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Sensory attributes, physicochemical and antioxidant characteristics, and protein profile of wild prickly pear fruits (*O. macrocentra* Engelm., *O. phaeacantha* Engelm., and *O. engelmannii* Salm-Dyck ex Engelmann.) and commercial prickly pear fruits (*O. ficus-indica* (L.) Mill.)

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ABSTRACT

Mexico presents the highest richness of *Opuntia* Mill. species. These species are an important economic factor for the country, and source of nutrients, bioactive compounds, pigments, and nutraceuticals which can be of interest for the food and pharmaceutical industry. However, there are some wild *Opuntia* species in the Chihuahua desert, that have not been analyzed to establish their properties and potential use. The aim of study was to evaluate the sensory, physicochemical and protein profile in wild prickly pear fruits (*O. macrocentra* Engelm. (OM), *O. phaeacantha* Engelm. (OP), and *O. engelmannii* Salm-Dyck ex Engelmann. (OE)) from Samalayuca, Chihuahua and compare them with two commercial prickly pear fruits (*O. ficus-indica* (L.) Mill. (green-OFG, red-OFR). The sensory profile of wild species was characterized by highest color, odor, and sour taste compared to the commercial fruits. Pulp, peel, and seeds from wild prickly pear fruits showed lower pH, and higher titratable total acidity, total phenolic compounds, total flavonoids, antioxidant capacity, protein, lipids, ash, carbohydrates (only peel), and crude fiber content than commercial *Opuntia* species. Furthermore, *O. engelmannii* showed a tendency to present the highest betacyanins, betaxanthins, and betalains contents. A total of 181, 122, 113, 183 and 140 different proteins were identified in OM, OP, OE, OFG, OFR species, respectively. All species showed the highest enrichment in three main pathways such as amino acids biosynthesis, glycolysis (dark)/gluconeogenesis (light), and the citric acid cycle. The wild prickly pear fruits of this study showed important nutritional, protein, and antioxidant properties with biological interest, and can be a potential source of functional ingredients and nutraceuticals.

1. Introduction

Opuntia Mill. (1754) is one of the most diverse and widely distributed genus in America, but the highest richness of wild species are found in Mexico, with at least 126 species reported with different degrees of domestication (Santos, Barba, Héliès-Toussaint, Guéraud, & Nègre-Salvayre, 2017). This genus is a dominant component of vegetation of the Mexican area of Chihuahua Desert, but little is known about wild species despite their economic, cultural, and environmental value. Lately, there is a special interest to evaluate the use of underutilized and/or neglected

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species due to different reasons. One of them is to use available and underutilized resources in specific regions (Joshi, Singh, Laobangdisa, & Kulkarni, 2020; Kunyanga, Vellingiri, & Imungi, 2014) that can impact human nutrition and diet (Hunter et al., 2019). Another reason is to improve sustainable development, eradicate hunger and to enhance rural development maintain natural resources and safeguard biodiversity (FAO, 2018). The opuntias vegetation communities represent an essential role in modulating local microclimates, maintaining the hydrological regime of the basins, and providing edibles cladodes and fruits, both used as food for associated wildlife and domestic livestock communities (Illoldi-Rangel et al., 2012). Traditionally the *Opuntia* fruit is consumed in the local market and exported to the U.S., Canada, Japan, and some European countries. Fruits and cladodes are used as ingredients in traditional Mexican cuisine, and in the production of foods such as juices, jams, nectars, and fructose. Also, different parts of *Opuntia* are used in traditional folk medicine (Vigueras & Portillo, 2001).

Wild and domesticated *Opuntia* species represent a great interest and possible uses due to their high nutritional value (e.g. minerals, lipids, protein, and dietary fiber content) and the potential effects on health, mainly related to the high content of antioxidant compounds, pigments, phenolic acids, biopeptides, and soluble fibers from these plants (Santos et al., 2017). *Opuntia ficus-indica* (L.) Mill. (1768) is the most domesticated and cultivated species, its chemical composition and nutritional value have been well established (Aragona, Lauriano, Pergolizzi, & Faggio, 2018). The domestication process has improved the flavor, size, shape, and pulp texture of the fruit, in addition to reducing seed hardness and quantity (Reyes-Agüero & Rivera, 2005), but other changes in the chemical composition of the plant have been observed. Different studies have reported that lipids, fiber, total sugars, and phenolic content were highest in the wild *Opuntia* species compared with the domesticated species (Astello-García et al., 2015; Guevara-Figueroa et al., 2010; Pichereaux et al., 2016). Many factors such as maturity stage, fruit harvest time, environmental conditions, pre- and post-harvest treatment, and the species are important in the modulation of the chemical composition of *Opuntia* fruit (Guevara-Figueroa et al., 2010; Hernández-Urbiola, Pérez-Torrero, & Rodríguez-García, 2011), and additional studies of wild and domesticated species are necessary considering that the vegetative parts exhibit variations in the chemical composition and properties (Santos et al., 2017).

Currently, *Opuntia* fruit, whole or its parts (peel, seed and pulp) is an important resource as ingredient to enrich foods (Oniszczuk et al., 2020), in pigments (betanin) and pectin production (Ciriminna et al., 2019), and due to its biological activity such as antimicrobial, anti-inflammatory, antioxidant, antidiabetic, anticancer, neuroprotective (Tilahun & Welegerima, 2018) or hepatoprotective effects (González-Ponce et al., 2016; Kang et al., 2016). Furthermore, several nutraceuticals benefits of the fruit have been related to its polyphenolic compounds, such as phenolic acids, flavonoids, ascorbic acid or its pigments such as betaxanthin and red betacyanin (Albano et al., 2015; Guevara-Figueroa et al., 2010; Khatabi, Hanine, Elothmani, & Hasib, 2016; Mena et al., 2018). However, many of these properties have been studied in *Opuntia ficus-indica* (L.) Mill fruits and studies in other underutilized wild species are necessary to establish their importance and potential uses.

O. engelmannii Salm-Dyck ex Engelmann. (1850), *O. macrocentra* Engelm. (1856), and *O. phaeacantha* Engelm. (1849) are the three largest wild *Opuntias* species found growing in the Chihuahua Desert. Although the fruits from these species are collected and consumed by local people, their sensory attributes, physicochemical properties, phytochemical content, and antioxidant capacity are little known. A previous study in our working group indicated that seeds of *O. phaeacantha* showed to be a good source of health-promoting polyunsaturated fatty acid, and its use in arid and semi-arid regions should be encouraged (Núñez-Gastélum et al., 2018). In this sense, the characterization of the edible (pulp) and inedible (peel and seed) tissues from these wild fruits is an important topic to study and define those properties of great interest. Therefore, whole fruits or the individual tissues from these wild species could be a new source of functional ingredients or bioactive compounds. In this study, physicochemical, sensory, antioxidant, and protein profiles of three wild prickly pear fruits (*O. macrocentra* Engelm. (OM), *O. phaeacantha* Engelm. (OP), and *O. engelmannii* Salm-Dyck ex Engelmann. (OE)) from Samalayuca, Chihuahua, Mexico were determined and compared with two commercial prickly pear fruits (*O. ficus-indica* (L.) (green-OFG and red- OFR).

2. Materials and methods

2.1. Biological material collection

The two commercial prickly pear fruits (OFG and OFR) were obtained from a local market in Ciudad Juárez, Chihuahua, Mexico. Wild prickly pear fruits (OM, OP, and OE) used in this study were sampled in Samalayuca Médanos area situated at 50 km south of Ciudad Juárez, Chihuahua State, Mexico at latitude 31°39′36″-29°25′12″N and a longitude 109°02′24″-107°14′24″. In this area, 60 plants of each wild species were randomly collected. The selection of plants consisted of detecting healthy and vigorous plants. For each plant, ten fruits distributed throughout the cladodes were collected. A total of 300 undamaged and homogeneous fruits were collected per specie, based on their presentation of maximum fruit maturation color. The same criteria such as undamaged, homogeneity and maximum maturation color were applied when the commercial fruits were purchased. All fruits were stored in an airtight polyethylene bag and immediately transported to the laboratory and they were stored at 4 °C. After wild and commercial prickly pear fruits were cleaned and the prickles and glochids located on the peel surface of fruits, they were removed by rubbing. In this condition, 50 fruits for each specie were randomly selected and were weighed (Supplementary Fig. S1). Furthermore, prickly pear fruits were cut longitudinally, and peel, pulp, and seeds were separated, and the weights of these fractions were recorded. Peel and seed were separately homogenized using a commercial homogenizer at normal speed for 2 min and samples, including peel, and seed were stored at −20 °C. Likewise, samples of the peel, pulp, and seeds were lyophilized (Labconco freeze dry/shell freeze system, Labconco Corp., Kansas City, MO), milled in a Nutribullet® household mixer (Nutribullet®, LLC, USA), and stored at −80 °C.

2.2. Sensory characterization

Commercial and wild *Opuntia* fruits were characterized by a descriptive analysis with a trained panel of 10 judges. The attributes in the olfactory phase were first impression, odor intensity and descriptors determined by focus group technique. In the oral phase, mouth characteristics were evaluated in the edible part of fruit such as hardness, moistness, and astringency; taste: such as sweet, sour, and bitter. Color, brightness, and texture attributes such as firmness, roughness and surface moisture were also evaluated. All tests were conducted in individual booths and the judges used a 150 mm linear scale, labeled at the end as “Not all…” and “Extremely…” for each attribute or descriptor. Each judge was provided with a fruit or 1 g of the edible portion (according to the test), and they were placed in 2 oz plastic cups, at room temperature and identified with three-digit random numbers. The samples were served to the judges in a balanced and randomized form, together with evaluation sheets. Judges rinsed their mouths with purified water (Alaska®, Chihuahua, Mexico) at the beginning and between samples for the oral phase and they used eye covers in all tests, except in the visual phase. Also, Pantone® scale was used in a color test. Two attributes or descriptors were evaluated per session of 60 min, standards for each attribute or descriptor were used at the beginning of the test and each test was performed by duplicate (Lawless & Heymann, 2010; Meilgaard, Civille, & Carr, 1999).

