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Review article

Cactus (*Opuntia* and *Nopalea*) nutritive value: A review

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A B S T R A C T

Cactus is an important fodder option for semiarid regions of the world. The energy and water supplied by this forage has long been used by livestock, and cactus cultivation has increased food security and reduced hunger and poverty in semiarid areas. The environmental and management practices affect the nutritive value of cacti and animal performance. The major species of cacti used for livestock includes *Opuntia ficus-indica* Mill., *O. lindheimeri* Engelm, *O. ellisiana, O. engelmannii* Salm Dyck, *O. chrysacantha* Berg, *O. amyclae*, *O. rastrera* Weber, *O. stricta* Haw, and *Nopalea cochenillifera* Salm Dyck. Under similar environmental conditions, *N. cochenillifera* usually presents greater dry matter (DM), water-soluble carbohydrates, and *in vitro* digestible organic matter concentrations, and lesser crude protein (CP) when compared with *O. ficus-indica.* The planting density also affects cactus growth and its chemical composition: a greater plant N concentration was observed in a population of 5000 plants/ha (11.2 g/ kg) compared to a population of 40,000 plants/ha (9.0 g/kg). Young cladodes are present in greater proportions in less dense plant populations, presenting greater nutrient concentration and lesser DM than older cladodes. Fertilizer application also affects the chemical composition. Nitrogen fertilization increased cladode N concentration (ranging from 6.7 g/kg to 13.9 g/kg) in *Opuntia ficus-indica*, with a positive linear response (0 up to 300 kg N/ha/year) occurring in three out of four locations in NE Brazil. The harvest management may affect the nutritive value, as a reduced harvest intensity will increase the proportion of younger cladodes. However, as cactus maintains its nutritive value for a longer period compared to other forages, the harvest frequency has little influence on overall nutritive value. Cladodes may be stored in a dry and shaded location without losing its nutritive value for at least two weeks, which may facilitate the logistics of

Abbreviations: ADF, acid detergent fiber; B, boron; Ca, calcium; CAM, crassulacean acid metabolism; CF, crude fiber; CN, non-structural carbohydrates; CP, crude protein; Cu, copper; DM, dry matter; EE, ether extract; Fe, iron; HCN, hydrocyanic acid; IVDMD, *in vitro* dry matter digestibility; K, potassium; Mg, magnesium; Mn, manganese; N, nitrogen; Na, sodium; NDF, neutral detergent fiber; NE, northeast; NFC, non-fiber carbohydrates; OM, organic matter; P, phosphorus; S, sulphur; TC, total carbohydrate; TDN, total digestible nutrients; WSC, water soluble carbohydrate; Yr, year; Zn, zinc.

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transportation, reducing the total costs. Therefore, this review provides an overview of how agronomic and environmental factors affect the chemical composition and nutritive value of cacti with the potential to improve livestock productivity in arid environments.

1. Introduction

Drylands occupy approximately 40 % of terrestrial surface and 2 billion people live in these areas. In addition, climate change is increasing temperatures and the frequency and severity of droughts in different regions of the world (FAO, 2019). At the same time, there is an increasing demand for high-quality animal protein in the world. Adapted fodder crops able to thrive in drylands might have a significant impact in the years to come, providing fodder to increase animal-source food in dry areas of the globe (Mudgal et al., 2018). Cactus is an important forage resource for arid and semiarid regions. In Mexico, cactus utilization as a forage is based on wild cactus population. In other countries such as Brazil, Tunisia, South Africa, and Morocco, cactus fodder is produced in cultivated orchards, which could have a multi-use purpose (fruit/forage/industrial processed products) or only fodder. It is a source of water and energy for ruminants and other type of animals, mainly during the dry season of the year. Cactus represents a live forage reserve and is an important resource to increase food security in semiarid regions (Ben Salem et al., 2002). Cacti produce a high amount of succulent biomass, with a high palatability, even under environmental conditions that are limiting for other types of forage (Ben Salem et al., 2002).

Crassulacean acid metabolism (CAM) is the photosynthetic mechanism of cacti (Leegood, 2013). The CAM mechanism typically confers efficient water use and slow growth to the Cactaceae, with a longer persistence of their nutritive value. However, some of the genera of this family, such as *Opuntia* and *Nopalea*, were domesticated long ago and are used by humans for both food and fodder. Indeed, selection by humans is likely the reason these genera are more productive than other cacti species.

The chemical composition of cactus cladodes varies with the season, plant age, cladode order (position), cultivar, fertilization and harvest management, planting density, and environmental factors (Dubeux et al., 2010; Alves et al., 2016a; Souza et al., 2017; Pessoa et al., 2020). The typical chemical composition of cacti includes low concentration of dry matter (5–15% DM), crude protein, fiber (ADF, acid detergent fibre and NDF, neutral detergent fibre), with digestibility being usually greater than other warm-climate forages (Batista et al., 2009; Monteiro et al., 2018; Inácio et al., 2020).

Forage nutritive value affects animal production and may change under the different agronomic practices and with the range of environments where cacti are cultivated. Therefore, this review provides an overview of how agronomic and environmental factors affect the chemical composition and nutritive value of cacti and the resulting effects on animal production.

2. Germplasm

The major species of cacti used for livestock includes *Opuntia ficus-indica* Mill., *O. stricta* (Haw.) Haw., *O. lindheimeri* Engelm,

Table 1
Cactus chemical composition (cladodes) according different authors and location.

Species/age	DM[a] g/kg	CP	NDF	ADF	CF	NFC	IVDMD	Reference/Location
O. stricta	107	47	311	167	–	521	852	Pessoa et al. (2020)/Brazil
O. stricta/4 year	140	33	202*	200	202	667	–	Silva et al. (2017)/Brazil
O. stricta	–	59	397	–	–	–	834#	Dubeux et al. (2019)/Madagascar
N. cochenillifera	156	39	217	–	–	659	–	Inácio et al. (2020)/Brazil
N. cochenillifera	123	40	252*	137	253	564	–	Lopes et al. (2020)/Brazil
O. ficus-indica cv. Gigante/2 years	91	49	318	203	340	500	–	Wanderley et al. (2012)/Brazil
O. fícus-indica/1 year	137	74	185	107	–	638	–	Rodrigues et al. (2016)/Portugal
O. fícus-indica f. Inermis	97	44	306	–	–	–	–	Rekik et al. (2010)/Tunisia
O. fícus-indica (Miller, TX 1279)/4 year	–	71	260	211	–	–	–	Mayer and Cushman (2019)
O. ficus-indica/90 days	63	104	319	217	–	–	667	Pinos-Rodriguez et al. (2010)/Mexico
O. ficus-indica	135	38	351	–	85	582	865	Nefzaoui and Ben Salem (2001)/Tunisia
Opuntia spp.	92	116	–	–	93	689	754	Tegegne (2001)/Ethiopia
Opuntia spp.	100	38	197	–	154	–	900	Azócar (2001)/Chile
O. ficus-indica cv. Italiana/455 days	37	73	252	235	–	–	–	Adapted from Ramos et al. (2011)/Brazil
O. ficus-indica cv. Gigante	126	44	262	200	–	618	–	Wanderley et al. (2002)/Brazil
O. ficus-indica cv. IPA-20	138	60	284	194	–	467	–	Batista et al. (2003)/Brazil
O. imbricate	930	33	513	147	–	–	–	Cerrillo and Juárez (2004)/Argentina
O. leptocaulis	940	34	448	164	–	–	–	Cerrillo and Juárez (2004)/Argentina
N. cochenillifera	120	62	269	165	–	462	–	Batista et al. (2003)/Brazil
N. cochenillifera/2 years	103	55	373	202	–	424	–	Torres et al. (2009)/Brazil

[a] DM = dry matter; CP = crude protein; NDF = neutral detergent fiber; ADF = acid detergent fiber; CF = crude fiber; NFC = non-fiber carbohydrates; IVDMD = *in vitro* dry matter digestibility.
[*] Neutral detergent fiber corrected for ash and protein.
[#] *In vitro* organic matter digestibility.

O. ellisiana, O. engelmannii Salm Dyck, *O. chrysacantha* Berg, *O. amyclae*, *O. rastrera* Weber, and *Nopalea cochenillifera* Salm Dyck. The nutritional value varies according to the cactus species; in general, *Nopalea cochenillifera* presents greater dry matter and soluble carbohydrate concentrations compared to cultivars of *O. ficus-indica*. From the agronomic point, *Opuntia stricta* has presented less demand of nutrients and it has been more tolerant to drought conditions than *Nopalea cochenillifera* (Inácio et al., 2020). Nevertheless, *Nopalea cochenillifera* Salm-Dyck. has typically shown greater nutritive value than *Opuntia stricta* (Haw.) Haw (Silva et al., 2018). *Opuntia* species, however, are the most cultivated in the world for fodder production. The chemical composition of cacti by species and location are presented in Table 1.

