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RABBIT HERBIVORY AND ITS EFFECT ON CLADODE, FLOWER AND FRUIT PRODUCTION OF *OPUNTIA VIOLACEA* VAR *MACROCENTRA* (CACTACEAE) IN THE NORTHERN CHIHUAHUAN DESERT, NEW MEXICO

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ABSTRACT—We studied the timing and effect of black-tailed jackrabbit and desert cottontail herbivory on a platyopuntia species, *Opuntia violacea* var *macrocentra* at a site on the Jornada del Muerto, 35 km north of Las Cruces, New Mexico in the northern Chihuahuan Desert. Total monthly fecal pellet dry mass collected around the base of individual opuntias over 15 months indicates that both rabbit species exhibit a seasonal preference for this opuntia with the greatest grazing pressure evident during dry seasons or when little annual or new growth of other perennial plants is present. Neither rabbit species appears to graze small opuntias possessing less than three cladodes. They also appear to avoid grazing new cladodes, since more than 80% of the cladodes produced in May 1990 survived for six months. The proportion of individual opuntias grazed increases with increasing cladode number size class as does the mean fecal-pellet dry mass collected around the base of individual opuntias. Spinescence did not affect grazing intensity over the 15-month study period. Instead, plant size and grazing history appear to be the most important determinants of grazing intensity. Although statistically not significant, there is a trend in our data which suggests that above-average rabbit herbivory may negatively affect cladode, flower and fruit production in intermediate opuntia size-classes only. For individuals with either very few or very many cladodes these parameters appear unaffected by rabbit herbivory. However, the strongly-skewed size-class frequency distribution indicates that recruitment of juvenile opuntias into the population is little affected by rabbit herbivory.

Black-tailed jackrabbits (*Lepus californicus*) and cottontail rabbits (*Sylvilagus* spp.) are widespread in the deserts of North America and play an important ecological and economic role in these ecosystems. Not only are they important prey items for many predators (MacCracken and Hansen, 1982) but, being predominantly herbivorous, they also consume a wide variety of range plants as well as planted crops (Sparks, 1968; Westoby and Wagner, 1973; Fagerstone et al., 1980; Anderson and Shumar, 1984; Roundy et al., 1985). They are thus competitors for food with domestic livestock and wildlife.

Although a number of studies have investigated the seasonal range of food items in jackrabbit and cottontail rabbit diets (Uresk, 1978; Westoby, 1980; Johnson and Anderson, 1984; MacCracken and Hansen, 1984), few have looked at the influence of rabbit herbivory on the growth, reproduction and population dynamics of rangeland plants (but see Anderson and Shumar, 1984). This is particularly true for northern Chihuahuan desert plants such as *Opuntia violacea* var *macrocentra* which appears to form an important component of rabbit diets. This is evidenced from the mass of rabbit fecal pellets which accumulates beneath the canopies of this plant as well as the clear lagomorph graze-marks present on their succulent cladodes.

Opuntia violacea var *macrocentra* (hereafter called *O. violacea*), a platyopuntia, is widely distributed in southern Arizona and southern New Mexico and is one of three varieties of the species (Earle, 1980). Adult plants may consist of up to 180 or more jointed flattened photosynthetic stems, called cladodes, each of which may be up to 0.2 m long. Although the jointed cladodes form ascending branches, adults seldom reach more than 0.75 m in height. In southern New Mexico, where this study was conducted, the yellow flowers, up to 65 mm in diameter first appear in May with the long (30 to 60 mm) fleshy fruits developing in June.

We asked three main questions in this study. First, when do rabbits graze *O. violacea*? Specifically, we sought to understand if there were preferred seasons or times in the year in which rabbits turned to this species as a forage source. Second, which individuals of this plant species do rabbits prefer, and can their choices be explained by reference to the size of the plant, level of spinescence or grazing history? Finally, what are the effects of rabbit herbivory on new cladode growth, flower and fruit production and plant mortality of *O. violacea*, and is this affected by plant size?