2.3. Physicochemical analyses

Pulp, peel, and seeds were analyzed in triplicate according to standard methods outline by AOAC (2000) methods: moisture was determined in an oven (VWR®, Model 1324, Irving, TX, USA) at 105 °C for 5 h; ash was determined in a muffle furnace (Felisa®, Model FE-340, Jalisco, Mexico) at 550 °C for 5 h; crude protein by Kjeldahl method (Labconco®, Model RapidStill II, Kansas City, MO, USA); fat by Soxhlet method (Soxtec™, Model 2043, Foss™, Hilleroed, Denmark); total carbohydrates by difference method; crude fiber by gravimetric method; water activity in AQUA LAB® (Model Serie 3, Meter Food, Washington, D.C., USA) equipment; pH and titratable acidity by potentiometric method (Accumet®, Model AB15 Plus, Westford, MA, USA). The titratable acidity results were reported as the percentage of citric acid.

The color of peel and pulp was evaluated by colorimetric equipment (Konica Minolta®, model CR-400, NJ, USA). Briefly, 10 g of sample was placed in a small petri dish for further analysis by the instrument, which was based on the CIELAB color system. This system determines the Cartesian coordinate defined by three colorimetric coordinated "L*", "a*," and "b*" of samples. L*, a*, and b* data were used to determine the color index (ΔE) and color tolerance (CMC) using the equations proposed by Mokrzycki and Tatol (2011).

2.4. Phytochemicals and antioxidant capacity

Ascorbic acid (AA) content of peel, pulp, and seeds was determined by triplicate, according to the methodology reported by Moreno-Escamilla et al. (2017). Briefly, 0.2 g of lyophilized samples were weighed into a test tube Falcon® and 5 mL of 5% metaphosphoric acid (Merck®, Toluca, Estado de México, Mexico) was added, stirred and sonicated (Branson®, Model 5800 Fisher Scientific, West Palm Beach, FL, USA) for 20 min in the dark. Afterward, the extract was centrifuged (Eppendorf®, Model 5810 R, Alto da lapa, Sâo Paulo, Brazil) at 3500 rpm for 10 min at room temperature, and the supernatant was collected into a new test tube. For AA quantification, 300 μL of the standard extract was taken into a test tube and 200 μL of 6.65% (w/v) trichloroacetic acid (Merck®, Toluca, Estado de México, Mexico) and 75 μL of DNPH (2,4-dinitrophenylhydrazine) reagent (Merck®, Toluca, Estado de México, Mexico) was added. Then, the mixture was incubated at 37 °C for 3 h. Afterward, 0.5 mL of 65% (v/v) H_2SO_4 (JT Baker®, West Palm Beach, Fisher Scientific, FL, USA) was added. Absorbance was measured at 520 nm in the UV–Vis microplate reader (BioRad®, Model xMark, Ciudad de México, Mexico), using AA as a standard. Results were expressed as mg AA by 1 g of sample (fresh weight, FW).

To determine betacyanins, betaxanthins, and betalains contents, 0.10 g of lyophilized samples (peel or pulp) were weighed into a test tube and 10 mL of 80% (v/v) methanol (JT Baker®, Fisher Scientific, West Palm Beach, FL, USA) was added. The samples were acidified with 0.5% (v/v) HCl (Merck®, Toluca, Estado de México, Mexico), stirred and sonicated for 15 min. Afterward, the extract was centrifuged at 3500 rpm for 10 min at room temperature, and the supernatant was collected into a new test tube. Finally, 300 μL were collected and placed in spectrophotometry cuvette and the absorbance was measured at 490 and 547 nm in the UV–Vis microplate reader. The concentration was determined according to the methodology proposed by Castellanos-Santiago and Yahia (2008) and were reported as milligrams per 1 g of sample (dry weight, DW).

Total phenolics (TPC), flavonoids (TF), and antioxidant capacity (AC) were determined in the peel, pulp, and seeds. Standard extracts were obtained according to the methodology described by Kähkönen et al. (1999). Briefly, for each tissue 0.25 g of lyophilized sample was weighed into a test tube and 10 mL of 80% methanolic solution (JT Baker®, Fisher Scientific, West Palm Beach, FL, USA) was added, stirred and sonicated for 30 min at 4 °C in the dark. Afterward, the extract was centrifuged (3500 rpm) for 15 min at 4 °C, and the supernatant was collected into a new test tube. Extraction was repeated and a total volume of 25 mL was finally completed. All samples were kept at −20 °C until the experimental analysis.

TPC and TF contents were determined according to the methodology reported by Georgé, Brat, Alter, and Amiot (2005). A calibration curve was performed using gallic acid as a standard for TPC and results were expressed as mg gallic acid equivalents (GAE) by 1 g of sample DW. For TF, a calibration curve was performed using catechin as a standard and results were expressed as mg catechin equivalents (CE) by 1 g of sample DW. The antioxidant capacity (AC) was determined by 2, 2-diphenyl-1-picrylhydrazyl (DPPH) radical (190 μM in methanol; Merck®, Toluca, Estado de México, Mexico), ferric reducing antioxidant power (FRAP) and 2,2-azinobis-(3-ethylbenzothiazoline-6-sulfonic acid) ($ABTS^{\bullet+}$) scavenging assays were determined using the methodology according to Moreno-Escamilla et al. (2017). All determinations were made in triplicate.

2.5. Protein extraction, gel electrophoresis, and protein identification

Proteins were extracted from 500 mg of pulp using the TCA/acetone-phenol methodology determined by Valero-Galván, Fernández, Valledor, Cerrillo, and Jorrin-Novo (2014). The final pellet was solubilized in 100 μL of a solution of 7 M urea (Jalmek Cientifica, Nuevo León, Mexico). The insoluble material was removed by centrifugation, and the protein content in the supernatant was quantified according to the Bradford method using BSA (Merck®, Toluca, Estado de México, Mexico) as standard (Ramagli & Rodriguez, 1985). Samples were stored at −80 °C until electrophoresis separation. Protein extracts (25 mg BSA equivalent) were subjected to SDS-PAGE on 13% polyacrylamide gels by using PROTEAN® II xi Cell (Bio-Rad, Hercules, USA). Gels were stained employing a Colloidal Coomassie procedure as reported in Görg, Postel, Baumer, and Weiss (1992) and protein profile was cut manually and placed in a tube of a microcentrifuge (Jalmek Cientifica, Nuevo León, Mexico) and was stored at 4 °C until protein identification (Maldonado, Echevarría-Zomeño, Jean-Baptiste, Hernández, & Jorrín-Novo, 2008).

The digestion of protein bands and MS analysis were determined as reported in Swaney, McAlister, & Coon, 2008 and Frese et al., 2011. Mass spectra were analyzed with the Proteome Discoverer 2.1 (PD, Thermo Fisher Scientific®, San Jose, CA, USA). The subsequent searches were carried out using the Mascot server (version 2.4.1, Matrix Science, Boston, MA, USA). The searches were conducted against the UniProt Viridiplantae database reviewed version. The analysis parameters comprised: full-tryptic protease specificity, two missed cleavage allowed, static modifications covered carbamidomethylation of cysteine (+57.021 Da). Furthermore, dynamic modifications included methionine oxidation (+15.995 Da) and deamidation in asparagine/glutamine (+0.984 Da). For the MS2 method, in which identification was performed at high resolution in the Orbitrap, precursor and fragment ion tolerances of ± 10 ppm and ± 0.2 Da were applied. Resulting peptide hits were filtered for a maximum of 1% FDR using the Percolator algorithm (Käll, Canterbury, Weston, Noble, & MacCoss, 2007). Protein function was analyzed using GO annotation through Metascape online tool (http://metascape.org/gp/index.html#/main/step1), and an enrichment cluster analysis was made using these settings: p-value < 0.01, minimum count of 3, enrichment factor >1.5, and FDR 5%.

2.6. Statistical analyses

The data obtained from the physicochemical and phytochemical determinations were analyzed using Levene's test and one-way ANOVA with Fisher's multiple comparisons (LSD). Furthermore, sensory profile data were analyzed using Levene's test and repeated measures analysis of variance (ANOVA) with Fisher's multiple comparisons (LSD). When the Levene's test was significant, Student's *t*-test for unequal variances was used. Also, data from phytochemicals concentration and antioxidant capacity were analyzed by Pearson's correlations. All the analyses were carried out using the statistical program XLSTAT version 2016.05

(Addinsoft®, Paris, France). The results are presented in mean values ± standard deviation (SD). The criterion for statistical significance was $p < 0.05$.

