

**HABITAT REQUIREMENTS FOR *ERIGERON KACHINENSIS*, A RARE ENDEMIC
OF THE COLORADO PLATEAU**

AND

**DEMOGRAPHY AND FACTORS INFLUENCING SEED SET IN *ERIGERON
KACHINENSIS*, A COLORADO PLATEAU ENDEMIC**

Manuscripts of Two Journal Articles.

**Presented to the Department of Botany and Range Science
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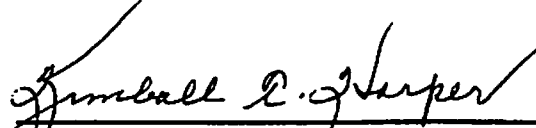
**In Partial Fulfillment
of the Requirements for the Degree
Master of Science**

by

Loreen Allphin

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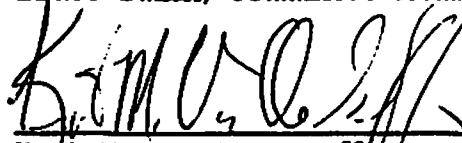
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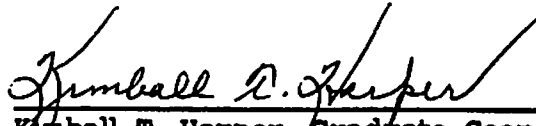
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**HABITAT REQUIREMENTS FOR *ERIGERON KACHINENSIS*, A RARE ENDEMIC
OF THE COLORADO PLATEAU**

Loreen Allphin

December 4, 1992

ABSTRACT

Erigeron kachinensis is a rare endemic of the Colorado Plateau, southeastern , Utah. This perennial composite grows in small, isolated populations at seeps and alcoves arising along the canyon walls in Cedar Mesa Sandstone substrates. The characteristics of six *Erigeron kachinensis* sites in Natural Bridges National Monument, San Juan County, Utah, were studied to describe habitats associated with this rare species in the deep canyons of Southeastern Utah. Sites were analyzed with respect to geology, soil chemistry, physical properties, and vegetational characteristics. The alcoves studied were very saline, often with soil surfaces covered with a white crust of salt. Total living cover was significantly correlated with percent soil moisture, soil salinity, and "available" phosphorus. Kachina daisies appear to more tolerant than associated species of differences in these abiotic factors. Most soil characteristics do not vary between the sites. The prevalent plant species on *E. kachinensis* sites were *Aquilegia micrantha*, *Calamagrostis scopulorum*, *Zigadenus vaginatus*, and *Erigeron kachinensis*. These species accounted for more than 75 percent of the total living cover in the alcoves studied. Attempts have been made to establish *Erigeron kachinensis* on sites which appear to have the necessary habitat conditions.

HABITAT REQUIREMENTS FOR *ERIGERON KACHINENSIS*, A RARE ENDEMIC OF THE COLORADO PLATEAU

The Kachina daisy (*Erigeron kachinensis* Welsh and Moore) was named in 1968 (Welsh et al. 1987). It is a rare perennial composite of the Colorado Plateau region of Utah and Colorado. The species grows in small, isolated populations at seeps and alcoves arising along the edges of deep canyons in these areas. No discussions of the habitat requirements of this species have appeared in the literature. The Kachina daisy was proposed as "endangered" by the U.S. Fish and Wildlife Service, June 16, 1976 (U.S. Dept. of Interior 1975, 1976). Later proposals down-graded the original proposal by recommending "threatened" status for the species (U.S. Dept. of Interior 1988). Currently, the Kachina daisy is listed by the US Fish and Wildlife Service as a category 2 species, a species for which more information is needed before assigning final designation (endangered, threatened or sensitive). My study was initiated to further document the abundance and ecology of *E. kachinensis*.

In 1984, an initial effort was launched to document locations of all populations of the Kachina daisy and their size in Natural Bridges National Monument, San Juan County, Utah. In that study, eight populations were recorded (Fagan, 1984). In 1988 and 1989, further study was made of these populations. Four of the populations were selected and the number of daisies in each was monitored for two years. The relative cover of Kachina daisy plants in those sub-populations was found to vary by almost 60 % between years (Belnap, 1988, 1989). Belnap's report to the National Park Service called for protection and

for further research to determine whether the observed declines in population size were due to natural fluctuations in temperature and precipitation between years or to more permanent stresses in the physio-chemical environment. It was also considered possible that the species was poorly adapted genetically to the surrounding environmental conditions. Concerns for the future of the species resulted in the research reported in this paper.

STUDY AREA AND METHODS

The Kachina daisy grows around seeps from the walls of natural alcoves in the Cedar Mesa Sandstone of White and Armstrong Canyons between 1680 and 1890m elevation. The Cedar Mesa Formation was deposited in Permian time (figure 2 and Hintze, 1975): the Cedar Mesa is a coarse grained, porous sandstone that stores considerable water within its massive deposits. In thickness, the Cedar Mesa varies from 500 to 1200m. Its depth is at a maximum in the Elk Ridge and Natural Bridges National Monument area. The Halgaito Formation is located below the Cedar Mesa Sandstone. It is a part of the Cutler group as is the Cedar Mesa Sandstone. The Halgaito Formation consists of mostly reddish-brown siltstone, sandstone and thin beds of limestone. It varies from 400-500m in thickness (figure 2 and Hintze 1975). Most of the alcoves where the daisy grows are developed in Cedar Mesa Sandstone immediately above the Halgaito Formation.

Where percolating water encounters finer textured lamina in the Cedar Mesa Sandstone, the water accumulates and moves laterally until it reaches the faces of vertical walls of deep, narrow drainage channels that cross outcrops of the Cedar Mesa Formation. In addition to

populations known in Natural Bridges National Monument (Welsh et al. 1987), other populations of the Kachina daisy have recently been found on lands administered by the Bureau of Land Management (Allphin 1991). Populations are now known in Fish, Arch, White, and Birch Canyons and in the Dark Canyon Primitive Area, San Juan County, Utah and on the lower portion of Coyote Wash, Montrose County, Colorado (Welsh et al., 1987).

Six study sites varying in respect to aspect, soil moisture, and soil salinity were chosen within Natural Bridges National Monument (figure 3). Two west-facing, two south-facing, and two north-facing alcoves were chosen for detailed study. All sites are located along the 1768 m (5800 ft.) contour line. These sites were monitored in June of 1990, 1991, and 1992.

At each site, individual daisy plants were selected for monitoring using the quarter method along a 100 m transect. These individuals were marked with numbered aluminum tags held at their base with a galvanized nail. The tags facilitated later relocation of specific plants. A minimum of 5 composite soil samples were taken per alcove. From those soil samples, soil moisture, percent coarse material (diameter > 2 mm), and concentrations of the biogenic elements were estimated. All chemical analyses were made by personnel of the Brigham Young University Soil Analysis Laboratory (managed by the Department of Agronomy and Horticulture).

Vegetational data were also collected at each study site in Natural Bridges National Monument. Percentage total living plant cover and frequency, and cover of individual species were determined at each

site. In addition, vegetative and floral characteristics of 600 tagged plants were recorded at each visit.

The soil samples from the various daisy sites were analyzed by one-way analysis of variance (ANOVA). The Tukey procedure was used to compare multiple means (Norusis, 1988). The vegetational data were also analyzed using a two-way analysis of variance for site and year. The Scheffe procedure was used to identify significant differences among means.

Correlations were run between important abiotic environmental variables and total living cover, species richness, and Kachina daisy characteristics. The Kachina daisy characteristics were standardized by setting the largest value for each variable at 100 and expressing the values for that parameter at all study sites as a percentage of the maximum value. These standardized values were summed for each of the alcoves to give an integrated estimate of vegetative and reproductive success of this species. Both simple and multiple linear regressions were performed and significant differences were determined. Multiple linear regressions permit an evaluation of interaction between different abiotic environmental variables and plant performance.

RESULTS

Physical Environment

Soils in the alcoves are sandy loams (table 1). The data show that *E. kachinensis* grows in saline conditions. Electroconductivity of soils from the study sites ranges from 6-31 mmhos/cm: those values indicate that the soils are very saline, since values of over 8 mmhos/cm are considered high enough to restrict yield of most crop plants (Richards 1954). Each of the alcoves studied had a crusty layer of white salt on the soil surface: the average electrical conductivity value for soils from the 6 alcoves was 13.6 mmhos/cm.

