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Final Report

Tracking Tallgrass Plant Population/Open Space and Mountain Parks

Kathleen H. Keeler
Professor
School of Biological Sciences
University of Nebraska-Lincoln
Lincoln NE 68588-0118
phone (402) 472-2717
fax (402) 472-2083
email kkeeler1@unl.edu

Summary: The 1999 project followed plants in permanently marked plots in the Open Space. Thirty one species of plants were remapped in tallgrass prairie areas associated with the Bock Permanent Markers.

For *Andropogon gerardii*, this represents a fifth year of observation: comparisons of polyploid cytotypes now include data from 1995-9. Higher polyploids are bigger, lower polyploids set more fertile seeds. Plant size is not significantly different between ploidy levels: some of both ploidy are very large individuals. There has been little change in plant size during the years studied: plants of *A. gerardii* are apparently quite old and stable. Seed counting and data entry from 1999 is not yet complete.

For 15 other species, plant number and location were recorded and compared to 1998 (and, where available, earlier) maps from a number of different plots. This data is gradually producing a picture of population dynamics within the Open Space, but analysis is still in progress for 1999. Another 15 species were incidentally mapped: they are too few to make a valid sample, but the information on individuals will be useful.

This project continued to follow mapped of species in Open Space prairies. This data indicates how large and healthy the populations are, notes changes, and compares the dynamics of different sites.

Permanent maps produced from this project provide the necessary baseline data for long-term monitoring of population health and for studying the demographics of these species.

The project can be seen as having three parts: 1) The comparison of the two chromosome types of *Andropogon gerardii* (big bluestem), begun in 1995, 2) remapping plants of 15 species that occur abundantly in two or more plots and 3) remapping incidental species found in insufficient numbers for a valid study but that are interesting nevertheless. The study of *Andropogon gerardii* addresses questions of the role of polyploidy in natural populations (e.g. Keeler and Davis 1999). The study of prairie plant populations address our general lack of knowledge about prairie plant species.

METHODS

Plots were established in 1995-6 to study *Andropogon gerardii* (big bluestem). Plots were associated with Carl and Jane Bock's permanent markers to allow / promote relocation (Table 1).

Table 1. Plot Locations. Plots are 10 m x 10 m., although not all of it may be included for any particular species.

Bock Plot Number	Description of Plot Location	Finding Plot from Bock Permanent Marker
28	Boulder Greens Venture, Shanahan Ridge	Marker is SW corner of plot
36	Bobolink Trail, Gebhard (South Boulder Creek Trail area)	Marker is SW corner of plot
45	Church Wildlife Transect (W of Cherryvale, S of Turnpike)	Marker is on the west edge of plot, 4 m lie S of marker, 6 N
52	Davidson Mesa	Plot is in same pasture as marker but orients to the fence line: it is 3 m N, 3 m W of the second post, running N & W
57	Open Space Maintenance, grazing exclosure	Marker 57 is in the same half of the exclosure as the plot but the plot orients to the fence: about 100 m from the NW corner of the exclosure; 8.4 m E of 20th fence post (counting all types of posts) or 9.8 m. at 300° from the 7th wooden fence post. Plot runs 10 m E and 10 S of that spot.
58	Sans Souci Trailer Park Site 3 Exclosure	Plot begins 4 m W of pole, runs 7 m S, 3 m N (& 10 m W)
61	Flatirons Vista Wildlife Transect	Marker is NW corner of plot
102	Chataqua Park Meadow	Plot begins 3 m N of Bock marker, runs 7 m S, 3 m N (10 m W)
BM	Bald Mountain Summit	From the bench at the summit, the plot is centered on the first pair of pine trees down the slope to the E. Beginning 2 m

		N of the tree, the plot is 9 m N, 5 m W (or 10 m W but the far 5 lack *A. gerardii*), 5 m S of the reference point at the tree, plot begins again: it runs 10 m S, 2 m E, 8 m W of the starting point. There's a permanent aluminum tag nestled close to the tree.
BW	Betasso Water Treatment Plant	Plot is up the two-tire track that continues E (and S relative to the Loop Trail) of the picnic table at the E entrance to the Loop Trail. At the crest of the hill is an open area with 5 pines in the curve of the trail as it turns more N and then more E. From the NE-most tree close to the trail, the plot is 6 m due E. From there it runs 6 m S, 4 m N (& 10 m E). There's a permanent tag nestled close to the pine tree.
FS	Flagstaff Summit	Long thin plot on sloping hillside. On Ute Trail above (lower end of trail, N side of road) parking lot, plot is just above the first place that the trail goes so far N that you can see out over the slope northward. The plot is on the ridge just E of that spot in the trail (uphill and slightly N) beginning with a young mature pine and going 13 m S and 13 m W (much space without *A. gerardii*). There's a permanent tag at the base of the pine tree.

In 1998, maps of the plots listed in Table 1 were expanded to include 31 additional species. Notes on flowering were taken, and some notes were made about plant size. These are being entered into the tables that ArcView constructs for its maps and in the future it will be possible to analyze them in relation to size, location etc.

RESULTS

Entering 1999 data into the 1999 maps (ArcView, the Macintosh based form of the GIS system ArcInfo) is about 70% complete for *Andropogon gerardii* and about 20% complete for most other species at this time (Table 2).