3. Results and discussion

3.1. Sensory characterization

The sensory characterization of *Opuntia* samples is shown in Table 1. For a better interpretation of the results obtained from the descriptive analysis, the linear scale (150 mm) was divided into five intensity levels: low intensity (L, 0 to 37 mm), medium low (ML, 38 a 74 mm), medium (M, 75 mm), medium–high (MH, 76 to 112 mm) and high (H, 113 to 150 mm). This analysis showed that in visual phase OM, OP, and OE species were perceived at H intensity level with more dark red color (Pantone® PMS, codes: OM 216, 221–222; OP 221,222 and OE 214–216,219,220–222), while OFR was perceived at MH intensity (Pantone® PMS, codes: 213–216, 220). OE was similar to OFR for the intensity of red color. Finally, OFG was perceived in ML intensity, with a wide range of colors from green-yellow to light green (Pantone® PMS, codes: 374–377). Furthermore, the fruits of OFR species presented a higher brightness (MH intensity) than OE and OFG species (ML intensity). In the tactile phase, wild OM (MH intensity) and OP (ML intensity) species were less firms than commercial species and OE wild fruit. The roughness of fruits from OP was the smoothest (L intensity) compared to the other wild (OM and OE) and commercial (ML intensity) species and the superficial moisture perceived by judges in the samples, both wild and commercial species were similar (ML intensity). In the olfactory phase, the wild species (OP and OE) were characterized by a higher odor (ML intensity) compared to commercial species (OFR and OFG) (L intensity). On the other hand, wild prickly pear fruits (OM and OP) were characterized by lower herbal odor than OE and commercial fruits. For taste attributes, the judges perceived greater differences among wild and commercial *Opuntia* fruits. Wild prickly pear fruits (OP, OM, OE) were characterized by lower sweetness (L and ML intensity) and higher sourness (MH and ML intensity) than OFR and OFG (L intensity). Wild OE fruit was perceived more bitter than other species, but all fruits had an L intensity. Finally, in the mouth tactile phase, wild prickly pear fruits (OM and OP) showed lower hardness than other species, and OE fruit was perceived with greater astringency among wild and commercial fruits. The sensory profile of wild and commercial prickly pear fruits is shown in Fig. 1.

Table 1
Sensory descriptive analysis from wild and commercial prickly pear fruits.

Attributes or descriptors	OM	OP	OE	OFR	OFG	*p*
Visual phase						
Red color intensity	126.7 ± 11.7^{a}	121.5 ± 10.8^{a}	114.4 ± 19.0^{ab}	99.9 ± 21.3^{b}	*	<0.01
Green color intensity	*	*	*	*	63.8 ± 20.3	
Brightness	78.2 ± 34.9^{ab}	76.5 ± 22.7^{ab}	56.1 ± 28.5^{b}	86.2 ± 17.3^{a}	61.5 ± 16.8^{b}	<0.01
Tactile phase						
Firmness	84.4 ± 23.4^{c}	69.5 ± 27.8^{c}	92.0 ± 29.1^{bc}	105.9 ± 24.1^{ab}	117.9 ± 19.8^{a}	<0.01
Roughness	71.6 ± 25.5^{a}	37.5 ± 14.9^{c}	52.7 ± 26.7^{abc}	43.8 ± 21.2^{bc}	58.0 ± 19.9^{ab}	<0.01
Superficial moisture	43.1 ± 21.5^{a}	43.2 ± 15.4^{a}	43.6 ± 17.0^{a}	44.7 ± 20.5^{a}	46.1 ± 19.8^{a}	0.91
Olfactory phase						
First impression	64.7 ± 30.1^{a}	66.4 ± 18.9^{a}	59.4 ± 23.5^{a}	70.1 ± 26.0^{a}	67.8 ± 30.1^{a}	0.75
Odor intensity	45.0 ± 16.8^{ab}	56.4 ± 24.5^{a}	50.2 ± 19.4^{a}	30.9 ± 10.0^{c}	33.3 ± 9.0^{bc}	<0.01
Fruits	52.1 ± 29.7^{a}	67.9 ± 36.3^{a}	53.7 ± 21.8^{a}	52.2 ± 26.4^{a}	46.5 ± 26.6^{a}	0.15
Sweet	60.4 ± 33.9^{a}	66.8 ± 30.7^{a}	55.3 ± 33.4^{a}	47.0 ± 26.2^{a}	47.2 ± 29.2^{a}	0.09
Fresh	53.8 ± 33.1^{a}	50.2 ± 36.0^{a}	50.8 ± 31.6^{a}	53.4 ± 30.3^{a}	70.1 ± 37.3^{a}	0.05
Herbal	39.6 ± 24.5^{b}	41.3 ± 22.9^{b}	53.4 ± 25.5^{ab}	57.0 ± 29.2^{ab}	66.9 ± 31.1^{a}	<0.01
Acid	23.6 ± 17.2^{a}	19.9 ± 10.4^{a}	29.6 ± 21.8^{a}	27.7 ± 16.7^{a}	29.6 ± 24.3^{a}	0.27
Taste						
Sweet	35.2 ± 20.6^{b}	49.7 ± 35.9^{b}	31.1 ± 12.8^{b}	76.0 ± 27.4^{a}	78.3 ± 27.4^{a}	<0.01
Sour	82.2 ± 32.2^{a}	64.4 ± 35.4^{a}	74.8 ± 24.6^{a}	21.2 ± 11.7^{b}	17.9 ± 5.9^{b}	<0.01
Bitter	24.8 ± 13.1^{ab}	24.2 ± 11.6^{ab}	28.1 ± 11.5^{a}	15.8 ± 6.3^{b}	19.3 ± 10.3^{b}	<0.01
Mouth tactile						
Hardness	14.9 ± 5.2^{b}	13.9 ± 3.7^{b}	36.6 ± 20.0^{a}	33.5 ± 10.3^{a}	49.1 ± 20.6^{a}	<0.01
Moisture release	112.7 ± 27.5^{a}	115.7 ± 24.7^{a}	104.3 ± 25.6^{a}	108.9 ± 17.6^{a}	110.5 ± 21.2^{a}	0.56
Astringency	28.0 ± 18.2^{ab}	25.1 ± 16.3^{ab}	35.3 ± 22.0^{a}	17.7 ± 9.7^{b}	18.6 ± 9.0^{b}	<0.01

O: *Opuntia*, OM: *O. macrocentra*, OP: *O. phaeacantha*, OE: *O. engelmannii*, OFR: *O. ficus-indica* (L.) "red", OFG: *O. ficus-indica* (L.) "green". Data are expressed as the mean ± SD with reference to linear scale (150 mm). Different letters indicate significant difference at $p < 0.05$.

In this study wild prickly pear fruits were characterized by intense red color (OM and OP), less firmness (OM and OP), intense odor (OP and OE) and in taste, they were less sweet and sour, and only OE was slightly more bitter and astringent compared to the commercial fruits (OFR and OFG). The sensory characteristics by descriptive analysis of *Opuntia* fruits have been poorly studied. The red color was an important attribute perceived by the judges and this characteristic has been related to high betacyanin concentration, which is the main source of natural food colorant E-162 (Castellar, Solano, & Obón, 2012). Another interesting attribute in wild fruits was the odor, where OP and EO were perceived with greater intensity, highlighting an attenuated herbal note in OM and OP fruits compared with OFG. A study in wild *Opuntia robusta* J.C. Wendl. (1835) and *Opuntia ficus-indica* (L.) showed that the fruits were perceived with similar notes such as vegetable and fruity, but no significant differences were observed (Torres-Bojórquez, García-Rubio, Miranda-López, & Cardador-Martínez, 2017). Odor descriptors such as green fruit, peach, green oxidized fruit, melon, cucumber, and wet straw were characteristic in two cultivates *O. joconostle* F.A.C. Weber. (1928) (Contreras, Jaimez, Castañeda, Añorve, & Villanueva, 2011). Differences in intensity and characteristic odor of the *Opuntia* fruits are related to its volatile composition. This composition depends on factors such as *Opuntia* species, cultivar, climatic conditions, maturity, and storage conditions, among others. In *Opuntia ficus-indica* (L.) fruits pulp 35 compounds were isolated, being mainly aldehydes, alcohols, and terpenes, but esters, ketones, linear hydrocarbons and terpenoids were also found. Volatile compounds such as nonanol, 2,6-nonadienal, 1-hexanol, 2-hexanal, and D-limonene were the predominant compounds (Andreu-Coll, Noguera-Artiaga, Carbonell-Barrachina, Legua, & Hernández, 2020). In taste, the wild fruits (OM, OP and OE) were characterized by low sweet and sour intensities, and only OE was slightly more bitter compare to commercial fruits. "Bittersweet" taste was an important attribute perceived in *Opuntia joconostle* samples (Contreras et al., 2011). Glucose (40–62%) and fructose (5.5–16%) were the predominant sugars in pulp and peel from *Opuntia ficus-indica* (L.), and these sugars are mediating for fruit sweet taste. Also, succinic acid was found to predominate in pulp and peel, and it can be responsible for sour taste (Farag, Maamoun, Ehrlich, Fahmy, & Wesjohann, 2017). Finally, bitter taste and astringency perceived in the wild fruits can be related to phenolic content. Phenolic acids such as coumaric, caffeic, gallic and protocatechuic acids, produce astringency and slight bitterness (Ferrer-

