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William K. Lauenroth
University of Wyoming, WLauenro@Uwyo.edu

R. L. Dougherty
Colorado State University - Fort Collins

J. S. Singh
Banaras Hindu University

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PRECIPITATION EVENT SIZE CONTROLS ON LONG-TERM ABUNDANCE OF *OPUNTIA POLYACANTHA* (PLAINS PRICKLY-PEAR) IN GREAT PLAINS GRASSLANDS

William K. Lauenroth

Department of Botany
University of Wyoming
Laramie, WY 82071
WLauenro@Uwyo.edu

R. L. Dougherty

Department of Rangeland Ecosystem Science
Colorado State University
Fort Collins, CO 80523

and

J. S. Singh

Department of Botany
Banaras Hindu University
Varanasi-221005, India

ABSTRACT—*Opuntia polyacantha* Haw. (plains prickly-pear) is a common cactus in the Great Plains of North America. We used two data sets, from Montana and Colorado, to test the hypothesis that there is a range of precipitation event sizes upon which *O. polyacantha* specializes. Events smaller than this range (>2 to ≤6 mm) do not moisten sufficient soil to be utilized, and larger events have negative effects on the status of *O. polyacantha* because they favor the development of taller and denser grass canopies. Multiple regressions of either green cladode density (northern mixed prairie) or *O. polyacantha* frequency (shortgrass steppe) with precipitation event sizes indicated negative effects of large precipitation events on the yearly changes in the either density or frequency of *O. polyacantha*. We suggest that weather conditions in the Great Plains may cause *O. polyacantha* to be controlled almost entirely by light competition from grasses and other negative biotic effects.

Key Words: cactus, northern mixed prairie, prickly-pear, shortgrass steppe, small precipitation events

INTRODUCTION

Several cactus species are common in the northern mixed prairie and shortgrass steppe of the Great Plains of North America (Weaver and Albertson 1956). *Opuntia polyacantha* Haw. (plains prickly-pear) is quite common in the prairie and steppe portions of Colorado, Wyoming, and Montana. Frequently the presence of *O. polyacantha* has been interpreted negatively because of its lack of forage value for livestock and the assumption that *O. polyacantha* is benefited by heavy grazing (Klipple and Costello 1960; Reed and Peterson 1961; Bement 1968). Recently the potential beneficial effects of *O. polyacantha* on other members of the plant community have received considerable attention (Rebollo et al. 2002, 2005). Rebollo et al. (2002) found that the presence of *O. polyacantha* provided sufficient protection from cattle grazing to allow many species to produce inflorescences. The degree to which this refuge effect is expressed is a function of grazing intensity and the cover of cladodes (an individual segment of a cactus stem) within cactus clones (Rebollo et al. 2005).

Several studies both in Montana and Colorado have failed to demonstrate strong grazing effects on the abundance of *O. polyacantha* (Turner and Costello 1942;

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Houston 1963; Bement 1968). In the shortgrass steppe, *O. polyacantha* had a slightly greater basal cover under grazing, but cladode density was not significantly different between grazed and ungrazed sites (Milchunas et al. 1989); in fact, highest cladode densities have been associated with lowest levels of disturbance (Milchunas et al. 1990). Hyder et al. (1975) observed that repeated heavy grazing in September and October increased, and repeated heavy grazing in April and July decreased, the frequency of occurrence of *O. polyacantha* in the shortgrass steppe in Colorado. However, in a wet year, cool-season grazing (November-April) resulted in large decreases that were attributed to damage by insects and other pathogens (Hyder et al. 1975). Precipitation thus seems to play an important role in the population dynamics of this species. Houston (1963) found a significant negative correlation between growing season precipitation and the percentage of *O. polyacantha* cladodes that were green. Bement (1968) attributed decreases in coverage of *O. polyacantha* to higher than normal annual precipitation, and Hyder et al. (1975) demonstrated a negative effect of spring and fall precipitation amounts, and a positive effect of summer amounts on the frequency, of *O. polyacantha*.

Grasslands of the Great Plains are characterized by growing seasons with frequent short to long periods of drought (Weaver and Albertson 1956; Sala et al. 1992; Lauenroth and Bradford 2006). Plants in these grasslands encounter frequent periods of water stress, most often in late summer, yet precipitation occurs more often than is evident from the low monthly totals, because most of the daily precipitation amounts are small (Sala and Lauenroth 1982; Sala et al. 1992; Lauenroth and Bradford 2006).

