

Ecological Characterization of *Opuntia* Clones in South Texas: Implications for Wildlife Herbivory and Frugivory

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INTRODUCTION

Prickly pear cactus (*Opuntia* spp.) is a common floristic component of arid and semiarid ecosystems of the southwestern United States and northern Mexico. Not surprisingly, in many of these regions it can be one of the dominant life forms, due primarily to its high water-use efficiency. Because of this dominance it can be an important element of wildlife habitats both as structure (shade, shelter, nesting substrate) and food for many mammal and avian species. In addition, it is utilized by other vertebrates (reptiles) and many invertebrates. Its structure provides shade and resting habitat for many birds. It can provide nesting substrate for birds, such as cactus wren, curve-billed thrasher and many other species. The importance of cactus structure for other wildlife species (e.g., small mammals, deer, reptiles) is not well documented, with few exceptions (e.g., woodrats *Neotoma* spp). As a food item, cactus cladodes are consumed by wildlife (deer, javelinas, lagomorphs) and livestock and are of considerable importance during some seasons to white-tailed deer (*Odocoileus virginianus*, Everitt and Gonzalez, 1979) and javelinas (Hellgren, 1994). The fruits are also consumed by a large number of animals including mammals (javelinas, some carnivores), birds (thrushes, woodpeckers), and at least one reptile (tortoises).

Prickly-pear cactus (*Opuntia* spp.) is present throughout south Texas and northern Mexico. Taxonomically, there are several species and many more varieties present (Benson, 1982); however, more important from an ecological perspective is the extensive polymorphism present in the genus *Opuntia* (Madams, 1972; Espinosa-Aburto, 1988). The many different morphological types (morphotypes) present in an area many times do not correspond to any known or established variety. In *Opuntia lindheimeri* there is a large variation in the morphological characteristics of individual plants ranging from nearly spineless plants to those with large spines and considerable variation in the densities of spines. The large variation in spine characteristics could have significant implications for predation by a variety of potential herbivores. In addition, there is also large variation in the timing of fruiting, fruit color, fruit sugar content, and seed concentrations in different morphotypes. The fruiting phenology and fruiting characteristics of different morphotypes could affect the number and types of animals that would visit a plant to feed on the fruit. The species that visit and consume fruit and their foraging and post-foraging behavior could influence the location of seed deposition and the possible establishment of new plants via active seed dispersal.

It is expected that the distribution, dispersion, relative abundance, and density of different *Opuntia* morphotypes throughout the landscape of south Texas can be explained, at least partially, by the interactions and influence of herbivores, including grazers and frugivores (fruit eaters). At one level, the size and density of specific morphotypes would be negatively affected if one, or more, had qualities that grazers preferred (few spines, short spines, high protein or

energy content, and low concentration of secondary chemicals). The distribution, dispersion, and abundance of different morphotypes would also be affected by the types of animals that consume the fruit and the quality of dispersal (probability that a seed consumed by a frugivore becomes a new plant) afforded to the plant by the species of animal that consume the fruit. Seed dispersal as an ecological process has received considerable attention for tropical and temperate-region plants (Howe and Smallwood 1982, Herrera 1985). However, knowledge of seed dispersal patterns and the importance of animals in the distribution of seeds for arid land plants is lacking. Many plants in arid ecosystems produce fruit, suggesting that their seeds have evolved to be consumed and dispersed by animals.

OBJECTIVES

The overall objective of this work was to characterize the variation in different morphotypes of prickly-pear cactus present on two south-Texas ranches. The characteristics evaluated were those believed to influence interactions of prickly-pear cactus with vertebrate herbivores through grazing activity and seed dispersal. We measured spiniscence, crude protein, and *in vitro* digestibility of cladodes, as well as fruit size, color, sugar content, and seed content. We discuss the potential implications that the variation of morphological and fruiting characteristics of prickly pear have to wildlife herbivory and frugivory in arid ecosystems of Texas and northern Mexico. Specific discussion is presented relative to the fruit and fruiting characteristics of *Opuntia* and the possible consequences to the potential seed-dispersal process.