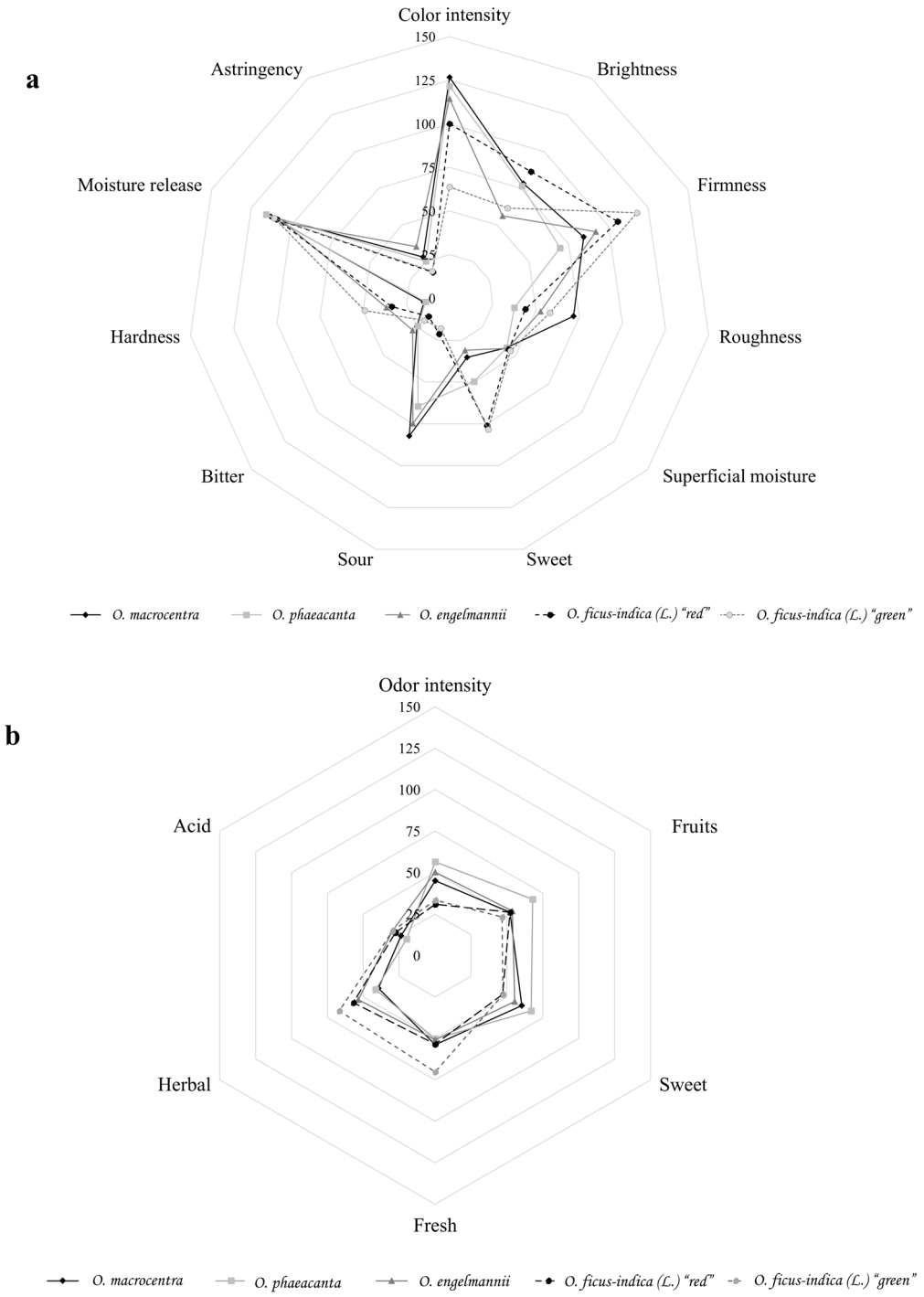

Fig. 1. Sensory profile of wild and commercial prickly pear fruits. **a**. Attributes from fruits in different sensory phases such as: visual, tactile, taste and mouth tactile. **b**. Descriptors from fruits in olfactory phase. Data are expressed as the mean with reference to linear scale (150 mm). Wild prickly pear fruits: *O. macrocentra* (OM), *O. phaeacantha* (OP) and *O. engelmannii* (OE), and commercial prickly pear fruits: *O. ficus-indica* (L.) "red" (OFR) and *O. ficus-indica* (L.) "green" (OFG).

Gallego, Hernández-Hierro, Rivas-Gonzalo, & Escribano-Bailón, 2014).

3.2. Colorimetry characterization

Colorimetry analysis showed that L* of wild prickly pear fruits (OM and OP) presented the highest values compared with the commercial (OFR) and the wild (OE) species (Table 2). On the other hand, wild OM species had more peel luminous than commercial (OFR), and wild (OP and OE) species. The results of chromatic coordinates of pulp and peel of wild species (OP and OM) presented a lower a* and the highest b*, but commercial (OFR) and wild (OE) species were highest for red color. The C* also confirmed that commercial species (OFR) had a more intense red in pulp and peel compared with the wild prickly pear fruits. Colorimetry characteristics of *Opuntia* fruits have been also poorly studied. However, the color characteristics of total fruits, pulp, and seed from different varieties of *O. ficus-indica* (L.) have been shown that the red-yellow pulp was appropriate to obtain colorants with high color intensity, whereas the whole fruit and red pulp reached powerful and stable yellow and red colors (Cejudo-Bastante, Chaalal, Louaileche, Parrado, & Heredia, 2014). Similar results were observed in juices of nine *Opuntia* spp.,

Table 2
Colorimetry characteristics of wild and commercial prickly pear fruits.

Fruit	L*	a*	b*	C*	Comparison	ΔE	CMC 1:1
Pulp					OM-OP	8.3 ± 0.3^{f}	10.4 ± 0.2^{e}
OM	38.1 ± 0.2^{a}	8.2 ± 0.0^{c}	18.7 ± 0.0^{b}	20.4 ± 0.0^{c}	OM-OE	23.6 ± 0.0^{d}	30.0 ± 0.1^{c}
OP	39.6 ± 1.5^{a}	1.8 ± 0.0^{d}	23.5 ± 0.1^{a}	23.6 ± 0.0^{b}	OM-OFR	27.6 ± 1.6^{c}	31.9 ± 1.1^{ab}
OE	24.9 ± 0.1^{c}	22.4 ± 0.0^{b}	5.1 ± 0.1^{d}	22.9 ± 0.0^{b}	OP-OE	31.3 ± 0.6^{b}	31.3 ± 0.4^{bc}
OFR	32.1 ± 1.5^{b}	34.2 ± 0.0^{a}	11.5 ± 0.5^{c}	36.1 ± 2.0^{a}	OP-OFR	35.4 ± 1.8^{a}	33.6 ± 1.3^{a}
					OE-OFR	15.3 ± 2.0^{e}	12.8 ± 1.9^{d}
Peel					OM-OP	10.7 ± 0.6^{d}	11.2 ± 0.6^{ab}
OM	39.6 ± 0.3^{a}	19.4 ± 0.0^{c}	4.4 ± 0.2^{c}	19.9 ± 1.0^{c}	OM-OE	12.8 ± 1.8^{c}	12.7 ± 1.6^{a}
OP	29.1 ± 0.3^{c}	18.8 ± 0.8^{c}	6.2 ± 0.1^{d}	19.8 ± 0.8^{c}	OM-OFR	17.2 ± 0.7^{a}	12.9 ± 0.4^{a}
OE	28.1 ± 1.2^{c}	23.0 ± 0.5^{b}	8.3 ± 0.0^{b}	24.5 ± 0.5^{b}	OP-OE	4.9 ± 0.3^{e}	3.4 ± 1.2^{d}
OFR	31.0 ± 0.3^{b}	32.9 ± 0.0^{a}	10.6 ± 0.4^{a}	34.6 ± 0.1^{a}	OP-OFR	15.0 ± 0.7^{b}	9.4 ± 0.8^{b}
					OE-OFR	10.7 ± 0.3^{d}	7.1 ± 1.1^{c}

O: *Opuntia*, OM: *O. macrocentra*, OP: *O. phaeacantha*, OE: *O. engelmannii*, OFR: *O. ficus-indica* (L.) "red". Data are expressed as the mean ± SD. SD = 0.0 indicate that SD < 0.1. Comparisons among species by pulp or peel group. Different letters indicate significant difference at $p < 0.05$.

where the yellow-green juices coloration, showed the highest b* values and had low a* values, while, the purple and the orange-red colored juices presented the highest a* values, and the lowest L* and b* values (Chavez-Santoscoy, Gutierrez-Uribe, & Serna-Saldívar, 2009). Our results also showed that ΔE and CMC from OM-OP species had the lowest variation, while the relation of OP-OFR species was the greatest difference in both parameters. However, in the peel, the relations in both attributes were less variable between the analyzed samples. The relation of OM-OFR species presented the highest variation in both parameters, while OP-OE species presented the smallest differences (Table 2). These results agree with those obtained in the sensory analysis, where the judges perceived the same differences in the color intensity of the fruits.

Color is an important property of fruits, through which it can attract animals or insects to help disperse their seeds, protect themselves from oxidative stress and provide information on the degree of maturity, among others. Felker et al. (2008) reported that the color in *Opuntia ficus-indica* (L.) is derived from de betalain content rather than anthocyanin pathway, generating a range in color from lime green, orange, red to purple, and this is a result of varying concentrations of the betaxanthins and betacyanins. For example, when the color is yellow-orange betaxanthins predominate, and if the color is red-purple, betacyanins are dominant. Differences in color between the pulp and the peel of the fruits may be due to the pigmentation process of the fruit, where the pulp is first pigmented and then the pigments diffuse towards the peel. This characteristic has been observed in *Opuntia stricta* Haw. (1812), *Opuntia megacantha* Salm-Dyck. (1834) and *Opuntia ficus-indica* (L.) fruits (Castellar et al., 2012).

3.3. Physicochemical characteristics

The moisture content of OFG was higher in pulp and peel, and like OM in seed than other species (Table 3). However, the water activity (Aw) was similar in pulp for all fruits, but the peel of the wild species showed lower Aw than commercial fruits. The wild prickly pear fruits presented lower pH values than commercial species. The titratable acidity was higher in pulp and peel from wild prickly pear fruits than OFR and OFG species. Seed from OM and OP fruits had lower titratable acidity than other samples. These results are congruent with the sour taste perceived by the judges in the sensory test. However, the acidity and pH of the fruits can vary among species (Castellar et al., 2012), for example, the pH values determined in this study were lower than those found in the pulp of *O. ficus-indica* (L.). fruit (pH 6.3), but these were higher than those found in the pulp of *O. dillenii* (Ker Gawl.) Haw. (1819) fruit (pH 3.3) (Medina, Rodríguez, & Romero, 2007) and different from joconostle genotypes (pH 3.1) (Hernández-Fuentes et al., 2015). Titratable acidity was higher in the seed than those determined for peel and pulp (Table 3). These results disagree with those determined in *O. matudae* Scheinvar. fruit, where the peel and pulp determination did not show significant differences (Guzmán-Maldonado et al., 2010). But our results were lower than those determined in the pulp of *O. ficus-*

Table 3
Physicochemical parameters of wild and commercial prickly pear fruits.

