Clusters of commercial varieties of cactus pear and xoconostle using UPOV morphological traits

Clemente Gallegos–Vásquez[1*], Alejandro F. Barrientos–Priego[2], Juan A. Reyes–Agüero[3], Carlos A. Núñez–Colín[4], and Candelario Mondragón–Jacobo[4]

[1]Centro Regional Universitario Centro–Norte, Universidad Autónoma Chapingo. Cruz del Sur Núm. 100, Col. Constelación, El Orito. Apartado Postal 196, CP 98085. Zacatecas, Zac., México
[2]Departamento de Fitotecnia, Universidad Autónoma Chapingo. CP 56230. Chapingo, Estado de México, México
[3]Universidad Autónoma de San Luis Potosí, Instituto de Investigaciones en Zonas Desérticas. CP 78377. San Luis Potosí, SLP. México
[4]Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias; Campo Experimental Bajío. Apdo. Postal 112. CP 38110. Celaya, Guanajuato. México

* Corresponding author: e–mail, cgallegosvazquez@gmail.com

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Abstract

Twenty nine cactus pear varieties and four xoconostle varieties were evaluated using 24 quantitative traits. Measurements of cladodes, flowers and fruits were performed according to the International Union for the Protection of New Varieties of Plants (UPOV) guidelines for tests of distinctness, uniformity and stability of cactus pear and xoconostles. Database conformed by 29 varieties and 24 traits was used in order to carry out a cluster analysis based on the Euclidian distance and the Ward's method, and a discriminant canonical analysis. Three well–defined groups were evidenced and confirmed by the cubic criteria of clustering. Four xoconostle varieties formed an independent group, and the rest of varieties were divided in the other two groups. The second group included nine varieties used mainly for "nopalitos" production and cactus pear production ('Burrona', 'Cristalina', 'Naranjón Legítimo', 'Fafayuca', 'Pico Chulo' and 'Torreoja'). The third group included 16 varieties: 9 and 7 varieties with yellow and green fruits, respectively. The first canonical function (CF1) accounted for 88% of the total variation, and the two estimated functions together explained all the variation. CF1 was related with peel thickness, pulp weight, fruit weight/peel weight ratio and maximum fruit diameter; meanwhile CF2 structure was defined mainly by receptacle diameter and peel weight. Thus *Opuntia* spp. fruit characters, and to a lesser extent, the receptacle diameter could be the most discriminating characteristics. Our results suggest at least one group of cactus pear varieties are closely related to the degree of human use or domestication.

Keywords: *Opuntia*, UPOV, grouping, multivariate analysis.

Introduction

The genus *Opuntia* refers to cacti with flat pseudostems or cladodes, cyathiform perianths exceptionally tubular with stamens shorter than tepals (Stuppy, 2002; Wallace and Dickie 2002), and comprises 191 species (Anderson, 2001); although some authors (e.g. Hunt, 2002) estimate that this genus contains as many as 215 species.

Opuntia is a complex genus that includes species used for their edible young cladodes called "nopalitos" obtained mainly from *O. ficus–indica*, or for their fruits (from many species) known as cactus pears (tunas in spanish) and "xoconostles". Xonocostle fruit differs from cactus pear in having very thick edible pericarp, almost absent and highly acidic pulp, and long shelf life. The word "nopal" refers to each plant of most of the *Opuntia* species disregarding if they are used for fresh fruit, vegetable or as animal feed. The wild stands of *Opuntia* are known as "nopaleras" which were the initial source of variability of domesticated variants.

From both biological and cultural points of view, *Opuntia* is important since: a) 29 species of *Opuntia* are found in Mexico; b) 16 out of 29 are native to Mexico; c) the majority of the wild stocks of *Opuntia* contain remnants of vegetation known as crasicaule or "nopaleras"; d) there is a large genus' genetic variability; e) some varieties are cultivated, at variable intensities, in pastures, "milpas" (mixed crop fields based on maize and sometimes on maize and dry beans), backyards and commercial plantations (Rzedowski, 1978; Colunga *et al*., 1986; Flores and Gallegos, 1994; Guzmán *et al*., 2003; Gallegos *et al*., 2004; Reyes–Agüero *et al*., 2005b).

Control of genetic resources around the world represents a leverage in agricultural markets and could play an important role in international relations (Gallegos *et al*., 2005).This is especially relevant as Mexico is considered centre of origin and diversity of many agricultural species, cactus pear (*Opuntia* spp.) included. *Opuntia* genus is closely associated to the cultural development of the Mexican people as demonstrated by the archaeobotanical findings (McNeish, 1972). Cactus pear has been used as a human food in the semi–arid regions of the south–west of Tamaulipas and in the Tehuacán valley from 9,000 to 11,000 years ago (Heiser, 1981).

At present, cactus pear is the most important cultivated cactus in the world (Mizrahi *et al*., 1996) occupying about 100,000 ha of five countries (Mondragón and Pérez, 2002). Mexico, is the main producing country, with 51,112 ha of plantations for the commercial production of fruit (Gallegos *et al*., 2009), 10,500 ha for the vegetable cactus pear ("nopalitos") and close to 15,000 ha for forage production (Flores, 2002).