Four major grasses and one minor, five other monocotyledon species, eight composite species (Asteraceae), four legumes (Fabaceae) and eight other dicotyledons were remapped in 1999. The total number of mapped plants is in excess of 1000. Droppped in 1999 were *Convolvulus arvensis*, *Iris missouriensis,* and an annual grass from plot 45. Added were yarrow (*Achillea lanulosa*) and yellow sweet clover (*Melilotus officinalis).*

Table 2. Status of data analysis.

r= remapped, a = entered into Arcview, c = seeds collected, d = seed count done

Plant species	Plot										
1999 data	28	36	45	52	57	58	61	102	BM	BW	FS
Andropogon gerardii (Poaceae) remapped (r), into arcview (a)	r	a	a	a	r	r	r	a	r	r	r
Andropogon gerardii seeds collected(c), counted (d)	d	c	c	c	c	d	c	d	c	d	c
Remapped 99 (r) On Arcview (a)											
Ambrosia psilostachya * (Asteraceae)	r	0	r	0	r	r	r	a	-	-	0
Artemisia frigida (Asteraceae)	0	0	0	0	0	0	r	a	r	r	r
Artemesia ludoviciana (Asteraceae)	r	0	0	0	0	r	0	r	0	0	0
Cirsium undulatum (Asteraceae)	r	0	r	r	r	0	r	0	0	r	0
Corypantha missouriensis (Cactaceae)	r	0	0	r	r	0	r	a	r	r	r
Dalea purpurea (Fabaceae)	r	0	0	0	r	0	r	r	0	0	0
Eriogonum alatum (Polygonaceae)	0	0	0	0	r	0	r	r	0	0	0
Liatris punctata (Asteraceae)	r	0	0	r	r	0	r	a	r	r	r
Opuntia fragilis (Cactaceae)	r	0	0	r	r	0	r	a	r	r	0
Opuntia macrorhiza (Cactaceae)	r	0	0	r	r	0	r	a	r	r	r
Panicum virgatum (Poaceae)	r	0	r	r	r	r	r	r	0	r	0
Psoralea tenuifolia (Fabaceae)	r	0	0	0	r	r	r	r	0	0	0
Schizachyrium scoparium (Poaceae)	r	0	r	r	r	r	r	r	r	r	r
Sorghastrum nutans (Poaceae)	r	0	r	r	r	r	r	r	0	0	0

Yucca glauca (Agavaceae)	r	0	0	r	r	0	r	r	0	0	r
	28	36	45	52	57	58	61	102	BM	BW	FS

Some species were too infrequent to occur in many plots but are being followed anyway (Table 3). Distribution of plant families studied is given in Table 4.

In the case of species with well over 100 individuals in the 10 x 10 meter plot, I subsampled the plots, following that species in only a limited part of the plot. This applies to *Psoralea tenuifolia* and *Ambrosia psilostachya* in particular. *Ambrosia psilostachya* is sufficently mobile (resprouting from perennial roots but on long rhizomes) that there was little agreement between the position in 1998 and 1999: I opted for counting shoots in each 1 m^2 quadrat.

Table 3. Incidentally mapped species (too few or rare to follow in detail)
e = exotic, n = noxious

Species	Plot(s)	Number of Plants
Achillea lanulosa (Asteraceae)	36, 102	8, 5
Amorpha fruiticosa (Fabaceae)	36	10
Apocynum androsaemifolium (Apocynaceae) e, n	36	>250
Asclepias speciosa (Asclepiadaceae)	36, 45, 52	6, 1, 1
Asparagus officinalis (Liliaceae) e	36	7
Dicanthelium oligosanthes (Poaceae)	45	<10
Euphorbia robusta (Euphorbiaceae)	52	25
Gailardia aristata (Asteraceae)	61, BM	1, 1
Hypericum perfoliatum (Hypericaceae) e n	28, 52, 61	10, 3, 2
Lithospermum caroliniense (Boraginaceae)	BM	1
Lupinus argenteus (Fabaceae)	102	20
Melilotus officinalis (Fabaceae)	45	2
Populus deltoides (Salicaceae)	45, 52	2, 2
Tragopogon dubius (Asteraceae) e	102	10

Table 4. Summary of Demographic Studies

Family	Number of Major Species	Number of Incidental Species
Dicotyledons		
Apocynaceae	0	1
Asclepiadaceae	0	1
Asteraceae	5	3
Boraginaceae	0	1
Euphorbiaceae	0	1
Fabaceae	2	2
Hypericaceae	0	1
Polygonaceae	1	0
Portulaceae	0	1
Salicaceae	0	1
Monocotyledons		
Agavaceae	1	0

Cactaceae	3	0
Iridaceae	0	1
Liliaceae	0	1
Poaceae	4	1
TOTAL SPECIES	16	15

1) *Andropogon gerardii* Cytotype Comparison

Andropogon gerardii plants in all plots were remapped and seeds counted. Clone areas were calculated from the Arcview maps and compared statistically using analysis of variance using PC SAS (1998). As shown in Table 5, there is no significant difference in either the mean clone size by cytotype or the change in cytotype between 1996 and 1998. This will be recalculated when the 1999 data is available.

Maps of this data are reproduced as Fig. 1 (plot 52, Davidson Mesa), and Fig. 2 (Plot 102 Chataqua Park Meadow). Fig. 1a is change in the plant shapes 1995-1999; Fig. 1b is shows change 1995-9 by cytotype, by superimposing first 1995 on 1999 to show where the clone has increased in area, and then 1999 on 1995 to show where the plant has contracted. (The numerical analysis through 1998 is in Table 5 as change in area).

Table 5. Clone Size compared between ploidy levels (ANOVA)

Area 98	DF	SS	F	P
Ploidy	2	2103109	0.02	0.98
Error	253	17121104772		
Change in Area 98	DF			
Ploidy	2	4655276	0.34	0.71
Error	251	169611411		

Fig. 1a Plot 52, Davidson Mesa: change in shapes of *Andropogon gerardii* clones 1995-1999. Striped: rocks.