Fruit tissues	Moisture (%)	Water activity (Aw)	pH	Titratable acidity (% Citric acid)	Protein* (%)	Lipids* (%)	Ash* (%)	Total carbohydrates* (%)	Crude fiber* (%)
Pulp									
OM	90.6 ± 0.2^{b}	0.984 ± 0.0^{a}	4.4 ± 0.1^{c}	0.012 ± 0.0^{a}	3.4 ± 0.2^{a}	0.4 ± 0.0^{b}	9.2 ± 0.1^{a}	86.8 ± 0.2^{d}	2.2 ± 0.0^{d}
OP	88.9 ± 0.9^{c}	0.992 ± 0.0^{a}	4.7 ± 0.0^{b}	0.007 ± 0.0^{c}	2.1 ± 0.2^{bc}	0.6 ± 0.0^{a}	10.4 ± 0.6^{a}	86.7 ± 0.8^{d}	9.4 ± 0.1^{a}
OE	89.6 ± 0.1^{c}	0.984 ± 0.0^{a}	4.2 ± 0.1^{d}	0.011 ± 0.0^{b}	2.3 ± 0.0^{b}	0.4 ± 0.0^{b}	7.4 ± 0.2^{b}	89.8 ± 0.2^{c}	5.3 ± 0.2^{b}
OFR	89.2 ± 0.2^{c}	0.972 ± 0.0^{a}	5.5 ± 0.1^{a}	0.001 ± 0.0^{d}	1.5 ± 0.0^{d}	0.1 ± 0.0^{c}	2.6 ± 0.1^{d}	95.7 ± 0.1^{a}	2.3 ± 0.0^{c}
OFG	91.1 ± 0.1^{a}	0.993 ± 0.0^{a}	5.2 ± 0.0^{a}	0.001 ± 0.0^{d}	1.7 ± 0.0^{c}	0.1 ± 0.0^{c}	5.4 ± 0.0^{c}	92.7 ± 0.1^{b}	1.5 ± 0.0^{e}
Peel									
OM	79.6 ± 0.3^{e}	0.985 ± 0.0^{b}	4.8 ± 0.0^{c}	0.008 ± 0.0^{b}	2.3 ± 0.0^{c}	1.9 ± 0.0^{a}	19.2 ± 0.2^{c}	76.4 ± 0.2^{b}	9.8 ± 0.1^{b}
OP	80.6 ± 0.1^{d}	0.984 ± 0.0^{b}	4.8 ± 0.0^{c}	0.008 ± 0.0^{b}	1.4 ± 0.0^{d}	1.6 ± 0.0^{b}	18.9 ± 0.3^{c}	77.8 ± 0.3^{a}	9.9 ± 0.0^{b}
OE	87.2 ± 0.0^{c}	0.988 ± 0.0^{ab}	3.8 ± 0.0^{d}	0.015 ± 0.0^{a}	2.3 ± 0.0^{c}	1.5 ± 0.0^{c}	24.5 ± 0.1^{b}	71.5 ± 0.1^{c}	5.8 ± 0.1^{c}
OFR	88.5 ± 0.0^{b}	0.992 ± 0.0^{a}	5.1 ± 0.0^{a}	0.004 ± 0.0^{d}	2.8 ± 0.1^{b}	1.0 ± 0.0^{d}	24.2 ± 0.3^{b}	71.8 ± 0.3^{c}	10.3 ± 0.3^{ab}
OFG	90.5 ± 0.0^{a}	0.991 ± 0.0^{a}	5.0 ± 0.0^{b}	0.006 ± 0.0^{c}	3.9 ± 0.1^{a}	0.7 ± 0.0^{e}	26.7 ± 0.1^{a}	68.5 ± 0.0^{d}	11.4 ± 0.4^{a}
Seed									
OM	50.8 ± 1.6^{ab}	0.990 ± 0.0^{a}	4.5 ± 0.0^{c}	0.045 ± 0.0^{c}	5.2 ± 0.0^{d}	8.5 ± 0.2^{b}	1.7 ± 0.0^{b}	84.5 ± 0.1^{b}	50.5 ± 0.2^{a}
OP	48.2 ± 2.2^{b}	0.987 ± 0.0^{ab}	4.4 ± 0.0^{d}	0.040 ± 0.0^{d}	6.3 ± 0.1^{c}	7.1 ± 0.0^{c}	1.9 ± 0.0^{a}	84.5 ± 0.2^{b}	50.6 ± 2.0^{ab}
OE	44.4 ± 1.3^{c}	0.984 ± 0.0^{b}	4.2 ± 0.0^{e}	0.057 ± 0.0^{a}	8.2 ± 0.2^{a}	10.6 ± 0.4^{a}	1.9 ± 0.0^{a}	79.1 ± 0.5^{c}	46.5 ± 0.5^{b}
OFR	48.4 ± 1.4^{b}	0.985 ± 0.0^{b}	5.2 ± 0.0^{b}	0.049 ± 0.0^{b}	8.0 ± 0.2^{a}	5.5 ± 0.0^{d}	1.5 ± 0.0^{c}	84.8 ± 0.3^{b}	51.2 ± 0.9^{a}
OFG	52.0 ± 2.5^{a}	0.990 ± 0.0^{a}	5.4 ± 0.0^{a}	0.051 ± 0.0^{b}	7.3 ± 0.4^{b}	4.6 ± 0.1^{e}	1.3 ± 0.0^{d}	86.5 ± 0.4^{a}	52.0 ± 0.6^{a}

O: *Opuntia*, OM: *O. macrocentra*, OP: *O. phaeacantha*, OE: *O. engelmannii*, OFR: *O. ficus-indica* (L.) "red", OFG: *O. ficus-indica* (L.) "green". Data are expressed as the mean ± SD. SD = 0.0 indicate that SD < 0.1. Comparisons among species by pulp, peel or seed group. *Data in dry weight (DW). Different letters indicate significant difference at $p < 0.05$.

indica (L.) and *O. dillenii* (Medina et al., 2007), and various joconostle genotypes (Hernández-Fuentes et al., 2015). The high acidity of wild fruits may be due in part to the presence of succinic acid, one of the most abundant organic acids found in pulp and skin of *Opuntia ficus-indica* (L.). This primary metabolite, together with sugars (e.g. sucrose and turanose) and amino acids (e.g. proline) help to mitigate water stress in creeping bent grass and is likely to function similarly function in *Opuntia* fruits (Farag et al., 2017; Yang, Chang, Sun, Yu, & Huang, 2014).

Protein, crude fiber, and total lipids were highest in seed than those determined in the peel and pulp (Table 3). Wild prickly pear pulp was characterized by higher protein, lipids, and ash content than the commercial species, and OP and OE pulps had the highest crude fiber content. On the other hand, wild prickly pear peel was characterized by higher lipids, and ash than commercial prickly pear peel. These results agree with those found in *O. ficus-indica* (L.) (El-Kossori, Villaume, El Boustani, Sauvaire, & Méjean, 1998; Salim, Abdelwaheb, Rabah, & Ahcene, 2009), *O. joconostle* and *O. matudae* fruits (Medina et al., 2007). On the contrary, the results determined of protein and total lipids of seeds were lower than those determined previously in *O. engelmannii*, *O. phaeacantha*, *O. macrocentra* (Núñez-Gastélum et al., 2018), and *O. dillenii* pulp (Morales et al., 2012). The total carbohydrates determined in the seeds were higher than those determined in *O. engelmannii*, *O. phaeacantha*, *O. macrocentra*, *O. heliabravoana* Scheinvar (1974), *O. joconostle*, and *O. ficus-indica* (L.) (Núñez-Gastélum et al., 2018; Prieto-García et al., 2006).

According to the proximal composition, the pulp, peel, and seed from wild prickly pear fruits (OM, OP, and OE) of this study, could be a source of functional ingredients. Linoleic acid (C18:2n6, 54.35–66.27 mmol TE/100 g dry seed), oleic acid (C18:1n9, 15.70–19.42 mmol TE/100 g dry seed), palmitic acid (C16:0, 11.01–13.72 mmol TE/100 g dry seed) and stearic acid (C18:0, 3.77–5.60 mmol TE/100 g dry seed) were the most abundant fatty acids found in the lipids from the seed of these wild fruits. Also, palmitoleic acid (C16:1n7), alpha linoleic acid (C18:3n3) and eicosanoid acid (C20:1n9) were reported (Núñez-Gastélum et al., 2018). Other components from *Opuntia ficus-indica* (L.) fruits have been obtained such as a mucilage with important pectin content (Matsuhiro, Lillo, Sáenz, Urzúa, & Zárate, 2006) or a biopolymer (gum) with potential application as thickener, stabilizer, and antioxidant agent in the food industry (Salehi, Emam-Djomeh, Askari, & Fathi, 2019). Additional studies in these wild species are necessary to evaluate in specific their carbohydrates and fiber composition.