The nutritive value also varies among cactus cultivars. In NE Brazil, Batista et al. (2009) evaluated the chemical composition of eight cactus cultivars. They observed greater dry matter and lesser ADF concentrations in *Nopalea cochenillifera* cv. 'Miuda' compared to *Opuntia* cultivars ('Gigante', 'IPA-20', 'Additional 1258', 1267 Algeria and 1317 Chile). *Opuntia* cv. 'Gigante' and 'Algerian' presented greater CP concentration compared to other cultivars (Table 2). Additionally, Batista et al. (2003) also compared three cactus cultivars ('Miuda', 'Gigante', and 'IPA-20') and observed that true protein concentration was similar among cultivars, averaging 511 g/kg CP, indicating a great proportion of non-protein N. The cultivars also varied in ADF, ranging from 160 g/kg for the *Nopalea cochenillifera* cv. 'Miuda' to 189 g/kg for *Opuntia ficus-indica* cv. 'Gigante'. In South Africa, Mokoboki and Sebola (2017) observed that the cactus nutritive value varied among different varieties within the same genus (Table 3). In Argentina, Guevara et al. (2004) observed that cactus nutritive value varied not only with environmental factors, but also within and among species, mainly among *O. inermis* clones (Table 4).

The major form of calcium (Ca) in cacti is calcium oxalate. Tovar-Puente et al. (2007) evaluated 15 cactus cultivars (*Opuntia* and *Nopalea*) and observed no difference in the oxalate crystal density among the different cladode areas, but the authors found differences among cultivars. Oxalates render Ca unavailable for livestock production, therefore, Ca supplementation is needed when feeding cactus, despite the usual great Ca concentration observed in *Opuntia* and *Nopalea*.

Du Toit et al. (2018) observed that the calcium oxalate crystal morphology was different as the crystals were bigger (ranged from 30 to 100 μm) and more abundant in the fresh cladode tissues of the three *O. ficus-indica* cultivars (Algerian, Morado and Gymno-Carpo) than in *O. robusta*, which were smaller (ranging from 6 μm to 35 μm), rounder, very scarce, and mostly observed close to the epidermis. This had an effect reducing calcium concentration in *O. robusta*.

3. Environment

3.1. Water

The environment, mainly the soil and climate, may exert a major effect on the quality of forage. Air temperature and humidity, soil moisture, and light are often the main factors affecting forage quality in a given location, season, or growth stage.

Abidi et al. (2009) observed that cactus chemical composition was affected by the season of the year. In general, the chemical composition presented greater values during the rainy season compared to the dry season. The chemical composition during the year varied more for *Opuntia ficus indica* f. inermis compared to *Opuntia amyclae* (Table 5). The authors explained that during the summer the reduction in organic matter may be explained by water loss and Ca accumulation.

Differences in chemical composition of cactus cladodes may result from the physiological adjustment of the plant to the environmental conditions. Because Ca is important for the stomatal opening mechanism, Contreras-Padilla et al. (2011) observed that Ca accumulation in cladodes may be related to water-deficit stress. The apoplastic Ca concentration must be kept at low levels to avoid stomata opening, and this mechanism is essential for CAM plants, which must keep their stomata closed during the daylight when water deficit occurs. This Ca behavior may also be explained by the increased mucilage during the dry season (Table 5). The mucilaginous components contain polymers such as chains of (1–4)-linked β-D-galacturonic acid and R(1–2)-linked L-rhamnose residues

Table 2
Chemical composition of cactus cladodes from different species/cultivars in northeast Brazil.

Variable	Gigante g/kg	Miúda	IPA-20	IPA-90−92	IPA-90−155	Additional 1258	1267 Algeria	1317 Chile	SEM
DM	153 bc	187 a	156 bc	165 ab	170 ab	148 bc	126 c	138 bc	7.1
Ash	81 b	81 b	72 bc	78 bc	68 c	76 bc	94 a	79 bc	2.6
EE	24	20	20	23	23	19	17	23	1.9
NDF[a]	248	241	247	255	263	241	246	249	6.3
ADF[a]	179 ab	148 c	185 ab	178 ab	207 a	162 bc	183 ab	158 bc	7.1
Lignin	13 ab	13 ab	13 ab	12 ab	13 ab	17 ab	7 b	10 b	1.4
Starch	207	205	198	194	204	190	193	195	14.2
WSC[a]	154	146	166	150	153	161	141	165	12.2
TC[a]	625 b	660 ab	690 a	690 a	711 a	666 ab	617 b	633 b	14.0
CN[a]	398 bc	439 abc	439ab	462 ab	468 a	445 abc	381 c	404 abc	15.0
CP	44 a	33 b	33 b	34 b	37 b	36 b	44 a	39 b	1.3

The means followed by the same letter in the same row do not differ (P > 0.05) by the Tukey Test.
[a] NDF = neutral detergent fiber; ADF = acid detergent fiber; WSC = water-soluble carbohydrate; TC = total carbohydrate; CN = Non-structural carbohydrates.
Source: Batista et al. (2009).

Table 3
Nutritive value from cladodes of different varieties of *Opuntia* sp. Grown in South Africa.

Varieties	OM g/kg, DM basis	CP	ADF	NDF	Hemicellulose	NFC	TDN
Algerian	777 c	81 c	76 e	137 c	60 d	622 c	766 a
Morado	788 d	95 b	104 b	209 a	104 b	550 e	745 c
American giant	731 a	62 d	112 a	187 c	74 c	632 b	739 d
Redtan	797 c	102 a	91 d	199 b	107 a	557 d	755 b
CrossX	816 b	61 d	93 c	167 d	74 c	645 a	698 e
SE	004	0051	0039	0026	0058	0019	0004

OM – Organic matter, CP – Crude protein, ADF – Acid detergent fibre, NDF – Neutral detergent fibre, NFC – Non fibre carbohydrates, TDN – Total digestible nutrients.
Source: adapted from Mokoboki and Sebola (2017).

Table 4
Nutritive value from cactus cladodes of different species grown in Argentina.

Clone	DM[a] *g/kg, DM basis*	OM	*In vitro* OM Digestibility	CP	NDF	ADF
O. inermis (SR)[b]	89	868 a	695 c	42	238	143
O. inermis (C)	91	868 a	805 a	41	271	146
O. inermis (SJ)	87	845 b	818 a	50	236	160
O. paraguayensis (LC)	115	837 b	802 a	32	238	148
O. paraguayensis (LR)	110	837 b	821 a	36	227	120
O. robusta (R)	73	816 b	814 a	43	227	153
O. spinulifera (S)	74	835 b	767 b	37	229	160

[a] DM, dry matter; OM, organic matter; CP, crude protein; NDF, neutral detergent fiber; ADF, acid detergent fiber.
[b] *(SR) – O. ficus-indica L. f. inermis (Web.) clone San Rafael, collected in Argentina; (C) – O. ficus-indica L. f. inermis (Web.) clone Cuenca, introduced from Mexico; (SJ) – O. ficus-indica L. f. inermis (Web.) clone San Juan, collected in Argentina; (LC) – O. paraguayensis K. Sch clone La Consulta, collected in Argentina; (LR) – O. paraguayensis K. Sch clone La Remonta, collected in Argentina; (R) – O. robusta Wend., collected in Argentina; (LR) – O. spinulifera Salm-Dyck f. nacuniana, introduced from México*.
Source: adapted from Guevara et al. (2004).

Table 5
Chemical composition (g/kg dry matter) of cactus cladodes in different seasons.