The soils are all basic with pH values ranging from 7.8-9.1. They were found to have high values for calcium, magnesium, potassium, and sodium (table 1). The ANOVA and multiple range tests demonstrate that alcove 3 is significantly different from the other alcoves studied. This difference may be related to the fact that the floor of alcove 3 is developed in the Halgaito Formation which consists of reddish-brown siltstone (figure 2). Even though alcove 3 differs from the others, the daisy population is thriving and seems to be unaffected by soil differences.

Percentage soil moisture in the alcoves varied from 5.8 - 25.6 % of dry weight (table 1). The moisture in the soils arises from water percolating through the sandstone. Since Natural Bridges National Monument gets most of its precipitation during the months of November through March (figure 1 and Brough et al., 1987), water accumulates in the sandstone during those months and is available for plant growth in all seasons as it flows from the sandstone along seep lines.

Alcoves 3 and 6 had the most moist soil. This is perhaps related to the fact that those alcoves receive only about 1 hour of direct sunlight per day. Site 2 was found to have the driest soil. The sample transect at site 2 is not within the alcove, but occurs on the slope directly below the alcove. Site 2 receives the most sunlight daily and is further from a seep line than other study sites. Site 2 faces north and is exposed to direct sunlight only during afternoon hours.

Soil temperatures (taken at ~1 cm depth) at the study sites are cool, ranging from 13.2-15.8C in June. Soils in alcoves are always cooler than surrounding soils, because they receive less direct sunlight and stay reasonably moist. The soil temperatures at the several sites vary only slightly depending primarily on the amount of direct sunlight.

Biotic Associates

Total living cover at locations that support *E. kachinensis* ranged from 17.8- 62.4 % in the six alcoves in growing seasons 1990-1992. (table 2). Most of the living cover was contributed by *E. kachinensis*, *Aquilegia micrantha*, *Calamagrostis scopulorum* and *Zigadenus vaginatus*. Frequency and cover values for those species are reported in table 2.

Several species were found to occur regularly with the Kachina daisy in both Natural Bridges National Monument and on lands managed by the Bureau of Land Management in that part of San Juan County, Utah (table 4). Considering all known locations for the Kachina daisy in San Juan County, Utah, only four species were found to coexist with it at 75 % or more of the occupied sites. Those species were *Aquilegia micrantha*, *Calamagrostis scopulorum*, *Cirsium calcareum*, and *Zigadenus*

vaginatus. These species are thus good indicators of habitat suitable for the Kachina daisy .

Kachina Daisy Characteristics

The characteristics of the average daisy in each of the alcoves studied are noted in table 2. The average number of rosettes per individual varied from 1.4-2.5 among the 6 sites. Statistical differences among the sites with respect to the number of rosettes per daisy plant in the different alcoves is noted in table 2. Alcoves 3 and 4 supported the largest plants, while the smallest plants grew in alcoves 2 and 5.

Average clump diameter for the Kachina daisy ranged from 3.6-7.3 cm in the field seasons 1990-1992. Alcove 2 plants had the smallest diameters among the 6 alcoves. This result perhaps reflects the fact that alcove 2 had the driest soil observed among the alcoves (table 2).

Average leaf lengths ranged from 1.9 to 3.6 cm among the 6 study sites. Alcove 2 plants had the smallest leaves observed. Average number of leaves per plant ranged from 9.9-23.6 among the study sites. As might have been expected, the number of leaves per plant was smallest for alcove 2, the driest of the alcoves (table 2).

The statistical differences seen among plant characteristics from these alcoves reflect the fact that the alcoves were chosen because of apparent differences in moisture, aspect, and direct sunlight. The alcoves which receive little direct sunlight (Sites 3, 4, and 6, table 1) had plants with larger leaves and clump diameters than plants from alcoves 1, 2, and 5 which received more sunlight. The amount of sunlight could also be expected to affect soil moisture which should also produce differences in vegetative characteristics.

DISCUSSION

Three abiotic variables were found to have a significant effect on total living cover in the six alcoves. Those were soil moisture, soil salinity (EC mmhos/ cm), and "available" phosphorus (ppm). Results for correlation analyses between these three important environmental variables and total living plant cover, integrated vegetative response of the Kachina daisy, and species richness are reported in table 3.

Salinity, considered alone, had a positive effect on total living cover and species richness. Total "available" phosphorus also had a significantly positive affect on total living cover in six alcoves. When soil salinity and soil moisture were considered together in multiple correlation, there was a significant correlation with total living plant cover. Partial correlation coefficients show that soil moisture represents significantly more of the variation in total living plant cover than soil salinity [$\% \text{ total cover} = 3.6(\% \text{ moisture}) + .015 (\text{EC})$]. The combined effects of soil moisture, soil salinity, and "available" phosphorus were also significantly correlated with total living cover.

In this study, increased soil moisture appearrd to reduce the effect of salinity on plants in the alcoves, and permitted good growth of most adapted species in soils of high salinity. Daisy response was not found to be significantly influenced by any of the foregoing abiotic variables. Kachina daisies appear to be more tolerant of differences in important abiotic environmental variables than other species contributing to total living plant cover in the alcoves (table 3).

The U.S. Park Service has encouraged attempts to transplant the species into what appear to be suitable habitats in Natural Bridges National Monument. A transplant site was selected near the Sipapu Bridge. There are no known natural Kachina daisy sites near this bridge in the Monument. The transplant site is a west-facing alcove along the 1768m (5800 ft.) contour level. The habitat resembles other Kachina daisy sites in that salinity is high, and many species occur on the site that are known to consistently grow with the daisy. Six daisies were transplanted in the summer of 1991. Four of the six survived to the summer of 1992. More transplants have been made and the Park Service is considering seeding the Kachina daisy into other alcoves which appear to have suitable habitat within Natural Bridges National Monument. Many new locations for the Kachina daisy have been found on BLM lands in the region by searching for physical habitats and associated species known to be compatible with the existence of the species.

The ecological data reported in this paper will ultimately permit workers to determine whether seed set in this species is limited by abiotic resources, predation, inadequate populations of pollen vectors, or genetic load. Variation in seed set among these alcoves and evidence concerning possible controlling variables will be presented in another paper.

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TABLE 1. Chemical and physical characteristics of soil from alcoves that support *Erigeron kachinensis* at Natural Bridges National Monument, San Juan County, Utah. Each value represents an average of five samples from each alcove. Means followed by the same letter do not differ at the $p < .05$ level of significance. Soil temperature and moisture values represent average conditions for mid-June in summers of 1990-1992.

	ALCOVE NO.					
	1	2	3	4	5	6
Elevation (m)	1768	1768	1768	1768	1768	1768
Aspect(deg.)	302	328	160	197	252	225
Hr.Direct Sun- light/day in June	5.0	5.75	1.0	4.5-5.25	4.6	0-1.5
Texture	sandy lm	loamy snd	sandy lm	sandy lm	sandy lm	sandy lm
Sand (%)	89.6 a	76.7 b	80.3 b	70.4 b	80.1 b	71.7 b
pH	8.6 a	8.8b	9.1 b	8.6 a	7.9 c	7.8 c
EC (umhos/cm)	13.1 a	17.1 a	31.1 b	7.6 a	6.9 a	6.0 a
Ave. Soil Temp (C)	14.1	15.8	13.9	15.1	13.9	13.2
Soil Moisture (%)	12.3 a	5.8 ab	18.4 ac	12.2a	12.7a	25.6 c
Organic Matter (%)	1.8 ab	1.1 ac	2.0 b	2.2 b	0.8 ac	1.6 ab
Skeletal Mtl. (% by wt.)	12.1 ab	15.1 ab	17.2 b	6.8 a	7.2 a	7.2 a
	Essential Elements					
P (ppm)	11.4 a	10.7 b	9.8 b	10.9 b	7.5 b	8.0 b
K (ppm)	197.0 a	229.5 a	640.2 b	153.0 a	80.4 a	82.0 a
Ca(ppm)	9590 a	7886 b	6758 b	10508 a	10884 a	10282 a

Table 1. Cont.

