

# Herbivory of clonal populations: cattle browsing affects reproduction and population structure of *Yucca elata*

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Abstract. The hypothesis that cattle browsing on inflorescences of the soaptree Yucca elata reduces reproductive success was investigated by comparing recruitment and population structure in six populations protected from grazing, six grazed during the flowering season and five grazed outside the flowering season. Cattle consumed 98% of inflorescences, which were found to be highly nutritious. Reduced recruitment in flower-grazed populations could not be attributed to reduced flower survival, as recruitment in non-flower grazed populations was also reduced. Changes in population structure were due to cattle browsing small caudices, including both genets and ramets. An alternate hypothesis of limited germination in soils compacted by cattle was not supported. Cattle browsing of inflorescences reduced reproductive effort, which may be due to the inability of the plants to resorb nutrients after flowering. Browsing also increased branching, probably through lack of apical dominance, whereas physical trampling increased procumbency. Cattle browsing implies a lack of genetic recruitment, possible local extinction of the yucca moth Tegeticula yuccasella, the exclusive pollinator of Y. elata, and local reduction in insect and bird biodiversity.

**Key words:** Herbivory – Cattle – *Yucca elata* – Biodiversity – Nutritional value of inflorescences

The effects of herbivores on the structure and population attributes of plant communities are well documented. Few studies, however, have provided mechanisms for such effects (Kershaw and Looney 1985).

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Cattle browsing the flowers of Yucca elata could cause reduced seed production and recruitment, resulting in an increase in large clonal individuals (Smith and Ludwig 1976). We tested this hypothesis by measuring inflorescence consumption and population structure in yucca populations protected from cattle browsing, browsed by cattle during the flowering season, and browsed by cattle outside the flowering season. Alternative hypotheses dealing with browsing of vegetative material and soil compaction were explored, and the implications of browsing on clonal populations are discussed.

#### Natural history of Y. elata

The soaptree yucca Y. elata (Agavaceae) is a common perennial in the Chihuahuan Desert, occurring throughout south-west Texas, southern New Mexico, southern Arizona and northern Mexico. The tall (up to 10 m), succulent caudex is surmounted by a rosette of narrow, sharp-tipped leaves, and has a large, fleshy tuber (Kearney and Peebles 1969). Yucca elata is iteroparous, flowering in May, June and July, but also grows clonally. The large (1-4 m) inflorescence stalk grows rapidly (Campbell and Keller 1932), and bears up to 1300 flowers (mean = 310 - C.D. James, M.T. Hoffman, D.C. Lightfoot, G.S. Forbes and W.G. Whitford unpubl.). It is pollinated exclusively by the mutualistic yucca moth Tegeticula yuccasella, but few fruits mature (James et al. unpubl.). Seeds are wind-dispersed and do not appear to have any mechanism for dormancy (McCleary and Wagner 1973).

Young inflorescence stalks and flowers are highly palatable to cattle (Herbel and Nelson 1966), and ranchers actively manage herds to utilize the annual Y. elata flower crop (K.M. Havstad, pers. comm.). Cattle also browse Y. elata leaves, which may form up to 20% of cattle diet in winter and spring (Herbel and Nelson 1966).

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**Table 1.** Locations, treatments and sample sizes of *Yucca elata* populations sampled in this study

Site	Tenure and	Treatment	Sample	
no	management unit <sup>1</sup>		size	
1	CR, exclosure 8	Exclosure	104	
2	CR, pasture 7	Flowering season grazed	102	
3	JER, pasture 9	Non-flowering season grazed	50	
4	CR, pasture 3N	Flowering season grazed	50	
5	CR, pasture 3S	Non-flowering season grazed	52	
6	CR, exclosure 3N	Exclosure	48	
7	CR, exclosure 5	Exclosure	50	
8	CR, pasture 5	Flowering season grazed	49	
9	CR, pasture 2	Flowering season grazed	50	
10	CR, exclosure 3S	Exclosure	49	
11	CR, pasture 3W	Non-flowering season grazed	48	
12	CR, pasture 15	Flowering season grazed	50	
13	CR, exclosure 14N	Exclosure	54	
14	CR, pasture 14N	Flowering season grazed	50	
15	CR, exclosure 15	Exclosure	51	
16	CR, pasture 12	Non-flowering season grazed	50	
17	CR, pasture 8	Non-flowering season grazed	48	

<sup>&</sup>lt;sup>1</sup> CR = New Mexico State University College Ranch, JER = US Department of Agriculture Jornada Experimental Range

#### Methods

# Study area

The study was conducted in the Jornada Basin in southern New Mexico. Study populations were located on the New Mexico State University College Ranch and the adjacent U.S. Department of Agriculture Jornada Experimental Range (Table 1), 40 km northwest of Las Cruces. Annual precipitation averages  $210\pm77$  mm, mainly as summer convective storms (Houghton 1972). Vegetation of these sites was dominated by grass (Sporobolus flexuosus, S. cryptandrus and Bouteloua eriopoda); honey mesquite Prosopis glandulosa was the most common woody perennial.