The contribution of a day's precipitation to the soil-water resource of a plant is influenced by the penetration of water in the soil and the vertical root distribution of the plant (Walter 1973; Lauenroth et al. 1993; Lauenroth and Bradford 2006). At the Central Plains Experimental Range, a shortgrass steppe site in Colorado, 52% of the length of *O. polyacantha* roots occurred in the top 2.5 cm of soil; 97% occurred in the top 10 cm (Dougherty 1986). A wetting front to 2.5 cm will moisten half the total length of roots of *O. polyacantha*. Using the equation given by Hanks and Ashcroft (1980), Dougherty (1986) predicted that a wetting front of 2.5 cm will result from a precipitation event of 2-4 mm, and that an event of 6 mm will wet sufficient soil to moisten 65% to 87% of the root length of *O. polyacantha*, depending on initial conditions. However, water in the top centimeter of soil may evaporate too quickly to be available to roots of any vascular plant. Also, canopy and litter interception may prevent up to 1 mm of precipitation from reaching the soil (Clark 1940). There is clearly a lower limit to the size of precipitation event that is available to even the shallow-rooted *O. polyacantha*.

Depth distributions of roots vary with plant functional types and species (Walter 1973; Lauenroth et al. 1993; Sun et al. 1997). Soil water resulting from large precipitation events may be utilized most efficiently by grasses, which are more deeply rooted than *O. polyacantha* (Dougherty et al. 1996; Sun et al. 1997). We propose that the smallest precipitation event that is utilized by *O. polyacantha* is 2 mm. Smaller events either do not reach the rooting zone of *O. polyacantha* or do not replenish its water content for long enough to significantly influence its water status. Also, based upon root density and wetting front penetration, 6 mm may be the upper range of events that are more efficiently utilized by *O. polyacantha* than by grasses. In the shortgrass steppe, 55% of the root biomass of grasses was found in the top 10 cm of soil; 69% in the top 20 cm (Bartos and Sims 1974). Although precipitation events larger than 6 mm contribute to the soil-water resource of *O. polyacantha*, they also promote grass growth, which can have a negative effect on *O. polyacantha*. We hypothesize that the negative effects of grasses exert more control over *O. polyacantha* than the positive effects of its own resource.

These considerations lead to the hypothesis that precipitation event sizes between 2 and 6 mm have a positive effect on the growth and survival of *O. polyacantha*: events smaller than this do not wet sufficient soil or are too rapidly lost to evaporation to be utilized, and larger events promote grass growth, which has negative effects. Where *O. polyacantha* coexists with grasses, we hypothesize that soil water is partitioned between the two functional types. Patterns of precipitation that favor the development of grass canopies are expected to result in decreases in local populations of *O. polyacantha*. *O. polyacantha* should benefit only from patterns of precipitation that provide relatively little benefit to grasses. Our objective is to discover the relationship between the distribution of precipitation event sizes and the abundance of *O. polyacantha* in two Great Plains grasslands.

METHODS

We used two data sets collected over periods of several years. Data from the Fort Keogh Livestock and Range Research Station in Montana are counts of green *O. polyacantha* cladodes in permanent 120 m^2 plots during 14 of the years between 1937 and 1962 (Houston 1963). Data from the Central Plains Experimental Range

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(CPER) in Colorado consist of frequencies of *O. polyacantha* sampled in 48 exclosures, each 1.5 ha in size. The CPER data set spans two studies. From 1963 through 1972, the effects of season of grazing and nitrogen fertilization were evaluated (Hyder et al. 1975). From 1973 to 1982 the effects of burning, atrazine, and nopalmate herbicides, in addition to grazing time and nitrogen fertilizer, were studied (USDA-ARS unpublished results). The burned and nopalmate herbicide treatments had significant effects on the frequency of *O. polyacantha*; our analysis therefore includes only the 12 pastures not burned or treated with nopalmate. The same size quadrat was used to sample frequency in both CPER studies.