Mg(ppm)	2498 a	2754 a	11904 b	2030 a	870 a	730 a
Na(ppm)	648.96 a	822.4 a	2535.0 b	322.6 a	126.7 a	127.4 a
Cu(ppm)	0.48 a	0.36 a	0.56 a	0.32 a	0.36 a	0.60 b
Fe(ppm)	1.8 ab	0.96 a	1.4 ab	1.9 ab	1.9 ab	2.2 b
Mn(ppm)	6.8 a	6.0 a	1.8 b	6.6 a	2.4 b	4.8 ab
Zn(ppm)	0.60 ab	0.44 a	0.72 ab	0.88 b	0.96 b	0.72 ab
Na Saturation (%) of ex- changeable bases	2.5 a	3.5 ab	6.0 b	1.2 a	0.5 a	0.6 a

TABLE 2. Vegetational characteristics and average characteristics of 100 randomly selected *Kachina* daisy plants at each of the six alcoves shown in table 1. All values are based on data taken during field seasons 1990-1992. Means followed by the same letter do not differ significantly at $p < .05$.

	ALCOVE NO.					
	1	2	3	4	5	6
Total Living	42.5 a	17.8 ab	45.5 ac	62.4 ac	18.1 ab	37.7 abc
Cover (%)						
Species	6.3 a	5.3 a	4.7 ab	9.0 ac	4.3 ab	7.0 abc
Richness *						
Ave. # Spec./ 100cm ² quad	2.8 a	1.8 b	1.6 b	2.6 a	1.4 bc	2.1 ab
Characteristics of <i>E. kachinensis</i>						
No. Rosettes/ plant	1.6 a	1.4 ab	2.5 c	2.1 d	1.6 ab	1.9 ad
Plant Diam. (cm)	4.8 a	3.6 b	6.2 c	7.3 d	4.4 a	6.6 cd
Leaf Length (cm)	2.7 a	1.9 b	2.5 a	3.6 c	2.1 b	3.4 c
No. Leaves/ plant	13.2 a	9.9 ab	23.6 c	22.2 c	13.5 ab	17.3 d
Characteristics of Prevalent Species						
<i>Erigeron kachinensis</i>						
Frequency (%)**	66.7 a	44.0 ab	38.7 b	54.7 ab	53.3 ab	72.0 ac (4.00)
Ave. Cover (%)	6.3 a	2.9 a	7.5 a	7.0 a	3.4 a	6.0 a
No. Plants/m ²	15.1	12.7	6.1	15.7	7.9	27.4

Table 2. cont.

Aquilegia micrantha

Frequency	73.3 a	56.0 a	57.3 a	26.7 b	8.0 c	56.0 ab
(%)**						

Ave. Cover	18.2 a	8.7 b	16.2 ab	2.9 b	2.5 b	17.3 ac
(%)						

Calamagrostis scopulorum

Frequency	40.0 a	16.0 a	32.0 a	40.0 a	9.3 a	41.3 a
(%)**						

Ave. Cover	4.6 a	2.7 ab	16.8 c	15.0 ac	2.2 ab	8.1 abc
(%)						

Ligadenus vaginatus

Frequency	53.3 a	33.3 a	30.7 a	61.3 ab	68.0 ab	2.7 c
(%)**						

Ave. Cover	10.6 a	2.97 ab	4.7 abc	22.4 ad	10.0 abc	0.05 abc
(%)						

* Species Richness = Number of species per 25m transect

** Frequency = Percentage of 100cm² sampling quadrats placed per 25 m transect that included any amount of this species

TABLE 3. The influence of three important environmental variables (soil moisture, soil salinity and "available" phosphorus) on total plant living cover and integrated vegetative response of the Kachina daisy. Significance level is shown by each r-value.

Independent Variable(s)	% Living Cover	Daisy Response	Species Richness
r-value for simple regression			
Soil Moisture (%)	0.15 NS	0.29 NS	0.11 NS
Salinity (EC)	0.79 **	0.09 NS	0.75 **
Available P (ppm)	0.75 **	0.02 NS	0.14 NS
Multiple r-value for multiple regression			
Soil Moisture & Salinity (EC)	0.95 *	0.66 NS	0.79 NS
Soil Moisture, Salinity (EC), & Available P (ppm)	0.99 *	0.80 NS	0.86 NS

* Regression significant at $p < .05$ level of significance

**Regression significant at $p < .10$ level of significance

NS Regression not significant

TABLE 4. Species associated with *Erigeron kachinensis* at all (100+) sites of occupancy on Bureau of Land Management Lands and the six study sites at Natural Bridges National Monument, San Juan County, Utah.

<i>Aquilegia micrantha</i> ****
<i>Calamagrostis scopulorum</i> ****
<i>Cirsium calcarum</i> ****
<i>Zigadenus vaginatus</i> ****
<i>Epipactus giganteus</i> ***
<i>Helianthella microcephala</i> ***
<i>Heterotheca villosa</i> ***
<i>Adiantum capillus var. veneris</i> **
<i>Carex aurea</i> **
<i>Castilleja linarifolia</i> **
<i>Cirsium rhybergii</i> **
<i>Gilia subnuda</i> **
<i>Hymenopappus filifolius var. cinereus</i> **
<i>Mimulus castwoodii</i> **
<i>Senecio multilobatus</i> **
<i>Swertia radiata</i> **
<i>Galium stellatum</i> *
<i>Gilia congesta var. palmifrons</i> *
<i>Habenaria sparsiflora var. sparsiflora</i> *
<i>Juncus arcticus</i> *
<i>Leptodactylon puegens</i> *
<i>Solidago sparsiflora</i> *
<i>Aster chilensis</i> ~
<i>Comandra umbellata</i> ~
<i>Penstemon watsonii</i> ~
<i>Ranunculus cymbalaria</i> ~
<u>Trees and Shrubs</u>
<i>Pinus edulis</i> ***
<i>Rhamnus betulaeifolia</i> ***
<i>Cercocarpus intricatus</i> **
<i>Juniperus osteosperma</i> *
<i>Pinus ponderosa</i> *
<i>Alnus utahensis</i> ~
<i>Clematis ligusticifolia</i> ~
<i>Mahonia fremontii</i> ~
<i>Populus fremontii</i> ~
<i>Salix exigua</i> ~

****	> 75 %	of Kachina daisy populations
***	50-75 %	of Kachina daisy populations
**	25-50 %	of Kachina daisy populations
*	5-25 %	of Kachina daisy populations
~	< 5 %	of Kachina daisy populations

FIGURE LEGENDS

Figure 1 Climatic
 diagram for Natural Bridges National Monument. The data represent
 average values for the period 1987- 1991. The shaded areas represent
 periods of accumulating soil moisture.

Figure 2 Geologic
 formations of Cedar Mesa Formation Sandstone at Natural Bridges
 National Monument, San Juan County, Utah (Hintze 1975).

Figure 3.....Location of
 Kachina daisy sites monitored in this study and a site where Kachina
 daisy plants have been transplanted in Natural Bridges National
 Monument, San Juan County, Utah. (# 1 = North-facing alcove A, # 2 =
 North-facing alcove B, # 3 = South-facing alcove A, # 4 = South-facing
 alcoves B, # 5 = West-facing alcove A, # 6 = West-facing alcoves B, and
 # 7 = Transplant site)

Natural Bridges Nat. Mon. (Elev.=1768 m) Mean Ann. Temp.= 10.47 C
 Mean Ann. Precip.=316.8 mm