Variable	Spineless cactus (*O. ficus indica* f. inermis)		Spiny cactus (*O. amyclae*)	
	rainy season	dry season	rainy season	dry season
Mucilage, g/kg fresh wt.	6.0	13.0	6.4	14.0
Dry matter, g/kg	66.0	191.0	67.0	157.0
Organic matter, g/kg	856.0	697.0	742.0	740.0
Crude protein, g/kg	58.5	29.7	71.0	42.8
Neutral detergent fiber (NDFom), g/kg	248.0	270.0	253.0	246.0
Acid detergent fiber (ADFom), g/kg	205.0	155.0	196.0	166.0
Lignin, g/kg	69.0	41.0	63.0	42.0
Ca, g/kg	78.0	92.0	84.0	84.0
P, g/kg	1.1	0.4	0.8	0.5
K, g/kg	45.8	23.7	46.9	24.1
Na, g/kg	17.0	31.0	23.0	31.2
Mg, g/kg	9.4	11.5	1.2	1.3
Mn, mg/kg DM	40.2	27.3	25.1	27.7
Cu, mg/kg DM	4.6	8.5	10.6	10.2
Zn, mg/kg DM	23.2	11.9	17.9	14.5
Fe, mg/kg DM)	277.0	130.0	345.0	217.0
Total oxalates, g/kg	105.0	102.0	110.0	118.0

Source: adapted from Abidi et al. (2009).

(Trachtenberg and Mayer, 1981; Lee et al., 2003). Osuna-Martínez et al. (2014) suggested the physiological role of the plant mucilage is to regulate the cellular water content during prolonged drought and to regulate the calcium fluxes of the plant. These authors also reported the antioxidant activity of cactus (Opuntia ficus-indica) protecting cells against oxidative damage, acting as radical scavengers, reducing lipid peroxidation, and increasing glutathione levels. Among the most important phytochemicals found in *Opuntia ficus-indica* there are compounds such as flavonoids (*e.g.* quercetin, isorhamnetin, luteolin, and kaempferol), betanin, betacyanin, betalain, and beta-carotene.

Zañudo-Hernández et al. (2010) indicated that the thickness of parenchyma tissue in *Opuntia spp*., where most of the water is stored in the cladodes, was notably reduced as the drought conditions progressed, especially in cladodes exposed to full sunlight. However, the chlorenchyma thicknesses in cladodes presented only minor changes during the wet and dry periods, suggesting that the water transport proceeds from the parenchyma to the chlorenchyma, and the lateral movement of water from the parenchyma tissue during drought period will sustain stomatal opening, keeping the photosynthetic tissue active. Furthermore, the synthesis of chlorophyll is affected by reductions in tissue water potential, reducing daily net CO_2 uptake and decreasing susceptibility to photodamage. During this process, it is observed a decrease of tissue N, with the chlorenchyma becoming the source of N during the drought season and other occasions in which these resources are scarce (Zegbe and Serna-Pérez, 2017). The ability of the parenchyma tissue to release water towards the chlorenchyma to store, provides an efficient effect on many physiological responses to drought, whereas chlorenchyma thickness shows little changes between drought and wet periods (Scalisi et al., 2016). This mechanism was also observed for *Opuntia ficus-indica* Mill (Nerd and Nobel, 1995).

Alves et al. (2016a) showed in different cactus pear varieties of the genera *Opuntia* and *Nopalea* greater expressive levels of carbohydrates, glucoside substances, and phenolic compounds accumulated in the rainy season. This is an adaptation to withstand the dry season, that act in the osmotic adjustment and protection against reactive oxygen species, as well as to stabilize proteins and cell membranes in plants exposed to stresses in the dry season.

3.2. Light environment

Horibe et al. (2016) studied the effect of constant light with different wavelengths on the growth of *Opuntia sp*., red light emission of 660 nm and blue light emission of 440 nm all at a photosynthetic photon flux density of 180 mol/m^2/s. They observed that the starch concentration, cladode growth, and cladode number were enhanced at the longer wavelength. Starch and sugar play a major role in guard cell osmoregulation, increasing stomatal opening followed by an increase in photosynthetic activity, with the light being a strong modulator of these processes (Lee, 2010). Thus, the reduction in non-structural carbohydrates in shaded cacti is due to a reduction in the photosynthetic activity.

3.3. Soil nutrients

Cladode nutrient concentration may also be affected by soil nutrients. Galizzi et al. (2004) observed that the cladode N concentration displayed a positive correlation with soil Mg concentration. The authors argued that this result was due to Mg being a component of the chlorophyll molecule and is also associated with the enzyme RUBISCO (ribulose 1,5 biphosphate carboxylase-oxygenase), the most common protein in plants. Galizzi et al. (2004) also observed a positive correlation between the soil pH and concentrations of Ca, Mg, and K in the cladodes, likely due to the greater cation solubility with increasing soil pH.

4. Agronomic aspects

4.1. Planting density

Cactus chemical composition is also affected by planting density. Dubeux et al. (2006) evaluated different cactus (*Opuntia ficus-indica* Mill.) planting densities in NE Brazil and observed greater cladode N concentration at lesser population densities, *i.e.*, 5000 plants/ha (11.2 g/kg) as opposed to 40,000 plants/ha (9.0 g/kg). The authors explained this behavior by the larger number of younger cladodes in the less dense population. In contrast, Ramos et al. (2011) did not observe a significant effect of plant spacing on the DM, ash, OM, ADF, and CP values for the same species, whereas the NDF was affected by the plant spacing, with lesser values observed in the less dense population (10,000 plants/ha).

Souza et al. (2017) observed in *Nopalea cochenillifera* that increasing planting density resulted in greater productivity and reduced the concentration of most minerals (N, P and K), except sulphur (S), explained by dilution effect. Furthermore, competition for nutrients, water, and light among plants increase with greater plant density. Mello et al. (2019) indicated that plant competition might decrease growth rate of individual plants, which can increase nutrient concentration in the forage mass. Cladode P concentration increased from 1.59 to 3.31 g/kg DM at planting densities of 6944 and 41,646 plants/ha, respectively.

4.2. Fertilizer application

Cladode chemical composition is affected by fertilizer application, since the protein and mineral concentrations are sensitive to modifications in plant nutrient supply (Felker et al., 2006). Dubeux et al. (2006) demonstrated a CP increase in cactus cladodes with increasing N fertilization levels and with a reduction in plant population density. The CP ranged from 47 g/kg in the absence of N and P fertilization and at a dense population of 40 000 plants/ha increasing to 79 g/kg when N and P were applied at 5 000 plants/ha. Considering the greater DM productivity at more densely planted orchards, total N availability for livestock production will be greater at denser cactus population density, particularly when well fertilized (Silva et al., 2016).

Souza et al. (2017) observed an effect of N and P fertilization on cladode N and P concentration in *N. cochenillifera*, Salm Dyck. The concentrations of these elements in the cladodes increased with increasing levels of N and P fertilization. González (1989) reported a CP variation in *Opuntia*, ranging from 45 g/kg in the absence of fertilization to 105 g/kg when 224 kg N and 112 kg P were applied per ha. Cladode P concentration increased from 0.8 to 1.8 g/kg with the same treatments. It is important to notice that fertilization not only may improve cactus chemical composition, but also increases cactus biomass yield (Silva et al., 2016).

Dubeux et al. (2010) evaluated the effect of P and K fertilization on the chemical composition of *Opuntia* cladodes and reported that P fertilization promoted reductions in Ca, N, Mg, K, and S. Potassium fertilization reduced Ca and increased the S concentration in cactus cladodes (*O. ficus-indica* Mill. cv IPA 20). Conversely, Teles et al. (2004) did not find any effect of mineral fertilization on the Ca, Mg, and K concentrations in the cladodes of *O. ficus-indica* at six months of age. The authors observed that this result was likely due to the soil fertility of the tested soil. There are numerous research results also addressing the effect of soil fertility and fertilizer application on cactus biomass productivity, but the focus of the current review is on cactus nutritive value. The macro and micro mineral concentrations of cactus cladodes are presented in Tables 6 and 7, respectively. In general, it is noteworthy that K and Ca are present in greater concentrations compared to other nutrients. Often, semiarid soils are rich in these two elements, which may reduce problems of nutrient deficiency. Cactus micro mineral concentration is highly variable and depend on different factors, such as the species, soil characteristics, and method of analysis.

5. Harvest management

Harvest management includes two major aspects affecting cactus chemical composition: harvest frequency and harvest intensity. The harvest frequency defines the growth stage when the plants will be cut, and the harvest intensity refers to which portion of the plant will be cut. The chemical composition varies in both situations. Pinos-Rodríguez et al. (2010) evaluated the chemical composition and digestibility of cactus cladodes (*O. ficus-indica* Mill.) at different ages, 30, 37, 45, 60, 75, and 90 days, using cacti grown under irrigation and N fertilization (90 kg N/ha/yr). It was observed that the CP and digestibility of the cladodes decreased linearly with maturity, whereas the NDF and ADF increased linearly with increasing cladode maturity. Ramírez-Tobías et al. (2007) reported similar results.