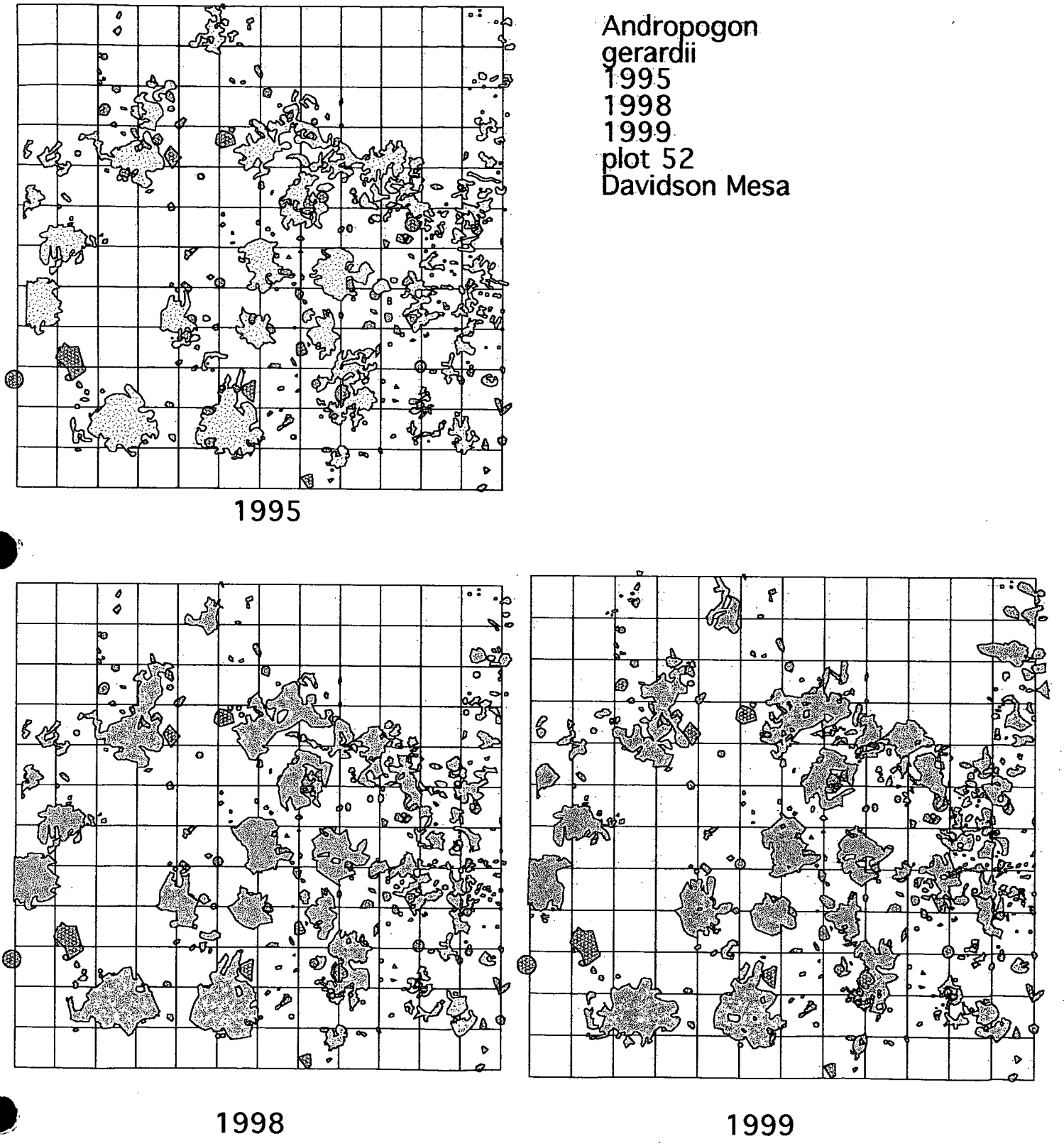
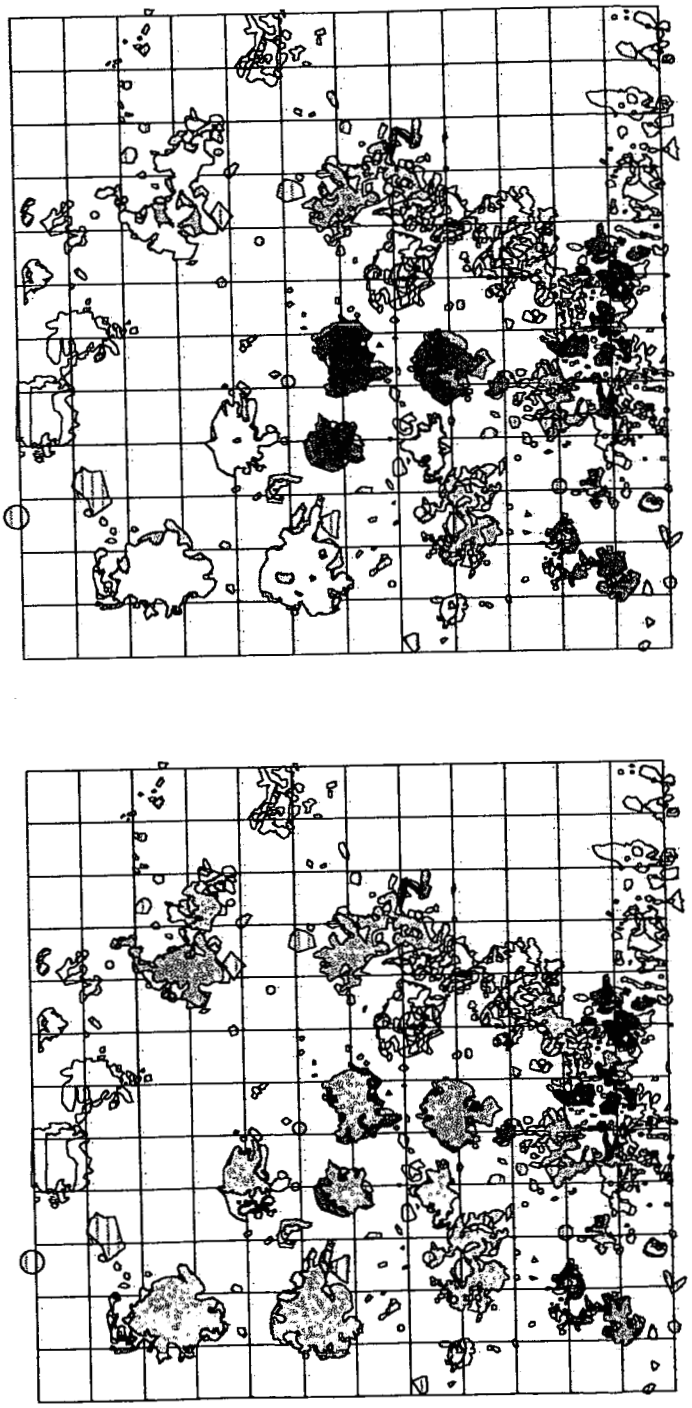