MATERIALS AND METHODS—The study was conducted from March 1990 to July 1991 on the Jornada del Muerto, 35 km NNE of Las Cruces, in Dona Ana County, New Mexico, at the New Mexico State University College Ranch. The study site is situated about 5 km south of the Jornada Long Term Ecological Research (LTER) site in the northern Chihuahuan desert (see Wondzell et al., 1987 for a description of the LTER site). The study site is on an alluvial piedmont, at the base of a bajada comprised of deep, coarse-grained, gravelly sediments. Mean annual rainfall for the region is 211 mm (SD = 77 mm) and monthly rainfall totals were determined from an on-site rain gauge. The study site is dominated by *Larrea tridentata* and *Prosopis glandulosa* var *glandulosa*. Other common plants include *Zinnia grandiflora, Yucca elata, Y. baccata* and *Opuntia violacea* var *macrocentra*.

A 1-ha site was randomly located on the bajada and subdivided into 100, 10-m × 10-m plots. Each of these contiguous plots was searched, and all *O. violacea* individuals present were numbered and mapped to assist in relocation. The number of jointed cladodes were counted and an index of cladode spinescence given for each plant. This index ranged from 1 (less than 20% of the areoles of the jointed cladodes contain spines) to 5 (80–100% of areoles contain spines) and was estimated independently by two observers and then averaged.

Black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus auduboni*) are present on the Jornada del Muerto. We assumed that these two lagomorphs were the main grazers on *O. violacea* cladodes in our study area since we found no evidence of other species having grazed this succulent. A permanent 1,000-m transect, situated 3 km north of the study site in a similar vegetation type and position on the bajada, exists as part of an on-going LTER rabbit monitoring program. This transect was sampled every month and rabbit densities were calculated using a modification of the method proposed by Emlen (1971). When walking the transect, the distance to a flushed rabbit was recorded and an average detection distance derived. This was then doubled to calculate the width of a sample belt that would encompass the animals detected and finally expressed as the number of animals per ha.

Initially, all rabbit fecal pellets were removed from a 0.75-m radius around the plants in the 1-ha site in March 1990. They were oven-dried at 60°C for three days and weighed. Thereafter all plants were visited monthly from May 1990 until July 1991 and the pellets were removed from the same area and oven-dried and weighed. The total number of grazing incidents on the jointed cladodes was noted in March 1990 and the number of new grazes determined each month for each plant until July 1991. We did not differentiate between heavily-grazed and lightly-grazed cladodes. To date accurately the time of grazing damage, we traced the graze outline on individual cladodes with a permanent ink marker. Any new grazing the following month could then be detected with ease. Since the dry mass of pellets collected from individual plants from May 1990 to July 1991 was highly significantly correlated with the number of grazed cladodes on individual plants (n = 144; Spearman rank correlation $r_s = 0.92$; $d.f.$ = 142; $P < 0.0001$; $y = 1.97x + 0.17$), we used fecal pellet dry mass to indicate the intensity of grazing on each plant. We assumed that fecal pellets were deposited while grazing on opuntias and not while resting in forms (shallow depressions) besides these plants. Observations of jackrabbit feeding behavior by Lechleitner (1958) indicate that this assumption is reasonable.

The number of cladodes, flowers and fruits produced on each plant in the period of May to June 1990 was counted. New cladodes produced in May 1990 were marked and their mortality was monitored for five months until October 1990. The mortality of individual plants during the course of study was also noted. We did not search for new individuals recruited into the plant population.

We determined the influence of herbivory on new cladode, flower and fruit production in May to June 1990, for each cladode-number size-class separately. Mean and standard error estimations of the number of new cladodes, flowers and fruits produced in individuals with less than the mean amount of fecal pellet dry mass collected from a 0.75-m radius around their base, were compared with individuals with more than the mean fecal pellet dry mass in each cladode size class.

RESULTS—One hundred and forty-four *O. violacea* individuals were counted on the 1-ha site. The population was strongly skewed towards juveniles, with 49% of the individuals having five or less jointed cladodes and only 10% possessing 36 or more jointed cladodes (Fig. 1).

Six individuals died during the course of the study. Five of these six plants had five or fewer cladodes and there was no evidence of grazing on these individuals. The sixth plant that died had 19 cladodes. Around the base of this plant we collected, an above average, 61.37 g dry mass of fecal pellets in March 1990. Grazing pressure was strongly implicated in the death of this individual.