# Study populations

A total of 17 Y. elata populations were studied (Table 1), of which 6 were protected from cattle grazing by exclosures, 6 had been routinely (for the past 25 years) grazed by cattle (stocking rate = 50 ha cow<sup>-1</sup>) during the summer flowering period (flower grazed), while the remaining 5 sites (non-flower grazed) had been routinely grazed during the winter, non-flowering season (J.A. Winder and K.M. Havstad, pers. comm.).

Site 6 was enclosed in 1939, and sites 7, 10, 13, and 15 in 1954 (R.E. Beck, pers. comm.). Site 1 was set up in 1969 for the IBP Desert Biome Project. The fencing does not exclude indigenous herbivores.

# Sampling

During June/July 1991 each Y. elata population was sampled in 100 × 15 m transects. All individuals, i.e., groups of caudices not further than 1 m apart, were located. Two initial samples (sites 1 and 2) each of 100 plants indicated that a sample of 50 plants per population was adequate to account for the variability in the number of caudices per plant. Thereafter, strip transects were replicated until approximately 50 plants were included for each population.

For each plant we recorded the number of caudices, height of each caudex, and the presence of inflorescences. Inflorescences were categorized as current, 1 and > 1 year old, based on the presence of fruit, weathering and proximity to the apex of the caudex. Grazed

inflorescences were determined by the presence of a chewed-off inflorescence stalk. The occurrence of branched, procumbent and dead caudices was recorded.

#### Nutritional value

Analyses were conducted on young inflorescence stalks, mature inflorescences, flowers, and young leaves. Material was dried and finely milled. Analyses were conducted at the Animal Nutrition Research Laboratories of the Department of Animal and Range Sciences, New Mexico State University, using standard techniques for moisture, ash, crude protein, neutral detergent fibre, acid detergent fibre and acid detergent lignin.

# Soil compaction

Soil compaction was measured with a proving ring penetrometer (Model LC-2B, Soiltest Inc, Evanston, Ill.), with a 0.983 inch<sup>2</sup> (6.34 cm<sup>2</sup>) basal area cone point. Fifty readings, about 2 m apart on a randomly located transect, were taken of undisturbed soil clear of vegetation or litter at each site.

# Height escape

A Y. elata population with a high proportion of tall plants was sampled at a location 27 km west of Deming, New Mexico on the south side of the I10 Highway. The site was grazed by cattle during the flowering season. At least 30 caudices that flowered in the 1991 season, in 20-50, 51-100, 101-150, 151-200 and >200 cm height classes, were sampled for inflorescence consumption.

# Data analysis

Proportional data were arcsine transformed before statistical analysis (Zar 1984). Differences between treatments were investigated using ANOVA and Students *t*-test, at the 95% level of significance. Correlation analyses were performed by least squares.

**Table 2.** Population attributes (means  $\pm$  SE) of Yucca elata populations sampled in this study and the results of ANOVA (df = 2,14) and Tukey's Range Test (data were arcsine transformed for testing)

Population attribute	Treatment	F	P			
	Grazed while flowering	Grazed while not flowering	Exclosures	_		
n	6	5	6			
Proportion of current flowers eaten (%) <sup>1</sup>	a 98.4±0.7	b 23.0 ± 5.1	b 9.9 ± 4.3	97.093	0.000	
Number of caudices per plant	a $3.24 \pm 0.22$	a $3.65 \pm 0.32$	b $2.18 \pm 0.11$	9.336	0.0027	
Proportion of single plants <20 cm (%)	ab 14.5 ± 2.7	a 6.1 <u>+</u> 1.1	b 19.4 <u>±</u> 4.0	4.914	0.0242	
Proportion of caudices < 20 cm, on multi-caudex plants (%)	a 20.5 ± 2.2	a 21.5 ± 1.9	b 37.6 ± 6.7	4.082	0.0401	
Proportion of branched caudices (%)	a 9.2 ± 2.5	a 14.6 ± 5.0	b 2.0 ± 1.5	7.225	0.0070	
Proportion of procumbent caudices (%)	a 2.4 <u>±</u> 1.1	a 2.2 ± 0.3	$\begin{matrix} b \\ 0.2 \pm 0.1 \end{matrix}$	5.663	0.0158	
Proportion of dead caudices (%)	a 11.1 ± 1.8	$a \\ 16.0 \pm 2.3$	$a \\ 13.8 \pm 1.8$	1.326	0.2969	
Proportion of multi-caudex plants with a dead caudex (%)	a 25.9 ± 3.1	$a \\ 36.6 \pm 7.3$	a 20.3 <u>+</u> 1.9	2.692	0.1025	
Proportion of caudices > 20 cm, currently flowering (%)	a 29.9 ± 1.7	b 49.2 ± 3.2	b 40.0 ± 1.7	15.509	0.0003	