METHODS

We evaluated five apparent morphotypes in each of two sites in Texas during the spring and summer of 1997. The sites were the Maltsberger Ranch, located south of Cotulla in La Salle county, and the Welhausen Ranch belonging to Texas A&M University-Kingsville approximately 35 km southwest of Freer in Webb county. Rancher Bill Maltsberger had identified many morphotypes of the native *Opuntia lindheimerii* from his ranch which he planted from pads in rows in an unreplicated "common garden." We selected contrasting types from this collection, some of which were almost spineless. These were propagated from cladodes; therefore, each of the morphotypes consisted of a single clone. In addition, selections also were made from the Welhausen Ranch. The clones (morphotypes) were given a Texas A&M University-Kingsville accession number that is listed in Table 1. The color of the cladodes was estimated using the Royal Horticultural Society Colour Chart and the spine characters were measured for 10 cladodes of 3 separate plants. After the fruits were mature, their sugar contents, pH, and seed contents were measured as previously described (Parish and Felker, 1997).

We evaluated spiniscence by measuring the number of areoles per side of the cladodes, number of areoles on the edge of cladodes, number of cladodes with spines, and length of longest spine. We also evaluated the nutritional value of cladodes from the different morphotypes using the Kjeldahl method (Horwitz, 1975) to estimate crude protein and the incubation step of Tilley and Terry (1963) method to index *in vitro* dry-matter digestibility (IVDMD). Protein in the samples was estimated as Kjeldahl nitrogen multiplied by 6.25. We determined *in vitro* digestibility of cactus samples using deer rumen fluid without a secondary treatment of pepsin-acid (Tilley and Terry, 1963) or neutral detergent (Van Soest, 1982). Fruit characteristics evaluated were: fruit weight, pulp-peel ratio, total soluble sugar, and weight of seeds per fruit. A literature review was conducted to locate citations dealing with wildlife consumption of prickly pear cladodes and

fruit. However, the review is not all inclusive and only selected references that are most relevant to the discussion presented are included in this paper.

RESULTS AND DISCUSSION

Spiniscence and Herbivory

We evaluated spiniscence of several clones from the Maltsberger and Welhausen Ranches and found considerable variation in number and length of spines and number of areoles per cladode (Table 1). Similar variation was found in prickly pears evaluated in Coahuila, Mexico (Espinoza-Aburto, 1988). The presence of spines in plants is commonly associated with deterrence of herbivory (Ricklefs, 1980; Janzen, 1986). In prickly pear, spines could be a function of both reduction of leaves, to reduce evapotranspiration, and as protection against herbivores. We believe that the presence and characteristics of spines should affect herbivory; therefore, we predict that the distribution, dispersion, and density of different morphotypes will be related to spiniscence as well as nutritional and water content.

Protein content of cladodes collected from the Maltsberger ranch was low compared to other forages and varied slightly between different morphotypes (Table 2) and has been found to be even more variable when compared to other studies (Gregory and Felker, 1992; Fuentes-Rodriguez, 1992). *In vitro* dry-matter digestibilities of 60% compare favorably with other forage resources. *In vitro* dry-matter digestibility also varied between morphotypes (Table 2) but the variation may not be biologically significant.

The use of prickly-pear pads by a large number of herbivores is a well known phenomena (Janzen, 1986). In arid areas of the U.S. and Mexico, prickly-pear cactus are consumed by deer (Ruthven et al., 1994), javelina (Theimer and Bateman, 1992), and other mammals such as carnivores (Best and Hoditschek, 1981; Gipson, 1974), and lagomorphs (Hoffman et al., 1993). In addition, small mammals (Shmidt-Nielson, 1964) and tortoises (Rose and Judd, 1983) are known to consume cactus cladodes.