Monthly estimates of rabbit abundance from the 1,000-m LTER transect show that the number of black-tailed jackrabbits in the area ranged from 0 to 2.1/ha (mean = 0.5/ha). Although desert cottontails were not seen in any month on the 1,000-m transect they were occasionally observed in our study area. The fact that two distinct fecal pellet size-classes were usually collected from the study site every month, suggests that desert cottontails were frequent visitors to the study area. The smaller pellet size class had a mean dry mass of between 0.05 and 0.075 g and probably reflected desert cottontail activity. Data of mean pellet dry weights of a single desert cottontail roadkill confirmed this. The mean for the second size class of dung, which we suggest were from black-tailed jackrabbits, was between 0.20 and 0.23 g.

Similarly, we observed two types of grazing on opuntia cladodes. In the first, only the epidermal layer between the glochids was removed and little internal supportive cladode tissue was consumed. In the second, epidermal as well as fibrous internal cladode tissue was consumed leaving a semicircular grazing shadow with varying amounts of the grazed cladode still intact. Pellet size was related to grazing type. We suspect that this might reflect different feeding behaviors of the two rabbits on *O. violacea,* with desert cottontails responsible for the former and black-tail jackrabbits the latter grazing type.

Irrespective of the type of grazing, the outer cladodes of opuntias were grazed most heavily

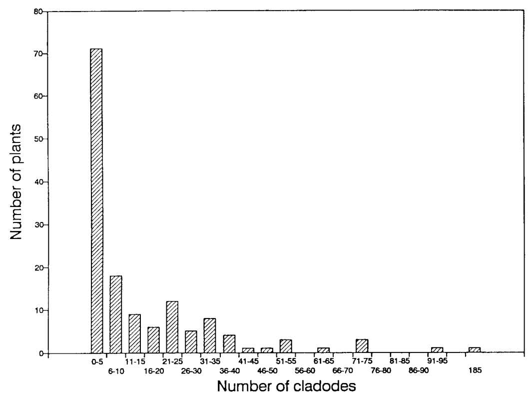

FIG. 1—Number of *Opuntia violacea* var *macrocentra* individuals (n = 144) in each size class on a 1-ha site in the northern Chihuahuan desert, New Mexico.

and grazing progressed from outer to inner cladodes. The specific architectural arrangement of cladodes on a plant and the way in which this was altered by grazing, appeared to be an important determinant of grazing intensity. We found it difficult, however, to quantify or measure this parameter.

The total monthly dry mass of fecal pellets collected around the base of the opuntias changed by two orders of magnitude between seasons and by an order of magnitude between some months (Fig. 2). Pellet dry-mass collected around *O. violacea* was 278 g for the 1-ha site in June 1990 (early summer) and then dropped to less than 30 g the next month. Pellet dry mass increased again from January to March 1991 (winter to early spring). There was a slight increase in pellet dry mass in June 1990 but this dropped again in July 1991. Monthly pellet dry mass and rainfall totals were not correlated ($n = 15$; $d.f. = 13$; $r = 0.25$; $P > 0.1$).

Fifty-one percent of *O. violacea* individuals in the 1-ha site were grazed at least once during the study. Grazing was observed only on individuals with three or more cladodes. The proportion of individuals grazed in each cladode-number size class was highest for the larger size classes (Fig. 3). More than 90% of *O. violacea* individuals with 21 cladodes or more were grazed at least once during the study. Mean dry mass (g) of pellets collected around the bases of individual plants generally increased with increasing cladode-number size class.

Grazing intensity (total dry mass of fecal pel-

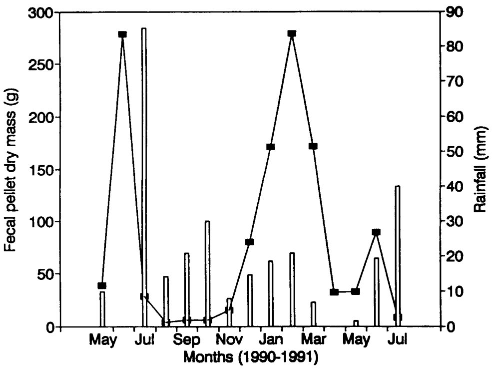

FIG. 2—Total monthly fecal pellet dry mass (g) collected from a 0.75-m radius around the base of 144 *Opuntia violacea* var *macrocentra* individuals and on-site monthly rainfall histograms for the period May 1990 to July 1991.