3.4. Phytochemical and antioxidant capacity

TPC content was higher in the pulp than the peel and seed, while TF was higher in the peel than the pulp and the seed (Table 4). Our results agreed with those determined in *O. ficus-indica* (L.) (Aruwa, Amoo, & Kudanga, 2019; Cejudo-Bastante et al., 2014; Khatabi et al., 2016), *O. stricta,* and *O. joconostle* fruits (Osorio-Esquivel et al., 2011; Yeddes, Chérif, Guyot, Sotin, & Ayadi, 2013). Furthermore, OE had higher TPC and TF contents than the commercial species. Although OFG and OFR (commercial species) showed the lowest values of TPC, OFG presented the highest content from pulp extracts, whereas OFR presented the highest one obtained from seed. Some studies have hypothesized that these variations in TPC and TF contents are depending on the type of compounds present in the extract, methods, and solvents used for the extraction, fruit maturity, climate, and quantification methodologies (Aruwa et al., 2019; Belviranl et al., 2019; Kuti, 2004). Additionally, green and yellow-skinned fruits had the lowest phenolic content in comparison with red and purple-skinned fruits in *O. ficus-indica* (L.) (Cejudo-Bastante et al., 2014; Khatabi et al., 2016; Stintzing et al., 2005). Our results of TPC were lower than those observed in two joconostle cultivars fruits (Morales et al., 2012) and the commercial *O. ficus-indica* (L.) fruits (Cejudo-Bastante et al., 2014) and *O. ficus-indica* (L.) seeds (Chougui et al., 2013). TF content determined in this study agreed with those determined in *O. ficus-indica* (L.), *O. stricta,* and *O. joconostle* (Osorio-Esquivel et al., 2011; Yeddes et al., 2013). Besides agreed with those determined in *O. joconostle* pulp but disagree with those determined in *O. matudae* pulp. However, our results were lowest than those observed *O. joconostle* seed and *O. matudae* seed (Morales et al., 2012).

AA content was higher in the peel than the pulp and the seed (Table 4). AA content was higher than those reported in the edible portion of *O. ficus-indica* (L.) (Butera et al., 2002; Kuti, 2004; Stintzing et al., 2005). The pulp extracts obtained from OP (wild species) and OFR (commercial species) presented the highest content and OM (wild species) and OFG (commercial species) showed the lowest ones. OM (wild species) and OFG (commercial species) showed the highest AA content

Table 4
Phytochemical profile and antioxidant capacity of wild and commercial prickly pear fruits.

Fruit (tissues)	TPC (mg GAE/g)	TF (mg CE/g)	AA* (mg AA/g)	Betacyanins (mg/g)	Betaxanthins (mg/g)	Betalains (mg/g)	Antioxidant capacity		
							DPPH (mmol TE/g)	FRAP (mmol TE/g)	$ABTS^{\bullet+}$ (mmol TE/g)
Pulp									
OM	8.42 ± 0.3^{a}	3.78 ± 0.0^{b}	0.76 ± 0.0^{d}	0.21 ± 0.0^{c}	0.12 ± 0.0^{c}	0.33 ± 0.0^{c}	13.59 ± 0.2^{a}	5.14 ± 0.2^{a}	19.96 ± 0.3^{c}
OP	7.76 ± 0.2^{b}	4.10 ± 0.0^{a}	1.92 ± 0.0^{a}	0.15 ± 0.0^{d}	0.09 ± 0.0^{d}	0.25 ± 0.0^{d}	13.53 ± 0.1^{a}	3.93 ± 0.7^{b}	22.78 ± 0.1^{b}
OE	8.14 ± 0.1^{a}	4.26 ± 0.1^{a}	1.53 ± 0.0^{c}	0.90 ± 0.0^{a}	0.45 ± 0.0^{a}	1.35 ± 0.0^{a}	11.43 ± 0.0^{b}	5.87 ± 0.4^{a}	28.43 ± 0.3^{a}
OFR	3.62 ± 0.1^{d}	3.14 ± 0.1^{c}	1.63 ± 0.0^{b}	0.25 ± 0.0^{b}	0.23 ± 0.0^{b}	0.49 ± 0.0^{b}	7.74 ± 0.0^{c}	1.38 ± 0.5^{c}	11.87 ± 0.2^{e}
OFG	5.00 ± 0.1^{c}	3.58 ± 0.0^{b}	0.67 ± 0.0^{e}	0.09 ± 0.0^{e}	0.07 ± 0.0^{e}	0.17 ± 0.0^{e}	6.74 ± 0.2^{d}	2.03 ± 0.1^{c}	16.33 ± 0.7^{d}
Peel									
OM	7.11 ± 0.1^{a}	3.60 ± 0.2^{b}	1.72 ± 0.0^{a}	0.11 ± 0.0^{d}	0.07 ± 0.0^{b}	0.18 ± 0.0^{c}	12.50 ± 0.2^{b}	4.42 ± 0.3^{bc}	28.17 ± 0.5^{b}
OP	3.70 ± 0.1^{c}	4.90 ± 0.0^{a}	1.20 ± 0.0^{d}	0.12 ± 0.0^{c}	0.06 ± 0.0^{c}	0.19 ± 0.0^{c}	13.08 ± 0.1^{a}	3.66 ± 0.3^{c}	28.01 ± 0.4^{b}
OE	6.95 ± 0.1^{a}	5.01 ± 0.1^{a}	1.19 ± 0.0^{d}	0.13 ± 0.0^{b}	0.06 ± 0.0^{c}	0.20 ± 0.0^{b}	12.89 ± 0.0^{a}	6.56 ± 0.2^{a}	29.19 ± 0.1^{a}
OFR	4.32 ± 0.1^{b}	3.18 ± 0.3^{c}	1.45 ± 0.0^{c}	1.16 ± 0.0^{a}	0.08 ± 0.0^{a}	1.19 ± 0.0^{a}	7.90 ± 0.1^{c}	5.18 ± 0.7^{b}	16.42 ± 0.3^{d}
OFG	4.34 ± 0.0^{b}	3.40 ± 0.1^{bc}	1.53 ± 0.0^{b}	0.09 ± 0.0^{e}	0.08 ± 0.0^{a}	0.17 ± 0.0^{d}	6.87 ± 0.0^{d}	7.37 ± 0.3^{a}	17.65 ± 0.2^{c}
Seed									
OM	6.96 ± 0.2^{a}	3.36 ± 0.1^{b}	0.26 ± 0.0^{b}	–	–	–	12.60 ± 0.0^{b}	3.46 ± 0.4^{a}	23.44 ± 0.9^{c}
OP	4.41 ± 0.1^{c}	4.02 ± 0.1^{a}	0.20 ± 0.0^{c}	–	–	–	13.46 ± 0.1^{a}	3.38 ± 0.4^{a}	27.38 ± 0.5^{b}
OE	4.96 ± 0.0^{b}	3.80 ± 0.1^{a}	0.15 ± 0.0^{d}	–	–	–	10.68 ± 0.0^{c}	2.07 ± 0.0^{b}	37.28 ± 0.2^{a}
OFR	4.30 ± 0.0^{c}	3.10 ± 0.2^{b}	0.30 ± 0.0^{a}	–	–	–	8.08 ± 0.0^{d}	0.80 ± 0.5^{c}	14.19 ± 0.1^{e}
OFG	2.93 ± 0.0^{d}	3.17 ± 0.2^{b}	0.15 ± 0.0^{d}	–	–	–	7.08 ± 0.0^{e}	2.08 ± 0.4^{b}	17.18 0.0^{d}

O: *Opuntia*, OM: *O. macrocentra*, OP: *O. phaeacantha*, OE: *O. engelmannii*, OFR: *O. ficus-indica* (L.) "red", OFG: *O. ficus-indica* (L.) "green". TPC: total phenolic compounds, GAE- gallic acid equivalents, TF: total flavonoids, CE: catechin equivalents, AA: ascorbic acid, TE: trolox equivalents. Data are expressed as the mean ± SD (dry weight, DW). *Data are expressed as the mean ± SD (fresh weight, FW). SD = 0.0 indicate that SD < 0.1. Comparisons among species by pulp, peel or seed group. Different letters indicate significant difference at $p < 0.05$.

obtained from the peel, however, OP and OE (wild species) presented the lowest ones. When the seed extracts were analyzed, OE (wild species) and OFG (commercial species) presented the lowest AA content, but OFR (commercial species) and OM (wild species) had the highest ones. These results agreed with those found in the edible portion of *O. ficus-indica* (L.), *O. lindheimeri* Engelm. (1850), *O. streptacantha* Lem. (1839), *O. stricta* var. *stricta* (Kuti, 2004). However, our results disagreed with those determined for the edible portion of Sicilian cultivars fruits of *O. ficus-indica* (L.), where no differences were shown between the different varieties (Butera et al., 2002). The betacyanin, betaxanthins, and betalains contents were higher in pulp than the peel (Table 4). These results agree with those found in the edible portion of *O. ficus-indica* (L.) fruits (Cejudo-Bastante et al., 2014). OE (wild species) presented the highest levels in both tissues, while OFG (commercial species) showed the lower ones.

The AC determined by DPPH was similar in the three tissues analyzed (Table 4). These results agree with those found in *O. ficus-indica* (L.) and *O. stricta* fruits (Yeddes et al., 2013). Although, the AC determined by $ABTS^{\bullet+}$ assay was highest in the seed and peel than those determined in the pulp, while AC obtained by FRAP assay was highest in the peel than those determined in pulp and seed. These results agree with those found in *O. ficus-indica* (L.) fruits (from Sicily/Italy), where peel showed higher AC than the pulp (Moussa-Ayoub, El-Samahy, Rohn, & Kroh, 2011). Furthermore, OM, OP and OE (wild species) presented the highest AC (DPPH and $ABTS^{\bullet+}$ assays) in the three extracts, while the OFG and OFR (commercial species) had the lowest ones. Besides, the AC determined by the FRAP assay also showed that wild species presented the highest AC values obtained from the pulp, while OFR (commercial species) had the lowest ones. OE and OFG showed the highest levels in peel and OP and OM presented the highest values in seed extracts, while OP (wild species) had the lowest in peel and OFR in seed. Interestingly, we observed a tendency of the increase in AC in wild species compared to commercial species in the three tissues analyzed. Our results disagree with those found in the peel and pulp extracts of *O. ficus-indica* (L.) and *O. stricta*, where the commercial species showed a tendency to present the higher AC than the wild species in both tissues (Yeddes et al., 2013). A comparison of the AC of pulp extract of different varieties of *O. ficus-indica* (L.) indicates that the total radical-scavenging ability of the methanolic extracts from the yellow fruit is significantly higher than the activity of the red and white ones (Butera et al., 2002). These results also have been observed in the estimation of the AC of the seed extract in *O. ficus-indica* (L.) species where the green and the yellow varieties had a better scavenging effect than the red ones (Cardador-Martínez, Jiménez-Martínez, & Sandoval, 2011; Chougui et al., 2013). A similar tendency was observed for peel and juicy pulp extracts (Butera et al., 2002; Cardador-Martínez et al., 2011). These results disagree with those obtained in the present study.