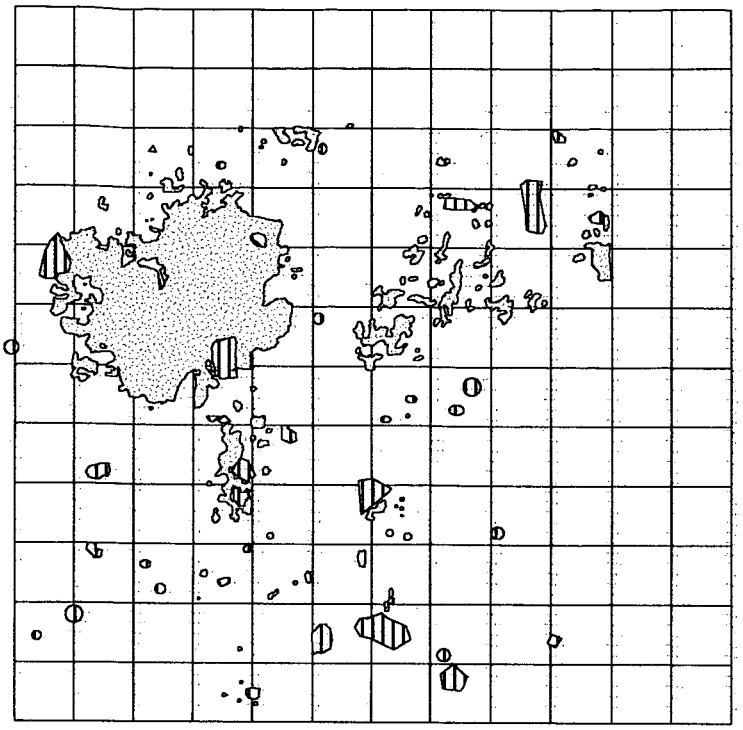


