An Overview of Genetic Resources for *Opuntia* Production in Mexico

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INTRODUCTION

During the last decade, cactus pear (*Opuntia* spp.) has become an important crop in the semiarid lands of the world. The increased interest in cactus pear is because of its ability to produce forage, fruit, vegetable, and other useful products as well as being a part of an ecological strategy to avoid or prevent the disastrous consequences of frequent, severe droughts and long-term degradation of ecologically weak environments, as is the case in arid environments (Pimienta *et al.* 1993). One of the main limitations for the development of cactus pear as a crop in the arid lands of countries with potential for the cultivation and utilization of this cacti is the lack of promotion of this crop. Field observations of wild and cultivated populations in Mexico and their comparison with the existing populations in other countries revealed that arid regions of Mexico host the greatest genetic diversity (Pimienta and Muñoz, 1995). Several reports have indicated variation in cactus pear based upon vegetative and reproductive morphology (Bravo, 1978), seed dormancy periods (Pérez , 1993), reproductive phenology (e.g., fruit-ripening time) (Pimienta, 1990), anatomical traits (Pimienta *et al.* 1993), fruit yield and quality (Gutierrez, 1987; Pimienta and Mauricio, 1989), chromosome number (Sosa, 1964; Muñoz, 1995) and sensitivity to biotic and abiotic factors that affect their growth and productivity (Pimienta, 1994). It is as though this variability arose via natural hybridization associated with polyploidy and geographical isolation (Gibson and Nobel, 1986). Because of the importance of cactus pear as genetic resource of high potential value for the sustainable agriculture in arid environments, it becomes important to understand the origin and causes of genetic and phenotypic variations in cactus pear. This information will be valuable in order to define future breeding strategies to overcome limitations for adaptation (e.g., drought and salinity) and productivity (e.g., pests and diseases). This paper presents information on the variability in the most important cactus-pear forms and varieties found in wild and cultivated populations in the arid lands of Mexico.

ORIGIN OF VARIABILITY ON CACTUS PEAR: THE ROLE OF THE BACKYARDS OF RURAL POPULATIONS

Cactus pear variability is commonly found in both wild and cultivated populations growing in the semiarid lands of the central part of Mexico. However, the highest variability is found in the backyards of rural homes dispersed on arid plateaus. Comparing recent field observations of cactus pear variability in the main producing countries with the varability in Mexico confirmed that the arid lands of Mexico host the largest variability in cactus pear phenotypes in the world and helped support the hypothesis that the actual variability of cactus pear found in Mexico is relatively recent and was not present when the Spanish conquerors arrived in Mexico. This hypothesis is supported because in most of the Mediterranean countries where this plant was introduced after the 16th century, cultivated varieties belong to one taxonomic specie, namely *Opuntia ficus-indica,* whereas, in México, the cultivated varieties belong to a least four different taxonomic species and to a large diversity of natural hybrids. In addition to *O. ficus-indica* (L.) Mill, the most important taxonomical species that produce edible fruits in wild and cultivated populations are *O. megacantha* Salm-Dyck, *O. amyclaea* Tenore, *O. streptacantha* Lemaire, and *O. lindheimeri* Engelm. Perhaps when the Spaniards first arrived in México, *O. ficus-indica* was the most abundant and representative specie in the natural populations, so when they collected vegetative material in México and introduced it to Spain, and later to Mediterranean countries, they dispersed phenotypes that belong mainly to *Opuntia ficus-indica.*

The variability of cactus pear is the result of the anthropogenic activity related to the domestication of this natural resource. It is thought that during the early stages of cactus pear domestication, outstanding phenotypes were collected for the inhabitants of the arid lands from wild populations and, further, were established vegetatively in the backyards (corrales) of the rural homes to satisfy human needs (e.g., ornamental, medical purposes, food, forage, and natural hedge). Through time, farmers collected an ample diversity of cactus pear phenotypes. However, because of the relatively small areas of the backyards, an artificial sympatric condition was created by the number and diversity of species that grow close together in small areas, so cross-pollination (gene flow) was greatly increased, and stimulated the creation of new hybrids or genetic combinations that were not possible to obtain in the natural populations. The backyards also contributed to the persistence of those new hybrids because their environments favored seedling establishment (Pimienta, 1994).

Recent cytological observations of pollen-grain germination, pollen-tube growth and embryo development following artificial crosses between wild and cultivated cactus pear species revealed a high degree of sexual compatibility notwithstanding the remarkable differences in plant morphology and ploidy levels between the crossed species. These observations revealed that in the members of the subgenus *Opuntia* there are few genetic barriers between species that would limit the exchange of genes and favors the creation of new genetic combinations in the backyards.