In the present study, the TPC determined in the pulp showed a positive correlation with the AC determined by DPPH ($r = 0.899$, $p = 0.03$) and FRAP ($r = 0.950$, $p = 0.01$) assays, while TF content was positively correlated with the AC determined by $ABTS^{\bullet+}$ ($r = 0.977$, $p = 0.001$) assay. Phenolic content of pulp extracts has been correlated previously with the AC in *O. ficus-indica* (L.) (green-skinned) ($r = 0.78$), *O. lindheimeri* (purple-skinned) ($r = 0.88$), *O. streptacantha* (red-skinned) ($r = 0.80$), *O. stricta* var. stricta (yellow-skinned) ($r = 0.76$), and *O. joconostle* ($r = 0.77$) (Kuti, 2004; Osorio-Esquivel et al., 2011). Although our results of AC in pulp extracts did not show a significant correlation with the AA and betalain contents, these results agreed with those determined in *O. ficus-indica* (L.), where not correlation was observed between the AC determined by ORAC method and AA content (Kuti, 2004). Furthermore, there was a significant correlation between the betalains and betaxanthins ($r = 0.996$, $p = 0.05$) contents, and betacyanin and betaxanthin ($r = 0.968$, $p = 0.05$) contents. These results agree with those determined in *Opuntia* clones, where a correlation was observed between the betalains and betaxanthins contents ($r = 0.928$) (Stintzing et al., 2005). In addition, when the methods used to determine the AC were correlated with each other, a positive correlation was observed between FRAP and $ABTS^{\bullet+}$ assays ($r = 0.900$, $p = 0.03$), and DPPH and $ABTS^{\bullet+}$ assays ($r = 0.977$, $p = 0.004$). But, when the phytochemicals obtained from peel were correlated with the AC, the betaxanthins content was negatively correlated with the AC determined by DPPH ($r = -0.931$, $p = 0.02$) and $ABTS^{\bullet+}$ ($r = -0.920$, $p = 0.02$) assays. Therefore, there was a significant correlation between betalain and betacyanin contents ($r = 1$, $p = 0.00$).

Together with all these results, the wild prickly pear fruits were characterized by the highest phenolic content in pulp (OM, OP, and OE), peel, and seed (OM and OE) compared with commercial prickly pear fruits (OFR and OFG). This phenolic content is highest compared with other edible fruits such as green globe grape (4.18 mg GAE/g DW), jackfruit pulp (1.27 mg GAE/g DW), and other berries from Nanjing (2.72–5.58 mg GAE/g DW), but similar with red globe grape (9.36 mg GAE/g DW) o pomegranate (9.55 mg GAE/g DW) and lower than mulberry (13.63 mg GAE/g DW) (Huang, Zhang, Liu, & Li, 2012; Olivas-Aguirre et al., 2017; Shrikanta, Kumar, & Govindaswamy, 2015). All tissues from OP and OE showed higher content of total flavonoids than grape skin (2.63 mg CE/g DW) or similar to mulberry (4.01 mg CE/g DW) (Shrikanta et al., 2015). Pulp, peel, and seed from wild prickly pear fruit had higher antioxidant capacity (AC), except in peel by FRAP assay, where only OE was higher than tissues from commercial fruits. Oniszczuk et al. (2020) reported some of the main phenolic acids in *Opuntia* fruits such as benzoic acid derivatives: protocatechuic, syringic, 4-OH-benzoic, vanilic, gentisic, salicylic, and cinnamic acid derivatives: caffeic, *trans*-sinapic and *cis*-sinapic, *p*-coumaric, ferulic, isoferulic, *m*-coumaric, and 3,4-dimethoxy cinnamic. *Opuntia* extracts have been used for centuries for medical purposes and the intake of these natural antioxidants has been related to significant health benefits due to their anti-atherogenic, anti-cancer, anti-bacterial, anti-inflammatory properties, among others (Santos et al., 2017).

On the other hand, pulp and peel from wild prickly pear fruits (OP and OM) showed the best content of ascorbic acid and OE pulp had the highest levels of betacyanins, betaxanthins, and betalains. These results agree with the color perceived by the judges in the sensory analysis and that determined by the colorimetric method. It has been argued that low pH values (3.1–3.8) promote the synthesis of betacyanins (Castellar et al., 2012), and in this study wild prickly pear fruits showed the lowest pH compared to commercial ones. Betacyanins are compounds of interest to be used as a natural coloring in confectionary, bakery, dairy, and frozen products. Currently, this pigment is obtained from *Beta vulgaris* L. var. *ruba* after 2 years of cultivation (Ciriminna et al., 2019), therefore the wild prickly pear fruits of this study could be a potential source of these compounds. Additional studies on the identification and quantification of the bioactive compounds of these wild fruits are necessary to determine their potential uses in the treatment of diseases, and/or as an ingredient in the development of new foods.

3.5. Protein identification

A total of 181, 122, 113, 183 and 140 different proteins were identified in OM, OP, OE, OFG, and OFR species, respectively (Supplementary File S1). Only 5 proteins were presented in the three wild *Opuntia* species, while 59, 43 and 31 proteins were unique in OM, OP, and OE, respectively (Supplementary Fig. 2). In the case of commercial species, 97 proteins were shared between the two commercial varieties, whereas 49 and 26 proteins were unique in OFG and OFR, respectively. Finally, only 17 proteins were detected in the five species. Furthermore, all species shown the highest enrichment in main pathways as biosynthesis of amino acids, glycolysis (dark)/gluconeogenesis (light), citric acid cycle, Calvin-Benson cycle (reductive pentose phosphate cycle), C4-dicarboxilic acid cycle, pentose phosphate pathway, pyruvate metabolism, photosynthesis, glyoxylate and dicarboxilate metabolism, and gluthatione metabolism, among others (Fig. 2) (Supplementary File S2).

In the Calvin cycle, the CO_2 is transformed into hexoses phosphate by

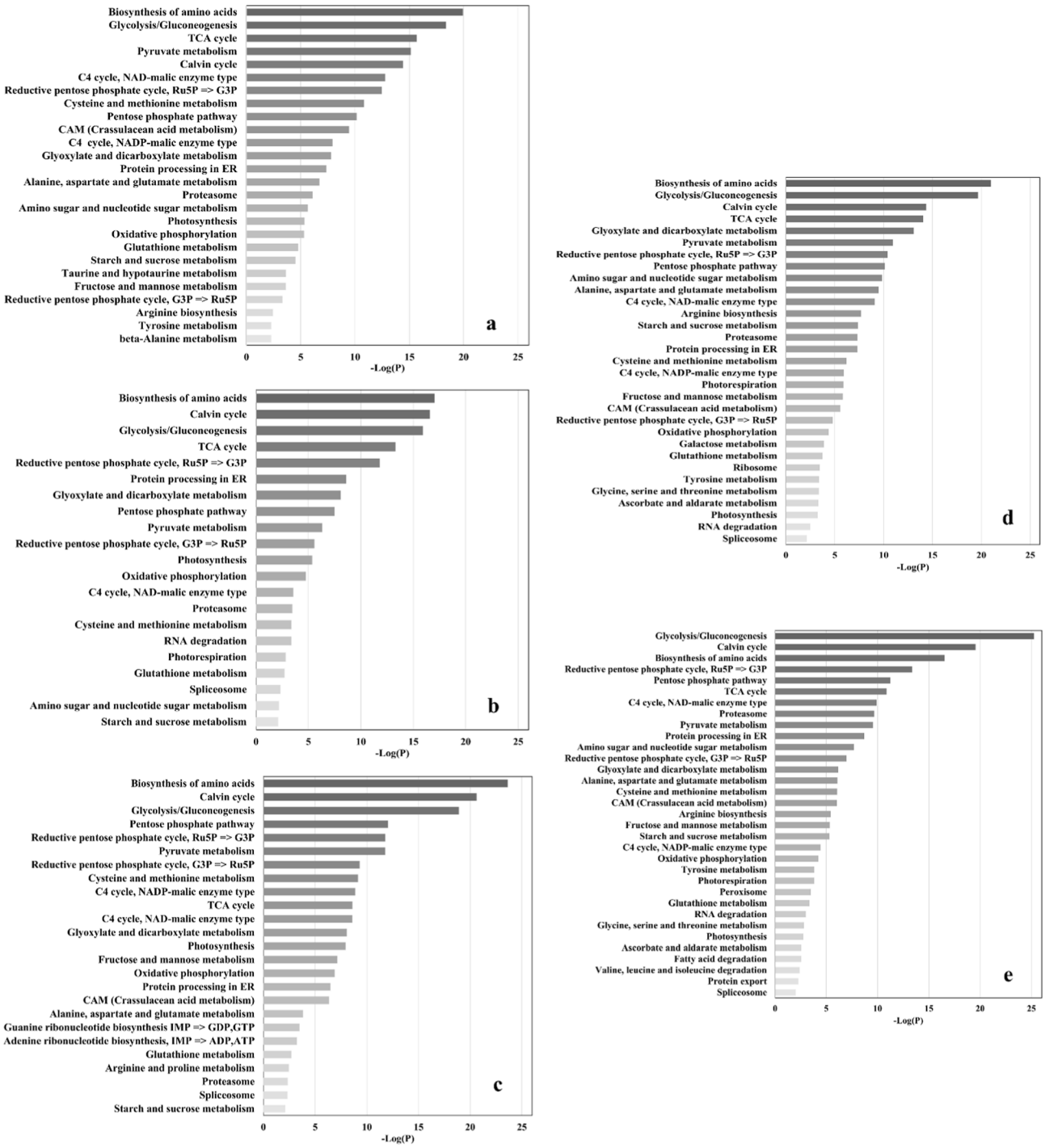

Fig. 2. Heatmap of enriched terms across input gene lists, colored by p-values. KEEG pathway enrichment analysis of identified proteins by Metascape from **a.** OM: *O. macrocentra*; **b.** OP: *O. phaeacantha*; **c.** OE: *O. engelmannii*; **d.** OFG: *O. ficus-indica* (L.) "green"; **e.** OFR: *O. ficus-indica* (L.) "red".