<sup>&</sup>lt;sup>1</sup> Site 17 excluded from this analysis, as cattle strayed onto this site during the 1991 flowering season Values with the same letter superscript do not differ at the 95% level according to Tukey's Range Test

# **Results**

What proportion of flower production was consumed by cattle?

At sites not grazed by cattle during the flowering season, a mean of 15% (n=10, range = 0-42%) of current inflorescences were consumed (site 17 was excluded from this analysis as cattle strayed onto this site, resulting in 66% of the inflorescences being eaten). We attributed this "natural" flower consumption to pronghorn antelope Antilocapra americana, mule deer Odocoileus hermionus, jack rabbits Lepus californicus, cottontail rabbits Sylvilagus auduboni and woodrats Neotoma sp.. Flower consumption did not differ between exclosure and non-flower-grazed populations (t=1.831, df=8, P=0.1044).

At sites grazed by cattle during the flowering season, 98% of current flower stalks had been consumed, significantly more than at exclosure and non-flower-grazed sites (Table 2). Cattle typically bit off the young inflorescence, or where the inflorescence was fully developed, ate the flowers. Where the inflorescence was too tall, the stalk was broken and the flowers eaten. Herbel and Nelson (1966) recorded cows standing on their hind legs to reach Y. elata flowers.

The attraction of cattle to inflorescences can be related to the nutritional value relative to other available foodstuffs. Young stalks and flowers are high in moisture and protein, with low fibre and ash loads (Table 3). The relatively low acid detergent lignin (largely lignin) indicates high ruminant digestibility of structural components (Van Soest 1982). The acid detergent fibre content of the young stalks and flowers was below that recorded in cattle diets on the Jornada at this time of the year, the height of summer drought, whereas crude protein levels were well above those recorded in Jornada cattle diets (Havstad 1977). The high protein levels observed here may be largely provided by heavy infestations of aphids, which cattle consume with the flowers.

Does grazing by cattle affect Y. elata population structure, and if so can this be attributed to reduced recruitment?

The prediction that flower-grazed Y. elata populations had more extensive cloning (more caudices per plant) than exclosure populations is supported (Table 2). This is associated with marginally decreased recruitment (fewer small individuals, Table 2). However, this cannot be attributed to reduced seed production as similar trends were observed for non-flower-grazed populations (Table 2), which did not have reduced reproductive success (flower survival). Thus it is not the loss of reproductive material that results in population changes, but some other interaction between cattle and Y. elata.

The finding that exclosure populations had more small shoots on multiple caudex plants (proportion of caudices < 20 cm on multiple caudex plants) than either the flower-grazed or non-flower-grazed populations

**Table 3.** Nutritional attributes (mean  $\pm$  SD) of Y. elata inflorescences, flowers and young leaves (n = 3, except where otherwise indicated)

	Mass g	Moisture %	Neutral detergent fibre %	Acid detergent fibre %	Acid detergent lignin %	Crude protein %	Ash %
Young stalk	$88.1 \pm 49.5$ $n = 5$	$65.4 \pm 4.4$ $n = 5$	$28.3 \pm 2.9$	$23.6 \pm 2.3$	$7.1 \pm 4.6$	$21.7 \pm 1.3$	6.4±0.7
Mature inflorescence	$ 1160.3 \pm 638.6 \\ n = 5 $	$73.0 \pm 2.9$ $n = 5$	$44.1 \pm 4.8$	$37.7 \pm 3.7$	$7.2 \pm 0.7$	$16.9 \pm 1.5$	$6.2 \pm 0.4$
Flowers	$600.3 \pm 385.7$ $n=5$	$78.7 \pm 3.5$ $n = 5$	$13.7 \pm 0.8$	$14.3 \pm 1.4$	$2.3 \pm 0.3$	$26.5 \pm 3.4$	$8.6 \pm 0.4$
Young leaves	$82.6 \pm 30.1$ $n = 4$	$70.1 \pm 3.3$ n = 4	$55.3 \pm 1.0$	$45.5 \pm 1.0$	$13.3 \pm 2.4$	$10.6 \pm 2.2$	$6.7 \pm 0.5$

