Traditional management and genetic diversity of *Cereus jamacaru* DC. subsp. *jamacaru* (Cactaceae) in the semi-arid region of Brazil

Camilla Marques de Lucena, Alejandro Casas, Natan Medeiros Guerra, Thamires Kelly Nunes Carvalho, Maristela de Oliveira Andrade, Reinaldo Farias Paiva de Lucena

Correspondence

Camilla Marques de Lucena[1], Alejandro Casas[2], Natan Medeiros Guerra[5], Thamires Kelly Nunes Carvalho[3], Maristela de Oliveira Andrade[4], Reinaldo Farias Paiva de Lucena[5]*

[1]Universidade Federal da Paraíba. Centro de Ciências da Saúde. Departamento de Ciências Biomédicas. Centro de Ciências Exatas e da Natureza. Programa de Pós-graduação em Meio Ambiente e Desenvolvimento (PRODEMA). Grupo de Pesquisa do CNPq "Meio Ambiente e Crenças: Pesquisas multidisciplinares em Ciências Ambientais, Ciências das Religiões e Teologia". João Pessoa, Paraíba, Brasil. CEP 58051-900.
[2]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México.
[3]Universidade Federal do Piauí – UFPI. Campus Professora Cinobelina Elvas – CPCE. Bom Jesus/PI- BR 135, KM 3, Planalto Horizonte.
[4]Universidade Federal da Paraíba. Centro de Ciências Exatas e da Natureza. Programa de Pós-graduação em Meio Ambiente e Desenvolvimento (PRODEMA). João Pessoa, Paraíba, Brasil. CEP 58051-900.
[5]Universidade Federal da Paraíba. Centro de Ciências Exatas e da Natureza. Grupo de Pesquisa do CNPq "Meio Ambiente e Crenças: Pesquisas multidisciplinares em Ciências Ambientais, Ciências das Religiões e Teologia". João Pessoa, Paraíba, Brasil. CEP 58051-900.

*Corresponding Author: reinaldolucena.dr@gmail.com

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Research

Abstract

Background: Cereus jamacaru subsp. *jamacaru* is a columnar cactus with high utilization potential. It is used as of animal feed in the semi-arid region of northeastern Brazil. This study aimed to characterize the knowledge, use, and management of this species in a rural community in the semi-arid region of Brazil.

Methods: Semi-structured interviews were conducted with 35 family heads (n = 104) of the village of Santa Rita. Genetic analyses were carried out to evaluate the structure and genetic diversity of populations exposed to different types of management. A total of 90 individuals, 30 in each stand (wild, managed and cultivated) were selected and georeferenced.

Results: Interviews revealed that fodder was the most important use category. Both *in situ* (gathering and tolerance) and *ex situ* (planting and transplanting) management were recorded. There was no significant difference in genetic diversity between the wild, cultivated, and managed stand. The analysis of molecular variance showed that most of the variation occurs within the populations (99.76%). Based on the Nei´s genetic distance matrix, it was possible to verify in the dendogram that the cultivated population is more distinct than the wild and managed ones.

Conclusions: The different types of use and management practiced demonstrate the high cultural and economic value of the mandacaru. *In situ* management, involves human selection in favor of individuals more robust and more and larger fruits.

This selection is not detected by the genetic analysis performed, although it is possible to infer that gene flow among populations is high thus counteracting effects of selection.

Keywords: Mandacaru; Caatinga; Ethnobotany; traditional population; Columnar cacti.

Background

Ethnobotanical studies have recorded and analyzed the interaction between people and plants, and a wide variety of use and management types of individuals (Nilsen *et al.* 2005; Villalobos *et al.* 2007; Blancas *et al.* 2009; Lins-Neto *et al.* 2010; Delgado-Lemus *et al.* 2014), populations (Casas *et al.* 2006; Yineger *et al.* 2008; Cruse-Sanders *et al.* 2013; Torres *et al.* 2015), forests (Casas *et al.* 1997), and even landscapes (Parra *et al.* 2012; Chen *et al.* 2015; Casas and Parra 2016; Casas et al 2024) have been observed and identified.

In traditional rural communities, there are some forms of management that can be classified as neither as agriculture nor as simple gathering, but as incipient management, less complex than the agricultural management and more complex than simple gathering (Casas and Cabalelero 1996; Casas *et al.* 1997; Casas *et al.* 2007; Casas *et al.* 2014; Casas *et al.* 2024). It is worth mentioning that the management can be classified as *in situ* or *ex situ*; the first one is carried out based on methods developed in areas where the plants occur naturally, such as forests, or in areas created by humans, such as grazing areas, and the second one is carried from the natural environment of the plants (Blancas *et al.* 2010). Mandacaru has the vegetative propagation as a mechanism of reproduction, and people use this mechanism as the main way of management. But sexual reproduction can also occur and is important to generate genetic variation in the population.

Studies on plant management are essential to analyze the process of plant domestication, making it possible to understand the practices related to human selection, their cultural reasons, and other evolutionary processes linked to human management that affect plant populations. In addition, the study of traditional management allows evaluating how it can contribute to biodiversity conservation and the sustainable use of natural resources (González-Soberanis and Casas 2004; González-Insuasti *et al.* 2008; Casas *et al.* 2016, Casas *et al.* 2024).

This process of traditional management can occur unconsciously, through which the individuals with desirable characteristics are moved to anthropic environments (e.g., backyards) which provide their maintenance, sometimes involving the elimination of individuals with undesirable traits (Zohary 2004). But also can occur with a clear intentionality, when individuals with favorable phenotypes are deliberately protected, preserved, or favored to be survive and reproduce, thus increasing their fitness in anthropogenic areas (Patiño-Lopez *et al.* 2022). Moreover, managment is influenced not only by the traditional knowledge about plants, but also by human cultural values, which can lead to changes in the availability and quality of plant resources (Blancas et al 2013). The following factors may also influence the management: 1) the role of the resources in subsistence, 2) the abundance or scarcity of wild resources to meet local human needs, 3) the duration of seasonal availability of wild resources, 4) the distance between the area where the needed resources occur and the place where people live, 5) the characteristics of the place where the resources are found, and 6) the possibility of management taking into account the biological characteristics of the plants, such as life cycle, ease of manipulation and success of establishment in anthropogenic areas (Casas *et al.* 1996; González-Insuasti and Caballero 2007).

Mesoamerica is one of the main areas of plant domestication, because of its high floristic diversity combined with the cultural inheritance of traditional people (e.g. indigenous or mestizo people who have been established in an area for a long time, in some cases several centuries, in others several millennia) who use and manage native plants, such as columnar cacti, to meet their cultural, social, economic and even technological needs (Casas *et al.* 1997; Casas *et al.* 1999; Arellano and Casas 2003). In Mexico, a number of studies have reported management practices related to several species of columnar cacti with coexisting wild and cultivated populations (Parra *et al.* 2012; Casas *et al.* 1999; Carmona and Casas 2005; Rodríguez-Arévalo *et al.* 2006; Parra *et al.* 2010; Patiño-Lopez *et al.* 2022) which are mainly used as human food (mainly fruits, sometimes flower buds and seeds) and for rural construction (e.g. hedges), medicine or fodder.