Fig. 1b Change 1995-9 by cytotype, by superimposing first 1999 on 1995 to show where the clone has decreased in area, and then 1995 on 1999 to show where the plant has expanded. Blue: 60 chromosomes (light 1995, dark 1999); purple 61-89 chromosomes (light 1995; dark 1999); red 90 chromosomes (light 1995; dark 1999). Striped: rocks.

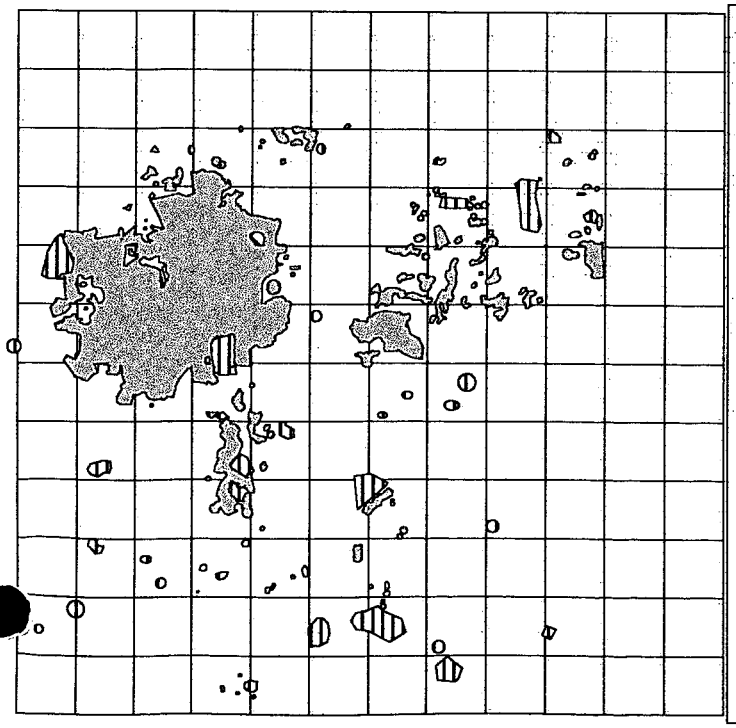


Plot 52
Davidson Mesa
Andropogon gerardii

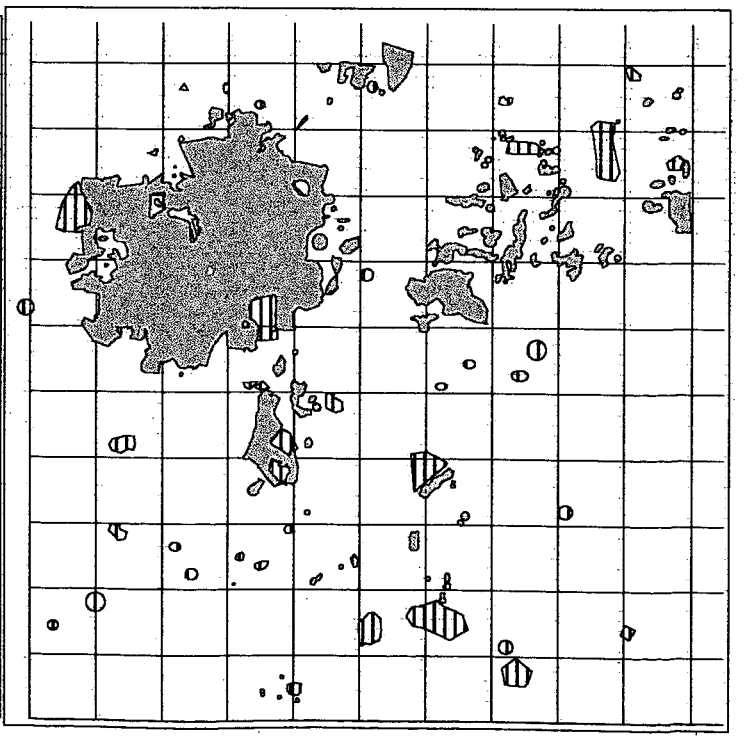
Fig. 2a Plot 102 Chataqua Park: change in shapes of *Andropogon gerardii* clones 1996-1999. Striped: rocks.



1996

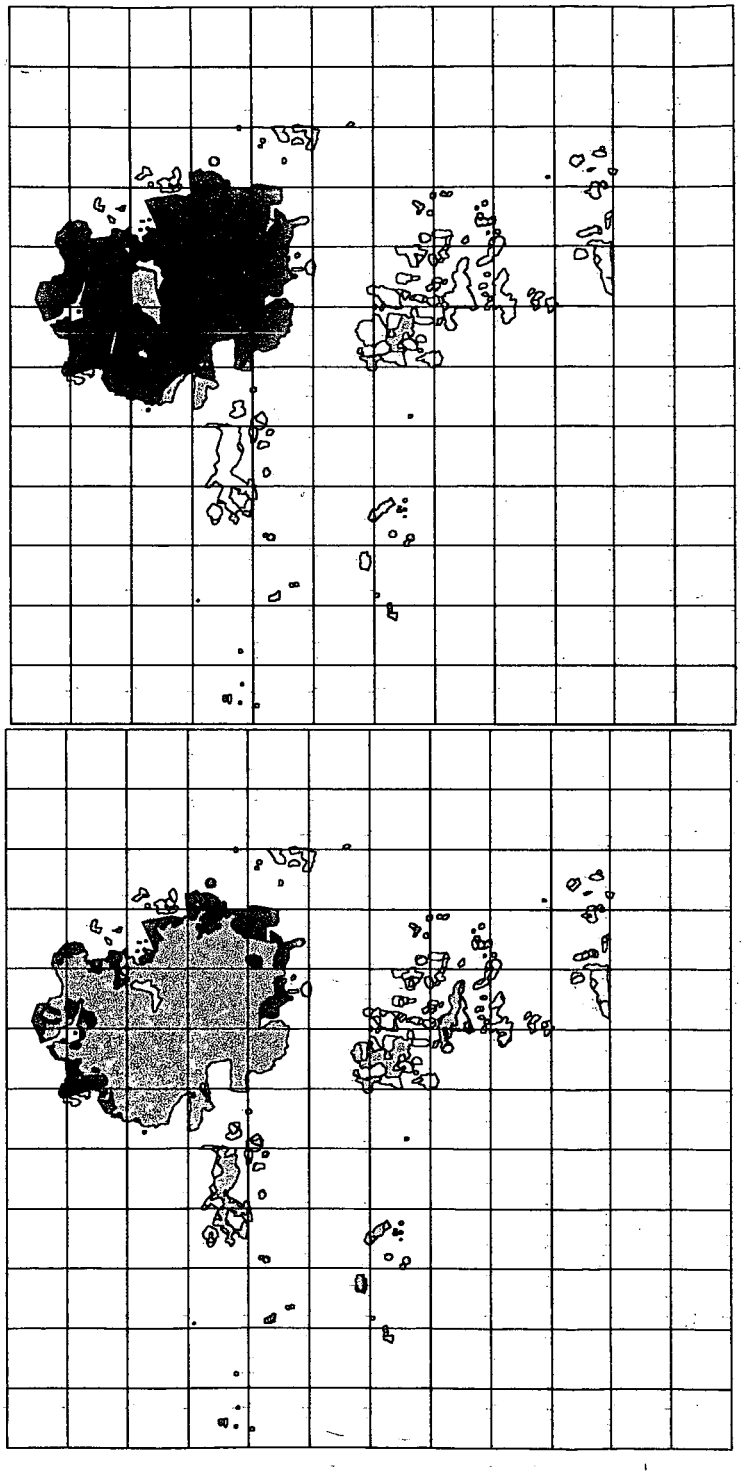


1998



1999

Fig. 2b Change 1995-9 by cytotype, by superimposing first 1999 on 1996 to show where the clone has decreased in area, and then 1996 on 1999 to show where the plant has expanded. Blue: 60 chromosomes (light 1995, dark 1999); purple 61-89 chromosomes (light 1995; dark 1999); red 90 chromosomes (light 1995; dark 1999).