Density and frequency are both quantitative descriptions of abundance, but they have different characteristics (Greig-Smith 1964). Cladode density is the number of cladodes per unit area. Frequency is the chance of finding a cladode in a particular size quadrat in one trial (Greig-Smith 1964). Frequency data require less effort to collect and considerable effort has been devoted to understanding their properties and utility as an indicator of density (Hyder et al. 1963; Greig-Smith 1964; Kershaw 1964; Heywood and DeBacker 2007). Although frequency and density are related indicators of abundance, an exact relationship is only possible if one can assume that individuals are distributed randomly (Hyder et al. 1963; Greig-Smith 1964). Few plants are randomly distributed, including *O. polyacantha*, therefore we avoided direct comparison between the Fort Keogh density data and the CPER frequency data. Our only assumption is that they are both quantitative indicators of *O. polyacantha* cladode abundance.

The vegetation on both the Montana and Colorado sites was dominated by *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths and *Buchloë dactyloides* (Nutt.) J.T. Columbus. All nomenclature and authorities follow the USDA PLANTS Database (USDA, NRCS 2008). The long-term mean annual precipitation is 326 mm at the Montana site and 321 mm at the Colorado site. Mean annual temperatures are 7.6°C at Fort Keogh and 8.6°C at the CPER. Winter is the dry season and early summer is the wet season at both sites. Data were collected from a range of soil types at the Montana site (see Houston 1963 for descriptions) and from sandy loam soils at the Colorado site (Hyder et al. 1975).

We summarized daily weather data from stations in Miles City, Montana, and the Central Plains Experimental Range in Colorado, and used regression analysis to test the response of *O. polyacantha* to precipitation (National Climatic Data Center 2002). The dependent variable was the difference between two consecutive years' measurements of green cladode density (Montana) or *O. polyacantha* frequency (Colorado). The independent variables were the number of precipitation events >2 mm and ≤6 mm, and the number of precipitation events >6 mm. Precipitation data were from the growing season (April 1–September 30) of the first of the two consecutive years. In the Great Plains, with rapid evapotranspiration between the characteristic late-afternoon precipitation, there is justification for the simplifying assumptions that the frequency of precipitation is as important as the amount, and that the number of events of a minimum size is a good indicator of the resource value of soil water for all but very deep-rooted plants (Lauenroth and Bradford 2006). We therefore use numbers of "small" (>2 and ≤6 mm) and "large" (>6 mm) precipitation events as easily measured indicators of the suitability of a growing season for *O. polyacantha* and its grass competitors.

For comparison with our analyses of the number of events, we calculated additional regressions between change in *O. polyacantha* and large precipitation amounts, and between *O. polyacantha* change and total growing season precipitation. We also tested the applicability of the seasonal model proposed by Hyder et al. (1975) to the complete CPER data and the Fort Keogh data.

RESULTS AND DISCUSSION

At both the Colorado and Montana sites, the size distributions of daily precipitation events are skewed toward the low end (Fig. 1). This pattern is characteristic of semi-arid and arid sites throughout the western United States (Loik et al. 2004). At the Colorado site, an average of 65% of the daily precipitation events from April 1 to September 30 are ≤6 mm, yet they account for only 22% of the total precipitation. The corresponding percentages for the Montana site were 75% and 28%. The coefficients of variability for total growing season precipitation among years were 34% for the CPER and 51% for Fort Keogh. There was also considerable variation among years in frequencies of large and small precipitation events.

O. polyacantha density in the Montana study varied by a factor of 2, and the highest frequency observed in the Colorado study was 1.5 times the minimum (Tables 1 and 2). The frequency data from Colorado showed less year-to-year variation than did the cladode density data from Montana. Frequency is expected to reflect variations in population size less readily than is density, especially for plants with highly aggregated distributions (Greig-Smith 1964).