Domestic livestock readily consume prickly pear; however, they appear to prefer varieties without spines or those from which spines have been eliminated through burning (Lehmann, 1969; Nobel, 1994). In Texas, for example, sheep and goats will consume *Opuntia* cactus that has not been singed by burning, but they can sustain chronic mouth injuries (Burt-Davy, 1920). Starving livestock will also browse on cacti with intact thorns, but will feed preferentially from those where spines have been removed (Dameron and Smith, 1939). In some areas of Mexico, prickly-pear pads are not readily consumed by goats but are made available to the goats by a herder walking around and cutting a small piece of the edge of the pads with a machete (pers. observ.). Apparently, the goats cannot get at the pad due to the spines on the edges but cutting a piece allows access to the pad. The fact that deer respond to an area where a gas burner has been utilized to burn spines of cactus (Maltsberger pers. comm.) suggests the elimination of spines facilitates the use of cladodes by this species also. These examples clearly suggest that spines can be an effective deterrent to at least some major herbivores, both native and introduced. The elimination of spines clearly facilitates prickly pear use by livestock which only under rare circumstance will feed directly on plants in the wild. It is believed that if cacti did not have spines, even with the current level of chemical defenses, it is likely that introduced livestock would have eliminated them just as thoroughly as they did many species of island plants that had never been exposed to browsing or grazing (Janzen, 1986).

Herbivorous activity on prickly pear may be related not only to its forage value but also to the high water content, which is an important consideration for organisms that live in the arid and semiarid environments where *Opuntias* are found. For example, wood rats (*Neotoma* spp), which require water on a daily basis obtain water from prickly pear, which, during the dry part of the year, can comprise 90% of the rats' diet (Schmidt-Nielson, 1964). High use of prickly pear cactus by deer and javelina in south Texas during the dry season is believed to be due to high demands of these species for preformed water (Zervanus and Day, 1977; Hellgren, 1994), rather than to the nutritional value of pads.

The effects of browsing by herbivorous animals on the distribution, dispersion, and density of different prickly pear morphotypes are not known. However, due to reasons cited above, the effects will likely vary for different morphotypes. In javelinas, for example, it is known that they select one morphological form of cactus over others based on spines and glochids, neutral detergent fiber, and fewer calcium oxalate crystals (Theimer and Bateman, 1992). This foraging pattern will affect the abundance and distribution of morphotypes differentially. A documented effect of browsing intensity has been the negative effect on flowering time (Kemp, 1983). Evolutionarily, flowering times may be influenced as much by browsing activity and disperser selection as by rainfall (Kemp, 1983).

While the spiny cactus has been declared a weed by the Government of South Africa, thereby making it illegal to own, plant, or transport spiny cacti, it has been observed to have been a valuable plant for wildlife. At the Double Drift Wildlife Preserve, giraffes were observed eating the tops out of 4-m-tall spiny *Opuntias*. At the Addo Elephant preserve, there are 3- to 4-m-tall spiny cactus all around the reserve, but there are no spiny cactus inside the reserve because they are aggressively sought out by the elephants. At Kruger National Park the elephants spread a low-growing spiny cactus (*O. stricta*) because they eat all of the fruits of the cactus. The widely prevalent red-colored feces of the elephants are a prominent indicator of this usage. The *O. stricta* in Kruger National Park has been enclosed with 2-m-tall electric fences to prevent its consumption and spread by baboons. Nevertheless, some baboons charge through the electric fence to eat the fruits of the *Opuntias*.

Even though the *Opuntias* are not native, perhaps some consideration should be given to their use in providing forage for game parks in dry seasons. Of course, such an option would not be desirable for government national parks. Alternatively, it is possible that foraging elephants might constitute an effective biological control for spiny *Opuntia* stands.