**Table 4.** Attributes (mean  $\pm$  SD) of grazed and ungrazed Y. elata populations and the results of Students t-test (df = 15)

Attribute	Grazed (n = 11)		Ungrazed (n = 6)	t	P
Mean caudex height (cm)	43.2±	9.63	30.8 ± 6.98	2.76	0.015
Soil compaction (Newtons cm <sup>-2</sup> )	$484.2 \pm 3$	36.4	$195.0 \pm 91.8$	1.94	0.036
Proportion of small plants (%)	10.7 ±	6.57	19.4± 9.87	2.04	0.031

(Table 2) indicates that cattle are actively selecting small rosettes. This might be a function of the protection afforded by larger leaves of bigger rosettes (Campbell and Keller 1932), which also have more inedible dry leaves. This could explain the paucity of small individuals in grazed populations, as a result of grazing of vegetative parts of the plant rather than decreased recruitment. This is expressed in the shift of mean caudex size between grazed and ungrazed populations (Table 4).

An alternate hypothesis is that physical soil compaction by cattle trampling may prevent Y. elata germination and recruitment. Soils at sites grazed by cattle (flower- and non-flower-grazed) were more compact than where cattle were excluded (Table 4). This is mirrored by reduced recruitment (proportion of small plants) at cattle grazed sites compared to exclosures (Table 4). However, recruitment of Y. elata is not a function of soil compaction (r=0.4203, F=3.218, df=15, P=0.0930), refuting this hypothesis.

# Does grazing influence reproductive effort?

Considerable reserves are required for flower production by Y. elata (Smith and Ludwig 1976). We hypothesized that populations stressed by grazing decrease flowering effort. Flowering of populations subject to vegetative grazing only (non-flower-grazed) did not differ from exclosure populations (Tukey's Range Test, Table 2). However, significantly fewer caudices flowered in flower-grazed populations (Table 2), suggesting that the loss of reproductive material is a significant drain on energy

reserves. Plants may resorb nutrients from unsuccessful flowers, aborted fruits, and inflorescence stalks, a process similar to the retranslocation of nutrients from leaves and roots.

# Does cattle grazing affect plant geometry?

Besides an increase in the number of caudices per plant, cattle grazing is associated with an increased propensity to branch (Table 2). We observed cattle grazing young vegetative growth at the centre of a rosette (see also Campbell and Keller 1932), causing the loss of apical dominance of the damaged rosette. Loss of apical dominance is known to generally cause an increase in branching (Harper 1977). Grazed populations also have a higher proportion of procumbent caudices (Table 2). This is a physical trampling effect, rather than a grazing effect.

# Does a high proportion of clonal individuals indicate senescence?

Populations with limited recruitment and an increase in individual cloning may display increased senescence (Symonides 1979). In our study this prediction was not supported by the proportion of dead caudices, nor the proportion of cloned plants with dead caudices, neither of which differed between grazed vs. ungrazed populations (Table 2).

# Do tall Y. elata escape flower browsing?

Tall caudices may bear inflorescences at heights unavailable to cattle (Smith and Ludwig 1976). In the Jornada basin populations, Y. elata caudices were relatively short ( $\bar{x} = 40.6 \pm 28.5$  cm (SD), n = 2843) with no indication of "height escape". The taller population near Deming displayed obvious height escape (Fig. 1). Caudices taller than 170 cm (n = 55) suffered no flower grazing by cattle. Flowers on all caudices shorter than 170 cm were consumed (n = 109). Only three caudices in the Jornada population were taller than this escape height.

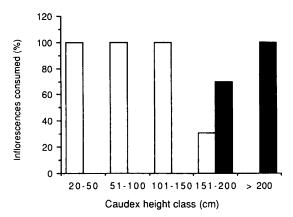


Fig. 1. Flower consumption of Yucca elata height classes, demonstrating height escape. Open bars = proportion of inflorescences consumed, solid bars = proportion of intact inflorescences

#### Discussion

Mechanism of change to population structure

Cattle significantly alter population structure and plant geometry of *Y. elata* by selectively grazing small caudices, whether these be ramets (sideshoots) or genets (recruited juveniles). These findings refute Smith and Ludwig's (1976) hypothesis that cattle browsing of the inflorescences has a major effect on *Y. elata* population structure.