In Northeast Brazil, cactus cladodes are usually harvested after two years of growth for animal fodder. The biomass produced above the primary cladodes is removed, and the remaining cladodes of the original plant are important to accelerate regrowth after harvesting. Thus, the chemical composition of the harvested material is a mixture of cladodes of different ages. Farias et al. (2000) tested different harvest management methods for *O. ficus-indica* Mill., reporting that, despite significant effects of harvest management on cactus productivity, differences regarding the chemical composition occurred at a lower magnitude (Table 8). The harvest intensity did not affect the DM concentration, but harvesting every four years (instead of every two) increased the DM concentration at 2×1 m plant spacing. In addition, the harvest intensity affected the crude protein, with greater values observed when the primary cladodes were not harvested.

Pessoa et al. (2020) evaluated the chemical composition of cladodes of five varieties of *Opuntia* in different phenological phases. In general, they observed greater concentrations of NDF in cladodes at the mature phase, which is possibly related to the complete development of the cladode. In addition, more mature cladodes produced lesser volumes of *in vitro* gas production, which is associated with lesser concentration of the indigestible fraction (C fraction) of carbohydrates, and greater availability of fast digestion carbohydrates. Conversely, younger cladodes had greater NFC concentration in comparison with intermediate and mature phase.

6. Storage and preservation

The storage of cactus after harvesting may reduce labor and transportation costs, depending on the distance from the field to the feeding area. The cladodes may be stored fresh, as harvested from the field, or they may be preserved as silage or dried. The storage of fresh cactus was evaluated by Santos et al. (1992). In that study, cladodes of different cactus cultivars were placed in piles and stored under the shade, being evaluated after different time periods. The results showed no effect of storage period up to 16 days on losses of DM, CP, crude fiber, and soluble carbohydrates (Table 9). Thus, a large quantity of cacti may be harvested at once and stored up to 16

Table 6
Macronutrient concentration of cactus cladodes.

Species	N g/kg	P	K	Ca	Mg	S	Source
O. ficus-indica	–	3.9	63.3	34.4	9.5	0.2	Hernández-Urbiola et al. (2011)
O. ficus indica f. inermis	9.4	0.4	23.7	92.0	11.5	–	Adaptado Abidi et al. (2009)
O. amyclae	6.8	0.5	24.1	84.0	1.3	–	Adaptado Abidi et al. (2009)
O. ficus-indica cv. Clone IPA-20	20.6	4.7	33.4	34.4	7.4	6.1	Dubeux et al. (2010)[a]
O. engelmannii	21.1	2.0	36.9	38.1	18.4	—	Nobel et al. (1987)[b]
O. ficus-indica	11.9	1.7	33.2	18.4	5.9	1.7	Teles et al. (2004)[c]
O. ficus-indica f. inermis		1.5	23.5	56.4	1.9		Ben Salem et al. (2005)
O. stricta	12.9	0.74	4.3	13.4	6.1	0.8	Alves et al. (2016b)
O. atropes	9.2	2.0	2.3	17.2	5.7	1.3	Alves et al. (2016b)
O. larreri	13.7	1.0	4.3	7.3	6.3	1.1	Alves et al. (2016b)
O. ficus-indica cv. Clone IPA-20	9.6	6.0		48.0	15.0		Batista et al. (2003)[d]
N. cochenillifera	9.9						Batista et al. (2003)[d]

[a] 400 kg N/ha.
[b] study performed in Texas, USA.
[c] N - 200 kg/ha; P_2O_5 −100 kg/ha; K_2O - 200 kg/ha; Ca - 250 kg/ha; Mg −80 kg/ha and S - 20 kg/ha.
[d] N−100 kg/ha; P_2O_5 −150 kg/ha and K_2O -100 kg/ha.

Table 7
Micronutrient concentration in cactus cladodes.

Species	Fe mg/kg	Zn	Mn	Cu	B	Na	Source
O. ficus-indica	84.5	108.6	686.9	6.5	–	–	Dubeux et al. (2010)
O. ficus-indica	1678	37	489	1.9	29.4	–	Lédo et al. (2020)
O. stricta	69.2	34.7	418.9	2.1	–	110	Alves et al. (2016b)
O. atropes	44.4	31.0	246.1	–	–	140	Alves et al. (2016b)
O. larreri	14.6	36.7	371.7	–	–	110	Alves et al. (2016b)
N. cochenillifera	28.2	27.9	450.3	–	–	110	Alves et al. (2016b)
O. engelmannii	73.0	31.0	92.0	4.3	23.0	179.0	Nobel et al. (1987) [a]
O. engelmannii	38–72	6–21	18–43	3.3–4.6	1–8	42–120	Nobel et al. (1987) [b]
O. ficus-indica f. inermis	1.38	35.53	17.48	5.55	–	4.0	Ben Salem et al. (2005)

[a] Texas, USA.
[b] Coahuila, México.

Table 8
Chemical composition of cactus cladodes (*Opuntia ficus-indica* Mill), as affected by plant spacing and harvesting management; São Bento do Una-PE, Brazil.

Treatment	DM *g/kg*	CP	CF	Cellulose
Plant spacing				
2.0 × 1.0 m	101a	45a	109a	138a
3.0 × 1.0 × 0.5 m	94b	45a	113a	142a
7.0 × 1.0 × 0.5 m	91b	48a	105a	138a
Harvest frequency				
Two years	94b	46a	98b	133b
Four years	97a	46a	119a	146a
Harvest intensity				
Preserving primary cladodes	95a	48a	106a	140a
Preserving secondary cladodes	96a	44b	112a	139a
Mean	95	46	109	139

The means followed by the same letter within each response variable and in the same column do not differ (P > 0.05) by the Tukey test.
Source: Adapted from Farias et al. (2000).

days, reducing both labor and transportation costs. After storage periods under the shade up to 16 days, a small variation was observed in the DM, CP, EE, ash, and non-N extract concentrations of cactus cladodes (*O. ficus-indica* Mill. cv. 'Gigante') harvested at four years of age (Santos et al., 1998). Silva et al. (2017) observed that *Opuntia stricta* maintains its nutritional value stable, when subjected to different storage times up to 21 days, and the intake behavior of Girolando heifers does not differ between treatments with *Opuntia stricta* (non-stored, or stored for 7, 14, and 21 days), and the *Nopalea cochenillifera* (control).

Carvalho et al. (2020) found that post-harvest storage for up to 60 days in cactus cultivars did not compromise forage quality. Longer storage periods (> 16 days) for cactus cladodes may further reduce operation costs; however, it is not known what effect long-term storage will have on the rate of deterioration, anatomy, and integrity of cactus cladodes.

The air temperature does affect the chemical composition of stored cladodes. Cantwell et al. (1992) evaluated the effect of the

Table 9
Chemical composition of cactus cladodes of different cultivars subjected to different post-harvest storage periods.

Cultivar		Storage period (days after harvest)					Mean	CV[b] (%)
		0 *g/kg*	4	8	12	16		
'Redonda'	DM[a]	153a	152a	176a	152a	161a	159	12
	CP	35[a]	36a	39a	36a	37a	37	14
	WSC	279a	309a	296a	282a	291a	291	12
'Gigante'	DM	138a	146a	170a	147a	153a	151	11
	CP	39[a]	41a	41a	40a	41a	40	10
	WSC	262b	330a	295ab	294ab	297ab	295	10
'Miúda'	DM	225b	228b	237ab	242a	238ab	234	3
	CP	22[a]	22a	22a	22a	21a	22	12
	WSC	566a	574a	588a	577a	592a	579	5

The means followed by the same letter in the same row do not differ (P > 0.05) by the Tukey Test.
[a] DM = dry matter; CP = crude protein; WSC = water-soluble carbohydrates.
[b] Coefficient of variation.
Source: Adapted from Santos et al. (1992).

storage temperature on the chemical composition of young cactus cladodes (*O. ficus-indica* and *O. inermis*), varying from 10−20 cm in length, which were stored for 30 days at different temperatures. The authors observed that the cladodes stored up to nine days at temperatures of 10, 15, and 20 °C presented reductions in the titratable acid content, and this variable increased when the cladodes were stored at 5 °C. The authors indicated that the principal respiratory substrates in CAM tissues held at high temperatures are organic acid. Therefore, warmer temperatures lead to greater respiration rates, depleting the organic acid reserves.

Rodriguez-Felix (2002) observed that cladodes develop chilling injury during storage at temperatures below 12 °C. Furthermore, cladodes of *Nopalea cochenillifera* are more chilling-injury sensitive than those of *Opuntia* spp., which is manifested as surface discoloration and softening of the cladode. Cold storage increases the postharvest life by retarding respiration, ethylene production, ripening, senescence, undesirable metabolic changes, and decay chemical composition.