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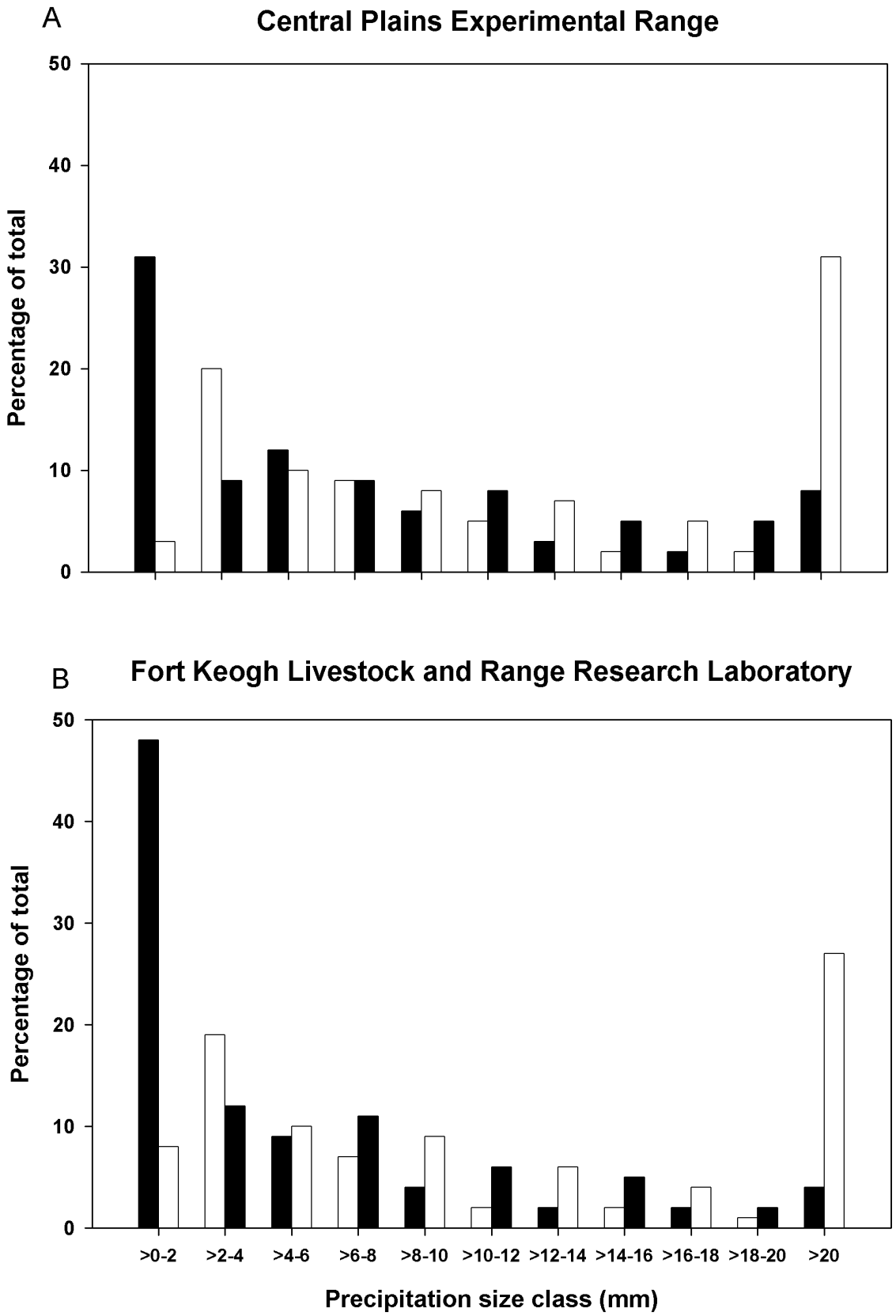

Figure 1. Distributions of frequencies and amounts of growing season precipitation associated with 11 event size classes at the Central Plains Experimental Range, Colorado (A) and Fort Keogh Livestock and Range Research Station, Montana (B).

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TABLE 1
SUMMARY OF PRECIPITATION, AVERAGE FREQUENCY OF *OPUNTIA POLYACANTHA* IN THE YEAR INDICATED, AND CHANGE IN FREQUENCY TO THE FOLLOWING YEAR, CENTRAL PLAINS EXPERIMENTAL RANGE, COLORADO

	Growing season precipitation				Annual precipitation		*Opuntia* frequency	
	Small (>2 mm and ≤6 mm)		Large (>6 mm)		Total (all days with precipitation)			
Year	Number	Amount	Number	Amount	Number	Amount	Average frequency (%)	Change in frequency (%)
1963	13	49	14	237	35	292	56.9	-1.7
1964	8	30	6	54	24	92	55.2	2.3
1965	13	52	20	283	43	343	57.5	-0.4
1966	14	58	11	185	40	255	57.1	2.5
1967	11	41	27	464	47	515	59.6	-7.6
1968	10	37	14	221	34	271	52.0	-4.6
1969	15	60	17	258	40	327	47.4	-1.9
1970	9	32	11	125	30	168	45.5	-0.2
1971	13	49	10	165	34	224	45.3	0.7
1972	13	54	20	244	50	314	46.0	0.0
1973	14	47	12	156	38	214	46.0	7.3
1974	12	47	7	153	25	205	53.3	1.9
1975	14	55	10	163	30	226	55.2	3.8
1976	21	77	13	156	40	240	59.0	1.8
1977	13	45	13	160	31	212	60.8	-2.5
1978	11	41	9	167	26	214	58.3	3.8
1979	15	57	21	334	44	397	62.1	0.7
1980	10	39	15	214	34	263	62.8	3.2
1981	14	51	15	272	37	334	66.0	NA

Notes: Precipitation data include the number of precipitation events and the amount of precipitation for three size classes during the growing season (April 1–September 30) of the year indicated.

