Between A Rock and A Hard Place:

Opuntia fragilis (Nutt.) Haw. (Cactaceae) in Stearns County, Minnesota

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Abstract

We surveyed the distribution of *Opuntia fragilis* (Nutt.) Haw. in Stearns County, MN, where it is restricted to a few rock outcrops. To compare the populations within three sites, we mapped clusters of pads and measured each individual pad within each cluster. Pads tended to be located in a narrow band of shallow soil between the bare rock and the angiosperm-dominated plant communities growing on adjacent deeper soils. Significant differences existed between the three populations in pad widths, average pad cluster sizes, and pad appearances. Although several pads flowered, none of the flowers set seed, indicating that persistence of these populations probably occurs primarily via asexual reproduction.

Introduction

Although the genus *Opuntia* has received considerable attention in warmer climates, little ecological attention has been given to the two species found in Minnesota. *Opuntia macrorhiza* Engelm. is on the Minnesota Species of Special Concern list, and is restricted to isolated populations on exposed rock outcrops in the Minnesota River valley (1). *Opuntia fragilis* (Nutt.) Haw. is more widespread, extending as far north as Manitoba. Within Minnesota it is found on scattered rock outcrops in southern Minnesota and in Stearns County, a disjunction of more than 80 miles. This study was designed to determine the current status and ecological niche of *Opuntia fragilis* within the rock outcrop communities of Stearns County.

Opuntia fragilis tolerates freezing, and has the greatest cold acclimation ability and the greatest freezing tolerance reported for any species of cactus. The physiological mechanisms permitting freezing tolerance are largely due to a reduction in water content, not to changes in the chemical composition of solutes within the plant tissues (2). Within outcrop communities in Manitoba, *Opuntia fragilis* colonizes secondary moss mats and lichen mats, and is eliminated when stress-tolerant perennial species dominate the site (3). The inability of *Opuntia fragilis* to coexist with grasses in a Nebraska grassland was found to be due not to competition for light (4) or water (5), but to increased insect herbivory under grass canopies (4). Thus, *Opuntia fragilis* appears to be a stress-tolerant species specialized for exposed shallow-soil habitats.

There is an apparent correlation between latitude and decreased sexual reproduction within *Opuntia fragilis* populations. Within the Nebraska sandhills *Opuntia fragilis* rarely reproduces sexually (4), and in Manitoba *Opuntia fragilis* reproduces entirely via asexual reproduction (3). Although *Opuntia fragilis* has not been examined for self-incompatibility, many species are self-incompatible, including *Opuntia imbricata* (6) and *Opuntia phaeacantha* (7). Furthermore, even self-compatible species often have significant reductions in pollination success in isolated populations (8). *Opuntia* pollination is typically performed by medium to large solitary bees (7).

Most new pad production on transplanted pad clusters occurs between May and the end of June (4). In one population in Manitoba, pad numbers increased over a four-year period at a 51% rate, and 6% of the pads were dispersed (via fragmentation) (9). Additionally, pad establishment was higher on south-facing slopes than other sites. Thus, over much of its range *Opuntia fragilis* may primarily spread via vegetative propagation, facilitated by the ability of pads to break away from the parent plant and become established.

Many questions about the ecology of this species remain unanswered. There are no published studies evaluating flower production and fate, pad turnover and fates, or presenting demographic tables for either species. Neither have any long-term comparisons of populations ever been presented. Therefore, our initial research goals were to search for *Opuntia fragilis* populations within Stearns County, evaluate the status of each population, particularly the population size and distribution within the community, and assess the frequency and success of flowering within each population.

Methods

During the summer of 1995, we assessed the status of prickly pear populations (*Opuntia fragilis*) in Stearns County, Minnesota. *Opuntia fragilis* is a prostrate prickly pear, growing in clusters of distinctly segmented stem sections, or pads, each less than five cm. in length. The pads are usually somewhat flattened, but new pads are often cylindrical (10). Spines are not sheathed, are strongly barbed, and the stem segments readily break off (9). Flowers are yellowish, up to 4 cm. wide, and fruits are dry, not fleshy (10).

We located four populations of prickly pears, all on granite outcrops (Table 1). Typically, these outcrops are exposed, with either partial shade from nearby trees or full sunlight. There is little to no soil accumulation on the surface of the outcrops, although some soil does accumulate in cracks and crevices. The outcrops are fringed by grasses and perennial forbs. Three sites are located on privately held property; one site (Quarry Outcrop) is located on land owned by Stearns County.