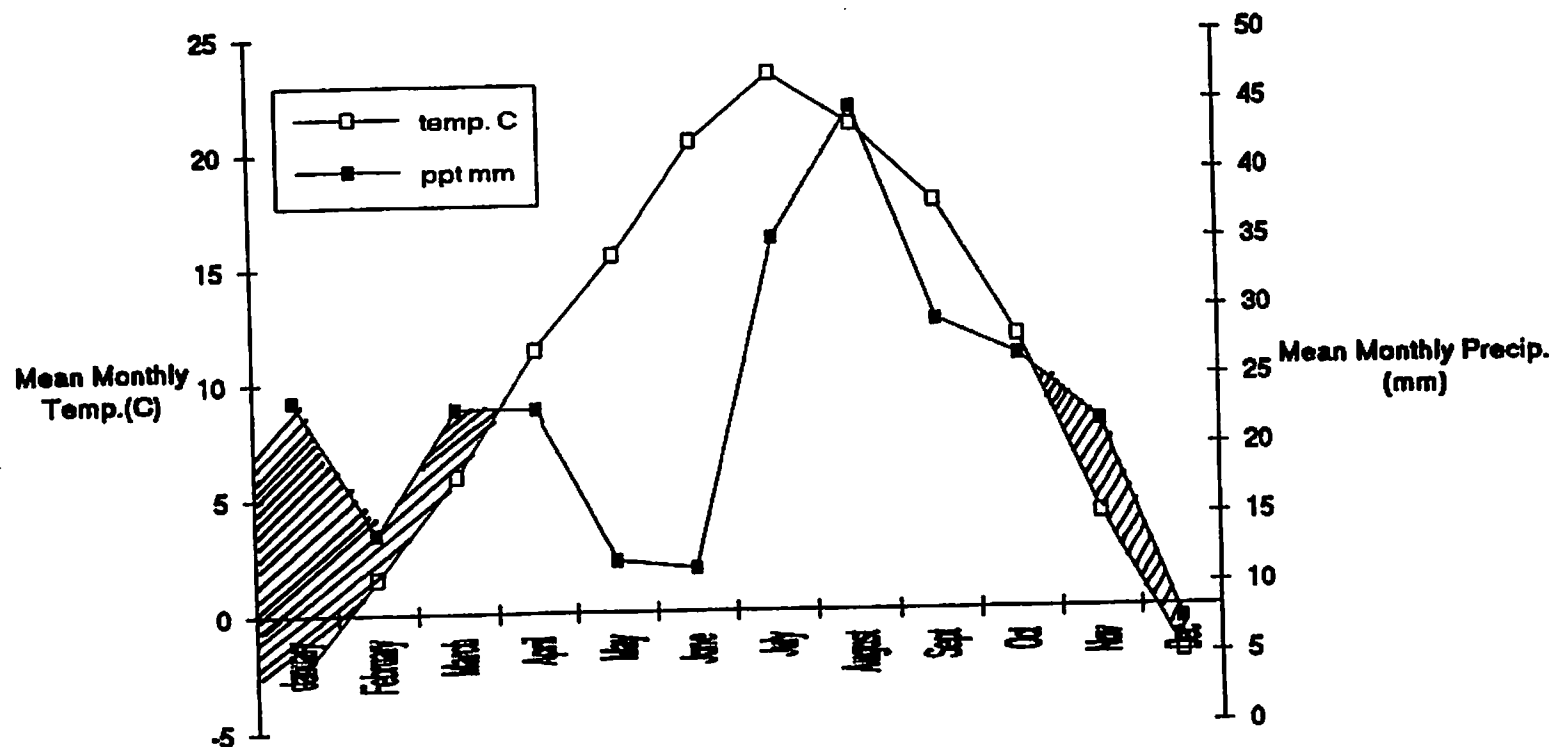


Figure 1.

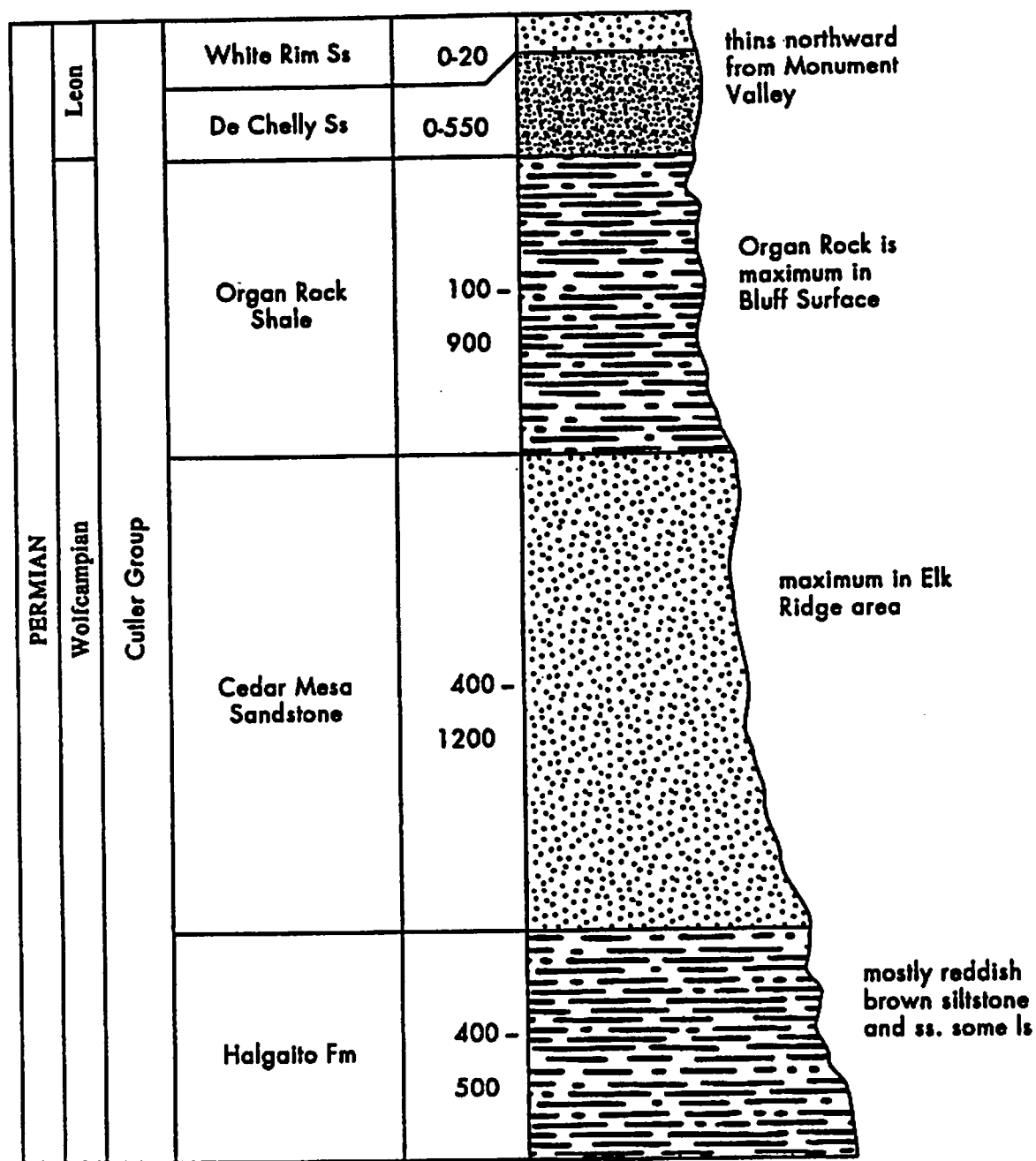


Figure 2.

**DEMOGRAPHY AND FACTORS INFLUENCING SEED SET IN *ERIGERON*
KACHINENSIS , A COLORADO PLATEAU ENDEMIC**

Loreen Allphin

December 4, 1992

ABSTRACT

The demography of six populations of *Erigeron kachinensis* in Natural Bridges National Monument, Utah is described. Mortality was greatest for the youngest size-classes recognized. Once established, individuals appear to have great longevity. Apparent pollination percentage is low (only about 48 %) and fruit abortion rates are high (~55 %). Abiotic resource availability appears to have no impact on abortion rates. As determined by pollinator exclosures, *Erigeron kachinensis* require animal vectors for successful pollination. The species is apparently self incompatible: plants in pollinator exclosures set almost no seed (<1 %). Few seeds (fruits) were observed to be destroyed by seed predators. It was observed through light microscopy demonstrated that aborted (shriveled) achenes included remnants of nonliving embryos. It seems likely that fruit abortions are tied to recessive alleles exposed in sexual recombination. Seed set limited primarily by genetic load and incomplete pollination.