Multiple regressions suggested important negative effects of large precipitation events on both cladode frequency and density (Table 3). The regression coefficients for the effect of small event frequency were all positive, and those for large events were all negative. The frequencies of large precipitation events explained more of the variation in changes in density and frequency than did those for small events. Regressions using amounts of precipitation from events over 6 mm explained more of the variability in density or frequency than regressions using total growing season precipitation (Table 4). At both sites, the numbers of large events and the amounts associated with them were more variable than the numbers and amounts of small events or the amounts of growing season precipitation, suggesting large events contained more explanatory potential. Sala et al. (1992) analyzed 33 years of precipitation data from the CPER and found that small precipitation events (≤5 mm) had low interannual variability compared to large events (≥10 mm).

Our results show that information about large precipitation events is more useful for explaining changes in *O. polyacantha* status than information about either small precipitation events or total precipitation. Removing the small precipitation information from total precipitation improved the utility of the totals for predicting *O. polyacantha* status (Table 4). The importance of the largest components of the precipitation regime and their negative effects on frequency and density is emphasized by the uniformly negative regression coefficients for both total precipitation and the amount contributed by large events.

Hyder et al. (1975) analyzed seven years of data and predicted *O. polyacantha* frequency using precipitation amounts from the spring, summer, and fall in the year prior to measurement. We found that if the Hyder et al. (1975) model was modified to predict change in frequency instead of frequency itself, results were still significant, but only spring precipitation was important and its effect was negative as in the original model. When the full 19 years of data from CPER were considered, the seasonal model was not significant (Table 5). We found that the seasonal model applied to change in density from the Fort Keogh data,

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TABLE 2
SUMMARY OF GROWING SEASON AND ANNUAL PRECIPITATION (NUMBER OF EVENTS AND AMOUNT), AVERAGE DENSITY OF GREEN *O. POLYACANTHA* CLADODES IN THE YEAR INDICATED, AND CHANGE IN DENSITY TO THE FOLLOWING YEAR, FORT KEOGH LIVESTOCK AND RANGE RESEARCH STATION, MONTANA

	Growing season precipitation				Annual precipitation		*Opuntia* density	
	Small (>2 mm and ≤6 mm)		Large (>6 mm)		Total (all days with precipitation)			
Year	Number	Amount	Number	Amount	Number	Amount	Density (cladodes/m^2)	Change in density (cladodes/m^2)
1937	11	47	8	125	40	190	9.57	2.13
1938	15	56	9	130	51	204	11.71	2.88
1939	16	54	9	136	57	217	14.58	4.45
1940	17	58	13	160	53	236	19.03	-2.48
1941	17	56	24	304	67	375	16.56	-5.05
1942	10	45	18	222	65	290	11.51	-1.17
1943	11	40	13	242	43	297	10.34	-1.12
1944	22	72	20	331	59	418	9.22	-2.51
1945	12	47	13	191	49	260	6.71	
1946	15	52	17	262	49	329		
1947	11	40	14	180	44	233		
1948	16	62	18	262	57	343		
1949	7	23	6	60	39	101	8.72	
1950	21	67	10	161	53	245		
1951	17	62	16	234	54	310		
1952	13	40	10	132	41	183		
1953	19	68	18	248	56	331		
1954	13	42	12	149	54	213		
1955	14	36	13	198	52	253	11.04	
1956	20	72	9	98	54	189		
1957	17	54	11	152	45	222	17.51	
1958	13	43	13	169	46	225		
1959	16	59	7	67	49	148		
1960	12	45	5	55	34	112	12.04	4.71
1961	15	48	10	130	53	198	16.75	

Notes: *Opuntia* data were recorded in 14 years, not all contiguous, resulting in only nine differences between adjacent years. Precipitation data include the number of precipitation events and the amount of precipitation for three size classes for the growing season (April 1–September 30) of the year indicated.