In Brazil, in semi-arid climates such as the Caatinga ecosystem, numerous native plant species are used by traditional populations (Albuquerque and Andrade 2002; Sousa Júnior *et al.* 2013; Campos *et al.* 2015; Nunes *et al.* 2015; Zank *et al.* 2015). Cacti that are native to this region, such as *Pilosocereus gounellei* subsp. *gounellei*, *Melocactus* sp. and *Pilosocereus pachycladus* F. Ritter subsp. *pernambucoensis* (F. Ritter) Zappi are cited in several ethnobotanical studies that have documented the economic, social and cultural importance of these species for human groups, such as local farmers (Lucena *et al.* 2013, 2014; Nunes *et al.* 2015); however, there are few studies that focus on the management of species belonging to the Cactaceae family.

In the case of *C. jamacaru* subsp. *jamacaru*, some studies have demonstrated the relevance of this columnar cactus by recording its potential of uses, but there is still no detailed information on the management of this species (Albuquerque and Andrade 2002; Magalhães 2006; Lucena *et al.* 2012 a,b, 2013, 2014; Bezerra-Silva *et al.* 2024), and the possible phenotypic and genotypic consequences of such management on populations. This cactus species, also known as "cardeiro" or "mandacaru", is found throughout the northeastern region of Brazil (Zappi and Aona 2014) and is one of the main sources of fodder for animals (e.g. use of cut branches) in the Brazilian semi-arid region during periods of drought (Cavalcanti and Resende 2007; Lucena *et al.* 2013). This plant is also used as human food, mainly its fruits consumed in nature (Lucena *et al.* 2013), for ornamentation of gardens and backyards for rural construction (e.g. hedges), for building houses (e.g. fences, doors and windows), and for making tools (e.g. tool handles), for medicinal purposes (e.g. treatment of inflammations), and for providing shade (Lucena *et al.* 2012a,b, 2013).

Based on this information, from the current use and potential benefits, and the socioeconomic and cultural importance of *C. jamacaru* subsp. *jamacaru* to traditional populations, it is relevant to investigate the management types and the likely occurrence of artificial selection associated with the management of this species, similar to what has been documented for other species in Mexico (Casas *et al.* 2007). The objectives of this study were to answer the following questions: Is there phenotypic variation among individuals of *C. jamacaru* subsp. *jamacaru* (mandacaru) in wild and anthropogenic environments? Is the phenotypic variation perceived by rural people? Do local farmers prefer to gather or collect *C. jamacaru* subsp. *jamacaru* (mandacaru) in certain areas? Do farmers plant or cultivate *C. jamacaru* subsp. *jamacaru* (mandacaru)? How do they do this? Do they select propagules from specific plants? If so, how?

The above questions raise the hypothesis that phenotypic variation, which is common in all biological populations, would be distributed differently in the wild and in anthropogenially influenced areas. If the phenotypes are perceived and preferred differently, then the phenotypes preferred by humans would be more abundant in managed environments. The different forms of use and management of the *C. jamacaru* subsp. *jamacaru* populations promote their artificial selection. In addition, the species can be managed both *in situ* in areas of secondary vegetation where other elements of the natural vegetation are removed and jamacaru is selectively left standing; and *ex situ* in areas where this plant is cultivated and may involve the propagation of selected sexual or asexual propagules. Therefore, this study aimed to characterize the knowledge, use, management, and selection on phenotypic variation, as well as the consequence of such selection on genotypic variation of *Cereus jamacaru* DC. subsp. *jamacaru* (mandacaru) in a rural community of the semi-arid region of Brazil.

Material and Methods

Study Area

This study was carried out in the rural community of Santa Rita, municipality of Congo, microregion of Cariri Ocidental and mesoregion of Borborema, in the State of Paraíba, Brazil, at the geographical coordinates 07º47'49'' S and 36º39'36'' W, at a distance of 212 km from João Pessoa, the state capital city (Figure 1). Its population is estimated at 4,785 inhabitants distributed in an area of 333,471 km², bordering the municipalities of Serra Branca (north), Coxixola and Caraúbas (east), Camalaú and Sumé (west), and Santa Cruz do Capibaribe in the State of Pernambuco (south) (IBGE 2016). The municipality has about ten rural communities (Riachão, Salina, Riacho do Algodão, Lagoa da Ilha, Santa Rita, Barra do Rio I, Barra do Rio II, Carmo I, Ventura, and Laginha). The economy of the people is based on agriculture and cattle raising.

The climate of the region is tropical semi-arid, with an average annual rainfall of 431.8 mm, high temperatures (between 18º C and 32º C) and evapotranspiration. The municipality has few water bodies and perennial rivers, and the reduced underground water storage increases the risk of desertification in the region (Sousa *et al.* 2012).

The municipality has rock outcrops in long fragments, in addition to slabs and stony soils with some pebbles. the predominant soil type is non-calcareous brown, but there are also vertisols, lithosols and saline soils (solonietz and solontchak) (AESA 2013). The vegetation is represented by open shrub-tree caatinga.

The community is located near a rocky mountain, called *Serra da Engabelada*, which has geoforms of granitic rock blocks with rupestrian records (about 22 inscriptions). The height of the mountain is about 820 meters, and it is known as *Engabelada* because of the optical illusion that it gives the impression of following its observers, i.e., from any place we observe the mountain, we have the impression of being facing it and, therefore, the people say that it deceives ("engabela" in Portuguese) its observer (Sousa *et al.* 2012).

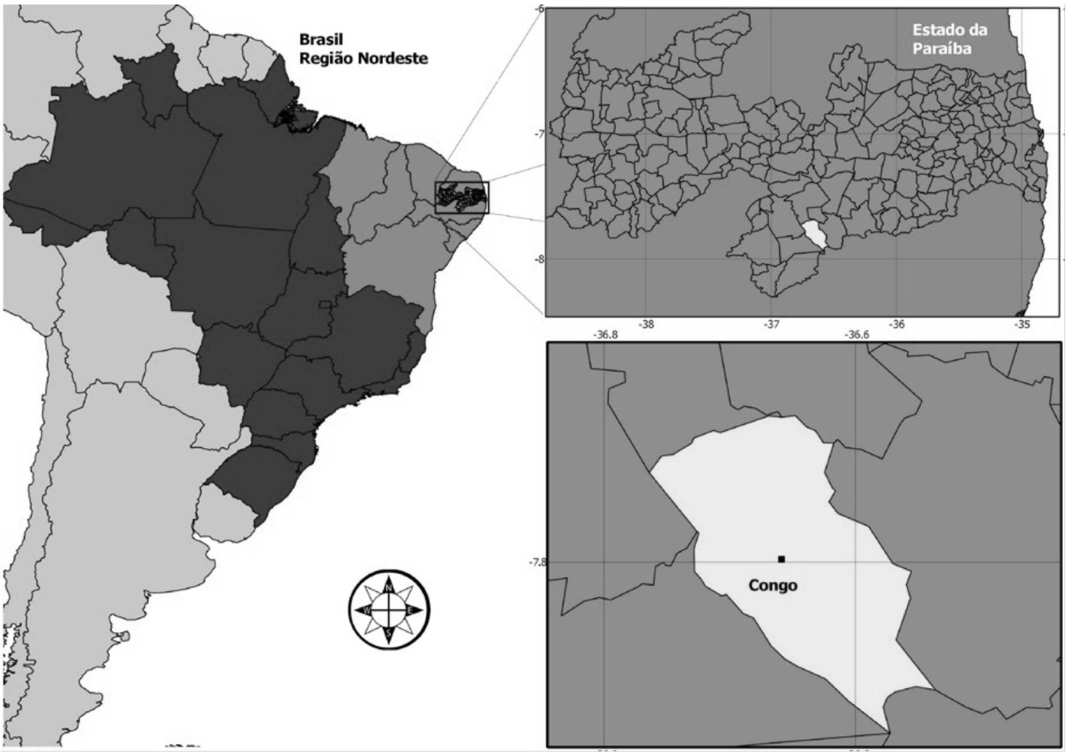

Figure 1. Location of the municipality of Congo, in the mesoregion of Borborema and microregion of Western Cariri, in the semi-arid region of the state of Paraíba, Northeast Brazil.