Fruit, Fruiting Characteristics, and Dispersal Syndromes

Fruit characteristics of morphotypes evaluated for this study were highly variable (Table 2). While the fruit characteristics of the domesticated fruit varieties of *Opuntia ficus-indica*, *O. amyoclea* and related species have been studied intensively (e.g., Parish and Felker, 1997), very little information is available on the fruit characteristics of the wild *O. lindheimerii*. The commercial fruit varieties range in color from red, orange, yellow, lime-green, to purple and have a minimum weight and sugar content of 110 g and 1 % sugar, respectively. There is a significant effort to reduce the seed content of the commercial varieties from current levels of 2.1 to 6.4 g/fruit (Parish and Felker, 1997). In contrast, fruits of the wild varieties are smaller (from 33 to 67 g), have less sugar (from 6.5 to 10.2 %), but have almost as much seed per fruit (1.9 to 3.97 g/fruit) as the commercial varieties. If the seeds were expressed on a g seed/g of fruit basis the wild varieties would have more seeds than the commercial varieties. Prickly pear cactus produces large fruits of varying colors and sugar contents that vary depending on the specific variety of cactus (i.e., Parish and Felker, 1997).

Details of seed dispersal mechanisms or the importance of seed dispersal in the life history of prickly-pear cactus are not well known. For humans, and apparently also for birds, the inner pulp is the portion of the fruit that is consumed. Therefore, a high pulp/peel ratio would be desirable. While many of the wild clones have a low pulp/peel ratio, clone 1504 was quite high in having more pulp than peel. It is unclear from a wildlife perspective whether high sugar content or high seed content is more important. For humans, at least, the hard *Opuntia* seeds are difficult to digest. The color of the fruits from all morphotypes was virtually the same in being yellow group 9A as judged using the Royal Horticultural Society Colour Chart.

In general, there are several seed dispersal syndromes that can be inferred from the fruit size, color, and period of ripening that gives an indication of the type of frugivores for which the fruit has evolved (van de Pijl, 1982). The size of the fruit in most prickly pears suggests it evolved for dispersal by large frugivores, because frugivore size is directly correlated with maximum fruit size (Wheelwright, 1985). Janzen (1986) has speculated that the production of large fruits and the location of the fruit on upper terminal pads is an adaptation of cacti for frugivory by large megaherbivores that were present in the area of north-central Mexico and the southern U.S. up to about 10,000 years ago. However, bright-colored fruits, such as red, are adapted to dispersal by birds (Howe, 1982; van der Pijl, 1982). But Janzen (1986) suggested that the bright coloration of ripe fruits in *Opuntia* may have also been used by the megaherbivore fauna to locate food sources.

Most *Opuntia* plants produce fruit with a large number of small seeds. The presence of large numbers of small seeds suggests consumption by small frugivores is also possible because small seeds are believed to be an adaptation to avoid predation by both large and small organisms (Snow, 1981; Hoppes, 1987; Janzen, 1986). The combination of large fruit with small seeds would suggest the fruit of *Opuntia* can be consumed by a large variety, in type and size, of frugivorous animals. Based on current assemblages of wildlife species present, and the seasonal availability of ripe fruit, opportunistic frugivory is what would be expected in *Opuntia* plants in south Texas. In contrast to the very few fruits still on the commercial fruit clones in December and January, we have noticed that some of the native *Opuntias* still have abundant fruits in January and February. These fruits were produced in April/May and continued to stay on the plants virtually all winter. In contrast, the commercial fruit varieties all abscise from the plant 60 days after reaching maturity (or about 150 days from flowering) (Felker, unpublished observations). As there is almost no fruit from any wild plants available after December, the fruits and seeds of *Opuntia* could be a significant resource for many kinds of wildlife.

A prediction based on fruit characteristics would be that a large number of species of different sizes will consume the fruit. The specific type and number of frugivores would depend on the time of year, especially with regard to birds, many of which present in the area are migratory. It remains to be determined what the quality of dispersal (probability that seed dispersed by a vector lands in a place suitable for germination) is for each of the different frugivores that consumes the fruit. The actual effect of combined seed dispersal by all species of animals will determine the quality of dispersal and ultimately dispersion patterns and demographics of morphotypes.