TABLE 3
RESULTS OF REGRESSION ANALYSIS TESTING THE IMPORTANCE OF THE NUMBER OF SMALL AND LARGE PRECIPITATION EVENTS ON YEARLY CHANGES IN *O. POLYACANTHA* FREQUENCY (COLORADO) OR GREEN CLADODE DENSITY (MONTANA)

Dependent variable	Independent variable(s)	Regression coefficients	R^2	d.f.	P
Change in frequency (CO)	# Small # Large	0.315 -0.406	0.426	2,15	0.016
Change in frequency (CO)	# Large	-0.379	0.357	1,16	0.009
Change in density (MT)	# Small # Large	0.036 -0.508	0.824	2,6	0.005
Change in density (MT)	# Large	-0.498	0.823	1,7	0.001

Notes: CO = Central Plains Experimental Range, Colorado; MT = Fort Keogh Livestock and Range Research Station, Montana. Small events are >2 mm and ≤6 mm, and large events are >6 mm.

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TABLE 4
RESULTS OF REGRESSION ANALYSIS TESTING THE IMPORTANCE OF TOTAL GROWING SEASON PRECIPITATION AND AMOUNTS FROM LARGE PRECIPITATION EVENTS TO PREDICT ANNUAL CHANGES IN *O. POLYACANTHA* FREQUENCY (COLORADO) OR GREEN CLADODE DENSITY (MONTANA)

Dependent variable	**Independent variable**	**Regression coefficients**	**r^2**	**d.f.**	**P**
Change in frequency (CO)	Total	-0.022	0.354	1,16	0.010
Change in frequency (CO)	Large (>6 mm)	-0.024	0.387	1,16	0.006
Change in density (MT)	Total	-0.030	0.695	1,7	0.005
Change in density (MT)	Large (>6 mm)	-0.032	0.723	1,7	0.003

Notes: CO = Central Plains Experimental Range, Colorado; MT = Fort Keogh Livestock and Range Research Station, Montana.

TABLE 5
RESULTS OF REGRESSION ANALYSIS TESTING THE APPLICABILITY OF THE SEASONAL MODEL OF HYDER ET AL. (1975) TO FREQUENCY FROM THE CENTRAL PLAINS EXPERIMENTAL RANGE, COLORADO

Dependent variable	**Independent variable**	**R^2**	**d.f.**	**P**
Frequency, 1964-1971 only	Spring Summer Fall	0.929	3,5	0.003
Change in frequency, 1964-1971	Spring Summer Fall	0.914	3,4	0.014
Frequency, 1964-1981	Spring Summer Fall	0.300	3,15	0.138
Change in frequency, 1964-1981	Spring Summer Fall	0.395	3,14	0.064

TABLE 6
RESULTS OF REGRESSIONS TESTING THE APPLICABILITY OF THE SEASONAL MODEL OF HYDER ET AL. (1975) TO CLADODE DENSITY AND THE ANNUAL CHANGE IN CLADODE DENSITY FROM FORT KEOGH LIVESTOCK AND RANGE RESEARCH STATION, MONTANA

Dependent variable	**Independent variable**	**R^2**	**d.f.**	**P**
Density	Spring Summer Fall	0.418	3,10	0.129
Change in density	Spring Summer Fall	0.940	3,5	0.002

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but not density itself (Table 6). We were unable to confirm Hyder et al.'s (1975) hypothesis about the positive influence of summer precipitation on *O. polyacantha*.

Further insight into the relationships between precipitation and *O. polyacantha* can be gained by investigating correlations of annual change in *O. polyacantha* with frequency of precipitation in a variety of size classes. We calculated the correlations with numbers of precipitation events in each of nine approximately equal frequency size classes. We found that change in *O. polyacantha* frequency or density was only significantly (negatively) related to the largest size classes. This analysis supported the results of the regression analysis; the largest precipitation events had the greatest effect on *O. polyacantha*.