the plants during photosynthesis (Bassham, 1979). In this study, the NAD-ME variation was the most enrichment in the five *Opuntia* species, especially in OM, although in the OE, this C4 cycle type was found over 3–4 times decreased. The NADP-ME type was also presented, except in OE. Additionally, the crassulacean acid metabolism (CAM) was found except in OP. This could mean that the CAM is not active in OP. Moreover, in this species, the C4 cycle NADP-ME type was not presented and the NAD-ME type was more decreased than in the other four species. Due to the *Opuntia* species live in desert ambient, it seems obvious that these plants should fix the CO_2 overnight through CAM. These results agree with those found by Pichereaux et al. (2016), where at least three isoforms of RuBisCO, one pyruvate phosphate dikinase (PPDK) and two phosphoribulokinase (PRK) were up-accumulated in the wild *O. streptacantha* cladodes.

Our data showed that the citrate synthase (CSY2), ATP-citrate synthase alpha chain (ACLA-1, ACLA-2, and ACLA-3), and ATP-citrate synthase beta chain (ACLB-2) were found in the pulp of *Opuntia* fruits. These proteins have been related to the synthesis of malic and citric acids. CSY2 was only found in OFG and OP species, while ACLA-1 was only found in OFG species, ACLA-2 was found in OM species and ACLA-3 was found in OP species. Furthermore, ACLB-2 was only found in OE, OM, OFR, and OP species. These enzymes also have been reported in

citrus juice cell sacs (Katz et al., 2007) and *Malus* Mill. (1754) fruits (Ma et al., 2019). We also identified three aconitate hydratase. The ACO 1 was only found in OE species, while ACO2 was only found in OE and OFG species, and ACO3 was only found in OE, OM, OFG and OP species. These enzymes also have been reported in citrus juice cell sacs (Katz et al., 2007). The oxidative decarboxylation of isocitrate into 2-oxoglutarate is mediated by the action of isocitrate dehydrogenase (IDH). In this study, we identified five isocitrate dehydrogenase [ICDH, cICDH, NADP-dependent, and NAD NAD + -dependent (IDH1 and IDH3)]. The ICDH was only found in OFR species, while cICDH was found in OM, OFG, and OFR species; NADP-dependent was only found in OE, OM and OFG species, while IDH1 was only found in OP and OFG species; finally, IDH3 was only found in OM and OP species. Pyruvate is a major product of glycolysis and is also an important intermediate during the transformation of sugars, organic acids, amino acids, and other compounds in fruits. Three proteins that participates in the pyruvate also were identified. The pyruvate dehydrogenase E1 (PDH2) which was only found in OM, OFG, OFR, and OP species, while the dihydrolipoyllysine-residue acetyltransferase component 2 was found in OM, OFG, OFR species, and the dihydrolipoyllysine-residue acetyltransferase component 4 (LTA2) was only found in OM species. In this study, also two succinyl-CoA ligases (ADP-forming subunit alpha-2 and subunit beta) were identified. Succinyl-CoA synthetase functions in the citric acid cycle (TCA), coupling the hydrolysis of succinyl-CoA to the synthesis of ATP and thus represents the only step of substrate-level phosphorylation in the TCA. The alpha subunit of the enzyme binds the substrates coenzyme A and phosphate, while succinate binding and nucleotide specificity is provided by the beta subunit. The subunit alpha-2 was only found in OE species, and the two commercial species (OFG and OFR), however, the subunit beta was only found in the wild OM species.

In this analysis, some enzymes related to malic acid synthesis were also identified. MDH was only found in OM species, while c-NAD-MDH1 was found in OE, OM, OFG, and OFR species; additionally, mMDH1 was identified in all the five species and PMDH2 only found in OM, OFG, OFR, and OP species. A variation in the accumulation NAD-MDH also has been observed in mature fruits of wild *Malus* species (Ma et al., 2019) and citrus juice cell sacs (Katz et al., 2007).

In our data, all *Opuntia* species varied in the sugar metabolisms, which may mean that the production of the different sugars is still active in the prickle pear pulp. But the starch and sucrose metabolism were found more enrichment in commercial species than in wild species. Although the fructose and mannose metabolism were present in OE, OM, OFG, and OFR species, this was not observed in OP species. Finally, the galactose metabolism was found only in OFG species. The fructose-bisphosphate aldose (FBA) participates in the glycolytic pathway and catalyzes the reversible reaction by converting fructose-1,6-bisphosphate into dihydroxyacetone phosphate and glyceraldehyde 3-phosphate. In this study, five FBA were observed. FBA1 was found in OFG, OFR, and OE species, while FBA2 was only observed in OE species, FBA4 was also found in commercial species and FBA5 was only observed in OFR and OM species. Furthermore, FBA6 was only observed in OFG, OFR, and OM species. A variation in the expression of five orthologs of FBA proteins has been observed among the protein cladodes analysis of wild and commercial *Opuntia* species (Pichereaux et al., 2016). Furthermore, a variation of FBA also have been differentially expressed in mature fruits of wild *Malus* species (Ma et al., 2019). The UDP-glucose pyrophosphorylase 1 (UGP1) converts the glucose 1-phosphate to UDP-glucose, which is the major glycosyl donor for polysaccharides. In this study, UDP-glucose pyrophosphorylase 1 was only identified in OFG and OE species, while UGP2 was only identified in OM species. The sucrose synthase enzyme catalyzes the reversible conversion of sucrose to fructose and uridine diphosphate glucose. The resulting fructose or glucose can be phosphorylated by fructokinase to generate fructose-6-phosphate or by hexokinase to produce glucose-6-phopshate, respectively. In our study, fructokinase-1, and hexokinase-6 were more abundant in the commercial OFG species. A variation in the accumulation of fructokinase-1 and hexokinase-6 also has been observed in mature fruits of wild *Malus* species (Ma et al., 2019). Three sucrose synthases (SUS) also were well represented in our study. SUS1 was only identified in OFG and OE species, while SUS2 was identified in OFG, OFR, OE and OP species. Finally, SUS4 was only found in OFG, OFR and OM species. Two up-accumulated orthologs of SUS have been also observed in the cladodes of wild *O. streptacantha* species (Pichereaux et al., 2016). Furthermore, a variation of the SUS also has been observed in mature fruits of wild *Malus* species (Ma et al., 2019). Other enzymes related to starch metabolism such as glucose-1-phosphate adenylyltransferase small subunit (ADG1) was only found in OFG, OFR, OM and OP species, while the glucose-6-phosphate isomerase 1 was only identified in OFG, OFR, OM species. Additionally, the ascorbate and aldarate metabolism (APX2, MDHAR, UGD1, ALDH7B4) was found only in the commercial species.

4. Conclusion

Wild prickly pear fruits, *O. macrocentra* (OM), *O. engelmannii* (OE) and *O. phaeacantha* (OP) from Samalayuca, Chihuahua showed differences with the commercial ones**,** but all were acceptable. These wild species were characterized by a red-purple color, intense odor, low sweetness and harness, and slightly sour which may enhance consumption. The chemical composition of these wild species pulp had higher contents in protein, lipids, and minerals than commercial species The OP and OE pulp could be a good source of dietary fiber and seed a good source of lipids. Wild prickly pear fruits also showed higher content of total phenolic compounds in pulp (OM, OE, and OP) and peel (OM and OE), while total flavonoids content (OP and OE) was higher in all tissues, but only OE pulp showed higher content in betacyanins, betaxanthins, and betalains. According to the phytochemical content, these wild prickly pear fruits showed a better antioxidant capacity which was more evident when determined by DPPH and $ABTS^{\bullet+}$ assays. Our data indicate that underutilized wild prickly pear species from Samalayuca area could be a promising source for functional ingredients in the enrichment and/or development of new healthy foods. Finally, the knowledge of their protein profile helps to better understand the metabolism of these desert species for their protection and conservation.

CRediT authorship contribution statement

José Valero-Galván: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization. **Raquel González-Fernández:** Methodology, Validation, Formal analysis, Data curation, Writing - review & editing, Visualization. **Alejandro Sigala-Hernández:** Methodology, Formal analysis. **José Alberto Núñez-Gastélum:** Methodology, Writing - review & editing. **Eliel Ruiz-May:** Methodology, Writing - review & editing. **Joaquín Rodrigo-García:** Methodology, Formal analysis, Writing - review & editing. **Alfonso Larqué-Saavedra:** Formal analysis, Writing - review & editing. **Nina del Rocío Martínez-Ruiz:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - review & editing, Visualization, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foodres.2020.109909.

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