Plot 102 Chataqua Park
Andropogon gerardii

Seed production was also determined for each plant each year. Andropogon gerardii produces many unfilled caryopses (single-seeded fruits). That data was collected but is not presented here. Of more importance is the comparison of good (= filled, viable) seeds produced by each cytotype (Table 6). There is no consistent significant effect of cytotype on seed production (analysis of variance, PC-SAS through 1998, Table 7). This will be redone to include 1999 when all the 1999 seeds have been counted.

The data also indicates the important but transient impact of burning on *Andropogon gerardii*. Plot 102 was burned in spring, 1996, plot 57 is spring 1997 and plot 58 in 1998. The effect of burning on the first two is quite dramatic, but gone the following year. Flowering by *A. gerardii* appeared to be normally stimulated at plot 58, but the plants within the study area showed no measurable effect.

Table 6. Mean Number of Filled (Viable) Seeds per Plant 1995-9.

	1995		1996		1997		1998		1999	
Plot	60 mean (std dev)	90 mean (std dev)	60 mean (std dev)	90 mean (std dev)	60 mean (std dev)	90 mean (std dev)	60 mean (std dev)	90 mean (std dev)	60 mean (std dev)	90 mean (std dev)
28			0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.9 (3.5)	0.0 (0)	3.11 (4.4)	0 (0)
36	2.7 (6.5)	1.4 (3.4)	78.3 (102.6)	60.9 (123.2)	0 (0)	0 (0)	76.0 (331.2)	32.3 (110.0)	*	*
45	13.9 (17.5)	1.1 (1.5)	18.8 (37.6)	688.7 (1487.6)	0.7 (1.4)	0.1 (0.3)	16.9 (58.9)	52.0 (123.5)	*	*
52	3.6 (5.1)	3.4 (7.5)	0.2 (0.6)	0.2 (0.5)	1.2 (0.4)	0.0 (0)	2.7 (8.2)	0.2 (0.4)	*	*
57			8.2 (10.7)	0.1 (0.4)	47.2 -	1.8 (3.0)	0.0 (0)	0.11 (0.33)	7.0 (8.7)	12.6 (9.3)
58	0.0 (0)	0.0 (0)	0.2 (0.6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	*	*
61			0.0 (0)	0.0 (0)	0.03 (0.2)	0 (0)	2.0 (4.6)	1.2 (3.4)	*	*
102			2143.7 -	45.7 (118.6)	0 -	0 (0)	0 -	0 (0)	0 -	0.3 (0.6)

- Incompletely analysed

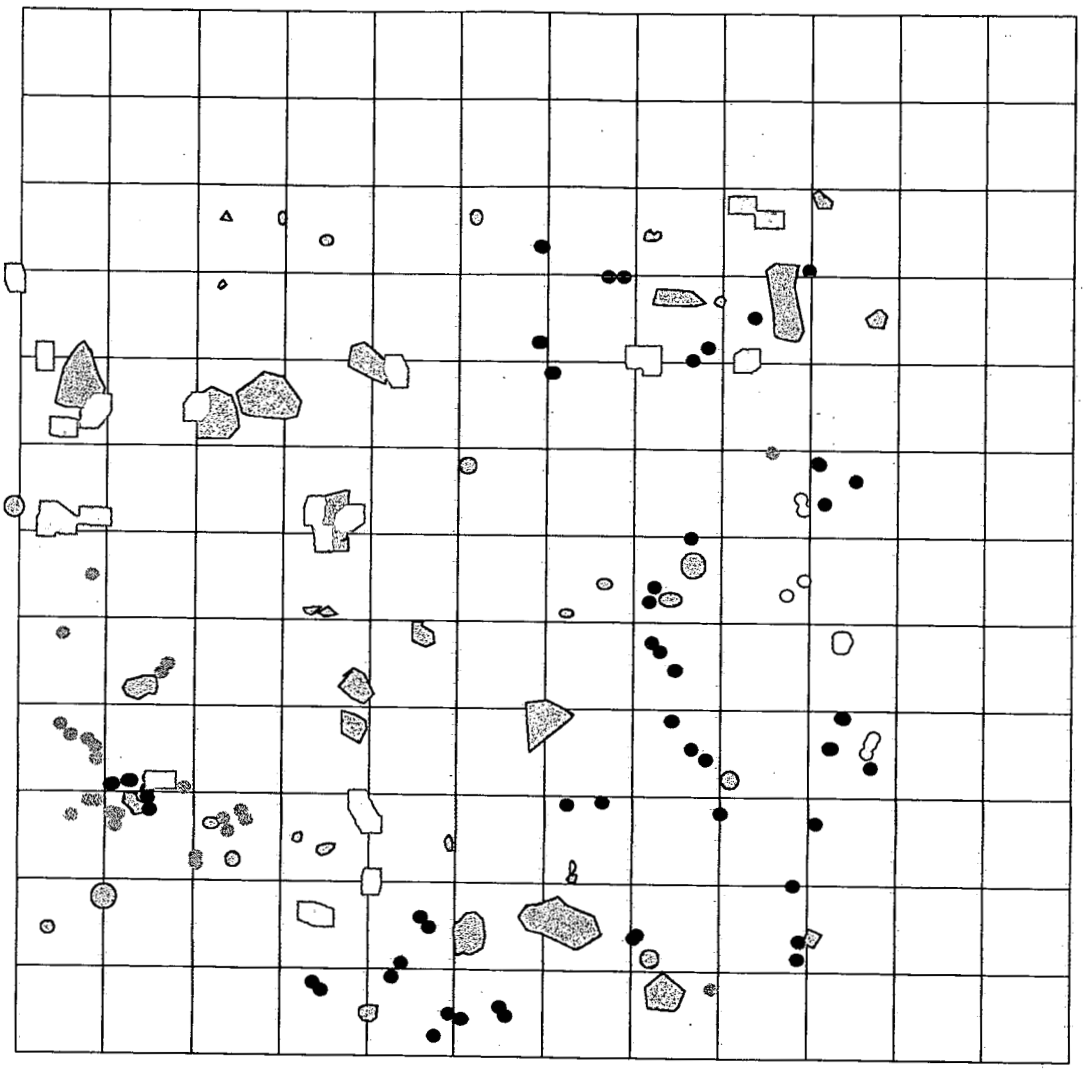
Table 7. Analysis of Variance of Seed Production by Chromosome, and Plot