Classification of cactus pear varieties and its wild relatives has been based on morphological features of the fruits (Valdez–Cepeda *et al*., 1996; Valdez–Cepeda *et al*., 1997; Fernández–Montes *et al.,* 1999; Mondragón, 2002; Gutiérrez–Acosta *et al*., 2003; Aguilar–Estrada *et al*., 2003; Valdez–Cepeda *et al*., 2003), chemical attributes (Molina *et al*., 2003; Scheinvar *et al*., 2003), and frost tolerance (Parish and Felker, 1998). Most of these studies used only a few commercially outstanding varieties and a low number of attributes. Reyes–Agüero *et al*. (2005a) used 69 fruit and cladode traits of 55 cactus pear varieties focusing on their degree of domestication and Colunga *et al.* (1986) analyzed the correspondence between the intensity of agricultural management and the degree of domestication. All these studies were based on quantitative methods that attempt to group varieties using similarities detected in the measured characteristics (Sokal and Sneath, 1963).

Other researchers have identified and described *Opuntia* spp. varieties using molecular markers such as isozymes (Chessa *et al*., 1997; Uzun, 1997), RAPDs (Mondragón and Bordelon, 2003), cpSSR (Chessa *et al.,* 2004) and ISSR (Luna–Paez *et al*., 2007).

There is widely recognized *Opuntia* genus involves a great genetic diversity. Then it is important to document and register different varieties under the basis of a reliable classification procedure. Therefore, the aim of this study was to classify 29 varieties of cactus pear and xonocostle using 24 morphometric cladode, flower and fruit traits as described by the UPOV guidelines through cluster and discriminant function analyses.

Materials and methods

Plant material

Mother cladodes of 29 of the most important commercial varieties for fresh fruit (cactus pear and xoconostle), vegetable or forage, belonging to six species of *Opuntia* were obtained from commercial plantations located in the main growing areas of Mexico (Table 1). They were planted at the experimental orchard of the Centro Regional Centro Norte de la Universidad Autónoma Chapingo located at El Orito, Zacatecas, Mexico (22° 44.7’ North latitude and 102° 36.4’ West longitude).

Measurements

Ten representative 9-years old plants of each of 29 varieties were chosen to measure twenty–four morphological attributes: seven describing the cladode, three the flower and 14 related to the fruit (Table 2). From each plant, 10 cladodes, 20 flowers and 20 fruits were used. All 24 traits were registered in accordance with the test guidelines for cactus pear and xoconostle of the International Union for the Protection of New Varieties of Plants (UPOV, 2004). A database was constructed with the 29 cases and means of the 24 traits.

Table 1. Mexican commercial varieties of the genus *Opuntia* evaluated in this study.

Species	Cultivar	Main use	Commercial importante
Opuntia albicarpa	‘Burrona’	Fruit	High
(syn. *O. amyclaea*)	‘Reyna’	Fruit	High
	‘Cristalina’	Fruit	Very high
	‘Chapeada’	Fruit	Medium
	‘Fafayuca’	Fruit	Medium
	‘Blanca la Gavia’	Fruit	Medium
	‘Esmeralda’	Fruit	Medium
	‘Villanueva’	Fruit	Medium
	‘Blanca San José’	Fruit	Medium
Opuntia ficus–indica	‘Milpa Alta’	Vegetable	High
	‘COPENA V1’	Vegetable	Very high
	‘Atlixco’	Vegetable	Very high
	‘COPENA F1’	Fodder	Medium
	‘Rojo Pelón’	Fruit	Medium
	‘Rojo Vigor’	Fruit	Low
	‘Roja San Martín’	Fruit	Low
	‘Rojo Lirio’	Fruit	Low
	‘Amarilla Plátano’	Fruit	Low
	‘Amarilla Diamante’	Fruit	Low
Opuntia joconostle	‘Xoconostle Cuaresmeño’	Xoconostle fruit	Very high
	‘Xoconostle Blanco’	Xoconostle fruit	Very high
	‘Xoconostle Colorado’	Xoconostle fruit	Very low
Opuntia durangensis	‘Xoconostle Chivo’	Xoconostle fruit	Very low
Opuntia megacantha	‘Pico Chulo’	Fruit	Very high
	‘Amarilla Montesa’	Fruit	Medium
	‘Torreoja’	Fruit	Medium
	‘Naranjón Legítimo’	Fruit	Low
	‘Amarillo Miquihuana’	Fruit	Low
Opuntia undulata	‘Bolañera’	Fruit	Low

Table 2. Plant features considered in this study based on the UPOV test guidelines for cactus pear and xoconostle (UPOV, 2004).