Modern commercial plantations in Mexico are relatively recent, starting in the middle 1940's. These plantations were established using vegetative material from outstanding phenotypes of the rural backyards. So the selection of outstanding phenotypes of the rural backyards for economic purposes was another important process in the domestication of cactus pear in Mexico that contributed to variability present in the modern commercial plantation and to the dispersion of the variability generated in the backyards.

VARIABILITY IN CACTUS PEAR

Cytological Observations

Differences in fruit size and cladode size are commonly observed between wild and cultivated cactus pear populations. Those differences are, in most cases, due to differences in ploidy levels rather than soil quality or climatic conditions. Cytogenetic studies showed the existence of different levels of ploidy that varied from 2x to 20x (Sosa, 1964; Yuasa *et al.* 1973). Pinkava *et al.* (1992), mention that about 63% of the species of the subfamily Opuntioideae are polyploids. An interesting observation that emerges from the cytological observations on *Opuntias* is that the cactus pear varieties and forms with the highest chromosome numbers are commonly found in cultivated populations (2n=6x=66 and 2n=8x=88). In contrast, the lowest chromosome numbers are found in wild populations (2n=2x=22 and 2n=4x=44) although in a few cases forms with higher chromosome numbers (2n=8x=88) are found in wild populations, as is the case of *O. streptacantha* (Pimienta and Muñoz, 1995).

Seed Germination and Apomixis

Seed germination observations in a representative number of wild and cultivated cactus pear varieties revealed variability in the rate of seed germination, length of the dormancy periods, final percentage of seed germination, and the percentage of polyembrionic seeds. Most of the varieties start seed germination 8 months after fruit ripening; a few of them started germination earlier. The highest percentages of germination were as recorded 12 months after fruit ripening. At this time, differences in the final percentage of germination between varieties were recorded. In varieties, such as "cristalina," "chapeada," and "negrita," percentages of germination greater than 80% were observed; whereas, in the remaining varieties the percentages were less than 50%. An extreme case was recorded in the variety "burrona," in which the final percentage was very low (3%). It is thought that low percentages of germination are an expression of sterility that may be related to the high number of chromosomes because varieties like "burrona" are polyploid (Muñoz, 1995) (Table 1).

Apomixis, known as somatic, sporofitic, or adventitious embryogenesis, is common in both wild and cultivated cactus pear species. However, the percentages are low. The percentages of polyembrionic seeds range from 1.5% to 16% and the number of plants that develop per seed varies from one to four (Perez, 1993), although cytological observations revealed that in some varieties it is possible to find more than six embryos per ovule (Garcia and Pimienta, in press). This situation is responsible for the increase in seed size and represents a serious drawback for marketing (Mondragon, 1993) (Table 2).

Cladode Anatomy

An anatomical study of mature cladodes in wild and cultivated cactus pear species growing in the semiarid zones of the central part of Mexico revealed variability in anatomical traits. Stomatal size ranges from 33 mm to 62 mm, although most of the species showed stomatal size close to or greater than 50 mm. Previous observations by Conde (1975) on stomatal size in different *Opuntia* species revealed that in species with stomatal size greater than 50 mm, the chromosome number varied from n=66 to n=88, indicating that polyploidy is a common phenomenon in *Opuntia*, and perhaps played an important role in speciation of cactus pear, because polyploidy contributed to reproductive isolation. On the other hand, like other cactus, stomatal density is relatively low because most of the species showed stomatal density of less than than 30 stomata/mm^2. Wild species showed highest stomatal density when compared to cultivated species. The lowest stomatal density was found in varieties than belong to *Opuntia ficus-indica*. Cuticular thickness ranged from 8 mm to 58 mm, but most of the species showed cuticular thicknesses of less than 20 mm. Sunken stomata is a common anatomical trait in most of the varieties, although the depth of the stomatal crypt varied from 8 mm to 50 mm (Table 3). An important fact is that the species collected in the driest regions showed the deepest stomatal crypt (Pimienta *et al.* 1993).

Cactus Pear Cultivated Varieties

The main commercial varieties are recognized primarily based on the color of both peel and pulp of the fruit. Varieties names are established by taking into consideration fruit color, fruit size, and cladode morphology, although, in some cases, the names are designed taking into consideration their response to environmental stresses. In addition to *O. ficus-indica*, the most important cultivated species belong to *O. amyclaea*, *O. megacantha*, and to different natural hybrids and are polyploids. Most of the cultivated varieties produce clear-green fruits, and are called "blancas". The majority of the varieties ripen fruits during August and September; a few of them ripen in early summer or during the fall (Table 4).