Cactus is usually fed to animals as fresh forage in a cut-and-carry operation, yet forage preservation may be an alternative for cactus cladodes that are fed as silage or hay (FAO, 2011). The dehydration of cactus cladodes, however, is not an easy operation, as it involves labor and costs associated with the chopping and drying of the cladodes. Cactus silage also presents limitations because of the high moisture of the ensiled material. Considering that cactus does not lose its nutritive value rapidly, preservation techniques should be used only if economic benefits associated with transportation and labor costs occur. Recent research has emerged in South Africa evaluating the potential use of sun-dried and coarsely ground cactus in feedlot diets (de Waal et al., 2006; Einkamerer et al., 2009; Menezes et al., 2010; de Waal et al., 2013). Inclusion of sun-dried cactus and sunflower oilcake meal resulted in similar lamb performance and carcass characteristics to animals on conventional feedlot diet (de Waal et al., 2013). de Waal et al. (2006) observed that the inclusion of sun-dried coarsely ground cactus (*Opuntia ficus-indica* var. Algerian) increased water intake and resulted in wet faeces, while urine excretion showed little increase. They concluded that the wetter faeces produced by sheep on sun-dried cactus diets occurred because larger quantities of water that were not reabsorbed from the lower digestive tract. In another research, Menezes et al. (2010) observed that inclusion of sun-dried coarsely ground cactus (*Opuntia ficus-indica*) from 0 up to 36 % led to production of wet faeces, and they indicated that occurred because of presence of mucilage in the cactus. However, this did not cause any detrimental effects and inclusion of sundried cactus increased intake and digestibility. This utilization has potential to establish a feed commodity market for cactus in semiarid regions. In fact, commercial farms are already using this process in South Africa with successful results in terms of animal performance in the feedlot.

The dehydration of cacti for use in animal feed has recently been studied (Aguilar-Yáñez et al., 2011; Andrade et al., 2016) because it has been suggested that, if cacti are to be transported for long distances, dehydration will drastically reduce the transportation costs. However, the water lost in such a process may reduce the benefit of the water contained in cacti that is utilized by animals during drought conditions. Cactus meal, the product after chopping and dehydrating cacti, may be used as an ingredient in total mixed rations or may be enriched with additives aiming to increase the protein concentration (Silva et al., 2017; Cruz et al., 2020).

Dehydration might have a negative effect on cactus nutritive value because of losses during the drying process. Andrade et al. (2016) evaluated the effect of cactus meal (dehydrated cactus) use on sheep performance by replacing Tifton 85 (*Cynodon* spp.) hay with fresh cactus (*Nopalea cochenillifera* Salm Dyck) or cactus meal. The authors did not report a difference between the chemical composition of the fresh cactus and cactus meal (Table 10), and the sheep performance and carcass yield were similar when the cactus was fed fresh or dehydrated. Véras et al. (2005) replaced maize with dehydrated cactus (0, 33, 67, and 100 %) and evaluated the performance of growing 'Santa Inês' lambs. The weight gain, energy intake and feeding conversion were reduced with increasing the proportion of cactus in the diet, whereas the dry matter and OM intake, CP intake, carbohydrate intake, and carcass yield were not affected by the replacement.

Combining additives with dehydrated cactus may increase its nutritive value. Araújo et al. (2008) evaluated the protein enrichment of cacti (*O. ficus-indica* Mill) with *Saccharomyces cerevisiae* in a semi-solid medium and found that yeast at 5, 10, and 15 % increased the cactus CP to 144, 220, and 260 g/kg, respectively. Also observed an increase in CP concentration of cactus cladodes from 44 to 104 g/kg after submitted to a semi-solid culture with *Saccharomyces cerevisiae* yeast (3% inoculum concentration on a fresh matter basis).

Aguilar-Yáñez et al. (2011) evaluated the inclusion of fresh or dehydrated cacti on lamb performance. In both situations, the cactus represented 17 % of the total diet on a DM basis. No significant differences were observed for weight gain, but an economic analysis showed a net gain of 25 and 37 % for the dehydrated and fresh cacti, respectively, compared to the diet without cactus.

Çürek and Özen (2004) evaluated the nutritive value of fresh cactus and silage by examining the chemical composition and *in situ* digestibility of both young and mature cladodes. The ensiled cactus had lower concentrations of organic matter (OM), CP, non-N extract, and total digestible nutrients (TDN) compared to the fresh cactus, and the mature cladodes produced a better silage compared to the young cladodes.

7. Antinutritional aspects

Cactus are known to be an important source of bioactive compounds, such as polyphenols, carotenoids and minerals, and due to a wide genetic diversity in *Opuntia* and *Nopalea* genera, there is a need to characterize the chemical profile and bioactive properties (Alves et al., 2017).

Alves et al. (2016a) evaluated secondary and tertiary cladodes of different 3-yr. old cactus species (*O. fícus-indica*, *O. stricta*, *O. atropes*, *O. larreri,* and *Nopalea cochenillifera*) regarding the presence of antinutritional compounds. They observed more expressive levels of glucoside substances and phenolic compounds (tannins and flavonoids) in the rainy season than in the dry season. This might be a physiological strategy to prevent oxidation by free radicals, reactive forms of oxygen and stabilize proteins and cell membranes in plants exposed to water stresses in the dry season. Lesser concentrations of bioactive compounds (total phenolics and condensed tannins), respectively, were found by Silva et al. (2011) in *O. ficus-indica*, which showed an average of 168 and 120 mg/100 g of

Table 10
Chemical composition of cactus cladodes (*Nopalea cochenillifera* cv 'Miuda') fed fresh or dehydrated.

Variable	Fresh Cactus	Dehydrated Cactus
DM, g/kg	73	822
OM, g/kg	815	808
CP, g/kg	80	80
EE, g/kg	10	9
NDF, g/kg	272	251
NFC, g/kg	454	467
Ash, g/kg	185	192
Ca, g/kg	23	23
P, g/kg	2	2

Source: Adapted from Andrade et al. (2016).

catechin, or 1.7 and 1.2 when expressed as g/kg DM. This concentration is below the level considered harmful to the health of animals.

Batista et al. (2009) evaluated the oxalate concentration from different cactus cultivar (Miúda genus *Nopalea* and Gigante, Chile, Algeria, IPA-20, IPA-90−92, IPA-90−155, and Additional 1258 genus *Opuntia*) harvested every 2 years. They observed that oxalate concentration was not affected by cultivar, getting an average of 1.7 g/kg. Oxalate synthesis is a mechanism that can reduce the negative impact of excessive calcium uptake by cactus.

Silva et al. (2020) found the oxalate concentration in *Nopalea cochenillifera* – varieties Miúda and IPA-Sertânia, and *O. stricta*, 18, 21, and 26 g/kg DM, respectively. They fed these cacti to lambs and observed that the presence of oxalates affected the morphological parameters of the fore stomach, that is, vacuolization in the keratinized layer. They considered oxalate an antinutritional constituent capable of triggering a tissue defense mechanism, suggesting an abrasive effect on the keratin of the ruminal mucosa, thus provoking an increase in the size of the dead cells that make up this layer.

In goat kid diets with *Nopalea cochenillifera*, the concentration of hydrocyanic acid (HCN) was 51 mg/kg, and that did not affect total digestible OM, nutrient intake, feeding behavior, productive performance, and carcass characteristics (Ferraz et al., 2018). Dessimoni et al. (2014) reported nitrate concentration of 83 mg/100 g DM in *O. ficus-indica*, however, this nitrate level does not present risks to animal health.

8. Conclusion

The germplasm, environment, and management practices affect the nutritive value of cacti, as do the plant spacing, season, harvest management, fertilization, cultivar, storage method, and preservation. Interactions between environment and management factors occur, resulting in contrasting nutritive values. These interactions are site specific and have been studied in different regions of the world. When the appropriate techniques are used, there is a potential to improve livestock productivity in dry environments by combining cactus productivity and its nutritive value. Future areas of research include utilization of invasive cacti (*e.g. Opuntia stricta*) as fodder, use of sun-dried cactus as a feed commodity for dry regions, and ensiling techniques for wasted fruits and cladodes from orchards dedicated to fruit production.

Declaration of Competing Interest

The authors report no declarations of interest.