DEMOGRAPHY AND FACTORS INFLUENCING SEED SET IN *ERIGERON*
KACHINENSIS, A COLORADO PLATEAU ENDEMIC

INTRODUCTION

Erigeron kachinensis is a rare endemic of the Colorado Plateau portions of southeastern Utah and southwestern Colorado. It is confined to sandy, saline substrates in alcoves of the walls of deep canyons. In this report, demographic relationships of the Kachina daisy are described from six populations. An attempt is also made to determine whether seed set in the Kachina daisy is limited by pollen availability, environmental stresses, predators, and/or deleterious genes exposed in the sexual recombination process.

It has long been recognized that seed set in plants could be limited by incomplete pollination, predators, and /or resources such as water, essential elements, or suitable temperatures (Stephenson 1981, Willson and Burley 1983, Marshall and Elstrand 1988, Dieringer 1992, Ehrlén 1992). Zimmerman and Pyke (1988) showed that the number of seeds produced by *Polemonium foliosissimum* was limited by resources other than pollen, but that pollen availability may have limited seed production to a lesser extent. Self incompatibility and inbreeding depression are known to limit seed set (Schlichting and Devlin 1992, Sork and Schemske 1992). It is also apparent that genetic load may limit seed set in outcrossed species (Charlesworth 1989).

Genetic load is considered to be greater in plants that habitually outcross than in species that are selfpollinated (Wiens et al. 1987). That

trend was supported by both fruit/flower ratios and mature, viable seed/zygote ratios. Outcrossing species are more heterozygous than inbred species and thus have more recessive alleles, some of which may be lethal or sublethal in the homozygous state (Wiens 1984, Charlesworth 1989). Such deleterious, recessive genes often appear in homozygous form as chromosomes are independently sorted in meiosis and result in lethal or sublethal combinations that produce abortion of developing seeds, inviable seeds, or seedlings that die before reproducing.

It has been suggested that rare, outcrossing species are often more heterozygous than more abundant and widespread relatives (Nickrent and Wiens 1989). Therefore, one must consider genetic load (undesirable alleles) in addition to inadequate pollination, insufficient essential resources, and seed predation in any attempt to account for incomplete conversion of flowers to viable seeds.

The Kachina daisy appears to have low fruit set and high abortion rates of pollinated ovaries. Since the species is rare, it is critical that managers know whether seed set is limited by inadequate pollination, insufficient essential resources in the habitat, seed predation, or by genetic load.

METHODS AND MATERIALS

Populations of the Kachina daisy considered in this study occur in six alcove seeps located in Natural Bridges National Monument, San Juan County, Utah. The alcoves occur at about 1768 m (5800 ft.) elevation. All occur in deep canyons that traverse Cedar Mesa Sandstone, and all of the alcoves are shaded for most of the day by high canyon walls. The daisies grow in sandy loam to loamy sands with pH-values ranging from 7.8-9.1 (table 1). The regional environment is semiarid (average annual precipitation is 316.8 mm) with an annual average temperature of 10.5 C (Allphin 1992). Common associated species in the alcoves were: *Aquilegia micrantha*, *Calamagrostis scopulorum*, and *Zigadenus vaginatus*. The populations differ in respect to amount and timing of direct sunlight received and amount of soil moisture. Two of the study alcoves faced west, two faced south, and the final two faced north. Each pair of alcoves that shares the same aspect (direction of exposure to the sun) differs in respect to soil moisture.

In each alcove, 100 Kachina daisy plants were permanently marked with numbered aluminum tags secured about 10-20 cm from plant bases with galvanized nails. Plants were monitored for three field seasons (summers of 1990 -1992). Data on vegetative characteristics of all 600 daisies were recorded each year (Allphin 1992). Characteristics of the soil associated with each population were determined by the Soil Analysis Laboratory at Brigham Young University. Data were taken on soil moisture, salinity, and "available" phosphorus at each population site to permit their correlation with plant size, reproductive success, and survival of daisy plants in the several alcoves. The number of

flower heads per plant, the number of flowers per head, the number of fruits that began to expand per head, and the proportion of aborted and filled achenes in mature heads were also determined for each population. Density of daisy plants in each population was determined and correlated with the resource base available to each population.

A size-class was assigned to each of the tagged daisies. These size-classes were based on number of rosettes per plant. Five size-classes are recognized: 1) a single rosette, 2) 2 rosettes, 3) 3 rosettes, 4) 4 rosettes, and 5) >4 rosettes per plant. The mortality of plants from year-to-year was determined by relocating numbered plants. The average number of flowers per plant by size-class and the percentage of ovaries that expanded into fruits were also determined for each plant. This information permitted a life table to be constructed for these populations.

Percentage of ovaries converted to fruits (seeds since the achene produces but a single seed) was determined by observing flower heads with a dissecting microscope immediately prior to fruit dispersal. The total number of fruits per head was determined. From that number, the proportions of ovaries which began to expand as fruits but aborted before the mature fruit stage and the percentage of fruits that produced plump, filled seeds were determined. This information permitted an estimate of efficiency of pollination, fruit abortion rates, and the number of filled seeds set by plants of each size-class. Microtome sections of both filled and shriveled fruits were observed under a light microscope to ensure that an abortion had actually taken place when ovary expansion ceased and a shriveled "seed" was produced. Sections were prepared by fixing the ovaries in both

glutaraldehyde and OsO_4 , dehydrating them in a graded series of ethanol, and embedding them in Spur's resin for sectioning with a glass knife.

It was also determined whether a plant could set seed with its own pollen (self) or whether it was obliged to outcross. In order to determine whether this species required an animal pollinator, cone-shaped pollinator exclosures were constructed from a fine mesh (0.5 mm diameter openings) to cover test plants. Cones were secured over the entire body of randomly chosen plants in each alcove. The exclosures were sealed off at ground level to preclude pollinators entering the exclosures from below. The percentage of fruits set by self-pollinated, outcrossed, and unmanipulated flowers of plants under the pollinator exclusion cones was determined. Hand pollination was accomplished by smothering the stigmas of receptive flowers in selected heads with pollen from another head on the same plant. Some heads were dusted with pollen from heads from other plants in the same population, while other heads were smeared with pollen from heads of plants from different alcoves. This was accomplished by rubbing flowering heads in anthesis together face-to-face. Hand-pollination ensures that pollen reaches all receptive stigmas (but not all flowers, since the head is an indeterminate inflorescence). Using this approach, fertilization will not take place if plants are self incompatible, if the pollen donor is too closely related (Manasse and Pinney 1991), or if stigmas are nonreceptive due to immaturity or senescence. Percentage seed set of hand-pollinated flower heads was determined for manipulated flowers in each of the treatments considered. From such data, one can determine whether flowers are self-compatible and whether pollen availability

affects the proportion of ovaries that begin to expand as fruits. One can also relate fertilization and abortion rates to pollen source.

RESULTS AND DISCUSSION

Results of soil characteristics shown to be significantly correlated with plant performance in the alcoves (Allphin 1992) are shown in table 1. Soil moisture, salinity, and available phosphorus were variables significantly correlated with vegetative response of the Kachina daisy (Allphin 1992). The demographic characteristics of *Erigeron kachinensis* collected in three field seasons (summers of 1990, 1991 and 1992) are reported in table 2.

Percent mortality of Kachina daisies each year was determined for each study alcove, and for each of the different size-classes defined earlier in this paper (table 3). The data show size-class 1 (plants with one rosette) to have the greatest percent mortality in both 1991 and 1992, followed by plants assigned to size-class 2 and size-class 3. No mortality was observed for plants in size-classes 4 and 5. It appears that once plants become well established, they can survive for great lengths of time. Large Kachina daisy plants must eventually die, but deaths were not observed among size-class 4 and 5 plants in my study. Death of large plants is probably related to stochastic disease or parasitism epidemics or to physical catastrophes such as the fall of roof spall caused by natural weathering of overhead rock or earthquakes or

to scouring due to flash floods. Flooding caused many of the deaths in alcove 2 in 1992.

Average mortality for the two years of observation varied greatly among alcoves (table 2), ranging from 4.5 % in alcove 5 to 20.1 % in alcove 2. Regression analysis demonstrated that mortality was positively and significantly ($p < .05$) correlated with soil temperature only among the environmental variables reported in table 1. As one might expect for a desert environment, mortality was negatively correlated with soil moisture, but that relationship was not statistically significant. The data support the reasonable hypothesis that mortality is greater where water stress is large (i.e., where soil moisture is scant and soil temperatures are elevated).