Plant part	Characteristic
Cladode	Length (cm)
	Width (cm)
	Thickness (cm)
	Ratio length/width
	Number of areoles in the central row
	Number of spines per areole
	Length of the longest spine
Flower	Number of flowers per cladode
	Length of the flower (cm)
	Number of stigma lobes
Fruit	Length (cm)
	Maximum diameter (cm)
	Ratio length/maximum diameter
	Density of areoles (areoles cm^{-2})
	Peduncle Length (cm)
	Depression of receptacle scar (cm)
	Receptacle diameter (cm)
	Peel thickness (cm)
	Peel weight (g)
	Pulp weight (g)
	Ratio weight of peel/fruit weight
	Number of normal seeds
	Number of abortive seeds
	Total soluble solids (°Brix)

Statistical analysis

Taking into account the mentioned database, a cluster analysis was performed by using the Euclidean distance as similarity index and the Ward's approach (Johnson, 1998) to conform groups of varieties. In addition, clustering criterion was applied to obtain a reliable number of groups or classes. Also, a canonical analysis (i.e. a multiple group discriminant analysis) was carried out in order to estimate some optimal combination of variables. Computationally, we performed a canonical correlation analysis to determine the successive functions and canonical roots (the eigenvalues).

The maximum number of discriminant canonical functions was two (three, the number of estimated groups, minus one). So that the first canonical function provided the most overall discrimination between groups, and the second provided the remnant (theoretically, these functions were independent or orthogonal, that is, their contributions to the discrimination between groups did not overlap). Later, for each case we computed the Mahalanobis distance from each of the group centroids (Johnson, 1998). Again, we classified the case as belonged to the group to which it was closest, that is, where the Mahalanobis distance was smallest.

Results

Cluster analysis

The dendrogram allowed us to identify three groups (Figure 1) and this was confirmed by the cubic clustering criterion (Figure 2). Groups 1 and 3 included varieties with the largest fruits, the highest density of areoles and larger receptacle diameters. Group 1 included 16 varieties with large fruits; they had higher contents of total soluble solids than varieties of the Group 3. Group 1 varieties had longer and thinner cladodes (41.06 and 2.52 cm, respectively) than those of the varieties of Group 3 (38.86 and 2.73 cm), and even those of Group 2 (31.45 and 2.62 cm).

Group 2 included four varieties of xoconostle, which possess fruits of a smaller size with thick peel and less total soluble solids. Main morphologic characteristics that separated the xoconostle's group from the other two groups were the absence of pulp and the presence of an edible thick pericarp.

Discriminant canonical analysis

Two estimated canonical functions explained all the variability; the first accounted for 88.16% of the total variance and the second one accounted for the remaining 11.84% (Table 3).

Intercorrelations between each variable and each of the eigenvector or discriminant canonical function were obtained with the main objective of identifying the discriminatory variables (Table 4). Their structure coefficients are marked in bold along the structure of each canonical function. In the first canonical function the most discriminatory variables were: peel thickness, pulp weight, ratio peel/weight, fruit weight, maximum fruit diameter, total soluble solids, fruit length, density of areolas in the fruit and number of flowers per cladode. Other important discriminant variables were identified by taking into account structure of the second canonical function 2; they were receptacle diameter, peel weight, and length/diameter ratio of fruit; thus, clearly these structure functions were clearly dominated by fruit variables. Taking into account that as larger the coefficient, the greater is the contribution of the respective variable to the discrimination between groups, these findings indicate that most of the discriminant attributes to differentiate *Opuntia* spp. groups are fruit measurements.

We were able to identify the nature of the discrimination for each discriminant canonical function by looking at the means for the functions across groups. We visualized how the two functions discriminate between groups by plotting the variety scores for the two discriminant functions (Figure 3). This plot confirmed that the cluster analysis had achieved reliable results.

Root 1 (canonical function 1) seems to discrimate mostly between Group 2, and Groups 1 and 3 combined. In the vertical direction (root 2 or canonical function 2), varieties of Group 1 and varieties of Group 3 fall below and over the center line (0), respectively, is apparent. It is explained because varieties included in Group 2 (Xonocostle) posses more flowers per cladode, larger peel thickness; shorter fruit length and diameter, higher density of areolas on the fruit, pulp weight, peel weight/ fruit weight ratio and total soluble solids. Varieties of Group 1 have lower peel weight, smaller receptacle diameter and a greater length/diameter ratio of its fruit in contrast to varieties of Group 3 like 'Cristalina' and 'Burrona'.

Estimated Mahalanobis distances for group centroids and its probabilities (Table 5) corroborate that there are indeed three different groups. Although Groups 1 and 3 have certain similarities, they are not enough to be included in the same group.