In the backyards of rural homes there is a large variability of varieties that are natural hybrids, that are early and even late ripening, and produce red-purple fruits or yellow-brown fruits, that are attractive to the international markets. However, in most of those varieties the fruits present low resistance to postharvest manipulation.

It is important to notice that in the backyards, early ripening (June) or late ripening (November-December) are commonly found. This is in contrast to most of the varieties growing in modern plantations where most fruit ripens between July and September (intermediate ripening).

In Table 5 the variability in fruit weights between cultivated prickly pear varieties is presented. The variation in fruit weight from 114 g to 240 g is particularly striking. Clear-green fruits are the heaviest. In most of the varieties the nonedible part constitutes from 40% to 60% of the total fruit weight.

Chemical analysis of the pulp of cultivated varieties showed that the percentage of total soluble solids varied from 11% to 14% and the total sugars from 12% to 17%. The reducing sugars had a greater range of variation from 5% to 14% and, in most varieties, the percentage was greater than 50%. Considerable variation was also found in the percentage of ascorbic acid. The highest content of this acid was 41 mg 100 g^{-1} and the lowest was 5 mg 100 g^{-1}. An interesting observation was that the highest content of ascorbic acid was found in varieties that produce fruits with a clear-green pulp. The pulp protein content is low and varied from 71 mg g^{-1} to 575 mg g^{-1}, although most of the varieties showed values close to or greater than 300 mg g^{-1}. Another interesting observation was that the fruits with a clear-green pulp contained the pigment chlorophyll (Delgado, 1985).

Physiological Activity

The evaluation of nocturnal acid accumulation as an indirect measure of photosynthetic activity in different cactus pear varieties revealed a large variability in the rate of photosynthesis among wild and cultivated varieties (Table 6). The highest rate of acid accumulation were recorded in cultivated varieties, such as "amarilla-huesona," "naranjona," and "copo de nieve." The rate of nocturnal acidification recorded in different cactus pear varieties matches the rate of growth observed in field conditions because varieties that showed the highest rate of growth also had the highest rate of nocturnal acidification, in contrast to varieties such as "tapona," which showed both low nocturnal acid accumulation and low growth rates, even under favorable growth conditions as observed when this variety was grown under nursery conditions. However, the relation between the rate of acidification and the growth of rate is not always positive, as in the case of the variety "fafayuco." This variety commonly shows high growth rates in the field and, in our observations, showed intermediate values of nocturnal acid accumulation.

Productivity

Among the cultivated varieties there are contrasting differences in fruit yield. Highly productive varieties are commonly found in the so-called "blanca" varieties, as is the case of "copena-1," "blanco" and "alfajaucan," in contrast with the so-called "roja" and "amarilla" varieties that show low productivity.

This, in part, explains why most of the commercial plantations in Mexico, produced the so-called green fruits, and few produced red and yellow varieties. Maximum fruit fresh productivity is obtained when the plants are over 10 years old and year to year there is great variation in yields due to the phenomenon of biennial bearing that is common in most of the cultivated varieties (Table 7).

Fruit yields are highly variable. Typical yields range from 2 to 8 ton ha^{-2}, although in some varieties, for example, the blanca varieties, yields may be 20 ton ha^{-2}. Recent trials showed that mineral fertilizers and manure increase fruit yield in cultivated plantations.

CONCLUSIONS

Although the variability of cactus pear varieties is relatively large in Mexico, this variation is considerably reduced in modern commercial plantations. Most of the commercial varieties produce the so-called green fruits. Few of them produce red and yellow fruits, notwithstanding the international markets showed demand for red and yellow fruits.

The rural backyards are authentic reservoirs of prickly pear variability in which exists a large variability in fruit color and date of ripening and other agronomically desirable traits. The Mexican researchers and growers may re-examine this variability in order to obtain new varieties.

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Table 1. Percentage of seed germination of wild and cultivated cactus pear varieties at different intervals of time after fruit harvest (Perez, 1993).

	Time after fruit harvest (months)					
Common Name	2	4	6	8	12	14
Naranjona[1]	0	0	0	5	42	5
Cristalina[1]	0	0	0	3	85	90
Burrona[1]	0	0	0	0	3	0
Chapeada[1]	0	0	0	0	3	0
Negrita[2]	0	0	13	55	67	100
Cardona Blanca[2]	0	0	3	23	40	30
Tapona[2]	0	0	8	3	80	32

[1] Fruits collected from cultivated populations.
[2] Fruits collected from wild populations.