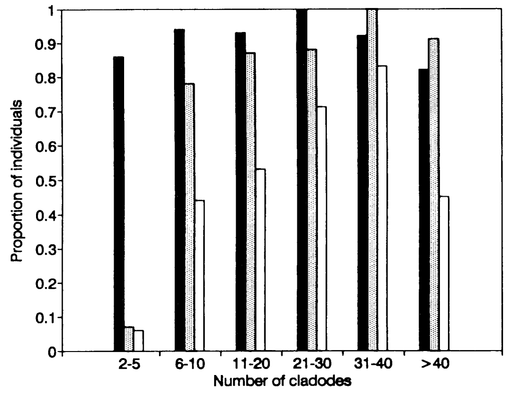

FIG. 4—Proportion of *Opuntia violacea* var *macrocentra* individuals producing new cladodes (filled bars), flowers (dotted bars) and fruits (open bars) in different size classes from May to June 1990 at a site in the northern Chihuahuan desert.

lets collected in a 0.75-m radius beneath an individual opuntia for the period May 1990 and July 1991) was not correlated with spinescence ($n = 144$; $r_s = 0.06$; $P > 0.49$), but was significantly correlated with the number of cladodes ($n = 144$; $r = 0.72$; $P < 0.0001$), and the total amount of fecal pellet dry mass collected beneath individuals in March 1990 at the start of the study ($n = 144$; $r = 0.59$; $P < 0.0001$). Fifty-two percent of the variance in grazing intensity on an individual opuntia for the period May 1990 to July 1991 could be accounted for in the following model ($d.f. = 141$; $F = 77.4$; $P < 0.0001$):

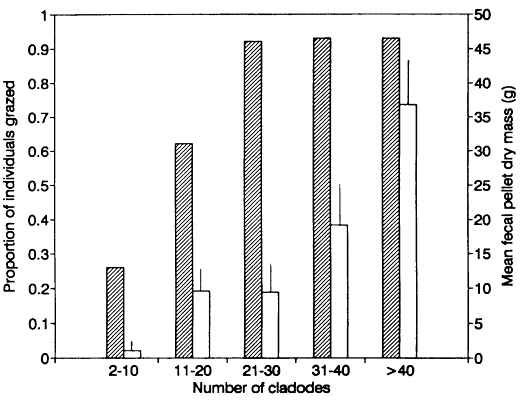

FIG. 3—Proportion of *Opuntia violacea* var *macrocentra* individuals grazed in different size classes (shaded bars) and mean fecal pellet dry mass (g) per size class (+*SE*) (open bars) at a site in the northern Chihuahuan desert for the period May 1990 to July 1991.

$$GI = -1.79 + 0.44N + 0.27F$$

where GI = Grazing intensity; N = Number of cladodes and F = Fecal pellet dry mass collected beneath *O. violacea* individuals in March 1990.

The proportion of individuals bearing new cladodes was high for all size classes (Fig. 4). The number of new cladodes produced was significantly positively correlated with the number of existing cladodes, flowers, fruits and fecal pellet dry mass (Table 1). More than 80.3% (*SE* = 2.7%) of those cladodes initiated in May 1990 survived until October 1990.

No flowers were initiated on individuals possessing less than three cladodes and only those plants having seven or more cladodes contributed substantially to the total number of flowers produced for the population (Fig. 4). The number of flowers produced was significantly correlated with number of existing cladodes, number of new cladodes and fecal pellet dry mass in May 1990 (Table 1).

Fruit production followed a similar pattern to that of flower production, increasing with increasing size class but then decreasing in the largest size class (Fig. 4). Fruit production was positively correlated with number of existing cladodes, flower production new cladode production and fecal pellet dry mass (Table 1).

Differences in the mean number of new cladodes produced in May 1990 between individual opuntias that had been grazed more heavily and individuals that had been grazed more lightly,

TABLE 1—Spearman rank correlations for 1990 between total number of cladodes, and numbers of new cladodes, flowers and fruits, and grazing intensity (rabbit fecal dry-mass from a 0.75-m plant radius) of 144 *Opuntia violacea* var *macrocentra* at a 1-ha site in the northern Chihuahuan desert. All coefficients are significant at $P < 0.0001$.