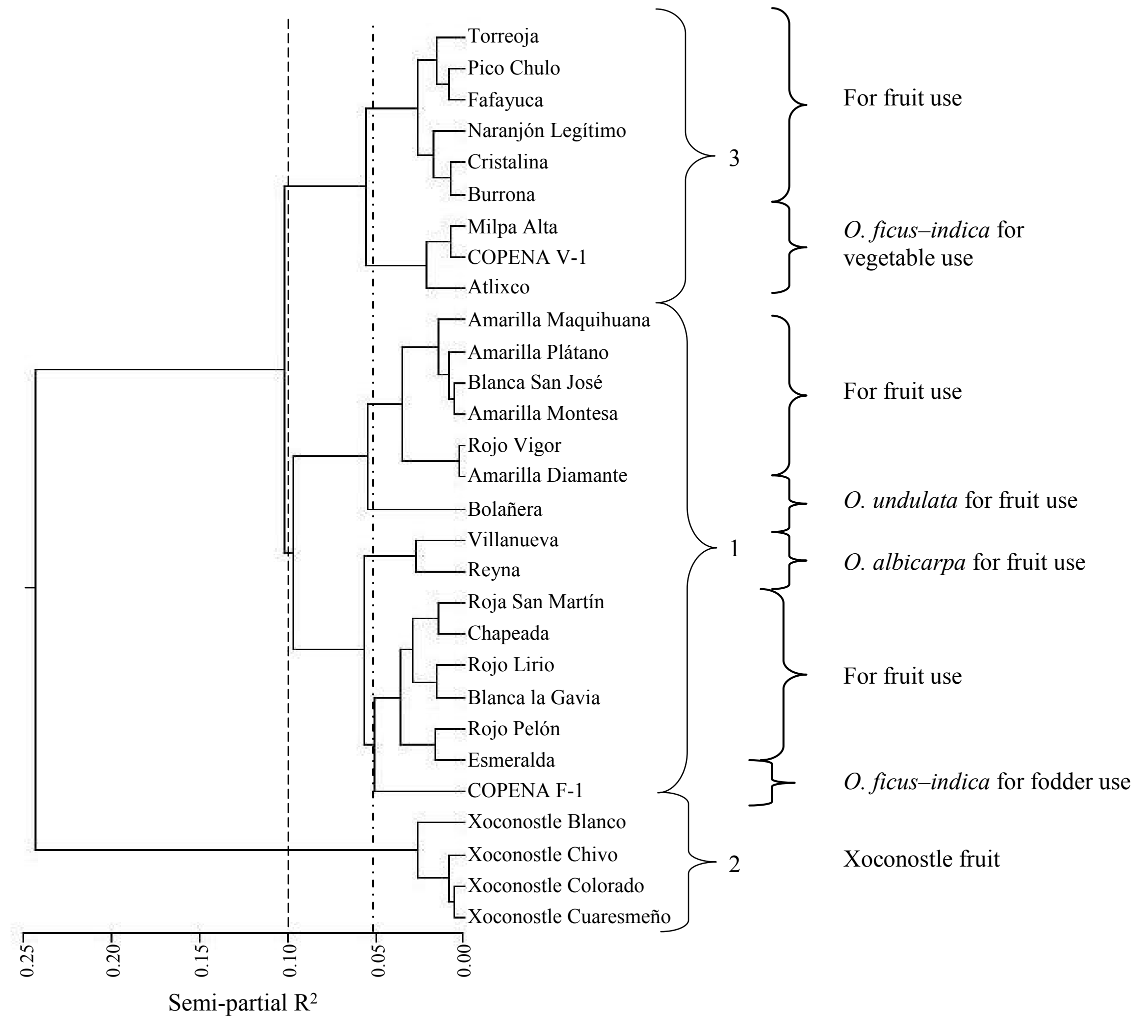

Figure 1. Dendogram of 25 varieties of cactus pear and four of xoconostle (*Opuntia* spp.) using 24 morphological characteristics, the Euclidean distance and the Ward's method.

Table 3. Eigen values of the discriminant canonical analysis of the three groups identified by cluster analysis of 29 varieties of *Opuntia* spp. using 24 morphological characteristics.

CF	Eigen value	Explained variance	Accumulated variance	Ratio of probability	Calculated *F*	*P*
1	188.78	0.88	0.88 (88.16%)	0.0002	11.62	0.0005
2	25.34	0.11	1.00 (100.00%)	0.0379	5.51	0.0332

CF, canonical function; *P*, probability.

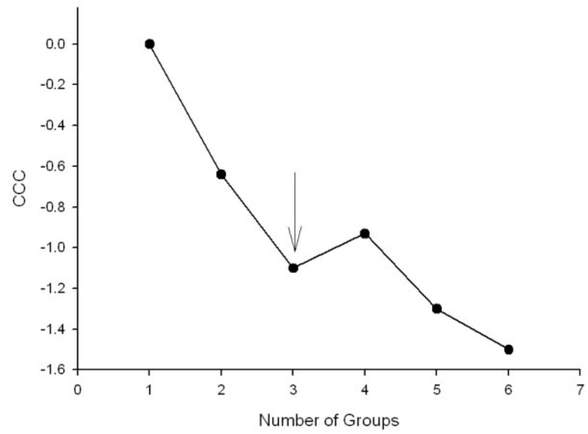

Figure 2. Cubic clustering criterion (CCC) as used for define number of groups in the dendrogram of 25 varieties of cactus pear and four of xoconostle (*Opuntia* spp.) computed using 24 morphological characteristics.

Table 4. Structure and eigen vectors from the discriminant canonical analysis of the three groups identified by cluster analysis of 29 varieties of *Opuntia* spp., using 24 morphological characteristics.