A life table was constructed for *Erigeron kachinensis* based on pooled information from the six different populations. Fecundity was taken as the average number of ovules that expanded into filled fruits in plants of each size-class (table 4). These results are based on data recorded in table 3. As might be expected, fecundity increases with size-class, with size-class 5 having the greatest fecundity. These are minimal estimates, however, since they are based on data collected in month of June only, and daisies continue to flower through September.

Selected reproductive characteristics of this daisy in the six alcoves are reported in table 2. A one-way ANOVA and the Scheffe test were used to determine whether percent abortion of pollinated ovaries and seed set differed among alcoves. No significant differences were found among the six sites or among years (1990-1992) as far as those reproductive characteristics were concerned. For that reason, reproductive data for the six alcoves and three years were pooled for

used in table 2 and figure 1. The average flower head in Kachina daisy contains about 25 ovules. Only about 48 % of those begin to expand. Failure of ovaries to expand suggests lack of pollination or pollination with inviable pollen. The data available are inadequate to distinguish between those two possible causes of reproductive failure. I will refer to unexpanded ovaries as "unpollinated" with the caveat that inviable pollen may also be involved. Of that 48 percent pollinated, about 55 % abort and fail to mature a seed. Therefore, only about 22 percent of the ovaries mature viable seeds. The result is a low fruit set for the Kachina daisy.

The results shown above are from data collected only in June 1990, 1991, and 1992. However, Kachina daisies begin flowering in mid-May and continue to flower through September. Fruit abortion rates were compared between heads produced in June and heads matured in September. The difference was not statistically significant.

Microtome sections of aborted and filled achenes were observed under a light microscope at the Electron Microscopy Laboratory at Brigham Young University (figures 2 and 3). Comparison of these figures illustrate that seed abortion has occurred in the shriveled achene.

To test the hypothesis that variation in filled fruit set is related to environmental conditions in the various alcoves, percent filled fruits was correlated with environmental variables known to affect plant vegetative growth in these populations (Allphin 1992). Percent fruit abortion was not found to be significantly correlated with soil moisture or soil salinity (figure 4), environmental factors that do significantly impact total living plant cover in the alcoves (Allphin 1992). Seed set

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in the Kachina daisy, therefore, does not seem to be limited by habitat conditions.

The hypothesis that predation limits reproductive success of the Kachina daisy was investigated for the six alcoves. Predation in seedheads was only observed in two of the alcoves (alcoves 1 and 3). In sites where predation occurred, it accounted for < 1% of the reproductive output of the alcoves and thus is not a major factor limiting seedset in this daisy.

Kachina daisies do not appear to set seed with their own pollen. Seed heads that developed under pollinator exclosures showed only 6.5 % ovary expansion; of expanded ovaries, about 90 % aborted during development (table 5). Significant reproductive success in the Kachina daisy is thus dependent on animal pollinators. A variety of small insect pollinators were seen visiting the study populations. Most visits occurred during the warmer parts of the day (noon to about three o'clock). The three most common pollinators observed were the common sawfly, a syrphid fly, and a bee fly (table 6).

The hypothesis that incomplete pollination limits the reproductive success of Kachina daisies in the study areas was investigated by correlating percent pollination of flowers with density of daisy populations in the six alcoves (figure 5). One might predict that more dense populations of flowers would attract more pollinators than sparse populations. Although some populations had 2 or 3 times (or even 4 times as in alcove 6) more plants per unit area than the most sparse population (alcove 3, table 2), there was no correlation between daisy density and percent pollination. This result suggests that pollinator

availability may not be a significant cause of observed differences in pollination among alcoves.

The results of the hand-pollination trials are reported in table 5. *Erigeron kachinensis* showed few expanded ovaries (13.3 %) in pollinator enclosures and most of the fertilized ovaries aborted (90.6 %) when pollen came from the same plant. In addition, percent of ovaries expanding significantly increased when pollen came from another source, either a plant in the same population or a plant from a different population. Ovule abortion in expanding fruits was also reduced when pollen came from another source.

Seed abortion rates, however, were still high, even when pollen came from another plant and fertilization had occurred. When fertilization was accomplished with pollen from another population, the daisy still aborted over half of the expanded ovaries. It is apparent that limitation in seed set is due to more than inadequate pollination. The data suggest that genetic load must be considered as another cause of limitation in reproductive success in the Kachina daisy.

When percent expansion of fruits and abortion of expanding fruits are compared between hand-pollination trials and open pollinated flowers, significant differences are found to occur (table 5). When natural insect pollinators provide the pollen to the stigmas, more of the ovules begin to expand (48.5 % rather than ~37 %). There is also a lower ovule abortion rate (~55 % rather than ~75 %). This result is probably related to two factors: 1) since the composite head is an indeterminant inflorescence, a single application of pollen does not encounter all potentially receptive stigmas, and 2) hand-pollination supplied pollen from only one donor, while insect pollination almost

certainly results in multiple paternal sources of pollen reaching each head.

It is common for plants which are outcrossers to have multiple paternity or pollen from many male donors (Janzen 1975, Janzen et. al. 1980, Dudash and Ritland 1991). There is known to be differential competitive ability among pollen grains from different donors (Bertin 1988, Snow and Mazer 1988). The success of one individual pollen grain will depend upon the genotypes of other pollen grains on the stigma. Such competition has been found to be related to differential growth rates of tubes from simultaneously germinating pollen grains from different donors in the style of the parent. Pollen tubes which grow down the style fastest will fertilize disproportionately more ovules (Mulcahy, et al. 1983). Percent fertilization was higher and abortion rate was lower in *Erigeron kachinensis* when insect pollinators provided pollen to the stigmas. Multiple paternity is a possible explanation for observed differences between insect and hand-pollination.

Since *Erigeron kachinensis* is rare, it is important that managers know whether seed set is limited by inadequate pollination, insufficient essential resources in the habitat, predation, or by genetic load. Fruit abortion in the Kachina daisy is not significantly affected by resources in the habitat. Although almost half of the ovaries fail to begin expansion and are apparently pollen limited, over half of the pollinated, expanding ovaries eventually abort. Therefore, limitations in fruit set of the Kachina daisy appear to be caused by lethal genetic recombinations. In rare perennials, there is a possibility that genetic polymorphisms will increase the frequency of lethal and sublethal

recombinations (Wiens 1984). Genetic load from such a source appears to be limiting proportion of fruits matured by *Erigeron kachinensis*.

The results of this study suggest that seed set in *Erigeron kachinensis* is limited by inadequate pollination and genetic load, but it is acknowledged that conclusions are based on inferences drawn from field observation. More definitive tests must be based on well controlled trials under growth chamber or greenhouse conditions. It is also critical that a direct evaluation of genetic heterozygosity be made of this species.

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TABLE 1. Important environmental characteristics of the six alcoves that support *Eriogon fasciculatus* at Natural Bridges National Monument. Each value represents an average of the five samples at each alcove. Means followed by the same letter do not differ at the $p = .05$ level or better.

	ALCOVES					
	1	2	3	4	5	6
Aspect (degrees)	302	328	160	197	252	225
Hrs. Dir. Sunlight in June	5.0	5.75	1.0	4.5-5.25	4.6	0-1.5
pH	8.6 a	8.8 ab	9.1 b	8.6 a	7.9 c	7.8 c
EC (mmhos/ cm)	13.1 a	17.1 a	31.1 b	7.6 a	6.9 a	6.0 a
Ave. Soil Temp.(C) *	14.1	15.8	13.9	15.1	13.9	13.2
Soil Moisture (%) *	12.3 a	5.8 ab	18.4 ac	12.2 a	12.7 a	25.6 c
Phosphorus (ppm)	11.4 a	10.7 b	9.8 b	10.9 b	7.5 b	8.0 b

* This is an average based upon samples taken in June of the summers of 1990, 1991, and 1992.

TABLE 2. Demographic characteristics of the six populations examined. Values reported are averages based on an initial inventory of 100 randomly selected plants in each alcove in 1990. Populations were reinventoried in 1991 and in 1992. Where possible, the standard error for each mean is shown in parenthesis below the mean.