References

Abidi, S., Ben Salem, H., Martín-García, A.I., Molina-Alcaide, E., 2009. Ruminal fermentation of spiny (Opuntia amyclae) and spineless (*Opuntia ficus indica* f. inermis) cactus cladodes and diets including cactus. Anim. Feed Sci. Technol. 149, 333–340. https://doi.org/10.1016/j.anifeedsci.2008.06.006.

Aguilar-Yáñez, M.I., Hernández-Mendo, O., Guerrero-Legarreta, I., Ramírez-Bribiesca, J.E., Aranda-Osorio, G., Crosby-Galvan, M.M., 2011. Productive response of lambs fed with fresh or dehydrated spineless cactus (*Opuntia ficus–indica* L.). J. PACD 13, 24–35.

Alves, F.A.L., Andrade, A.P., Bruno, R.L.A., Silva, M.G.V., Souza, M.F.V., Pessoa, C., Oliveira, F.C.E., Brito Filho, S.G., Santos, D.C., 2016a. Genetic diversity and seasonal chemical profile by 1H NMR and cytotoxic activity in *Opuntia* and *Nopalea* genres. J. Med. Plants Res. 10, 732–747. https://doi.org/10.5897/JMPR2016.6207.

Alves, F.A.L., Andrade, A.P., Bruno, R.L.A., Santos, D.C., 2016b. Study of the variability, correlation and importance of chemical and nutritional characteristics in cactus pear (*Opuntia* and *Nopalea*). Afr. J. Agric. Res. 11, 2882–2892. https://doi.org/10.5897/AJAR2016.11025.

Alves, F.A.L., Andrade, A.P., Bruno, R.L.A., Silva, M.G.V., Souza, M.F.V., Santos, D.C., 2017. Seasonal variability of phenolic compounds and antioxidant activity in prickly pear cladodes of *Opuntia* and *Nopalea* genres. Food Sci. Technol. 37, 536–543. https://doi.org/10.1590/1678-457x.19316.

Andrade, S.F.J., Batista, A.M.V., Carvalho, F.F.R., Lucena, R.B., Andrade, R.P.X., Lima Júnior, D.M., 2016. Fresh or dehydrated spineless cactus in diets for lambs. Acta Sci. Anim. Sci. 38, 155–161. https://doi.org/10.4025/actascianimsci.v38i2.29329.

Araújo, L.F., Silva, F.L.H., Brito, E.A., Oliveira Júnior, S., Santos, E.S., 2008. Enriquecimento protéico da palma forrageira com *Saccharomyces cerevisiae* para alimentação de ruminantes. Arq. Bras. Med. Vet. Zootec. 60, 401–407. https://doi.org/10.1590/S0102-09352008000200019.

Azócar, P., 2001. *Opuntia* as feed for ruminants in Chile. Cactus (*Opuntia spp.*) As forage, *Opuntia* as feed for ruminants in Chile. Cactus (*Opuntia spp.*) As forage. In: Mondragon-Jacobo, Perez-Gonzalez (Eds.), FAO Plant Production and Protection Papers N°169. FAO, Rome, 161p.

Batista, A.M., Mustafa, A.F., McAllister, T., Wang, Y., Soita, H., McKinnon, J.J., 2003. Effects of variety on chemical composition, in situ nutrient disappearance and in vitro gas production of spineless cacti. J. Sci. Food Agric. 83, 440–445. https://doi.org/10.1002/jsfa.1393.

Batista, A.M.V., Ribeiro Neto, A.C., Lucena, R.B., Santos, D.C., Dubeux Jr., J.C.B., Mustafa, A.F., 2009. Chemical composition and ruminal degradability of spineless cactus grown in Northeastern Brazil. Rang. Ecol. Man. 62, 297–301. https://doi.org/10.2111/07-099R1.1.

Ben Salem, H., Nefzaoui, A., Ben Salem, L., 2002. Supplementing spineless cactus (*Opuntia ficus indica f. inermis*) based diets with urea-treated straw or oldman saltbush (*Atriplex nummularia* L.). Effects on intake, digestion and growth. J. Agric. Sci. 138, 85–92. https://doi.org/10.1017/S0021859601001770.

Ben Salem, H., Abdouli, H., Nefzaoui, A., El-Mastouri, A., Ben Salem, L., 2005. Nutritive value, behaviour and growth of barbarine lambs fed on oldman saltbush (*Atriplex nummularia* L.) and supplemented or not with barley grains or spineless cactus (*Opuntia ficus-indica f. Inermis*) pads. Small Rum. Res. 59, 229–237. https://doi.org/10.1016/j.smallrumres.2005.05.010.

Cantwell, M., Rodríguez-Felix, A., Robles-Contreras, F., 1992. Postharvest physiology of prickly pear cactus stems. Sci. Hort. 50, 1–9. https://doi.org/10.1016/S0304-4238(05)80003-2.

Carvalho, C.B.M., Edvan, R.L., Nascimento, K.S., Nascimento, R.R., Bezerra, L.R., Jácome, D.L.S., Santos, V.L.F., Santana Júnior, H.A., 2020. Methods of storing cactus pear genotypes for animal feeding. Afr. J. Range For. Sci. 2020, 1–7. https://doi.org/10.2989/10220119.2020.1734084.

Cerrillo, M.A., Juárez, R.A.S., 2004. *In vitro* gas production parameters in cacti and tree species commonly consumed by grazing goats in a semiarid region of North Mexico. Liv. Res. Rural Devel. 16, 4–9.

Contreras-Padilla, M., Pérez-Torrero, E., Hernández-Urbiola, M.I., Hernández-Quevedo, G., Real, A., Rivera-Muñoz, E.M., Rodríguez-García, M.E., 2011. Evaluation of oxalates and calcium in nopal pads (*Opuntia ficus-indica* var. redonda) at different maturity stages. J. Food Comp. An. 24, 38–43. https://doi.org/10.1016/j.jfca.2010.03.028.

Cruz, A.A.C., Véras, A.S.C., Oliveira, J.C.V., Santos, D.C., Chagas, J.C.C., Neves, M.L.M.W., Monteiro, C.C.F., Ferreira, M.A., 2020. Sugarcane and cactus cladodes plus urea: a new option for Girolando dairy heifers. R. Bras. Zootec. 49, e20200016. https://doi.org/10.37496/rbz4920200016.

Çürek, M., Özen, N., 2004. Feed value of cactus and cactus silage. Turk. J. Vet. Anim. Sci. 28, 633–639.

de Waal, H.O., Zeeman, D.C., Combrinck, W.J., 2006. Wet faeces produced by sheep fed dried spineless cactus pear cladodes in balanced diets. South Afr. J. Anim. Sci. 36 (Issue 5, Supplement 1), 10–13.

de Waal, H.O., Schwalbach, L.M.J., Combrinck, W.J., Shiningavamwe, K.L., Els, J., 2013. Commercialisation of sun-dried cactus pear (*Opuntia ficus-indica*) cladodes in feedlot diets for Dorper wether lambs. Acta Hort. 995, 343–350. https://doi.org/10.17660/ActaHortic.2013.995.45.

Dessimoni, G.V., Batista, A.G., Barbosa, C.D., Dessimoni-Pinto, N.A.V., 2014. Bromatological and mineral composition and antinutritional factors of cactus pear. Tecnol. Cien. Agropec. 8, 51–55.

Du Toit, A., Wit, M., Hugo, A., 2018. Cultivar and harvest month influence the nutrient content of *Opuntia spp*. cactus pear cladode mucilage extracts. Molecules 23, 916. https://doi.org/10.3390/molecules23040916.

Dubeux Jr., J.C.B., Santos, M.V.F., Lira, M.A., Santos, D.C., Farias, I., Lima, L.E., Ferreira, R.L.C., 2006. Productivity of *Opuntia fícus-indica* (L.) Mill., under different N and P fertilization and plant population in North- east Brazil. J. Arid Environ. 67, 357–372. https://doi.org/10.1016/j.jaridenv.2006.02.015.

Dubeux Jr., J.C.B., Araújo Filho, J.T., Santos, M.V.F., Lira, M.A., Santos, D.C., Pessoa, R.A.S., 2010. Adubação mineral no crescimento e composição mineral da palma forrageira –Clone IPA-201. Rev. Bras. Ciênc. Agrár. 5, 129–135. https://doi.org/10.5039/agraria.v5i1a591.

Dubeux Jr., J.C.B., Schroth, W., Ruiz-Moreno, M., Ferreira, M.A., DiLorenzo, N., Gutierrez-Beltran, M.A., Queiroz, L.D., 2019. Nutritive value of raketamena (*Opuntia stricta*) as a fodder in Madagascar. Acta Hort. 1247, 73–80. https://doi.org/10.17660/ActaHortic.2019.1247.10.