1996	DF	SS	F	P
Chromosomes	1	81863	7.5	.007
Plot	4	857727	1.8	.12
Chrom X Plot	11	7772730	6.1	<.001
Residual	195	22605836		
1997	DF	SS	F	P
Chromosomes	1	405	.66	.42
Plot	4	414	.67	.61
Chrom X Plot	11	272	.44	.94
Residual	228	616		
1998	DF	SS	F	P
Chromosomes	1	20060	.38	.54
Plot	4	59658	.28	.61
Chrom X Plot	11	215868	.37	.96
Residual	164	8611361		

2) and 3) Demography of Open Space Plants

For this part of the study, the data exists but has not yet been adequately analyzed. A representation is given in Figure 3.

Fig. 3. Species in Plot 102 (Chataqua Park). *Liatris punctata* blue (1998 light, 1999 dark), *Lupinus argenteus* black (1998 light, 1999 dark), *Opuntia macrorhiza* red 1998. Rocks – gold.*Liatris* is unchanged from 1998, *Lupinus* showed substantial shift (for about 20% the 1999 dot covers the 1998 dot).



Three species were not found in 1999, having been marked in 1998. Those were *Talinum parviflorum* (Portulacaceae), *Sisyrinchium montanum* (Iridaceae) and *Grindelia squarrosa* (Asteraceae).

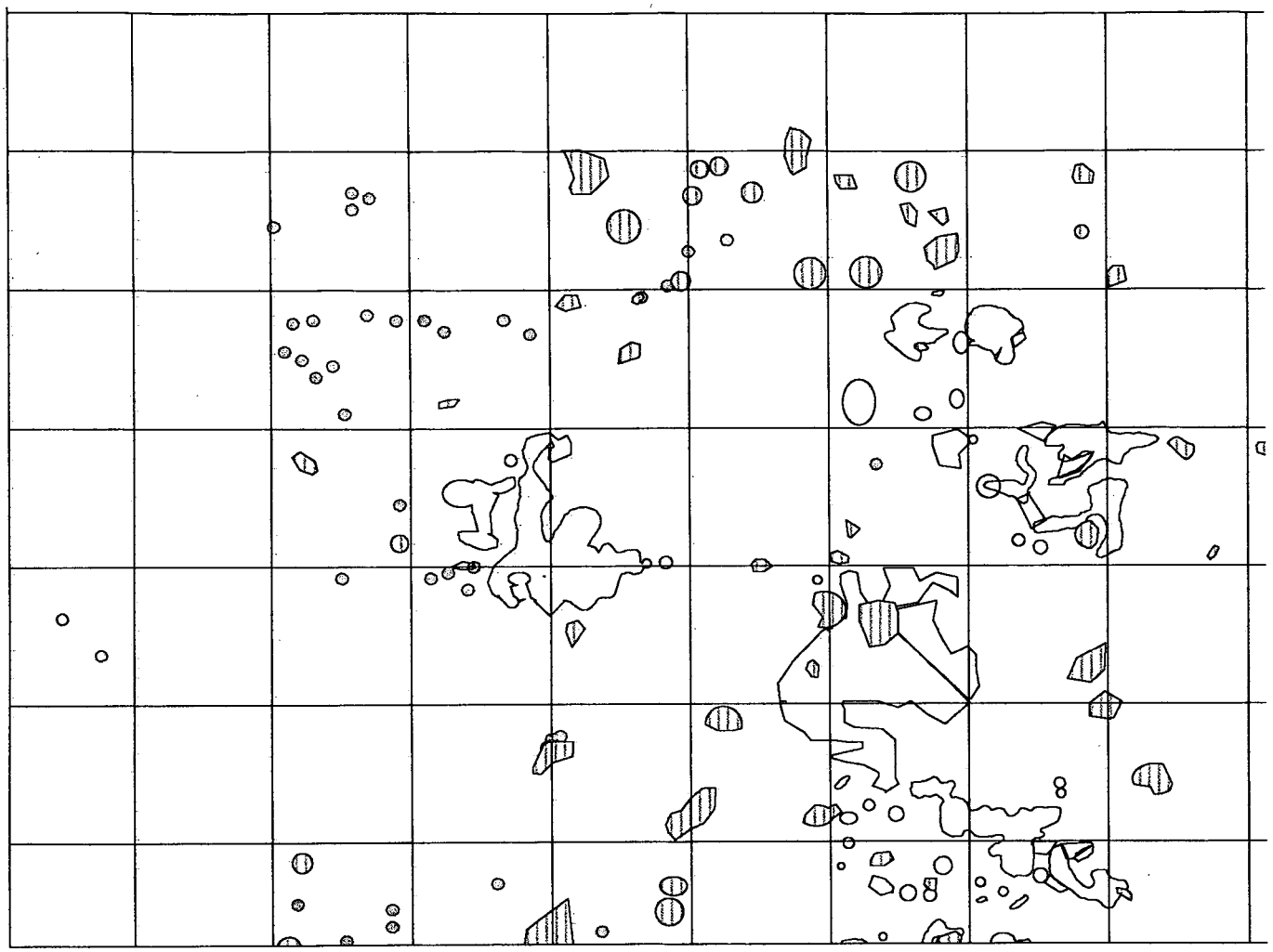
Talinum was known from six individuals at the north end of plot 57 (OCS grazing exclusion). Although not uncommon in Boulder County (Weber 1972 and pers. comm.), *Talinum* species are dramatically under-observed in the Great Plains (Great Plains Flora Association 1986). Probably a short-lived perennial, it will be interesting to see when it reappears.

