILITY OF SUPPORTING DATA
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

COMPETING INTERESTS
"The authors declare that they have no competing interests".

FUNDING
"Not applicable"

AUTHOR CONTRIBUTIONS

Writing-review, formal analysis, NLA; writing NED; conceptualization-writing DEG.

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