The urban center of the municipality of Congo is located about 8 km from the community of Santa Rita, which was chosen for this study because of its accessibility and the availability of its inhabitants to participate in this research.

The community's economy is based on subsistence agriculture, such as maize and bean, and livestock consisting of cattle, goats and sheep raising. However, these activities are currently being little explored in the region due to the low rainfall, which makes the planting and animal feeding difficult. Thus, benefits from the INSS (National Institute of Social Security) and the federal government (*Bolsa Familia*), as well as sewing activities, supplement the income of many families in the community (Sousa *et al.* 2012).

Regarding terms of education, students are transported daily by public transportation to the schools located downtown. In terms of health services, the community is monitored by a community health agent. All homes have electricity and running water.

Ethnobotanical assessment of *Cereus jamacaru* DC. subsp. *Jamacaru* management

Semi-structured interviews were conducted with 100% of the heads of household (104 = 45 men and 59 women) in the rural community of Santa Rita, at different times (Albuquerque *et al.* 2010). After the purpose of the study was explained to the participants, they were asked to sign the Free and Informed Consent Form, in accordance to the Resolution of the National Health Council required by the Research Ethics Committee (Resolution 196/96). This study was approved by the Human Research Ethics Committee (HREC) of the Lauro Wanderley Hospital of the Federal University of Paraíba.

The questionnaire used in the interviews included questions about the knowledge, use, and management of *Cereus jamacaru* DC. subsp. *jamacaru* in the region (e.g., forms of use, useful parts, morphological variations noticed by the informants, gathering areas, and planting methods). We considered the data from the informants who actually manage the species (97% of the interviews 100/104).

The categories of use recorded in the interviews were classified, based on the literature, as human nutrition, bioindication of natural phenomena (e.g. rain), fuel, construction, fodder, religious magic, medicinal, ornamental, shade, technology, and veterinary (Andrade *et al.* 2006; Sousa *et al.* 2012; Lucena *et al.* 2012a,b, 2015a,b,).

The categories *in situ* and *ex situ* management were considered, according to Casas *et al.* (1997, 2007, 2014) and Blancas *et al.* (2010). The managed population (population 2) can represent both "in situ" and "ex situ" management. Among the *in situ* management types we can mention:

- Gathering, which consists in obtaining useful parts of the plant (branches or fruits), from individuals in the population. This activity may be simple, or involves social agreements among members of the community, and it may also be selective, with some individuals being gathered and others do not.

- Tolerance, which occurs when individuals of certain species, and sometimes certain phenotypes, are left standing in areas of vegetation that have been cleared for other purposes (agriculture, establishment of grasslands or construction of houses);

Induction or enhancement of desirable individual plant species or particular phenotypes of thereof. Usually carried out by deliberate propagation of seeds or vegetative parts for asexual reproduction. This activity promotes an increase of the abundance of desirable plants;

- Protection of specific individual plants through various practices to protect them from herbivores (e,g. fencing around the plant, shading or clearing factors that determine quality, pruning, pest control, among others).

Among the types of *ex situ* management we identify:
- Sowing and planting of seeds and vegetative propagules from forests to areas of human influence, such as agroforestry systems, homegardens, grasslands;

- Transplanting, in which entire plants, usually young plants but in some cases also adult plants, are moved, from natural environments to human-made areas.

Genetic analyses of *Cereus jamacaru* DC. subsp. *jamacaru*

Sample of individuals

A total of 90 individuals forming the Santa Rita metapopulation were sampled, to have a general overview of the genetic variation in different environmental contexts. A total of 30 individuals were sampled per stand of wild, silvicultural managed and cultivated stands making up the metapopulation of Santa Rita (including wild, managed and cultivated stands of individuals coexisting in the areas). Each individual was georeferenced using GPS to elaborate a map of local distribution and availability.

The wild stand of the metapopulation (Stand 1) is represented by individuals found in sites of the “Serra da Engabelada” (the mountain located in the community), which are far from the residences, considered as individuals of difficult access by the residents. The silvicultural managed stand of the metapopulation (Stand 2) consists of individuals that are in sites not too far away from the residences, found in cultivation areas, roadsides and secondary forest, which are subjected to sporadic extraction. The cultivated stand of the metapopulation (Stand 3) was composed of individuals located in sites very close to the residences (in gardens, backyards, and hedges), which are regularly managed.

DNA Extraction

Two to three young areoles were collected from each individual. The spines of the areoles were removed and processed in a mill (MM 400) at a frequency of 30.0 (1/s) for up to 2:00 minutes, depending on the rigidity of the sample. The ground material was then used for the DNA extraction. After each grinding of the spines, the mill vessels were washed to avoid possible contamination.

The material was transferred from the grinding vessels to 2-ml Eppendorf tubes, by using a spatula. The DNA extraction was performed according to the CTAB method of Doyle & Doyle (1987), with modifications.
After DNA extraction, the quality and quantity of DNA was verified by electrophoresis in 0.8% agarose gels and by the NanoDrop 2000 (Thermo Scientific), respectively.

PCR amplification conditions

A total of nine primers were used, three of them from *Haageocereus tenuis* (Arakaki *et al.* 2010), three from *Pilosocereus machrisii* (Perez *et al.* 2011) and three from *Uebelmannia pectinifera* subsp. *pectinifera* (Moraes *et al.* 2014). Each reaction resulted in a final volume of between 5 and 6 µL, by using the QIAGEN Multiplex PCR Kit (www.qiagen.com) as the polymerase and using the cycle conditions and concentrations suggested by the manufacturer.

Then, 0.5 µL of the amplified PCR products were mixed with Liz in Hi-Di formamide (Applied Biosystem) and with Gene Scan LIZ-500 size standard (Applied Biosystem), and denatured at 95°C for 5 min. The PCR products were analyzed by capillary electrophoresis on the Genetic Analyzer 3130xl Sequencer (Applied Biosystem). Genotypes were obtained from electropherograms using the Peak Scanner software (Applied Biosystem).

Marker quality

The MicroChecker 2.2.3 software (Van Oosterhout 2004) was used to identify the presence of genotyping errors, such as the presence of null alleles at each locus per stand.

Deviations from the Hardy-Weinberg equilibrium were analyzed using ARLEQUIN (Excoffier *et al.* 2005). Linkage equilibrium (LE) deviations were assessed tby GenePop on the Web (Rousset 2008) using the Fisher's method for each locus pair (Raymond and Genepop 1995).

Genetic diversity

From the information of all loci, the following basic genetic diversity parameters were calculated for each stand: number of alleles per locus (Na), number of effective alleles (Ne), observed heterozygosity (Ho), expected heterozygosity (He), and weighted expected heterozygosity (uHe), which were analyzed using GenAlEx 6 (Peakall, *et al.* 2006).

Genetic structure

The fixation index (FST) was calculated using the FreeNa software, by the EMA method, allowing the null alleles (Chapuis and Estoup 2007), and the coefficient of inbreeding was calculated using the INEst software (Chybicki and Burczyk 2009).

The genetic distances (DC) (Cavalli-Sforza and Edwards 1967) were estimated for each pair of stands, through the INA correction described by Chapius & Estoup (2007), using the FreeNa software.