Einkamerer, O.B., de Waal, H.O., Combrinck, W.J., Fair, M.D., 2009. Feed utilization and growth of Dorper wethers on Opuntia-based diets. South Afr. J. Anim. Sci. 39 (Supplement 1), 53–57.

FAO, 2011. Successes and failures with animal nutrition practices and technologies in developing countries. In: Proceedings of the FAO Electronic Conference, 1-30 September 2010. Rome, Italy.

FAO, 2019. Trees, forests and land use in drylands: the first global assessment – full report. FAO Forestry Paper No. 184. Rome.

Farias, I., Lira, M.A., Santos, D.C., Tavares Filho, J.J., Santos, M.V.F., Fernandes, A.P.M., Santos, V.F., 2000. Manejo de colheita e espaçamento da palma-forrageira, em consórcio com sorgo granífero, no Agreste de Pernambuco. Pesq. Agropec. Bras. 35, 341–347. https://doi.org/10.1590/S0100-204X2000000200013.

Felker, P., Paterson, A., Jenderek, M.M., 2006. Forage potential of qpuntia clones maintained by the USDA, National Plant Germplasm System (NPGS) collection. Crop Sci. 46, 2161–2168. https://doi.org/10.2135/cropsci2006.02.0081.

Ferraz, L.V., Guim, A., Véras, R.M.L., Carvalho, F.F.R., Freitas, M.T.D., 2018. Cassava dreg as replacement of corn in goat kid diets. Trop. Anim. Health Prod. 50, 309–315. https://doi.org/10.1007/s11250-017-1432-3.

Galizzi, F.A., Felker, P., González, C., Gardiner, D., 2004. Correlations between soil and cladode nutrient concentrations and fruit yield and quality in cactus pears, *Opuntia ficus–indica*, in a traditional farm setting in Argentina. J. Arid. Environ. 59, 115–132. https://doi.org/10.1016/j.jaridenv.2004.01.015.

González, C.L., 1989. Potential of fertilization to improve nutritive value of prickly pear cactus (Opuntia lindheimeri Engelm.). J. Arid. Environ. 16, 87–94.

Guevara, J.C., Colomer, J.H.S., Estevez, O.R., 2004. Nutrient content of *Opuntia* forage clones in the Mendoza plain, Argentina. J. PACD 6, 62–77.

Hernández-Urbiola, M.I., Pérez-Torrero, E., Rodríguez-García, M.E., 2011. Chemical analysis of nutritional content of prickly pads (*Opuntia ficus indica*) at varied ages in an organic harvest. Int. J. Environ. Res. Public Health. 8, 1287–1295. https://doi.org/10.3390/ijerph8051287.

Horibe, T., Iwagawa, Y., Kondo, H., Yamada, K., 2016. Hydroponics culture of edible *Opuntia* 'Maya': effect of constant red and blue lights on daughter cladodes growth and spine development. Environ. Control Biol. 54, 165–169. https://doi.org/10.2525/ecb.54.165.

Inácio, J.G., Conceição, M.G., Santos, D.C., Oliveira, J.C.V., Chagas, J.C.C., Moraes, G.S.O., Silva, E.T.S., Ferreira, M.A., 2020. Nutritional and performance viability of cactus *Opuntia*-based diets with different concentrate levels for Girolando lactating dairy cows. Asian. Australas. J. Anim. Sci. 33, 35–43. https://doi.org/10.5713/ajas.18.0916.

Lédo, A.A., Donato, S.L.R., Aspiazu, I., Silva, J.A., Donato, P.E.R., Carvalho, A.J., 2020. Nutrient concentration and nutritional efficiency in 'Gigante' cactus pear submitted to different spacings and fertilizations. Rev. Bras. Eng. Agríc. Amb. 24, 154–161. https://doi.org/10.1590/1807-1929/agriambi.v24n3p154-161.

Lee, J.S., 2010. Stomatal opening mechanism of CAM plants. J. Plant Biol. 53, 19–23. https://doi.org/10.1007/s12374-010-9097-8.

Lee, E.H., Kim, H.J., Song, Y.S., Jin, C., Lee, K.T., Jungsook, C., Lee, Y.S., 2003. Constituents of the stems and fruits of Opuntia ficus-indica var. saboten. Arch. Pharm. Res. 26 (12), 1018–1023. https://doi.org/10.1007/BF02994752.

Leegood, R.C., 2013. Photosynthesis. In: Lennarz, W.J., Lane, M.D. (Eds.), Encyclopedia of Biological Chemistry. Academic Press, Cambridge, pp. 492–496.

Lopes, L.A., Ferreira, M.A., Batista, A.M.V., Maciel, M.V., Andrade, R.B., Munhame, J.A., Silva, T.G.P., Cardoso, D.B., Véras, A.S.C., Carvalho, F.F.R., 2020. Intake, digestibility, and performance of lambs fed spineless cactus cv. Orelha de Elefante Mexicana. Asian. Australas. J. Anim. Sci. 33, 1284–1291. https://doi.org/10.5713/ajas.19.0328.

Mayer, J.A., Cushman, J.C., 2019. Nutritional and mineral content of prickly pear cactus: a highly water-use efficient forage, fodder and food species. J. Agro. Crop Sci. 205, 625–634. https://doi.org/10.1111/jac.12353.

Mello, A.C.L., Silva, R.M., Souza, T.C., Dubeux Jr., J.C.B., Lira, M.A., Santos, M.V.F., Coêlho, J.J., Santos, D.C., Cunha, M.V., 2019. Nutrient concentration in spineless cactus under different planting densities and harvesting management. Acta Hort. 1247, 137–142. https://doi.org/10.17660/ActaHortic.2019.1247.19.

Menezes, C.M.Dda C., Schwalbach, L.M.J., Combrink, W.J., Fair, M.D., de Waal, H.O., 2010. Effects of sun-dried *Opuntia ficus-indica* on feed and water intake and excretion of urine and faeces by Dorper sheep. South Afr. J. Anim. Sci. 40 (Issue 5, Supplement 1), 491–494.

Mokoboki, K., Sebola, N., 2017. Chemical composition and feed intake of *Opuntia* cladodes varieties offered to goats. J. Anim. Plant Sci. 32, 5096–5103.

Monteiro, C.C.F., Ferreira, M.A., Véras, A.S.C., Guido, S.I., Almeida, M.P., Silva, R.C., Inácio, J.G., 2018. A new cactus variety for dairy cows in areas infested with *Dactylopius opuntiae*. Anim. Prod. Sci. 59, 479–485. https://doi.org/10.1071/AN17256.

Mudgal, V., Mehta, M.K., Rane, A.S., 2018. Lentil straw (Lens culinaris): an alternative and nutritious feed resource for kids. Anim. Nutr. 4, 417–421. https://doi.org/10.1016/j.aninu.2018.04.009.

Nefzaoui, A., Ben Salem, H., 2001. Opuntia spp. A strategic fodder and efficient tool to combat desertification in the WANA region. In: Mondragon-Jacobo, C., Perez-Gonzalez, S. (Eds.), Cactus (Opuntia spp) as Forage. Food and Agriculture Organization, Rome, Italy, pp. 73–89.

Nerd, A., Nobel, P.S., 1995. Accumulation, partitioning, and assimilation of nitrate in *Opuntia ficus-indica*. J. Plant Nutr. 18, 2533–2549. https://doi.org/10.1080/01904169509365083.

Nobel, P.S., Russel, C.E., Felker, P., Medina, J.G., Acuña, E., 1987. Nutrient relations and productivity of prickly pear cacti. Agron. J. 79, 550–555. https://doi.org/10.2134/agronj1987.00021962007900030030x.

Osuna-Martínez, U., Reyes-Esparza, J., Rodríguez-Fragoso, L., 2014. Cactus (*Opuntia ficus-indica*): a review on its antioxidants properties and potential pharmacological use in chronic diseases. Nat. Prod. Chem. Res. 2, 1000153 https://doi.org/10.4172/2329-6836.1000153.

Pessoa, D.V., Andrade, A.P., Magalhães, A.L.R., Teodoro, A.L., Santos, D.C., Araújo, G.G.L., Medeiros, A.N., Nascimento, D.B., Valença, R.L., Cardoso, D.B., 2020. Forage cactus of the genus *Opuntia* in different with the phenological phase: nutritional value. J. Arid. Environ. 181, 104243 https://doi.org/10.1016/j.jaridenv.2020.104243.