Population No.	No. Plants per 1.0m ²	No. Rosettes per plant	Leaf Length. (cm)	Clump Diam.(cm)	No. Heads per plant	No.Flower per Head	% Flowers Pollinated	Pollinated Ovaries Aborting%	% Ovaries Maturing Seeds per Head	% Mortality 1990-1991	% Mortality 1991-1992
1	15.1	1.6	2.7	4.8	1.3	21.1	51.2	54.2	24.0	9.0	15.4
		(0.06)	(0.07)	(0.13)	(0.08)	(0.65)	(14.09)	(8.72)	(11.54)		
2	12.7	1.4	1.9	3.6	0.9	21.5	53.4	62.3	22.4	11.0	29.2
		(0.03)	(0.06)	(0.10)	(0.10)	(0.87)	(18.79)	(14.66)	(13.42)		
3	6.1	2.5	2.5	6.2	1.9	28.4	42.2	57.7	18.5	5.0	7.4
		(0.10)	(0.06)	(0.18)	(0.19)	(0.86)	(11.96)	(7.47)	(6.28)		
4	15.7	2.1	3.6	7.3	2.3	27.2	47.4	48.8	24.3	7.0	10.8
		(0.07)	(0.08)	(0.18)	(0.20)	(0.91)	(4.61)	(6.05)	(2.06)		

TABLE 3. Summary of mortality and reproductive characteristics by size-class for June 1990- June 1991 and June 1991- June 1992. Data for six populations are pooled for this table. Average number of viable seeds per head was based on data taken only in June 1992.

Size-class	Initial No. Plants in 1990	% Mortality (1990-1991)	% Mortality (1991-1992)	Ave. No. Heads per Plant	Ave. No. Viable Seeds per Head
1	340	9.12	10.95	.60	5.7
2	165	3.03	7.51	1.4	5.1
3	67	1.49	1.72	2.7	5.0
4	18	0	0	4.0	5.3
5	10	0	0	6.7	5.7

TABLE 4. Life table for *E. laetevirens* based upon observation of 600 individuals over a three year period (1990-1992). Probability of survival (l_x) is based upon average mortality values by size-class for the intervals June 1990-June 1991 and June 1991- June 1992. Fecundity (b_x) was determined using the average number of filled seeds per plant as observed in June 1992 (See table 3).

SIZE CLASS (x)	NO. SURVIVING TO START OF CLASS (N_x)	PROBABILITY OF SURVIVAL (l_x)	FECUNDITY (b_x)	REPLACEMENT RATE ($l_x b_x$)
1	1000	1.0	3.4	3.4
2	900	0.900	7.1	6.4
3	853	0.853	13.5	11.5
4	839	0.839	21.2	17.8
5	839	0.839	38.2	31.9

TABLE 5. Reproductive success of unmanipulated flowers of Kachina daisies under pollination from pollinators but received hand-applied self pollen or pollen from two non-self sources. For comparative purposes, the average open-pollinated flowers is also shown. Means are given with standard deviations in parenthesis below.

	N for each Trial (N= 1 flower head)	% of Ovaries Expanded	% Abortion for Expanded Ovaries
Flower Heads without hand-applied pollen	44	6.5 (8.06)	87.2 (21.87)
Hand-pollination with pollen from heads from same plant	12	13.3 (14.69)	90.6 (26.52)
Hand-pollination with pollen from heads from same population	6	38.5 (14.87)	84.8 (12.86)
Hand-pollination with pollen from head from different alcoves	4	36.0 (17.3)	74.8 (31.47)
Open-pollinated flower heads	>100	48.5 (5.698)	55.9 (5.23)

TABLE 6. Insect pollinators seen visiting flowers of *Euphorbia* during field seasons 1990- 1992.

Insect Order	Insect Family	Common Name
Hymenoptera	Tenthredinidae	Common Sawfly
Diptera	Bombyliidae	Bee Fly
Diptera	Syrphidae	Syrphid Fly
Diptera	Bibionidae	March Fly

FIGURE LEGENDS

Figure 1.....Reproductive success of *Erigeron kachinensis* based on data pooled for six alcoves inventoried in three different growing seasons.

Figure 2.....Light microscope photograph of a microtome section from a filled, expanded fruit of *Erigeron kachinensis*. x 138

Figure 3.....Light microscope photograph of a microtome section from an expanded fruit with an aborted embryo. Note the disintegrating cells inside. x 175

Figure 4.....Correlation of fruit abortion with important resources in the habitat of *Erigeron kachinensis*.

Figure 5.....Relationship between population density and pollination of *Erigeron kachinensis* in six different alcoves.

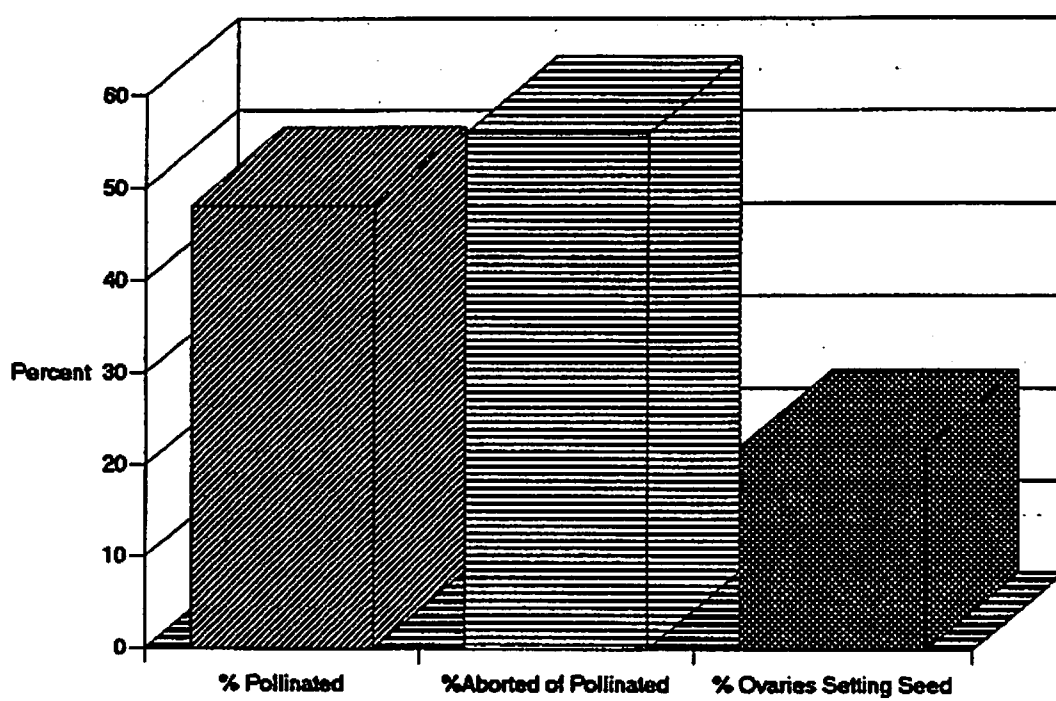
Reproductive Success of *E. kachinensis*

Figure 1.