In the Table Outcrop, all pads were located in one tight cluster, covering an area of about six m^2. Due to the difficulty of relocating individual pads, we did not map or measure pads on this outcrop. We measured pads in each of the other three sites. Within the smallest population (the Woods Outcrop), we located and mapped every pad. In the other two sites (the Quarry Outcrop and the Cold Spring Outcrop), we mapped subpopulations within the site. The pads were either scattered individually or linked to other pads in a cluster. Each cluster was identified with a letter, and each pad

within that cluster was given a number. Isolated individual pads were given both a letter and a number.

We drew a sketch illustrating pad appearance for each pad. The status of each pad was determined for pad dimensions (length and width) and pad appearance (green, dark green, pale green, yellow, or gray). Pad appearance was closely correlated with apparent pad health: green pads generally appeared healthy, yellow pads generally appeared to be dying, and the few gray pads we observed may be dead. Each outcrop was visited several times during the flowering season, and all five flowers observed were tracked to assess flowering fate. No fruit set occurred, so we were not able to assess fruit dispersion or seed predation.

Results

In addition to different population sizes between the populations, pad width varied significantly between outcrops. The difference in widths is mostly driven by narrower pads in the Cold Spring Outcrop than in the other two outcrops (Table 2). Regression analysis indicated that pad length and outcrop site both significantly predict pad width (Table 3).

Pad cluster sizes varied significantly between all three outcrops (Table 4). Indeed, one of the four original outcrops was excluded from data collection simply because the pads were all contained within one extended cluster. The Woods Outcrop had the largest cluster sizes, with 5.7 pads per cluster on average. The Quarry Outcrop

had the fewest pads per cluster, with 2.7 pads per cluster, and the Cold Spring Outcrop was intermediate, with a mean of 4.0 pads per cluster.

Most pads were healthy, especially those in the Woods Outcrop (Table 5). In the two larger populations, about 10-15% of the pads had substantial color shifts, to either a very dark green-gray or to a pale green color. Many of these pads were located near the base of a cluster of pads, and thus are probably older. About 5-7% of the pads were either dead or yellowing, and probably dying. These pads fell into two categories: either they were isolated pads which probably were not able to successfully establish themselves, or they were located near the base of a pad cluster. Clearly, not all pads are alike, and future studies should consider a possible correlation between pad appearance and pad survival.

There were very few flowers produced; we found only five flowers over all four outcrops. All flowers were produced in June, remained open for up to 8 days, and were produced by green pads on the terminal end of pad clusters growing in full sunlight. Although we planned controlled cross-pollination experiments, because we found only five flowers over all four entire populations, we did not have sufficient flowers to perform pollination experiments with any degree of confidence in the results; furthermore, we wanted to leave these five flowers undisturbed in order to investigate natural seed set. None of the flowers produced fruits. Thus, there was a complete absence of successful sexual reproduction.

We found that most pads were growing either on bare rock or within clusters of moss; sometimes pads grew adjacent to other vegetation. However, we did not find clusters growing in the midst of other herbaceous plants, and all clusters were exposed

to direct sunlight for at least a few hours per day. Therefore, we harvested 12 terminal green pads with similar dimensions, and planted the pads in two large terraria. One terrarium contained bare soil, and the other terrarium contained mats of live moss. Pads were watered weekly, and monitored for growth and survival. It quickly became apparent that the pads growing on bare soil required additional watering in order to survive. After four months, all pads had survived, but the pads growing on the moss mats had a healthier green appearance, and four of the six moss pads had developed a "daughter" pad. In contrast, the pads growing on bare soil looked more desiccated, and only two developed daughter pads.

Discussion

Within Stearns County, there are at least four populations of *Opuntia fragilis*, of which one is protected by public ownership. Two of the privately held populations are small and therefore potentially vulnerable to disturbance, but the third privately owned outcrop contains the largest known population in this county. All outcrops share a suite of common characteristics: they contain extensive areas of exposed granitic rock, often with high sunlight exposure. The rock outcrops are colonized in patches by moss mats, and the prickly pear clusters tend to be located on or near these mats. If enough mineral soil has accrued to permit the development of a complete herbaceous layer, competition has removed prickly pears as a component of the community.