Despite suppression of both recruitment into the population, and clonal growth of individuals, there was no associated increase in the mortality of caudices in clonal individuals, as would be expected in an ageing population. This suggests that the treatment may have been too short (>20 years) to show increased mortality, particularly in view of the slow growth (Campbell and Keller 1932) of this species.

# Implications of suppression of genet recruitment

Although recruitment of genets by sexual reproduction may not be vital to the maintenance of *Y. elata* in the relatively short time examined in this study, a dependence on clonal growth alone could be detrimental to the population. There would be no mechanism for replacement of individuals that die, and populations would not grow locally, or colonize new areas. There would also be no opportunity to express genetic variation, which could have a detrimental effect on the ability of populations to respond to new or evolving pathogens (Harper 1977). Although asexual reproduction, by reducing variance in recruitment, contributed to population stability in *Y. glauca* (Kingsolver 1989), dependence on clonal growth could prove to be limiting to *Y. elata*.

# Implications for yucca moths

The yucca moth *Tegeticula yuccasella* is an obligatory parasite on *Y. elata* seeds (Miles 1983) and is the ex-

clusive pollinator of its flowers (James et al. unpubl.). This tight mutualism is vulnerable to interference by cattle grazing. If cows eat all the flowers (as in sites 8, 9 and 16), the current cohort of moths will fail to reproduce. Long-term diapause in moth larvae may apparently occur (up to 17 years under artificial conditions for Paradoxus Y-inversus; Powell 1989), although it is not known whether moth emergence is triggered within any particular year (thereby depleting local stocks of diapausing larvae). Furthermore, the flight ability of the moths appears limited, suggesting poor dispersal between Y. elata populations. These circumstances may lead to local extinctions of yucca moths, resulting in an absence of pollinators for Y. elata. Thus, even if cattle grazing was removed to allow yucca flowering, no successful fruitset would occur. Local vucca populations may therefore be rendered permanently infertile and incapable of producing recruits by sexual reproduction, with the associated long term disadvantages of genetic inflexibility. A similar situation has arisen for Y. fillifera in Mexico where flower harvesting for human consumption has extirpated the particular yucca moth T. mexicana. There are consequently large regions where Y. fillifera flowers are not pollinated and no fruitset occurs (Ridaura-Sanz 1979).

# Implications of inflorescence loss for biodiversity

Yucca elata is the structural dominant on the Jornada Basin, and loss of inflorescences has severe implications for species diversity, besides local extinctions of yucca moths. Over 70 arthropod species associate with Y. elata inflorescences, including sap-feeders, nectivores, and predators (G.S. Forbes, D.C. Lightfoot, C.D. James, M.T. Hoffman and W.G. Whitford unpubl.). The availability of inflorescence stalks limits nesting success of the large carpenter bee Xylocopa californica (Smith and Whitford 1978). A variety of birds, including Swainson's hawk Buteo swainsoni, loggerhead shrike Lanius ludovicianus, northern mockingbird Mimus polyglottus and western kingbird Tyrannus verticalis, use the dry inflorescences for perches (pers. obs). In large areas of grassland these are the only perches available, and their loss may reduce local populations of these important predators. Furthermore, numerous bird species nest in the inflorescences. The impact of the loss of Y. elata inflorescences on local biodiversity needs to be quantified and incorporated into regional conservation models.

# Implications for grazing management

Although Y. elata can avoid cattle browsing its flowers through the mechanism of "height escape" described here, this may not be possible in all yucca populations (vide the small size and lack of "height escape" in the Jornada populations). For those populations with "height escape", local yucca moth populations will be maintained, ensuring the ability of the yuccas to produce fertile seed. For shorter Y. elata populations it will be

necessary to modify grazing management to allow partial rather than total flower removal. However, since the main impact of grazing is upon small caudices, whether genets or ramets, recruitment will remain suppressed, and the populations threatened by lack of replacement and the loss of genetic flexibility. To maintain *Y. elata* populations in the long term, lengthy periods of rest will be necessary to allow new recruits to reach sufficient sizes to escape removal by cattle.

# Herbivory of clonal populations

A mechanism has been proposed to explain observed changes in population structure of Y. elata when grazed by cattle. The loss of ramets and genet recruits may be the primary mode whereby clonal populations are modified by herbivory, and this model should be tested on other clonal species subject to herbivory. Clonal populations appear to be useful tools to resolve the effects of herbivory on the reproductive versus vegetative phases of plants.

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