		CF1		CF2	
Plant part	Characteristic	Structure Coefficient	Eigenvalue	Structure Coefficient	Eigenvalue
Cladode	Length	**0.5081**	15.0294	–0.2938	–10.8511
	Width	0.2576	–7.7442	0.2595	9.0137
	Thickness	0.2688	–15.5268	–0.4321	11.1386
	Length/width ratio	0.3347	1.3419	0.1936	0.4329
	Number of areoles in the central row	–0.4234	–1.8756	–0.1701	–0.5049
	Number of spines per areola	–0.1472	–2.1948	–0.0489	–1.1504
	Length of the longest spine	0.1023	2.3232	–0.1727	1.8235
Flower	Number of flowers per cladode	**–0.6102**	–2.3218	–0.1552	–1.2216
	Length of flower	**0.5345**	–2.0870	–0.2937	–3.0973
	Number of lobes of the stigma	0.3709	–1.5287	–0.4927	–0.3297
Fruit	Length	**0.6610**	–26.2137	–0.0280	–14.0356
	Maximum diameter	**0.6726**	31.0975	0.4215	20.2704
	Length/width ratio	0.2312	18.4647	**–0.5702**	9.9397
	Density of areolas	**0.6126**	2.4307	–0.0026	–1.4480
	Length of peduncle	0.3578	–1.3192	–0.3648	0.1826
	Depression of the flower scar	0.1226	–1.5580	–0.0873	–4.3493
	Diameter of receptacle	0.0393	–1.8957	**0.6244**	–3.9407
	Thickness of peel	**–0.9255**	–3.9827	0.2719	1.5468
	Weight of peel	0.4020	–2.7311	**0.6233**	3.8406
	Weight of pulp	**0.7556**	–5.1282	0.1581	–8.0697
	Weight of peel/Weight of pulp ratio	**0.6738**	1.0990	–0.2693	1.0916
	Number of normal seeds	0.4736	1.2581	0.2595	1.3697
	Number of abortive seeds	0.3331	–2.1273	0.2958	0.7983
	Total soluble solids	**0.6643**	3.5147	–0.2384	–0.4412

¶Significant coefficients are in bold

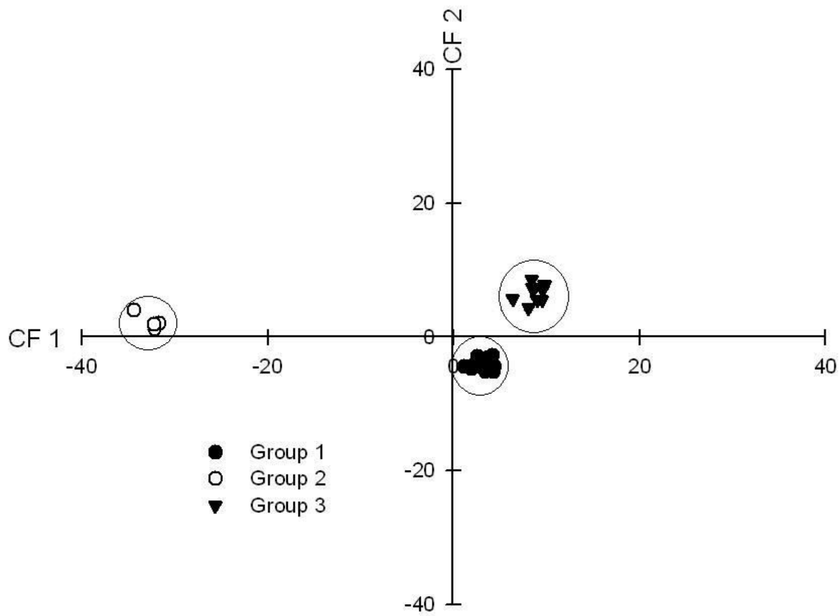

Figure 3. Position of three *Opuntia* spp. groups on the plane defined by two canonical functions (CF).

Table 5. Mahalanobis distances and their probabilities (P) of the groups identified by cluster analysis of 29 *Opuntia* spp. varieties, using 24 morphological characteristics.

Group	1	2	3
1		1318	143
2	P = 0.0029		1722
3	P = 0.0602	P = 0.0024	

Discussion

Clearly, our results suggest Group 2 is different of both Groups 1 and 3. Group 2 included *O. durangensis* and *O. joconostle* which are known as "xoconostles". They have a thick edible pericarp and acid fruits, with a pH from 1.5 to 3.1 (García–Pedraza *et al*., 2005).

The closest varieties were 'Rojo Vigor' (red fruit) and 'Amarilla Diamante' (yellow fruit) 8Group 1), both classified as *O. ficus–indica*; they are candidates for molecular studies aimed to discover markers of single–gene traits. Also, in the same Group 1, 'Villanueva' and 'Reyna' joined at 0.25 of semi-partial R^2; both are spiny, posses medium size cladodes, and their fruits are lime green; then we suppose only DNA fingerprinting could help to explain their morphological similarities.