The Molecular Variance Analysis (AMOVA) was performed to evaluate the genetic differences of the different types of stands of *C. jamacaru* subsp. *jamacaru* through by the stepwise mutation model (SMM), using the Arlequin software version 3.11 (Excoffier *et al.* 2005).

The genetic distances and identities of Nei (1972) were estimated through the Tools for Population Genetic Analysis (TFPGA) 1.3 software (Miller 1973) and, thus, a Unweighted Pair Group Method with Arithmetic Mean (UPGMA) dendrogram was constructed (Sneath and Sokal, 1973).

Results

Use and management of *Cereus jamacaru* DC. subsp. *jamacaru*

All informants (97% of the 100/104 interviewed) reported knowing *Cereus jamacaru* DC. subsp. *jamacaru* (mandacaru). When the informants were asked about the types of mandacaru they knew, only 7% stated that in addition to knowing the native species (*C. jamacaru* subsp. *jamacaru*) they also knew the thornless species (*Cereus* sp.), which was introduced to the community in 2011 (Figure 2). In this study, however, only the native species was considered for recording the uses and management.

Regarding the planting of the species, 50% of the informants have already planted at least one individual of *Cereus jamacaru* DC. subsp. *jamacaru*, in places such as gardens, backyards, hedges, and areas of agro-pastoral activities.

However, almost half of the inhabitants (47%) stated that they do not plant this species because when they need its useful parts (e.g., branches and fruits) to feed their animals or themselves, they gather such parts from the individuals that already exist on their land, or on neighboring land. Therefore, only a minority of informants (3%) do not carry out any type of management, that is, they do not plant and do not gather the “mandacaru” native to the region.

Although the community of Santa Rita has a great diversity of Cactaceae species, the farmers reported that they prefer to plant the “mandacaru” because it is useful for feeding animals (49%) and because it is also used as an ornament in the gardens of the houses (15%). The most useful part of the tree is its branches (48%), which are mainly used as fodder (78%).

Regarding the morphological aspects of “mandacaru” (e.g., height, number of branches, and fruit size), 53% of the respondents did not notice any difference between the individuals found in the community. However, 23% of them reported that the individuals near the residences are generally larger, greener, and have thicker fruits and branches, different from those found in the mountain and in the local forests (the wild stand). According to the residents, such differences can be explained by the fact that the individuals near the houses are often irrigated and fertilized, which may explain these morphological changes. There may also be other reasons, such as density diversity, which creates competition for light, air, and micronutrients in the soil.

Figure 2. Species of “Mandacaru” recorded in the rural community of Santa Rita, municipality of Congo, Paraíba State, Northeast Brazil. **A.** “Mandacaru” with spines (*Cereus jamacaru* DC. subsp. *jamacaru*); **B.** “Mandacaru” without spines (*Cereus* sp.).

Incipient management forms were recorded in the studied community, and they were divided into four categories (Figures 3 and 4). With regard the *in situ* management, farmers gather the branches of “mandacaru” to feed animals (e.g., goats), especially during periods of low rainfall. Sporadically, they gather the fruits for human consumption. It is worth mentioning that, between November (2016) and January (2017), the “mandacaru” was frequently used, since, according to the inhabitants, it was a period of intense drought.

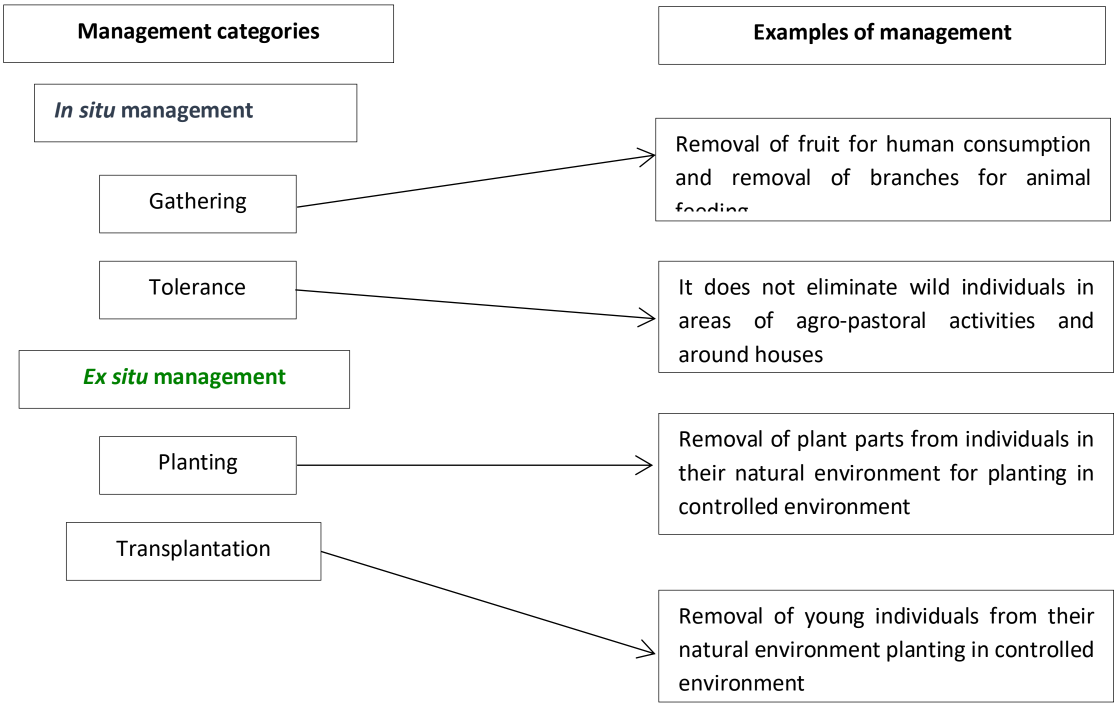

Figure 3. Forms of management of *Cereus jamacaru* DC. subsp. *jamacaru* recorded in the rural community of Santa Rita, municipality of Congo, Paraíba State, Northeast Brazil.

It was also possible to record other forms of management such as tolerance, planting, and transplanting, which demonstrates the high importance of “mandacaru” for the community studied. It should be noted that these forms of management are carried out with the aim of conserving the species in the region, so that it can be used in animal feeding as an emergency food (mainly used during periods of lack of rain).

Most of the informants (78%) said that when they use the “mandacaru” to feed their animals, they do not completely eliminate the plant, thus demonstrating a sustainable use of the species.

When they were asked about the possibility of (large-scale) cultivation of this species in the community, 59% of them had never thought about this possibility; however, 41% had already intended to cultivate it, since they believe such practice would contribute to the animal feed safety.

Figure 4. Main forms of management of *Cereus jamacaru* DC. subsp. *jamacaru* (“mandacaru”) in the rural community of Santa Rita, municipality of Congo, Paraíba State, Northeast Brazil. **A.** Record of the removal of branches to be used as fodder; **B; W; D**. Branches to be used as fodder; **E.** Animal eating “mandacaru” branches. **F.** Planting of “mandacaru” branches in the fence; **G; H.** Planting of “mandacaru” around the residences.

Genetic diversity

When comparing the mean values of the parameters Na, Ne, Ho, He and uHe between the wild, cultivated and managed stands, there was no statistically significant difference between these stands (Table 1).

Table 1. Parameters of genetic diversity estimated in wild, managed and cultivated stands of the metapopulation of of *Cereus jamacaru* DC. subsp. *jamacaru* of Santa Rita. The results are based on nine microsatellite loci.