	Cladodes	New cladodes	Flowers	Fruits
New cladodes	0.61			
Flowers	0.81	0.58		
Fruits	0.58	0.47	0.77	
Fecal pellet dry mass	0.68	0.37	0.59	0.42

were highest for individuals possessing 11 to 40 cladodes (Fig. 5a) There was little difference between the two groups in the smallest and largest cladode size classes. Although the trend suggests a greater influence of grazing on intermediate size classes, non-parametric Mann-Whitney two-sample tests showed no significant differences between the two groups in any of the size classes.

Differences in the mean number of flowers and fruits produced in May 1990 between the two grazing groups were greatest for individuals with 11 to 30 cladodes (Fig. 5). There was little difference between the two groups in the smallest and two larger cladode size classes. There was, however, considerable variation between individuals in the same group for most size classes. Again, while the trend is evident, non-parametric Mann-Whitney two-sample tests showed no significant differences between the two groups in any of the size classes (Fig. 5).

DISCUSSION—Rabbits do not graze opuntias continuously at this site, but instead exhibit a seasonal preference, shifting to these succulents as a forage source during dry season or when little annual or new growth of other perennial plants in present. This confirms the general conclusions of MacCracken and Hansen (1984) and Westoby (1980) who suggest that, since jackrabbits obtain much of their water from their food, particularly during dry periods, they are likely to select for succulence. These and other studies (e.g., Uresk, 1978) all suggest that rabbits switch between grasses, forbs, succulents and shrubs depending on seasonal moisture, temperature and dormancy conditions.

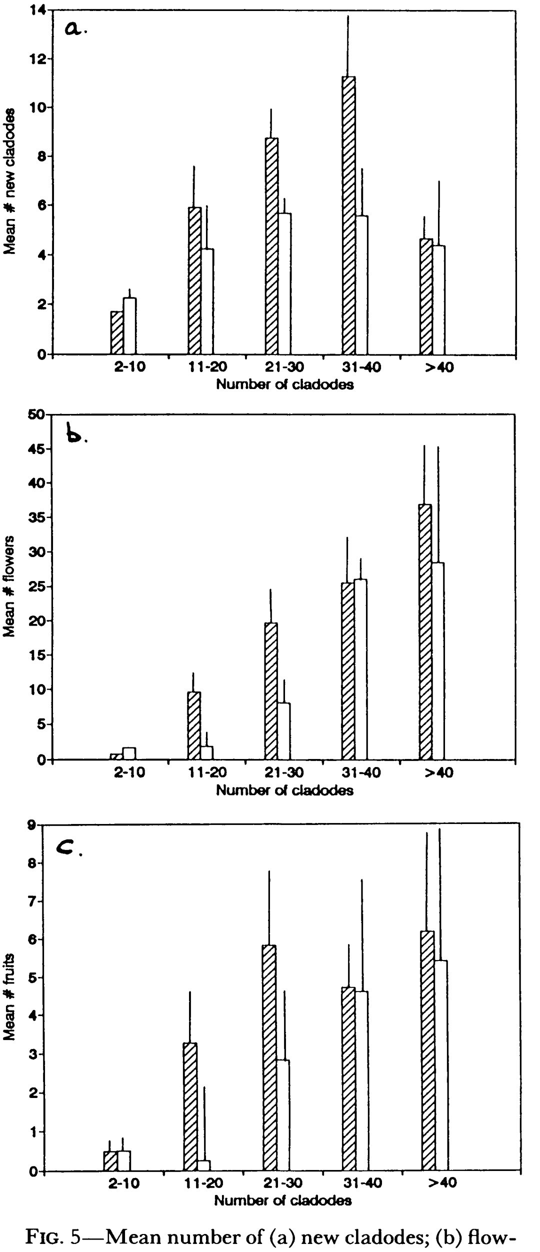

FIG. 5—Mean number of (a) new cladodes; (b) flowers and (c) fruits (+*SE*) produced in May 1990 by *Opuntia violacea* var *macrocentra* individuals in each cladode size class for individuals with less than the mean amount of fecal pellet dry mass (g) collected from a 0.75-m radius around their bases (shaded bars) and for individuals with greater than the mean amount of fecal pellet dry mass (g) collected from around their bases (open bars).