There were no general clustering botanical patterns revealed in Groups 1 and 3. As appreciated in Figure 1, both groups included varieties of *O. megacantha*, *O. albicarpa* (*O. amyclaea*) and *O. ficus–indica*. These species belong to the series Streptacanthae and Ficus–indicae (Britton and Rose, 1919). Group 1 also included *O. undulata* (series Streptacanthae).

In general, the cluster analysis carried out with morphological characteristics formed groups according to the degree to which the commercial importance of varieties. Group 3 included more varieties with very high and high commercial importance, while Group 1 included varieties with medium and low commercial importance, with the exception of 'Reyna' which is widely cultivated in México over an area that exceeds 20,000 ha (Gallegos *et al*., 2004) concentrated in one specific region. In the case of Group 2, only very low–spread varieties are included. Groups according to the spread of the varieties as a crop could be related to the level of domestication of the *Opuntia* as found in other studies (Colunga *et al*., 1986; Reyes–Agüero *et al*., 2005b). Thus, the spread of the *Opuntia* varieties could be related to desirable attributes of fruits, young cladodes used as vegetable, and number of spines in the plant, that is, to desirable characteristics during the domestication process (Griffith, 2004). There is known *Opuntia ficus–indica* is one of the most domesticated species (Reyes–Agüero *et al*., 2005a) as well as the varieties used for fruit production clustered in Group 3.

Two estimated canonical functions explained all the variability; the first accounted for 88.16% of the total variance and the second one accounted for the remaining 11.84%. Aditionally, most of the discriminant attributes to differentiate *Opuntia* spp. groups are fruit measurements. Then, our results agree with those pointed out by Colunga *et al*. (1986) and Valdez–Cepeda *at al*. (2003) who reported that fruit size was found to be important for ordination and numerical classification of cactus pear varieties. These findings explain human tendency to select plants with bigger fruits and higher pulp/peel ratio, fewer areoles and sweeter pulp are typical in the process of domestication of *Opuntia* (Colunga *et al*., 1986; Reyes–Agüero *et al*., 2005b). A similar preference has been reported for the edible cacti "pitaya" (*Stenocereus griseus*) (Luna–Morales, 2004).

The earlier evidence of human consumption and domestication of cactus pear and xoconoxtle dates back to at least 9,000 years (Heiser, 1981). According to Reyes–Agüero *et al*. (2005a) *O. ficus–indica* is the most domesticated as no wild plants of this species have been found (Reyes–Agüero *et al*., 2005b) and, as a consequence, it has been proposed that is derived from *O. amyclaea* (sin. *Opuntia albicarpa*) (Britton and Rose, 1919) or from *O. megacantha* (Benson and Walkington, 1965).

Evidence for sub–clustering was found within each of the main clusters at a low level (0.05 value of semi–partial R^2). In Group 3, a sub–cluster was found containing six of the main varieties for fruit purposes and another sub–cluster that included 'Milpa Alta', 'COPENA V–1' and 'Atlixco', which are cultivated for vegetable production (Saénz–Hernández *et al*., 2002), belongs to *O. ficus–indica*. Within Group 1, five sub–clusters were detected. Two sub–clusters were 'Bolañera' (*O. undulata*) and 'COPENA F–1' (*O. ficus–indica*), this last used for fodder. The other three sub–clusters contained varieties for fruit production. No sub–clustering was found in Group 2.

Attributes chosen here fulfill the recommendations of González–Andrés (2001), as they are derived from several different organs of the plant: cladode, fruit and flower. It was an objective assessment since all the characteristics and ratios between fruit characteristics were quantitative and determined by physical measurement. The present study demonstrated, with this collection of *Opuntia* spp.; that peel thickness and pulp weight and to a lesser extent the diameter of the receptacle were the most discriminating of the UPOV guidelines traits.

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References

Aguilar–Estrada, A., J.A Reyes–Agüero, and J.R. Aguirre–Rivera. 2003. Caracterización de la semilla de 403 variantes de nopal (*Opuntia* spp.). *In*: *Memoria IX Congreso Nacional y VII Congreso Internacional Sobre Conocimiento y Aprovechamiento del Nopal*. Zacatecas, México: Universidad Autónoma de Zacatecas. pp. 117–120.

Anderson, E.F. 2001. The Cactus Family. Timber Press. Portland, USA.

Benson, L. and D. Walkington. 1965. The Southern California prickly pear invasion, adulteration and trial–fire. Annals of the Missouri Botanical Garden 52: 262–273.

Britton, N. and J. Rose. 1919. The Cactaceae. Vol I. Carnagie Institution of Washington. Washington, USA.

Chessa, I., G. Nieddu, P. Serra, P. Inglese, and T. La Mantia. 1997. Isozyme characterization of *Opuntia* species and varieties from Italian germplasm. Acta Horticulturae 438: 45–52.

Chessa, I., G. Nieddu, M. Nieddu, P. Erre, and G.F. Cocco. 2004. Genetic diversity of *Opuntia* spp. growing in the Mediterranean area as described by molecular markers. In: *Memorias del X Congreso Nacional sobre el Conocimiento y Aprovechamiento del Nopal y 5º. Internacional Congreso on Cactus Pear and Cochineal. Chapingo*, Mexico: Universidad Autónoma Chapingo.