Pinos-Rodríguez, J.M., Velázquez, J.C., González, S.S., Aguirre, J.R., García, J.C., Álvarez, G., Jasso, Y., 2010. Effects of cladode age on biomass yield and nutritional value of intensively produced spineless cactus for ruminants. S. Afr. J. Anim. Sci. 40, 245–250.

Ramírez-Tobías, H.M., Reyes-Agüero, J.A., Pinos-Rodríguez, J.M., Aguirre-Rivera, J.R., 2007. Efecto de la espécie y madurez sobre el contenido de nutrientes de cladodios de nopal. Agrociencia 41, 619–626.

Ramos, J.P.F., Leite, M.L.M.V., Oliveira Junior, S., Nascimento, J.P., Santos, E.M., 2011. Crescimento vegetativo de *Opuntia ficus-indica* em diferentes espaçamentos de plantio. R. Caatinga. 24, 41–48.

Rekik, M., Ben Salem, H., Lassoued, N., Chalouati, H., Ben Salen, I., 2010. Supplementation of Barbarine ewes with spineless cactus (*Opuntia ficus-indica* f. inermis) cladodes during late gestation-early suckling: effects on mammary secretions, blood metabolites, lamb growth and postpartum ovarian activity. Small Rum. Res. 90, 53–57. https://doi.org/10.1016/j.smallrumres.2009.12.051.

Rodrigues, A.M., Pitacas, F.I., Reis, C.M.G., Blasco, M., 2016. Nutritional value of *Opuntia ficus-indica* cladodes from Portuguese ecotypes. Bulg. J. Agric. Sci. 22, 40–45.

Rodriguez-Felix, A., 2002. Postharvest physiology and technology of cactus pear fruits and cactus leaves. Acta Hort. 581, 191–199. https://doi.org/10.17660/ActaHortic.2002.581.18.

Santos, M.V.F., Lira, M.A., Farias, I., Burity, H.A., Tavares Filho, J.J., 1992. Efeito do período de armazenamento pós-colheita sobre o teor de matéria seca e composição química das palmas forrageiras. Pesq. Agropec. Bras. 27, 777–783.

Santos, M.V.F., Farias, I., Lira, M.A., Nascimento, M.M.A., Santos, D.C., Tavares Filho, J.J., 1998. Colheita da palma forrageira (*Opuntia ficus indica* Mill) cv. Gigante sobre o desempenho de vacas em lactação. R. Bras. Zootec. 27, 33–39.

Scalisi, A., Morandi, B., Inglese, P., Lo Bianco, R., 2016. Cladode growth dynamics in *Opuntia ficus-indica* under drought. Environ. Exp. Bot. 122, 158–167. https://doi.org/10.1016/j.envexpbot.2015.10.003.

Silva, V.L., Costa, L.S., Bastos, M.P.V., Facuri, L.M.A.M., Rêgo Júnior, N.O., Silva, M.V., 2011. Forrage palm round meal (*Opuntia ficus*) chemistry physical and biochemical characterization, fed to ruminants. Pubvet 5, 999–1002.

Silva, N.G.M., Santos, M.V. Fdos, Dubeux Jr., J.C.B., Cunha, M.Vda, Lira, Mde A., Ferraz, I., 2016. Effects of planting density and organic fertilization doses on productive efficiency of cactus pear. Rev. Caatinga 29 (4), 976–983.

Silva, E.T.S., Melo, A.A.S., Ferreira, M.A., Oliveira, J.C.V., Santos, D.C., Silva, R.C., Inácio, J.G., 2017. Acceptability by Girolando heifers and nutritional value of erect prickly pear stored for different periods. Pesq. Agropec. Brasil. 52, 761–767. https://doi.org/10.1590/s0100-204x2017000900008.

Silva, R.C., Ferreira, M.A., Oliveira, J.C.V., Santos, D.C., Gama, M.A.S., Chagas, J.C.C., Inácio, J.G., Silva, E.T.S., Pereira, L.G.R., 2018. Orelha de Elefante Mexicana (*Opuntia stricta* [Haw.] Haw.) spineless cactus as an option in crossbred dairy cattle diet. S. Afr. J. Anim. Sci. 48, 516–525. https://doi.org/10.4314/sajas.v48i3.12.

Silva, T.G.P., Batista, A.M.V., Guim, A., Silva Jr, V.A., Carvalho, F.F.R., Barros, M.E.G., Sousa, D.R., Silva, S.M.C., 2020. Histomorphometric changes of the fore-stomach of lambs fed with diets containing spineless cactus genotypes resistant to *Dactylopius* sp. Trop. Anim. Health Prod. 52, 1299–1307. https://doi.org/10.1007/s11250-019-02129-0.

Souza, T.C., Santos, M.V.F., Dubeux Jr., J.C.B., Lira, M.A., Santos, D.C., Cunha, M.V., Lima, L.E., Silva, R.R., 2017. Productivity and nutrient concentration in spineless cactus under different fertilizations and plant densities. Ver. Bras. Cienc. Agrar. 12, 555–560. https://doi.org/10.5039/agraria.v12i4a5473.

Tegegne, F., 2001. Nutritional value of Opuntia ficus-indica as a ruminant feeding in Ethiopia. In: Mondragon-Jacobo, Perez-Gonzalez (Eds.), Cactus (Opuntia spp.) as Forage. FAO, Rome. FAO Plant production and protection papers N°169: 161p.

Teles, M.M., Santos, M.V.F., Dubeux Jr., J.C.B., Lira, M.A., Ferreira, R.L.C., Bezerra Neto, E., Farias, I., 2004. Efeito da adubação e do uso de nematicida na composição química da palma forrageira (*Opuntia ficus indica*, Mill). R. Bras. Zootec. 33, 1992–1998. https://doi.org/10.1590/S1516-35982004000800010.

Torres, L.C.L., Ferreira, M.A., Guim, A., Vilela, M.S., Guimarães, A.V., Silva, E.C., 2009. Substituição da palma-gigante por palma-miúda em dietas para bovinos em crescimento e avaliação de indicadores internos. R. Bras. Zootec. 38, 2264–2269. https://doi.org/10.1590/S1516-35982009001100028.

Tovar-Puente, A., Pando-Moreno, M., González-Rodríguez, H., Scott-Morales, L., Méndez-Gallegos, S.J., 2007. Density of calcium oxalate crystals in 15 prickly pear cultivated species. J. PACD 9, 91–98.

Trachtenberg, S., Mayer, A.M., 1981. Composition and properties of Opuntia ficus-indica mucilage. Phytochemistry 20, 2665–2668.

Véras, R.M.L., Ferreira, M.A., Cavalcanti, C.V.A., Véras, A.S.C., Carvalho, F.F.R., Santos, G.R.A., Alves, K.S., Maior Júnior, R.J.S., 2005. Substituição do milho por farelo de palma forrageira em dietas de ovinos em crescimento. Desempenho. R. Bras. Zootec. 34, 249–256. https://doi.org/10.1590/S1516-35982005000100029.

Wanderley, W.L., Ferreira de, M.A., Andrade, D.K.B., Véras, A.S.C., Farias, I., Lima, L.E., Dias, A.M.A., 2002. Replacement of Forage Cactus (Opuntia ficus indica Mill) for Sorghum Silage (Sorghum bicolor (L.) Moench) in the Dairy Cows Feeding. Revista Brasileira de Zootecnia 31 (1), 273–281. https://doi.org/10.1590/S1516-35982002000100030.

Wanderley, W.L., Ferreira, M.A., Batista, A.M.V., Véras, A.S.C., Bispo, S.V., Silva, F.M., Santos, V.L.F., 2012. Intake, digestibility and ruminal measures in sheep feed silage and hay in association with cactus pear. Rev. Bras. Saúde Prod. Anim. 13, 444–456. https://doi.org/10.1590/S1519-99402012000200013.

Zañudo-Hernández, J., Aranda, E.G.C., Ramirez-Hernández, B.C., Pimenta-Barrios, E., Castillo-Cruz, I., Pimienta-Barrios, E., 2010. Ecophysiological responses of Opuntia to water stress under various semi–arid environments. J. PACD 12, 20–36.

Zegbe, J.A., Serna-Pérez, A., 2017. Seasonal changes and nutrient concentrations of "cristalina" cactus pear cladodes in response to NPK fertilization. Commun. Soil Sci. Plant Anal. 48, 769–777. https://doi.org/10.1080/00103624.2017.1298783.