Stands	***Na***	***Ne***	***Ho***	***He***	***uHe***
Wild	9.778±0.795	4.569±0.498	0.493±0.043	0.758±0.029	0.772±0.030
Silvicultural Managed	8.556±0.801	4.379±0.479	0.475±0.051	0.753±0.024	0.766±0.024
Cultivated	9.444±1.168	5.220±0.844	0.453±0.066	0.773±0.029	0.787±0.029

Legend:

Na = number of alleles per locus, ***Ne*** = number of effective alleles, ***Ho*** = observed heterozygosity, ***He*** = expected heterozygosity, ***uHe*** = weighted expected heterozygosity.

Genetic structure

The Global F_{ST} was 0.014 with a confidence interval (CI) of 0.000519-0.027621, indicating a low genetic differentiation. The inbreeding coefficient (F_{IS}) values were practically the same for the managed (0.1827) and cultivated (0.1813) stands of the metapopulation, whereas the wild stand had a lower value (0.1207).

In the molecular variance analysis (AMOVA) it was possible to observe that in the stepwise mutation model (SMM), most of the variation occurs within the stands of the metapopulation, being 99.76% (Table 2).

Table 2. Molecular variance analysis (AMOVA) for three stands of the metapopulations of *Cereus jamacaru* DC. subsp. *Jamacaru* of Santa Rita. The results were obtained from the stepwise mutation model (SMM).

Mutation model	Source of variation	Sum of squares	Variation component	Variation Percentage	Statistic
SMM	Between the stands	15215.128	15.95019	0.2326	R_{ST} = 0.00233**
	Within the stands	1173883.767	6839.72940	99.76734	

When analyzing the dendrogram (UPGMA), based on the genetic distance of Nei, it was notorious that the stand 3 (the cultivated groups of individuals) is more different from stand 1 (wild groups of individuals) (Nei's *D*= 0.1465) and stand 2 (silvicultural managed groups of individuals) (Nei's *D*= 0.1369), and it was possible to observe two groups (Figure 5).

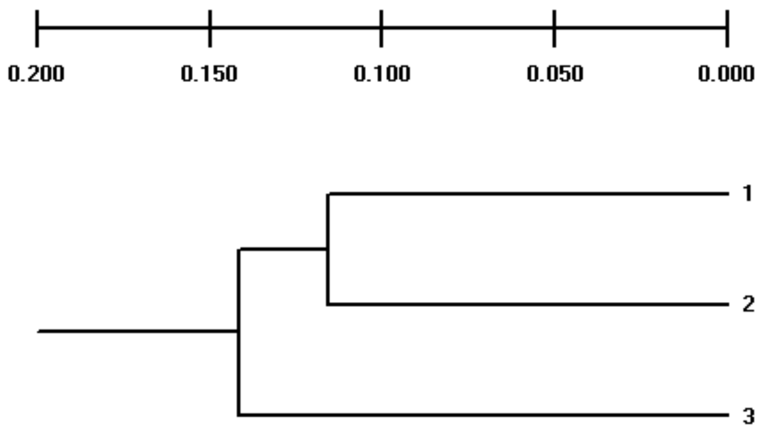

Figure 5. Dendrogram (UPGMA) based on the genetic distances of Nei (1978) with nine microsatellite loci of nucleus, estimated for three stand of individuals making up the metapopulation of *Cereus jamacaru* DC. subsp. *jamacaru* in the rural community of Santa Rita, municipality of Congo, Paraíba State, Northeast Brazil.

Discussion

Use and management of *Cereus jamacaru* DC. subsp. *jamacaru*

The farmers' preference for *Cereus jamacaru* DC. subsp. *jamacaru* for planting and animal fodder is related to its morphology, as it is one of the columnar cacti with larger size compared to other species and because it is easy to handle, since it has fewer thorns than other native species. Other studies carried out in traditional communities in the Northeastern semi-arid region of Brazil also report the intense use of "mandacaru" for feeding animals (Andrade *et al.* 2006; Lucena *et al.* 2012a,b, 2013, 2015a,b; Nunes *et al.* 2015; Lima-Nascimento *et al.* 2021), although they do not clearly show this preference of use.

The management of this species, both *in situ* and *ex situ*, can be explained by the fact that it is the most versatile species among those present in the community (Lucena *et al.* 2015a,b; Lima-Nascimento et a. 2021) and that it is mainly found in areas of lower altitude and in well-anthropized environments (e.g. gardens and backyards) (Lucena *et al.* 2015a,b). The abundance of individuals in anthropized areas is usually associated with the process of artificial selection, which implies the selection of individuals with traits relevant to human groups to be managed or cultivated (Lima-Nascimento et a. 2021). Such selection can, over time, cause significant differences in morphological (Arellano and Casas 2003) and even in genetics traits (Otero-Arnaiz *et al.* 2005), as has been reported in some studies of columnar cacti native to Mexico (Casas *et al.* 2006, 2016; Parra *et al.* 2008).

Similarly to the present study, the cultivation of branches of columnar cacti in gardens for use as human food and fodder has already been recorded in some villages in the Tehuacán-Cuicatlán Valley, in Mexico (Blancas *et al.* 2010; Parra *et al.* 2010).

Considering the useful parts of "mandacaru", several studies have documented the prominent use of its branches for human consumption (Andrade *et al.* 2006; Chaves e Barros 2015), as fodder (Lucena *et al.* 2012 a,b, 2013; Sales *et al.* 2014), and for therapeutic purposes (Andrade *et al.* 2006; Júnior 2011; Lucena *et al.* 2014). However, some ethnobotanical studies carried out with columnar cacti from Mexico report the intense use of the fruits for human consumption, which is one of the most relevant categories (Arellano and Casas 2003; Carmona and Casas 2005).

The different forms of management recorded in Santa Rita show the interest in the conservation of the studied species in the region, because of its economic and cultural importance for the farmers.

Considering the forms of *in situ* management, similar to the gathering, the tolerance was also well demonstrated in the interviews. According to Casas *et al.* (1997; 2014), plants with desirable traits are generally tolerated, even in cultivated areas.

Similar to the *in situ* management, the *ex situ* management recorded in Santa Rita can be considered as a practice involving artificial selection. Casas *et al.* (2016) point out that these forms of cultivation of wild plants in controlled environments differ from the agricultural management, which is a form of cultivation involving domesticated plants.

Genetic diversity and structure

The low genetic differentiation among the different types of mandacaru stands observed by the Global F_{ST} (0.014) and SMM (0.23%) values can be explained by the intensity and type of management, geographical distance between the populations, and the permanence of the gene flow. The influence of these aspects has already been reported in studies with other columnar cacti in Central Mexico (Otero-Arnaiz *et al.* 2005; Casas *et al.* 2006; Cruse-Sanders 2013).

From the ethnobotanical research carried out in the community, it is evident that the form of management carried out by the farmers it cannot influence the genetic dissimilarity between the populations (wild, managed and cultivated). This is because the use of plant parts for the planting of individuals that make up the cultivated population generates the genetic similarity within the population and, consequently, the divergence and dissimilarity in relation to the managed and wild populations. According to González-Insuasti & Caballero (2007), the intensity of the management follows an ascending scale, depending on the type of management carried out and the number of people involved in this practice. In addition, the intensity of management is influenced by the level of risk and uncertainty of the availability of the resource, resulting from its economic and/or cultural importance and even from the scarcity of the resource in the region (Blancas *et al.* 2013). These aspects may explain what is happening with the "mandacaru" in the community of Santa Rita; since it is an economically and culturally important species, the farmers have planted and transplanted it more and more.