Annual changes in *O. polyacantha* are influenced only slightly by variations in favorability of its soil water resource (events ≤6 mm). Of more apparent importance is the effect of large precipitation events. Our results suggest that the negative effect of large precipitation events may be mediated by direct and indirect influence of the grasses that more efficiently utilize soil water supplied by these events. Although we do not have associated data for grass growth from either site, results from the literature support this idea. Lauenroth et al. (1978) and Dodd and Lauenroth (1975) reported negative effects of spring and summer water additions on *O. polyacantha* and positive effects on grasses from and experiment at CPER. Both the negative and positive effects were enhanced when nitrogen was added in combination with water. Grass biomass increased by 150% with the addition of water and 475% when both water and nitrogen were added (Lauenroth et al. 1978). It is plausible that at least part of the negative response of *O. polyacantha* was the result of shading by grasses (Cook 1942; Dodd and Lauenroth 1975). Burger and Louda (1994, 1995) conducted a field shading experiment with *Opuntia fragilis*, a common cactus in the northern mixed prairie. They found increased live cladode numbers when grasses were prevented from shading the cactus and increased mortality from *Melitara dentata* in the presence of grass canopies. Experiments using detached cladodes of *Opuntia ficus-indica* indicated that shading by 94% completely eliminated initiation of daughter cladodes (Nobel 1996), which is consistent with field observations of whole plants that found a positive relationship between CO_2 fixation and incident daily photosynthetically active radiation (Acevedo et al. 1983). Confirmation of negative effects of shading of *O. polyacantha* by grasses will require additional field experiments of the kind reported by Burger and Louda (1994, 1995).

Indirect negative effects of grasses on *O. polyacantha* are also possible if grass canopies enhance the microclimate of insect herbivores of *O. polyacantha* (Cook 1942; Dodd and Lauenroth 1975). Although the exact mechanism involved in the relationship of moisture and insect pests of *O. polyacantha* is not known, they apparently thrive in humid microclimates (Cook 1942; Bugbee and Riegel 1945; Dodd and Lauenroth 1975; Speirs 1978). Cook (1942) noted that emergence of adult *Melitara dentata*, the blue cactus borer, was hindered by dry conditions.

The succulent nature of *O. polyacantha* may be important in moderating its reliance on frequent replenishment of the soil-water resource. Internal storage of water may allow *O. polyacantha* to function normally in drought periods of up to a month. Krishnamoorthy et al. (1979) reported average water residence times on the order of months in *Opuntia* species. The frequent inputs to and rapid loss of water from the shallow rooting zone of *O. polyacantha* represents a high-frequency temporal pattern of an important resource. Through its ability to quickly take up water when it is available and store it internally, *O. polyacantha* can impose a lower temporal frequency on its water resource (Dougherty et al. 1996). This new frequency is low enough to allow the relatively energy-inefficient metabolic pathways of *O. polyacantha* to fuel its slow but steady growth. Variations in the frequency of availability of soil water to *O. polyacantha* may thus be damped out by the plant to the extent that they are not associated with noticeable variations in population status. Possibly, there was sufficiently frequent precipitation for the modest requirements of *O. polyacantha* in most of the years in these studies; effects of precipitation frequency on *O. polyacantha* may only be noticed in years of drought, when there is little inhibition of growth from grasses. Milchunas et al. (1989) have indeed reported an increase in the abundance of this species in the shortgrass steppe during dry years on ridge tops.

The presence of *O. polyacantha* can deter the use of associated forage plants. The interpretation of the value of this effect can be negative (Mueller et al. 1994) or positive (Rebollo et al. 2002, 2005). A question that is often asked but not clearly answered is: What accounts for the abundance of *O. polyacantha* in Great Plains grasslands? One answer, that *O. polyacantha* increases in response to livestock grazing and is an indicator of overgrazing, seems to have originated in the writings of John Weaver (Weaver and Albertson 1956). The idea that *O. polyacantha* is an indicator of overgrazing has been perpetuated through three generations of rangeland management textbooks (Stoddard and Smith 1955; Stoddard et al. 1975; Holochek

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et al. 1989). Much of the literature in the past half-century has not found clear relationships between grazing treatment and the abundance of *O. polyacantha*. Hyder et al. (1975) reported positive and negative interactions between grazing and weather on *O. polyacantha* abundance, Houston's (1963) and Bement's (1968) research implicated weather as the key control on abundance, and Milchunas et al. (1989) and Hart and Ashby (1998) found no relationship between grazing intensity and abundance. From our research, our answer to the abundance question is that weather conditions seem to cause *O. polyacantha* to be controlled by light competition from grasses and other negative biotic effects such as damage by insect herbivores. Heavy grazing by itself does not seem to promote increases in *O. polyacantha* abundance, although decreased light competition from grasses as a result of heavy grazing may have some influence.

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