Colunga P., E. Hernández–Xolocotzi y A. Castillo–Morales. 1986. Variación morfológica, manejo agrícola y grados de domesticación de *Opuntia* spp. en el Bajío guanajuatense. Agrociencia 65: 7–49.

Fernández, M. R., C. Mondragón, J. Luna, L.A. Sáenz, J.A. Zegbe, S.J. Méndez y J.C. Martínez. 2000. Principales Cultivares Mexicanos de Nopal Tunero. Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Centro de Investigación Regional del Centro, Campo Experimental Norte de Guanajuato. San Luis de la Paz, Gto., México. 34 p.

Flores–Valdés, C.A. and C. Gallegos–Vázquez. 1994. The production of prickly–pear in the north–central region of Mexico. In: *Proceedings 5th Annual Texas Prickly Pear Council*. Texas Prickly Pear Council. Kingsville, TX, USA. pp. 13–30.

Flores–Valdés, C.A. 2002. El nopal y la lucha contra la desertificación. Reporte de Investigación 59. Universidad Autónoma Chapingo, Centro de Investigaciones Económicas, Sociales y Tecnológicas de la Agroindustria y de la Agricultura Mundial. Chapingo, México. 39 p.

Gallegos–Vázquez, C., J. Cervantes–Herrera and S.J. Méndez–Gallegos. 2004. Producción de tuna en el Centro Norte de México. Revista de Geografía Agrícola 33: 143–158.

Gallegos–Vázquez, C., J. Cervantes–Herrera y A.F. Barrientos–Priego. 2005. Manual Gráfico para la Descripción Varietal del Nopal Tunero y Xoconostle (*Opuntia* spp.). Servicio Nacional de Inspección y Certificación de Semillas – Secretaría de Agricultura, Ganadería, Desarrollo Rural y Pesca (SNICS–SAGARPA) y Universidad Autónoma Chapingo (UACh). Tlalnepantla, México.

Gallegos–Vázquez, C., C. Mondragón–Jacobo, and J. A. Reyes–Agüero. 2009. An update on the evolution of the cactus pear industry in Mexico. Acta Horticulturae 811: 69–76.

García–Pedraza, L.G., J.**A.** Reyes–Agüero, J.R. Aguirre–Rivera, and J.M. Pinos–Rodríguez. 2005. Preliminary nutritional and organoleptic assessment of the xoconostle fruit (*Opuntia* spp.) as a condiment or appetizer. Italian Journal of Food Science 17: 333–340.

González–Andrés, F. 2001. La Caracterización Morfológica. *In*: González–Andrés, F. and M.J. Pitalúa–Villamil. (Eds.). *Conservación y Caracterización de Recursos Filogenéticos*. INEA. Valladolid, España. pp. 199–217.

Griffith, P.M. 2004. The origins of an important cactus crop, *Opuntia ficus–indica* (*Cactaceae*): new molecular evidence. American Journal of Botany 91: 1911–1921.

Gutiérrez–Acosta, F., R.D. Valdez–Cepeda, F. Blanco–Macías, J.L. García–Hernández and J.D. López–Martínez. 2003. Clases de accesiones de nopal de tuna blanca considerando atributos de fruto. *In*: *Memoria IX Congreso Nacional y VII Congreso Internacional Sobre Conocimiento y Aprovechamiento del Nopal*. Universidad Autónoma de Zacatecas. Zacatecas, Zac. México. pp. 101–110.

Guzmán, U., S. Arias y P. Dávila. 2003. Catálogo de Cactáceas Mexicanas. Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México, D.F., México. 315 p.

Heiser, Ch.B. 1981. Seed to Civilization: The History of Food. W.H. Freeman and Company. Second edition. San Francisco, USA.

Hunt, D. 2002. Alphabetical List of Currently Accepted Species. *In*: Hunt, D. and N. Taylor (Eds.). *Studies in the Opuntioideae*. The Manse and Chapel Lave. Sherborne, UK. pp. 250–255.

Johnson, D.E. 1998. Métodos Multivariados Aplicados al Análisis de Datos. International Thompson Editores. México, D.F., México.

Luna–Morales, C. del C. 2004. Recolección, cultivo y domesticación de cactáceas columnares en la Mixteca Baja, México. Revista Chapingo, Serie Horticultura 10(2): 195–102.

McNeish, R.S. 1972. The Prehistory of the Tehuacan Valley: Chronology and Irrigation. University of Texas Press. Austin, TX, USA. 290 p.

Molina–Velásquez, M., R.D. Valdez–Cepeda, R.E. Vázquez–Alvarado, G. Salinas–García, R. González–González, F. Blanco–Macías, J.L. García–Hernández and F. Gutiérrez–Acosta. 2003. Agrupamiento de 51 accesiones de nopal con base en atributos físicos y bromatológicos. *In*: *Memoria IX Congreso Nacional y VII Congreso Internacional Sobre Conocimiento y*

Aprovechamiento del Nopal. Universidad Autónoma de Zacatecas. Zacatecas, Zac., México. pp. 107–110.