A study carried out in the State of Pernambuco, Northeastern Brazil, with a native tree species of the Caatinga (*Spondia tuberosa* Arruda), popularly known as umbu, showed that the individuals of this species are in the process of incipient domestication due to the forms of management to which they are subjected (Lins-Neto *et al.* 2013), but with regard to "mandacaru", we did not analyze the effects of a possible incipient domestication in the present study.

In addition to the management type, geographic factors (topography, barrier, and distance) should also be considered (Parra *et al.* 2010). These factors can influence the natural gene flow between populations of individuals of the same plant species and thus influence the genetic variation.

According to the dendrogram (UPGMA) (Figure 4), the genetic similarity of the cultivated stand of individuals, in relation to the managed and wild stands, indicates that gene flow is very active, which can be explained by the geographic distance between the individuals of the groups of individuals making up the metapopulation of Santa Rita., as it was mentioned above. Some studies carried out with columnar cacti native to Mexico have found that the geographic distance was more relevant than the form of management to explain the genetic distance between the populations (Otero-Arnaiz *et al.* 2005; Casas *et al.* 2006), which is similar to what we found in this study. There are still questions to be answered, which could be explored by comparing several metapopulations throughout the range of the species analyzed. Especially because ecological and cultural factors can vary in the region. But this is an advance for understanding a process that is happening on an interesting plant species in an important region of Northeastern Brazil.

Conclusion

From the forms of use and management carried out by the farmers of Santa Rita, using the individuals of *Cereus jamacaru* subsp. *jamacaru*, it is possible to prove that it is a species of high cultural and economic value.

The forms of management, especially the patterns of preferences associated to gathering can be in turn related to human selection in other contexts where the species is managed. However, geographic factors and the occurrence of gene flow between wild and cultivated populations may be factors influencing an absence of genetic differences detectable between the populations of "mandacaru". This fact confirms that even when people practice selection favoring certain individuals with certain phenotypes, the gene flow occurring in all these contexts leads to consider all these stands as part of a metapopulation, which is similar to those patterns found for several species of columnar cacti in Mexico.

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Declarations

List of abbreviations: N/A
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Literature cited

AESA – Agência Executiva de Gestão das Águas do Estado da Paraíba. Disponível em: http//www.pb.gov.br/aesa. Acesso em: 05 de Agosto de 2013.

Albuquerque UP, Andrade, LHC. 2002. Uso de recursos vegetais da caatinga: o caso do agreste do estado de Pernambuco (nordeste do Brasil). Interciencia 27: 336–346.

Albuquerque UP, Lucena RFP, Alencar NL. 2010. Métodos e técnicas para a coleta de dados etnobiológicos. In: Albuquerque, UP; Lucena, RFP; Cunha, LVFC (Eds). Métodos e técnicas na pesquisa etnobotânica. Recife: NUPEEA. p. 40-64.

Andrade CTS, Marques JGW, Zappi DC. 2006. Utilização de cactáceas por sertanejos baianos. Tipos conexivos para definir categorias utilitárias. Sitientibus. Série Ciências Biológicas (Etnobiologia) 6:3–12. doi:10.13102/scb8142

Arakaki M, Soltis PS, Speranza PR. 2010. Characterization of polymorphic microsatellite loci in *Haageocereus* (Tricocereeae, Cactaceae). American Journal of Botany 97(3):17-19. doi: 10.3732/ajb.1000026

Arellano E, Casas A. 2003. Morphological variation and domestication of *Escontria chiotilla* (Cactaceae) under silvicultural management in the Tehuacán Valley, Central Mexico. Genetic Resources and Crop Evolution 50(4):439-453. doi:10.1023/A:1023902704131

Bezerra-Silva A, Albuquerque-Lima S, Fagundes ACA, Gomes MTD, Santos-Neves PS, Costa JS, Costa-Neto EM, Funch LS. 2024. Mapping ethnobotanical aspects of the iconic Mandacaru cactus, *Cereus jamacaru* DC. in Brazil: a scientometric review. Brazilian Journal of Biology 84(2): e287299. doi:10.1590/1519-6984.287299

Blancas J, Casas A, Lira R, Caballero J. 2009. Traditional management and morphological patterns of *Myrtillocactus schenckii* (Cactaceae) in the Tehuacán Valley, central Mexico. Economic Botany 63(4):375-387. doi: 10.1007/s12231-009-9095-2

Blancas J, Casas A, Rangel-Landa S, Torres I, Pérez-Negrón E, Solís L, Delgado-Lemus A, Parra F, Arellanes Y, Caballero J, Cortés L, Lira R, Dávila P. 2010. Plant management in the Tehuacán-Cuicatlán Valley. Economic Botany 64(4):287–302. doi:10.1007/s12231-010-9133-0

Blancas J, Casas A, Pérez-Salicrup D, Caballero J, Vega E. 2013. Ecological and sócio-cultural factors influencing plant management in Náhuatl communities of Tehuacán Valley, Mexico. Journal of Ethnobiology and Ethnomedicine 9(39):1-22. doi: 10.1186/1746-4269-9-39

Campos LZO, Albuquerque UP, Peroni N, Araújo EL. 2015. Do socioeconomic characteristics explain the knowledge and use of native food plants in semiarid environments in Northeastern Brazil? Journal of Arid Environments 115(1):53-61. doi:10.1016/j.jaridenv.2015.01.002

Carmona A, Casas A. 2005. Management, phenotipic patterns and domestication of *Polaskia chichipe* (Cactaceae) in the Tehuacán Valley, Central Mexico. Journal of Arid Environments 60: 115-132. doi:10.1016/j.jaridenv.2004.03.007

Casas A, Vázquez C, Viveros JL, Caballero J. 1996. Plant management among the Nahua and the Mixtec in the Balsas River Basin, México: An ethnobotanical approach to the study of plant domestication. Human Ecology 24(4):455–478. doi: 10.1007/BF02168862

Casas A, Caballero J. 1996. Traditional management and morphological variation in *Leucaena esculenta* (Moc. et Sessé ex A.DC.) Benth. In the Mixtec Region of Guerrero, Mexico. Economic Botany 50(2):167-181. doi: 10.1007/BF02861449

Casas A, Caballero J, Mapes C, Zárate S. 1997. Manejo de la vegetación, domesticación de plantas y origen de la agricultura em Mesoamérica. Boletín de la Sociedad Botánica del México 61(1):31-47. doi: 10.17129/botsci.1537

Casas A, Caballero J, Valiente-Banuet A, Soriano JA, Dávila P. 1999. Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in Central México. American Journal of Botany 84(4): 522-533.

Casas A, Cruse-Sanders J, Morales E, Otero-Arnaiz A, Valiente-Banuet A. 2006. Maintenance of phenotypic and genotypic diversity in the managed populations of *Stenocereus stellatus* (Cactaceae) by indigenous peoples in central Mexico. Biodiversity and Conservation. 15(3): 879-898. doi: 10.1007/s10531-004-2934-7

Casas A, Otero-Arnaiz A, Perez-Negron E, Valiente-Banuet A. 2007. *In situ* management and domestication of plants in Mesoamerica. Annals of Botany 100(5):1101- 1115. doi: 10.1093/aob/mcm126

Casas A, Camou A, Otero-Arnaiz A, Rangel-Landa S, Cruse-Sanders J, Solís L, Torres I, Delgado A, Moreno-Calles AI, Vallejo M, Guillén S, Blancas J, Parra F, Farfán-Heredia B, Aguirre-Dugua XA, Arellanes Y, Pérez-Negrón E. 2014. Manejo tradicional de biodiversidad y ecosistemas en Mesoamérica: el Valle de Tehuacán. Investigación Ambiental 6(2): 23-44.