Kemp's (1983) study of plants at a nearby and comparable site provides details of plant phenological activity in the northern Chihuahuan desert and places the results of our study in a broader community context. Kemp (1983) showed that very little new growth is present in these communities from winter to early spring (November to February), particularly during dry years. Not surprisingly, therefore, we found in our study that this period coincided with one of the two peaks in rabbit grazing intensity on opuntias.

The second peak in grazing intensity occurred in June but this was not consistent between years. The nearly three-fold discrepancy in the fecal pellet dry mass collected from the population in June 1990, (an unusually low monthly rainfall record for June see Kemp, 1983) and June 1991 (an average monthly rainfall record) suggests that rabbit grazing intensity varies considerably from year to year. It also suggests that moisture availability and temperature as well as the availability of other forage sources may all influence the intensity of rabbit herbivory on this species. The role that seasonal variations in chemical composition of opuntia cladodes has on jackrabbit and cottontail grazing intensity (Potter et al., 1986; Retamal et al., 1987) may also be important.

Irrespective of the season, however, plant size and not spinescence seems to be a key determinant of whether a plant is grazed or not by these lagomorphs. Grazing on individuals also appears reasonably consistent between years.

Herbivory influences new cladode, flower and fruit production and mortality differently in different *O. violacea* size classes. Rabbit herbivory appears no to be directed at seedlings or individuals with 10 or fewer cladodes. Growth, reproduction and mortality in this cladode size class appear little influenced by the low grazing intensity. It is more likely that, in this size class, subtle microhabitat differences rather than differences in levels of herbivory influence these measures. Individuals with 30 or more cladodes also appear to be little affected by herbivory. The greater volume and specific architecture of large individuals, as well as the fact that grazing occurs predominantly on peripheral, older cladodes, ensures that there remains enough photosynthetically-active material and primordia for new cladode, flower and fruit production. Individuals in this cladode size-class may be above a threshold level where growth and reproduction are affected by rabbit grazing intensity. However, for individuals in size classes between these two extremes, rabbit herbivory may have an important influence on the number of new cladodes, flowers and fruits produced, as well as on plant mortality. In these size classes, rabbit herbivory may delay the onset of reproductive maturity largely through the retardation of biomass production and through the removal or damage of cladodes containing reproductive primordia. Although not statistically significant, heavily-grazed individuals in these size classes showed reduced cladode, flower and fruit production and, in one case, even death, compared with lightly-grazed or ungrazed individuals.

Despite the effect that grazing may have on individual biomass and flower production in intermediate size classes, there is little to indicate that rabbit herbivory influences greatly the recruitment of new individuals into the population. Assuming that the number of cladodes on *O. violacea* is positively correlated with age, then the good negative exponential function fit to cladode size class distributions for the population indicates that there is continuous regeneration of the species at this site (Daubenmire, 1968).

While this study has focused on the influence of rabbit herbivory on opuntia growth, reproduction and mortality, the dependence of these animals on opuntias for survival during dry periods may be important. Johnson and Anderson (1984), for example, have shown that in southeastern Idaho, vegetation composition has a strong influence on jackrabbit densities. It is possible that the abundance of opuntias at any one site influences positively the number of rabbits that can be sustained by that site.

Finally, while rabbit fecal-pellet removal is used in a number of studies investigating the ecology of these mammals in their natural habitats (Roundy et al., 1985; Anderson and Shumar, 1986; McAdoo et al., 1987), two implications of this method, particularly for a study such as ours, need to be considered. Firstly, the effect of removal of pellets on trail marking and home range use is not known. Although Smith (1990) points to studies that have reported that jackrabbits move about their home ranges via a system of trails, little is known about how they would identify or mark such trails. The role of fecal pellets in this regard may be important. However, our study has shown that dry mass of pellets collected from beneath opuntias for the period May 1990 to July 1991 was significantly correlated with dry pellet mass collected in March 1990. It appears, therefore, that the presence of fecal pellets may not be an important criterion for trail demarcation since our data suggest that rabbits returned to the same plants irrespective of whether fecal pellets were present around their bases or not.

Secondly, one aspect that we did not consider was the potential beneficial effects to plant nutrition of rabbit pellets deposited around the base of opuntias. Nobel et al. (1987), for example, have shown that nitrogen additions can increase the productivity of some opuntias. Rabbit feces may, therefore, be an important nutrient complement and the continual removal of this material over a long period may confound observations of cladode, flower and fruit production during the course of study.

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