Mondragón–Jacobo, C. and J. Pérez–Gónzalez. 2002. Genetic resources and breeding cactus pear (*Opuntia* spp.) for fodder production. Acta Horticulturae 581: 87–93.

Mondragón–Jacobo, C. 2002. Caracterización genética de una colección de nopal (*Opuntia* spp.) de la región Centro de México. Agricultura Técnica en México 28: 3–14.

Mondragón–Jacobo, C., and B.B. Bordelon. 2003. Presencia de apomixis en cruzas de nopales mexicanos y su identificación molecular preliminar. Revista Fitotecnia Mexicana 25(3): 247–252.

Mizrahi, Y., A. Nerd, and P.S. Nobel. 1996. Cacti as crops. Horticultural Reviews 18: 291–320.

Luna–Páez, A., E. Valadez–Moctezuma, A.F. Barrientos–Priego and C. Gallegos–Vázquez. 2007. Caracterización de *Opuntia* spp. mediante semilla con marcadores moleculares RAPD e ISSR y su posible uso para diferenciación. Journal of the Professional Association for Cactus Development 9: 43–59.

Parish, J. and P. Felker. 1998. Fruit quality and production of cactus pear (*Opuntia* spp.) fruit clones selected for increased frost hardiness. Journal of Arid Environments 37: 123–143.

Rzedowski J. 1978. La Vegetación de México. Edit. Limusa. México, D.F., Mexico.

Reyes–Agüero, J.A., J.R. Aguirre–Rivera and H.M. Hernández. 2005a. Systematic notes and detailed description of *Opuntia ficus–indica* (L.) Mill. (*Cactaceae*). Agrociencia 39: 395–408.

Reyes–Agüero, J.A., J.R. Aguirre J.L. y Flores. 2005b. Variación morfológica de *Opuntia* (*Cactaceae*) en relación con su domesticación en la Altiplanicie Meridional de México. Interciencia 30: 476–484.

Sáez–Hernández, C., J. Corrales–García and G. Aquino–Pérez. 2002. Nopalitos, Mucilage, Fiber and Cochineal. *In*: Nobel, P.S. (Editor). *Cacti: Biology and Uses*. University of California. Berkeley, CA, USA. pp. 211–234.

Scheinvar, L., K. Filardo, L. Segura, G. Olalde–P., B. Mendoza, P. Ramírez, A. Chimal y J. Olivares. 2003. Importancia de las microestructuras y estudios bromatológicos como apoyo a la taxonomía del género *Opuntia* Mill. (*Cactaceae*). *In*: *Memoria IX Congreso Nacional y VII Congreso Internacional Sobre Conocimiento y Aprovechamiento del Nopal*. Universidad Autónoma de Zacatecas. Zacatecas, Zac., México. pp. 111–116.

Sokal, R.R. and P.H.A. Sneath. 1963. Principles of Numerical Taxonomy. H. Freeman & Co. San Francisco, USA.

Stuppy, W. 2002. Seed characters and the generic classification on the *Opuntioideae* (*Cactaceae*). *In*: Hunt, D. and N. Taylor (Eds.). *Studies in the Opuntioideae*. The Manse and Chapel Lave. Sherborne, UK. pp. 25–58.

UPOV. 2004. Cactus Pear and Xoconostles (*Opuntia*, Groups 1 & 2), Guidelines for the Conduct of Tests for Distinctness, Uniformity and Stability. *TG/217/1.* International Union for the Protection of New Varieties of Plants. Geneve.

Uzun, I. 1997. Fruit and cladode isozymes in cactus pear. Acta Horticulturae 438: 45–53.

Valdez–Cepeda, R.D., C. Gallegos–Vázquez y F. Blanco–Macías. 1997. Análisis multivariado en once variedades de nopal tunero: atributos de fruto. *In*: *Memorias del VII Congreso Nacional y V Internacional sobre Conocimiento y Aprovechamiento del Nopal.* FAO–Universidad Autónoma de Nuevo León, Facultad de Agronomía. Monterrey, N.L., México. pp. 118–119.

Valdez–Cepeda, R.D., C. Gallegos–Vázquez y F. Blanco–Macías. 1996. Clasificación numérica de *Opuntia* spp. mediante características de su fruto (tuna). Revista de Geografía Agrícola 22/23: 287–293.

Valdez–Cepeda, R.D., F. Blanco–Macías, and C. Gallegos–Vázquez. 2003. Ordering and numerical classification in prickly pear cactus using fruit attributes. Revista Chapingo Serie Horticultura 9(1): 81–95.

Wallace, R.S. and S.L. Dickie. 2002. Systematic Implications of Chloroplast DNA Sequence Variation in Subfam. *Opuntiodeae* (*Cactaceae*). *In*: Hunt, D. and N. Taylor (Eds.). *Studies in the Opuntioideae*. The Manse and Chapel Lave. Sherborne, UK. pp. 9–24.