Frugivory and Seed Dispersal

The presence of fruit is a clear indication that seed dispersal is intended in plants that produce them (van der Pijl, 1982). Fruit production is energetically expensive, and therefore, there must be a tradeoff for a plant to invest in fruit production. Fruit attracts frugivores who will consume the fruit and, in the process, consume the seeds as well, which, if not destroyed in digestion will

be dispersed. In exchange for seed dispersal, the frugivore obtains a nutritional reward (generally in the form of sugars, water, or protein). In the cactus family, the most common form of reproduction is by seeds (Went, 1982). The fact that seeds have high viability and germination after removal of the fruit pulp, and even greater germination after scarification (Went, 1982), suggests these seeds (and fruit) are adapted to consumption and dispersal by animals. In cactus, as in other plants (i.e., tomatoes), the fruit pulp contains a germination inhibitor (Went, 1982). The passage of seeds through the digestive systems of animals serves the dual purpose of removing the pulp and scarifying the seeds, thereby increasing germination rates. Rose and Judd (1983) reported that in south Texas cactus seeds had significantly greater germination rates after passing through tortoise alimentary canals.

The consumption of *Opuntia* fruit by a large number of animals (mammals, birds, and reptiles) is well known. However, the actual or potential seed dispersal quality afforded to *Opuntia* seeds has not been adequately evaluated. Frugivory in *Opuntia* has previously received attention from the perspective of fruit loss or destruction in plantations of prickly pear, although no studies have quantitatively evaluated fruit removal in wild plants. Mammals are the best known consumers of *Opuntia* fruit and have to some extent received attention as seed dispersal agents (Janzen, 1986). Some of the mammals whose diet has been quantified and that consume *Opuntia* fruit include javelinas (Corn and Warren, 1985), deer (Everitt and Gonzalez, 1979; Quintana, 1985), coyotes (*Canis latrans*, Best and Hoditschek, 1981; Gipson, 1974), and jackrabbits (Timmons, 1942) raccoons (*Procyon lotor*) and 13-lined ground squirrels (*Spermophilus tridecemlineatus*) (Lehmann, 1984). In some areas, woodrats (*Neotoma*) are considered to be the primary consumers of *Opuntia* fruits (Vargas-Mendoza and Gonzalez-Espinosa, 1992). For the most part, most mammals that consume fruit could be potential seed dispersers. However, some organisms are known to destroy large numbers of seeds through mastication and digestion, in which case they become seed predators rather than dispersers.

Birds, which include highly frugivorous species, are not well documented in the literature as consumers of *Opuntia* fruit with the exception of possible fruit predation problems. Frugivory by birds in commercial plantations in Estado de Mexico accounted for 30% of fruit loss (Fucikovsky and Luna, 1988). While not quantified, birds are known to be responsible for fruit damage in an *Opuntia* collection in Kingsville, Texas (P. Felker, pers. observ.) Observations in south Texas and northern Mexico show that thrashers, mockingbirds, woodpeckers, orioles, and white-winged dove (*Zenaida asiatica*) regularly consume fruit when ripe (Chavez-Ramirez, pers. observ.). In addition, flycatchers (*Tyrannus* spp., Fucikovsky and Luna, 1988), crows (*Corvus* spp., Quintana, 1985), bobwhite (*Colinus virginianus*), scaled quail (*Callipepla squamata*, Lehmann, 1984; Medina, 1988), and wild turkey (*Meleagris gallopavo*) (Lehmann, 1984) have been observed consuming fruit. Undoubtedly, many more species of birds consume fruit but have not been studied adequately. Regarding reptiles, tortoises are the only species documented as consuming *Opuntia* fruit (Rose and Judd, 1983) in North America.

The arid and semiarid ecosystems of North America support many mammals and birds that are primarily granivores and, as such, function as seed predators. In Mexico, at least seven species of birds are reported to consume *Opuntia* seeds (Quintana, 1985). What is not known is if the granivores consume seeds directly from the fruit or if they secondarily eat them after defecation by frugivores. Combined, mammals and avian granivores make up large portions of the animal biomass in arid environments and therefore have the potential to consume large quantities of seeds from *Opuntia* and other plants. The actual proportion of seeds that are ultimately destroyed by granivores would have significant consequences for overall dispersal and distribution of plants in the landscape.