Casas A, Parra F. 2016. La domesticación como proceso evolutivo. In: Casas A, Torres-Guevara J, Parra F. (eds.). Domesticación y agricultura en el continente americano: historia y perspectivas del manejo de recursos genéticos en el nuevo mundo. Universidad Nacional Autónoma de México/Universidad Nacional Agraria la Molina. Red Mexicana de Etnoecología y Patrimonio Biocultural, Conacyt, México/Perú.

Casas A, Torres-Guevara J, Parra F, Cruz A. 2016. Domesticación y agricultura en américa: historia y perspectivas del manejo de recursos genéticos en el nuevo mundo. In: Casas A, Torres-Guevara J, Parra F. [coord.]. Domesticación en el continente americano. Manejo de Biodiversidad y Evolución Dirigida por las Culturas del Nuevo Mundo. 1: 13-24.

Casas A, Vallejo M, Parra-Rondinel F. 2024. Domestication of Species and Landscapes in Mesoamerica. In book: Nature(s) in Construction (pp.15-34). doi:10.1007/978-3-031-60552-9_2.

Cavalcanti NB, Resende GM. 2007. Efeito de diferentes substratos no desenvolvimento de mandacaru (*Cereus jamacaru* P. DC.), facheiro (*Pilosocereus pachycladus* RITTER), xiquexique (*Pilosocereus gounelli* (A, WEBWR EX K. SCHUM.) BLY. EX ROWL.) e coroa-de-frade (*Melocactus bahiensis* BRITTON & ROSE). Revista Caatinga, Mossoró 20(1): 28-35.

Cavalli-Sforza LL, Edwards AWF. 1967. Phylogenetic analysis: models and estimation procedures. The American Journal of Human Genetics 19(3):233-257. PMID: 6026583; PMCID: PMC1706274.

Chapuis MP, Estoup A. 2007. Microsatellite null alleles and estimation of population differentiation. Molecular Biology and Evolution 24(3):621-631. doi: 10.1093/molbev/msl191

Chaves EMF, Barro RFM. 2015. Cactáceas: recurso alimentar emergencial no semiárido, Nordeste do Brasil. Gaia Scientia 9(2): 129-135.

Chen YH, Gols R, Benrey B. 2015. Crop domestication and its impacto n naturally selected trophic interations. Annual Review of Entomology 60: 35-58. doi: 10.1146/annurev-ento-010814-020601

Cruse-Sanders JM, Parker KC, Friar A, Huang DI, Mashayekhi S, Prince M.; Otero-Arnaiz A, Casas A. 2013. Managing diversity: domestication and gene flow in *Stenocereus stellatus* Riccob. (Cactaceae) in Mexico. Ecology and Evolution 3(5):1340-1355. doi: 10.1002/ece3.524

Chybicki IJ, Burczyk J. 2009. Simultaneous estimation of null alleles and inbreeding coefficients. Journal of Heredity 100: 106-113. doi: 10.1093/jhered/esn088

Delgado-Lemus A, Casas A, Téllez O. 2014. Distribution, abundance and traditional management of *Agave potatorum* in the Tehuacán Valley, Mexico: bases for sustainable use of non-timber forest products. Journal of Ethnobiology and Ethnomedicine 10 (63): 1-12. doi: 10.1186/1746-4269-10-63

Doyle JJ, Doyle JL. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemistry Bullerin 19:11–15.

Excoffier L, Laval G, Schneider S. 2005. Arlequin ver. 3.0: An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1(47):47-50.

González-Soberanis C, Casas A. 2004. Tradicional management and domestication of tempesquistle, *Syderoxylon palmeri* (Sapotaceae) in the Tehuacán-Cuicatlán Valley, central Mexico. Journal of Arid Environments 59(2): 245-258. doi: 10.1016/j.jaridenv.2004.01.018

González-Insuasti MS, Caballero J. 2007. Managing plant resources: How intensive can it be? Human Ecology 35(3): 303-314. doi: 10.1007/s10745-006-9063-8

González-Insuasti MS, Martorell C, Caballero J. 2008. Factors that influence the intensity of non-agricultural management of plant resources. Agroforestry Systems 74(1):1-15. doi: 10.1007/s10457-008-9148-z

IBGE. Instituto Brasileiro de Geografia e Estatística. IBGE cidades/População estimada 2016.

[http://cidades.ibge.gov.br/xtras/perfil.php?lang=&codmun=250470&search=paraiba|congo]. Accessed: 15 de Agosto de 2017.

Júnior WSF, Ladio AH, Albuquerque UP. 2011. Resilience and adaptation in the use of medicinal plants with suspected anti-inflammatory activity in the Brazilian Northeast. Journal of Ethnopharmacology 138: 238-252. doi: 10.1016/j.jep.2011.09.018

Lima-Nascimento AM, Silva JSB, Casas A, Lucena CM, Lucena RFP. 2021.Traditional management of Cactaceae: *Cereus jamacaru* DC as the native cactus most managed by rural communities in areas of Caatinga in Brazil. Ethnobotany Research and Applications 21:31. doi: 10.32859/era.21.31.1-12

Lins-Neto EMF, Peroni N, Albuquerque U. 2010. Tradicional knowledge and management of umbu (*Spondias tuberosa*, Anacardiaceae): an endemic species from the semi-arid region of northeastern Brazil. Economic Botany 64(1):11-21. doi: 10.1007/s12231-009-9106-3

Lins-Neto EMF, Almeida ALS, Peroni N, Castro CC, Albuquerque UP. 2013. Phenology of *Spondia tuberosa* Arruda (Anacardiaceae) under different landscape management regimes and a proposal for a rapid phenological diagnosis using local knowledge. Journal Ethnobiology and Ethnomedicine 9(1):10. doi: 10.1186/1746-4269-9-10

Lucena CM, Costa GM, Sousa RF, Carvalho TKN, Marreiros NA, Alves CAB, Pereira DD, Lucena RFP. 2012a. Conhecimento local sobre cactáceas em comunidades rurais na mesorregião do sertão da Paraíba (Nordeste, Brasil). Biotemas 25(3): 281-291. doi: 10.5007/2175-7925.2012v25n3p281

Lucena CM, Costa GGS, Carvalho TKN, Guerra NM, Quirino ZGM, Lucena RFP. 2012b. Uso e conhecimento de cactáceas no município de São Mamede (Paraíba, Nordeste do Brasil). Revista de Biologia e Farmácia (Biofar) (special volume):121-134.

Lucena CM, Lucena RFP, Costa GM, Carvalho TKN, Costa GGS, Alves RRN, Pereira DD, Ribeiro JES, Alves CAB, Quirino ZGM, Nunes EN 2013. Use and knowledge of Cactaceae in Northeastern Brazil. Journal of Ethnobiology and Ethnomedicine 9(62):1-11. doi:10.1186/1746-4269-9-62

Lucena CM, Carvalho TKN, Marín EA, Nunes EM, Oliveira RS, Melo JG, Casas A, Lucena RFP. 2014. Potencial medicinal de cactáceas en la región semiárida del Nordeste de Brasil. Gaia Scientia (Volume Especial Populações Tradicionais):36-50.

Lucena CM, Carvalho TKN, Ribeiro JES, Quirino ZGM, Casas A, Lucena RFP. 2015a. Conhecimento botânico tradicional sobre cactáceas no semiárido do Brasil. Gaia Scientia (Edição Especial Cactaceae) 9(2):77-90.