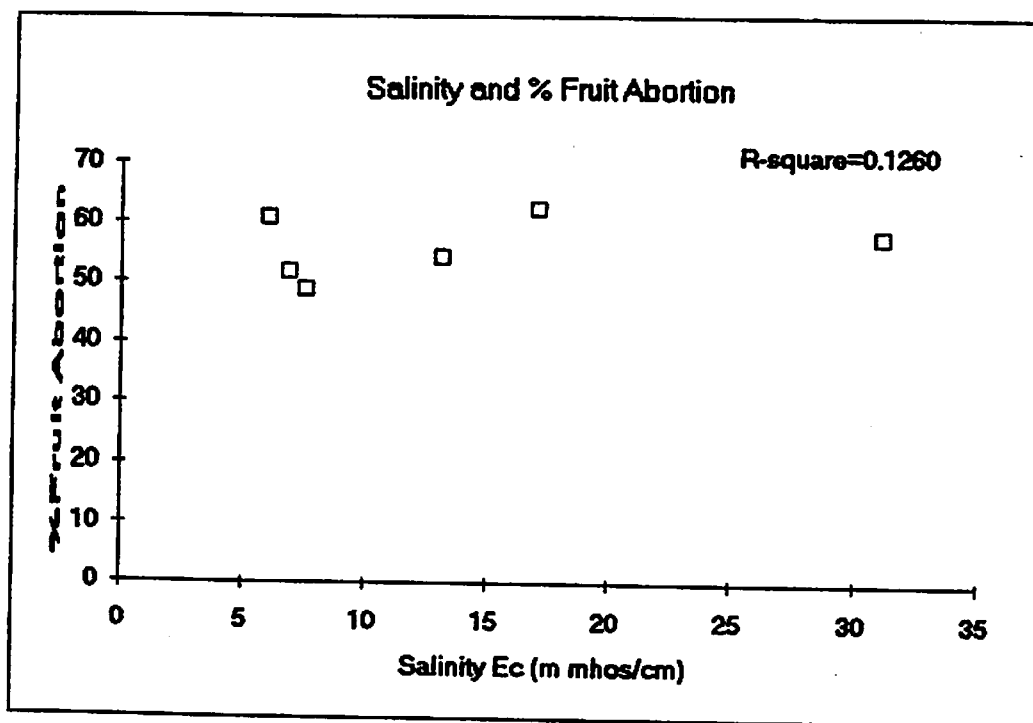
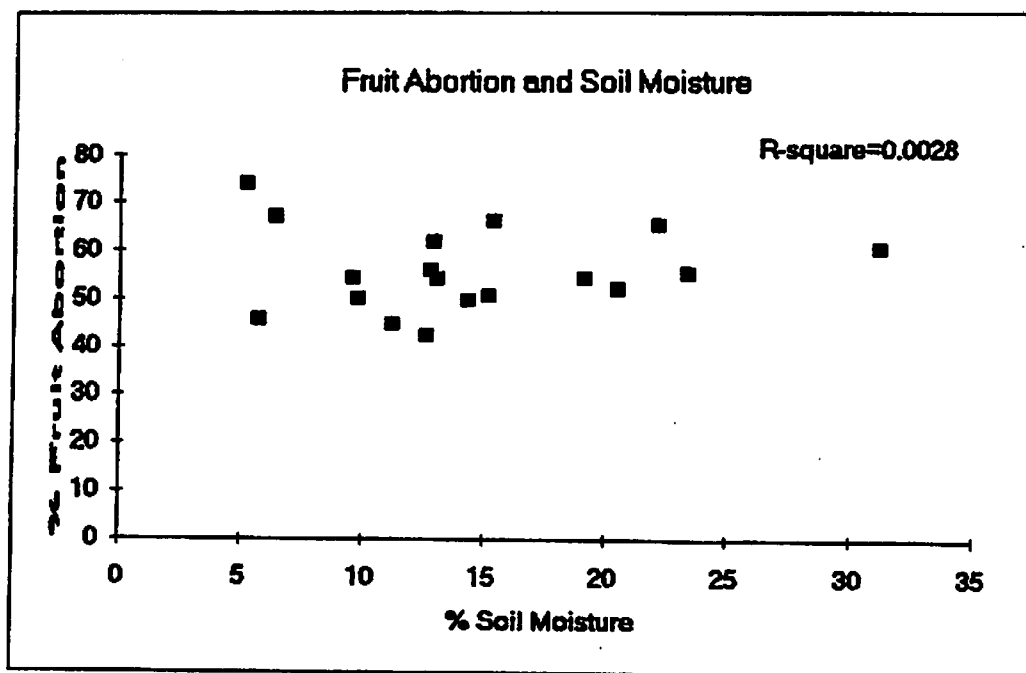


Figure 4.

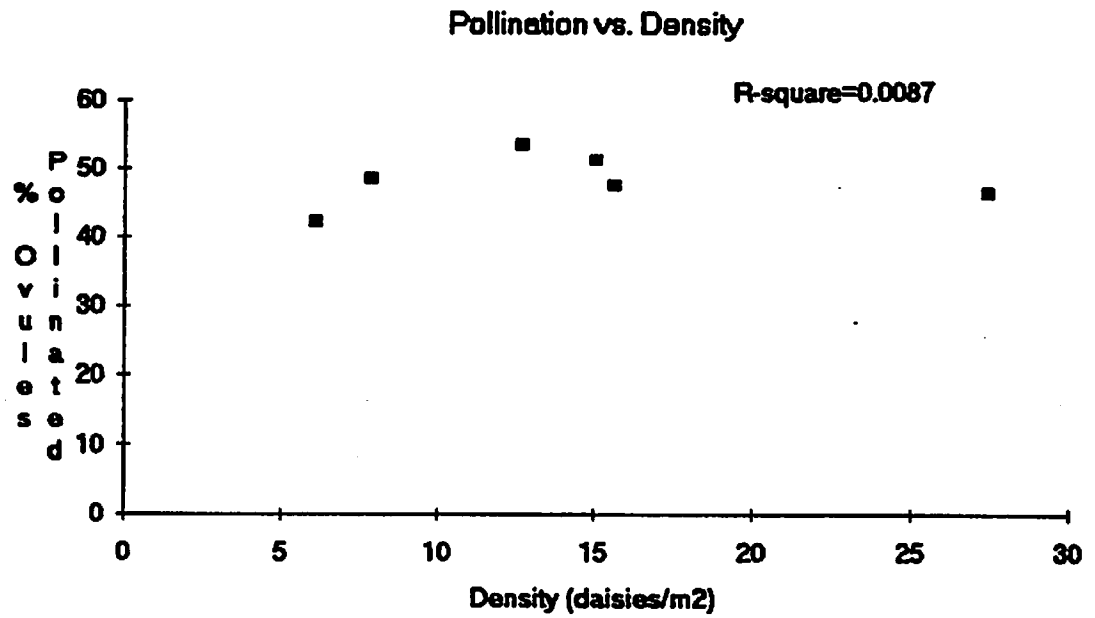


Figure 5.

HABITAT REQUIREMENTS FOR *ERIGERON KACHINENSIS*, A RARE ENDEMIC
OF THE COLORADO PLATEAU

Loreen Allphin

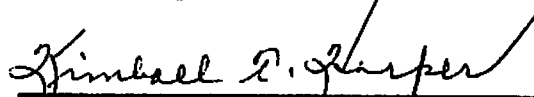
Department of Botany and Range Science

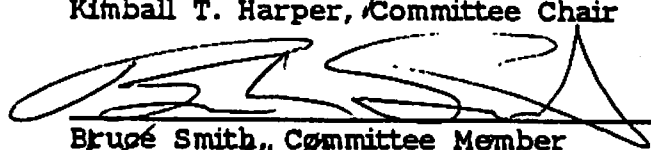
M. S. Degree, December 1992

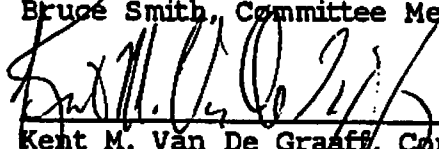
ABSTRACT

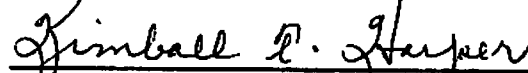
Erigeron kachinensis is a rare endemic of the Colorado Plateau, southeastern , Utah. This perennial composite grows in small, isolated populations at seeps and alcoves arising along the canyon walls in Cedar Mesa Sandstone substrates. The characteristics of six *Erigeron kachinensis* sites in Natural Bridges National Monument, San Juan County, Utah, were studied to describe habitats associated with this rare species in the deep canyons of Southeastern Utah. Sites were analyzed with respect to geology, soil chemistry, physical properties, and vegetational characteristics. Total living cover was significantly correlated with percent soil moisture, soil salinity, and "available" phosphorus. Kachina daisies appear to more tolerant than associated species of differences in these abiotic factors. Most soil characteristics do not vary between the sites. The prevalent plant species on *E. kachinensis* sites were *Aquilegia micrantha*, *Calamagrostis scopulorum*, *Zigadenus vaginatus*, and *Erigeron kachinensis*. These species accounted for more than 75 percent of the total living cover in the alcoves studied. Attempts have been made to establish *Erigeron kachinensis* on sites which appear to have the necessary habitat conditions.

COMMITTEE APPROVAL:


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