It is clear that prickly pear cactus is an important ecological element of arid and semiarid ecosystems of North America. The actual importance of *Opuntia* as a food source and structure for many species is recognized but has not been adequately studied in many instances. The fact that some *Opuntias* produce fruit that remains on the plant all year long offers significant opportunities for enhanced wildlife food plants. However, further studies are critically needed to determine the competition for fruits among animals as diverse as deer and curve-billed thrashers. For birds, it is critical to know if the protein and excellent seed oil can be digested. More detailed studies should be conducted to determine the importance of *Opuntia* for wildlife species, particularly as it relates to the ecological interactions between animals and prickly pear. Considering the large variation in animal assemblages present in arid and semiarid areas of North America (in relation to 10,000 years ago when megaherbivores were present), it is important to understand the effects that different herbivores (grazers and frugivores) have on the distribution, dispersion, and abundance of different *Opuntia* morphotypes. Better knowledge of the plant-animal interactions involving prickly-pear cactus may help us better understand the mechanism by which prickly pear has increased in many areas of Texas and Mexico, where it is considered a range problem when it becomes abundant and is found in high densities. A better understanding of the interactions involving grazers may also help in the potential management of this abundant resource as an economical source of forage, food, and structure for wildlife and domestic livestock.

The increasing interest in South Texas for food plots for wildlife should consider *Opuntia* cladodes as useful year-round for foraging and its fruit would be available from June through January for birds and other animals. The nearly spineless *Opuntia* morphotype 1506, with 4.9% protein, 60% IVDMD, and 53-g fruits containing 8.5% sucrose and 3.0 g seeds, should be given special consideration.

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Table 1. Spiniscence Characteristics of *Opuntia* Morphotypes

		Maltsberger Ranch, La Salle County, Texas					Wellhausen Ranch, Webb County, Texas			
Morphotype Number		1503	1504	1505	1506	1507	WR1	WR2	WR3	WR4
Aerioles	Number per side	22.5	19.8	17.2	19.3	19.4	13.2	21.6	20.5	27.8
	SD	2.5	3.5	2.6	0.6	3.8	2.6	2.5	3.1	3.0
	% with spines	13.5	15.2	30.1	1.4	3.2	99.0	69.9	77.9	78.0
	Number per edge	33.7	29.3	32.7	31.6	30.3	27.6	28.5	29.6	33.0
	SD	4.0	5.9	4.3	2.4	3.0	2.4	2.5	3.1	4.1
	% with spines	23.2	37.5	42.3	3.3	10.8	100.0	77.4	80.0	77.0
Spines	Length (mm)	23.0	22.9	28.0	27.5	31.0	57.9	32.7	38.4	36.7
	SD	6.3	4.5	5.6	6.0	8.5	4.7	5.1	6.2	6.3
Protein content (%)		5.76	5.18	4.9	4.87	5.74				
IVDMD		63.0	51.83	57.8	60.1	59.5				

IVDMD = In vitro dry-matter digestability

Table 2. Fruit and Fruiting Characteristics of Opuntia Morphotypes

		Maltsberger Ranch, La Salle County, Texas					Wellhausen Ranch, Webb County, Texas			
Morphotype Number		1503	1504	1505	1506	1507	WR1	WR2	WR3	WR4
Fruit	Weight (g)	39.5	47.7	33.7	53.1	59.3	43.4	51.8	41.5	67
	SD	5.44	10.4	0.7	14.7	9.86	7.1	10.8	6.4	9.3
Pulp to Peel	Ratio	0.8	1.2	0.37	0.36	0.48	0.43	0.61	0.39	0.62
	SD	0.07	0.12	0.05	0.07	0.21	0.07	0.13	0.05	0.11
Sugar	Content (%)	7.3	9.4	6.5	8.5	7.2	7.1	10.8	10.2	9.38
	SD	1.13	0.4	0.07	0.87	0.56	0.3	1.1	0.92	0.6
Seed	Content (grams/fruit)	2.9	2.16	2.07	2.95	1.9	2.49	3.57	1.64	3.97
	SD	0.48	0.5	0.3	1.06	0.41	0.47	1.09	0.47	0.62