The populations range in size from six clusters to several hundred clusters, with

up to 14 connected pads in a cluster. There are significant differences between the outcrops in pad widths, the percentage of healthy pads, and pad cluster sizes. Overall, the average cluster size is between 3-5 pads, and most of the pads are healthy in appearance. Flowering is rare, and fruiting did not occur.

Based upon both observations and experimental manipulation, it is clear that within these granite outcrop communities *Opuntia fragilis* is a specialist species occupying moss mats in the zone between bare rock and mineral soil. The spines both protect it from herbivory and enable dispersion of pads to occur via fragmentation.

Because it is likely that these populations are not sexually reproducing, they may have developed from a set of single-pad colonization events, and an entire population may be a single clone. Outcrop differences can be due to three different mechanisms: plasticity in response to different environmental conditions, genetic differences due to founder effects, or genetic differences due to site-specific natural selection and/or genetic drift. Until a thorough population genetic analysis is performed on these populations, we have no way of answering this question. If they did indeed arise from single-pad founder events, it is probable that genetic diversity is low; however, this remains to be determined. One possible consequence of limited genetic diversity is a depression of sexual reproductive effort. Recruitment of sexually produced propagules is frequently rare in cacti, and in the case of *Opuntia rastrera* there is strong inbreeding depression for fruit set (11). Thus, if these populations are derived from a few individual invading pads, it is entirely possible that there is low genetic variability within the population and a resultant high likelihood of self-incompatibility.

This study has laid the framework for determining patterns of temporal change

within this species. Ultimately, the development of demographic models of pad production, dispersion, and longevity will illuminate further the niche that these cacti occupy. We will then be able to more effectively manage these small populations and predict successional dynamics within these isolated rock outcrop communities.

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Tables

Table 1: Outcrops in Stearns County. Each site is named, described, and the *Opuntia fragilis* population size is estimated.

Outcrop Name	Outcrop Description	Population Size
Cold Spring Outcrop	a large steep-sided hill with numerous sections of exposed granite, mostly in full sunlight	several hundred clusters
Quarry Outcrop	several exposed sections of granite, partial to full sunlight	approximately 100 clusters
Table Outcrop	one exposed section of granite, full sunlight	one large cluster, 3x3m area, 100+ pads
Woods Outcrop	one exposed section of granite, partially shaded	six clusters, 44 pads

Table 2: Pad Dimensions. Means and standard deviations for pad lengths and widths in the three outcrops are presented, with the corresponding ANOVA statistics.

Outcrop	Pad Length (cm)		Pad Width (cm)	
	Mean	S.D.	Mean	S.D.
Cold Spring	2.82	1.19	1.28	0.38
Quarry	3.05	1.06	1.53	0.52
Woods	2.71	1.08	1.50	0.50
ANOVAs: $F_{2,277}$	1.80		11.58	
p(F)	0.1668		<0.0001	

Table 3: Regression Analysis of Pad Widths. Pad length and population source significantly predict pad widths (in cm).

Regression Statistics: $F_{3,276}=79.21$ $p<0.0001$ $r^2=.46$

Regression Equation: width= .27 * length + .53 + .19 (if Quarry) + .29 (if Woods)

Table 4: Pad Connectedness. The number of clusters and the percentages for pads in each cluster size are presented for the three outcrops.

	Outcrop					
Pads / Cluster	**Cold Spring**		**Quarry**		**Woods**	
	#	%	#	%	#	%
1	2	7.7	15	30.0	0	0.0
2	5	19.2	16	32.0	0	0.0
3	4	15.4	6	12.0	1	16.7
4	5	19.2	5	10.0	1	16.7
5	3	11.5	5	10.0	1	16.7
6	5	19.2	1	2.0	1	16.7
7	1	3.8	0	0.0	0	0.0
8	1	3.8	1	2.0	0	0.0
9	0	0.0	1	2.0	0	0.0
10-14	0	0.0	0	0.0	2	33.3
Total # Clusters	26		50		6	

ANOVA Statistics: $F_{2,80}=14.59$; $p<0.000$

Table 5: Pad Appearances. Percentages for pads in each appearance category are presented for the three outcrops.

	Outcrop		
Appearance	**Cold Spring**	**Quarry**	**Woods**
Green, Healthy	82.7%	78.2%	100%
Dark Green-Gray	5.8%	3.0%	
Pale Green	4.8%	13.5%	
Green-Yellow, Dying?	5.8%	4.5%	
Gray, Dead?	1.0%	0.8%	