Table 2. Percentage of polyembrionic seeds on wild and cultivated cactus pear varieties (Perez, 1993).

Common Name	Polyembrionic Seeds (%)
Blanca Lisa[1]	16.0
Negrita[2]	11.0
Sangre de Toro[1]	10.0
Cristalina[1]	7.0
Cardona Blanca[2]	3.5
Gomelilla[2]	1.5

[1] Fruits collected from cultivated populations.
[2] Fruits collected from wild populations.

Table 3. Variation on the anatomical traits of the epidermis of cactus pear species.

Common Name	Cuticular thickness (μm)	Stomatal density (mm^2)	Depth of Stomatal crypt (μm)
Cardon	58	34	42
Amarilla huesona	53	20	12
Copo de Nieve	27	22	11
Xoconostle	24	30	50
Tapón de Mayo	21	38	13
San Pedrito	11	19	0
Pelón-Liso	10	15	24
Fafayuco	8	24	24
Pelón-Liso	8	9	20
Blanco de Monte	8	23	0

[1] Fruits collected from cultivated populations.
[2] Fruits collected from wild populations.

Table 4. Variability in fruit color and chromosome number in the most important cultivated cactus pear varieties in Mexico.

Common Name	Fruit color	Chromosome Number
Alfajayucan (*O. amyclaea*)	Green-clear	2n=8x=88
Burrona (*Opuntia* sp.)	Green-clear	2n=8x=88
Cristalina (*Opuntia* sp.)	Green-clear	2n=8x=88
Blanca de Castilla (*Opuntia* sp.)	Green-clear	?
Amarilla-Huesona (*O. megacantha*)	Yellow-brown	2n=8x=88
Chapeada (*Opuntia* sp.)	Green-clear	?
Rojo-Pelón (*O. ficus-indica*)	Red-purple	2n=8x=88
Naranjona (*Opuntia* sp.)	Yellow-brown	?

Table 5. Variability of average fruit weight and edible part weight in cactus pear varieties growing on cultivated populations (Pimienta & Mauricio, 1989).

Common Name	Fruit weight (g)	Edible part weight (g)
Cristalina (*Opuntia* sp.)	240	152
Burrona (*Opuntia* sp.)	205	127
Alfajayucan (*Opuntia amyclaeae*)	187	106
Blanca de Castilla (*Opuntia* sp.)	148	75
Amarilla-Huesona (*O. megacantha*)	143	79
Papanton (*Opuntia* sp.)	130	70
Chapeada (*Opuntia* sp.)	128	63
Rojo-pelón (*O. ficus-indica*)	116	59
Amarilla-naranjona (*Opuntia* sp.)	114	59

Table 6. Nocturnal acid accumulation on wild and cultivated cactus pear varieties.

Common Name	Nocturnal Acidification (μmoles/m^2)
Amarilla-huesona (*O. ficus-indica*)[1]	532
Naranjona (*Opuntia* sp.)[1]	488
Charola (*O. streptacantha*)[1]	413
Copo de Nieve (*O. ficus-indica*)[1]	387
Pelon-liso (*O. ficus-indica*)[1]	385
Xoconostle (*O. joconostle*[1]	379
Papanton (*Opuntia* sp.)[1]	284
Tlaconopal (*O. ficus-indica*)[1]	269
Fafayuco (*Opuntia* sp.)[1]	217
Pepino (*Opuntia* sp.)[1]	215
Tapon (*O. robusta*)[2]	176
Cristalina (*Opuntia* sp.)[1]	150
Camuesa (*Opuntia* sp.)[1]	117
Rojo de Tonala (*O. ficus-indica*)[1]	100
Tapon de Mayo (*O. robusta*)[2]	38

[1] Vegetative material collected from cultivated populations.
[2] Vegetative material collected from wild populations.

Table 7. Long-term evaluation of fresh fruit yield on selected on cactus pear clones in Aguascalientes, Mexico (Gutierrez, 1987).

Clone	Year						Average Yield (ton/ha)
	1982	1983	1984	1985	1986	1987	
Copena-1	1.5	38.2	9.3	29.4	13.4	18.3	18.35
Blanco	1.4	51.1	7.4	29.8	20.5	20.0	21.70
Roja	5.1	45.6	8.8	35.6	25.1	24.0	24.03
Amarilla	2.4	6.6	3.9	6.0	10.8	5.9	5.93
Alfajayucan	3.4	46.0	10.7	32.0	23.5	23.1	23.11