Lucena CM, Ribeiro JES, Nunes EN, Meiado MV, Quirino ZGM, Casas A, Lucena RFP. 2015b. Distribuição local de *Cereus jamacaru* DC. subsp. *jamacaru* e *Pilosocereus pachyucladus* F.Ritter subsp. *pernambucoensis* (F.Ritter) Zappi (Cactaceae) e sua relação com uma comunidade rural no Município do Congo, Paraíba. Gaia Scientia (Edição Especial Cactaceae) 9(2):97-103.

Magalhães, A. 2006. Perfil etnobotânico e conservacionista das comunidades de entorno da Reserva Natural Serra das Almas, Ceará-Piauí, Brasil. Ceará. 81f. Dissertação (Mestrado em Desenvolvimento e Meio Ambiente) Universidade Federal do Ceará.

Miller MP. 1973. Tools for population genetics analyses (TFPGA) 1.3. A windows program for the analysis of allozymes and molecular population genetic data. Computer software distributed by author.

Moraes EM, Cidade FW, Silva GAR, Machado MC. 2014. Polimorphic microsatellite markers for the rare and endangered cactus *Uebelmannia pectinifera* (Cactaceae) and this congereneric species. Genetic and Molecular Research 13(4):10359-10366. doi: 10.4238/2014.December.4.31

Nei M. 1972. Genetic distance between populations. American Naturalist. 106(949): 283-292.

Nilsen LB, Dhillion SS, Camargo-Ricalde SL, Rendón-Aguilar, Heun M. 2005. Traditional knowledge and genetic diversity of *Opuntia pilifera* (Cactaceae) in the Tehuacán-Cuicatlán Valley, Mexico. Economic Botany 59(4):366-376. doi: 10.1663/0013-0001(2005)059[0366:TKAGDO]2.0.CO;2

Nunes AT, Lucena RFP, Santos MV, Albuquerque UP. 2015. Local knowledge about fodder plants in the semi-arid region of Northeastern Brazil. Journal of Ethnobiology and Ethnomedicine 11(12):1-12. doi: 10.1186/1746-4269-11-12

Otero-Arnaiz A, Casas A, Hamrick JL, Cruse-Sanders J. 2005. Genetic variation and evolution of *Polaskia chichipe* (Cactaceae) under domestication in the Tehuacán Valley, central Mexico. Molecular Ecology 14(6): 1603-1611. doi: 10.1111/j.1365-294X.2005.02494.x

Parra F, Pérez N, Lira R, Pérez-Salicrup D, Casas A. 2008. Population genetics and process of domestication of *Stenocereus pruinosus* (Cactaceae) in the Tehuacán-Valley, México. Journal of Arid Environments. 72(11):1997-2010.doi:10.1016/j.jaridenv.2008.06.007

Parra F, Casas A, Peñaloza-Ramírez JM, Cortés-Palomec AC, Rocha-Ramírez V, González-Rodríguez A. 2010. Evolution under domestication: ongoing artificial selection and divergence of wild and managed *Stenocereus pruinosus* (Cactaceae) populations in the Tehuacán Valley, Mexico. Annals of Botany 106:483-496. doi: 10.1093/aob/mcq143

Parra F, Blancas JJ, Casas A. 2012. Landscape management and domestication of *Stenocereus pruinosus* (Cactaceae) in the tehuacán valley: human guided selection and gene flow. Journal of Ethnobiology and Ethnomedicine 8(32):1-17. doi: 10.1186/1746-4269-8-32

Patiño-Lopez V, Bravo-Avilez D, Vargas-Mendoza CF, Blancas J, Rendón-Aguilar B. 2022. Evolution under domestication of correlated characters in populations of *Stenocereus stellatus* (Pfeiff.) Riccob., under different forms of management in central Mexico: genetic diversity, damage, and defense mechanisms. Genetic Resources and Crop Evolution 69(2): 601-618. doi: 10.1007/s10722-021-01245-x

Peakall R, Smouse PE. 2006. Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6(1):288–295. doi: 10.1111/j.1471-8286.2005.01155.x

Perez MF, Téo MF, Zappi DC, Taylor NP, Moraes EM. 2011. Isolation, characterization, and cross-species amplification of polymorphic microsatellite markers for *Pilosocereus machrisii* (Cactaceae). American Journal of Botany 98(8):204-206. doi: 10.3732/ajb.1100033

Raymond M, Rousset F. 1995. Genepop (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 68(3):248-249. doi: 10.1093/oxfordjournals.jhered.a111573

Rodríguez-Arévalo I, Casas A, Lira R, Campos J. 2006. Uso, Manejo y procesos de domesticación de *Pachycereus hollianus* (F.A.C. Weber) Buxb. (Cactaceae), en El Valle de Tehuacán-Cuicatlán, México. Interciencia 31(9):677-685.

Rousset F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. Molecular Ecology Resources 8(1):103-106. doi: 10.1111/j.1471-8286.2007.01931.x

Sales MSL, Martins LV, Souza I, Meireles Deus D, Deron AP. 2014. *Cereus jamacaru* De Candolle (Cactaceae), o mandacaru do nordeste brasileiro. Ciências Biológicas e da Saúde 20(2):135-142. doi: 10.5212/Publ.Biologicas.v.20i2.0006

Sneath PH, Sokal RR. 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification. 1st Edition, W. H. Freeman, San Francisco.

Sousa FS, Cruz KCM, Souza MMR. 2012. Congo. In: Lima AG, Sobrinho AM, Farias CMP, Freitas DK, Batista FA, Cruz KCM, Andrade VS. (Orgs.) Traços históricos e culturais do Cariri Paraibano, João Pessoa. p 115.

Sousa Júnior JR, Albuquerque UP, Peroni N. 2013. Traditional knowledge and management of *Caryocar coriaceum* Wittim. (Pequi) in the Brazilian Savanna, Northeastern Brazil. Economic Botany 67(3): 225-233. doi: 10.1007/s12231-013-9241-8

Torres I, Casas A, Vega E, Martínez-Ramos M, Delgado-Lemus A. 2015. Population dynamics and sustainable management of mescal agaves in central Mexico: *agave potatorum* in the Tahuacán-Cuicatlán Valley. Economic Botany 69(1):26-41. doi: 10.1007/s12231-014-9295-2

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P. 2004. Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4(3):535-538. doi: 10.1111/j.1471-8286.2004.00684.x

Villalobos S, Vargas O, Melo S. 2007. Uso, manejo y conservación de “yosú”, *Stenocereus griseus* (Cactaceae), in the Upper Guajira, Colombia. Acta Biologica Colombiana 12(1):99-112.

Yineger H, Kelbessa E, Bekele T, Lulekal E. 2008. Plants used in traditional management of human ailments at bale mountains national park, southeastern ethiopia. Journal of Medicinal Plants Research 2(6):132-153.

Zank S, Peroni N, Araújo EL, Hanazaki N. 2015. Local health practices and the knowledge of medicinal plants in a Brazilian semi-arid region: environmental benefits to human health. Journal of Ethnobiology and Ethnomedicine 11(11):1-13. doi: https://doi.org/10.1186/1746-4269-11-11

Zappi D, Aona L. 2014. Cactaceae in Flora brasiliensis revisitada. Available in: http://flora.cria.org.br. Acesso em: 10 nov. de 2014.

Zohary D. 2004. Unconscious selection and evolution of domesticated plants. Economic Botany 58(1): 5-10. doi: 10.1663/0013-0001(2004)058[0005:USATEO]2.0.CO;2