Sisyrinchium montanum was quite abundant in plot 58 (grazing exclosure by Sans Souci Trailer Park) in 1998. In 1999 I could not find a single individual flowering, and made no positive identification of the foliage, although that is more problematic. (Fig. 4)

Grindelia squarrosa was known from two plants in plot 61 (Flat Irons Vista). The death of two individuals in a plot the same year is not especially notable.

Other species have presumably changed in abundance between 1998 and 1999, the shorter lived species more dramatically than longer-lived species, on the whole (Fig. 3) This information will be available when the analysis is complete.

Fig. 4. *Sisyrinchium montanum* (Iridaceae) at plot 58 in 1998. None were found in 1999.



DISCUSSION

Data collection and analysis is in progress. The *Andropogon gerardii* populations are not changing much: maps from 1995 are pretty predictive of 1999 (Figure 1, 2). Seed production is highly variable: the effect of burning strongly marked, but transitory (Table 6). No significant differences were found in frequency of good seeds produced by the three polyploid levels.

Other species studied offer interesting insights into population dynamics of the Open Space grasslands, but the data is not yet fully entered into the computer and needs to be analyzed. This will be an important data set when fully entered and analyzed. I expect have it entered before spring.

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Poster - Ecological Society of America Meeting, Spokane WA. Aug 1999

Comparison of Co-occurring Big Bluestem Plants with 60 and 90 Chromosomes

Kathleen H. Keeler, School of Biological Sciences, University of Nebraska-Lincoln, Lincoln NE 68588-0118

ABSTRACT

Big bluestem, *Andropogon gerardii*, the dominant grass of the tallgrass prairie biome, has two common ploidy levels, with 60 and 90 chromosomes, which are frequently found in plants of the same population. Over a four year period this study compared the size, expansion and seed production of permanently marked plants of both ploidy levels in relict tallgrass prairie in Boulder CO. 90 chromosome plants were bigger and flowered more, but had significantly lower frequencies of viable seed. Clonal expansion was not significantly different among the cytotypes. While the 90 chromosome cytotype can be seen as contributing almost as many viable seeds to the population as 60's at present, since 60's breed true and 90's make gametes with a mean of 45 chromosomes, 90's are almost never recruited into the population. 90's apparently established many years ago and are only very slowly lost. Populations of this dominant grass have a substantial chromosome-based genetic load and are in very long term equilibrium.

INTRODUCTION

Polyploidy within local populations is widespread (Stebbins 1971, Lewis 1980, Keeler 1997) but is poorly understood. This study compares two cytotypes of the same species *in situ*.

Andropogon gerardii Vitman (big bluestem) was the dominant grass of the tallgrass prairie (e.g. Weaver and Fitzpatrick 1934). Populations of big bluestem often contain two polyploid morphs (cytotypes): hexaploid, $2n = 6x = 60$ chromosomes and enneaploid $2n = 9x = 90$ chromosomes (Keeler 1990, Norrmann et al. 1997). In NE, KS, and CO prairies, these two cytotypes are often in nearly equal proportions. Intermediate cytotypes are present but rare (Keeler 1992, Keeler and Davis 1999).

Both cytotypes are obligately outcrossing (Norrmann et al. 1997). When crossed, they produce viable offspring with intermediate chromosome numbers (Norrmann et al. 1997, Norrmann and Keeler unpub. data).

The two cytotypes cannot readily be distinguished morphologically.

This research compared the cytotypes *in situ* to evaluate their relative fitnesses under natural conditions.

METHODS AND SITES

PLOTS. The plots are in Boulder CO (Table 1). This is tallgrass prairie (Livingstone 1951) plus the advantage of gaps between *A. gerardii* plants at some sites, facilitating the identification of individuals. The permanent plots have various management regimes, to look at cytotypic effects, not response to management.

CYTOTYPE DETERMINATION. Cytotypes were determined by flow cytometry (Keeler et al. 1987, Norrmann et al. 1997). Fresh leaf material was sent by express mail to Dr. K. Arumuganathan, University of Nebraska Flow Cytometry Laboratory for analysis. We stained isolated nuclei with propidium iodide. Propidium iodide specifically stains for DNA, so the amount of stained material (nuclear DNA) is directly proportional to the number of chromosomes (Keeler et al. 1987, Norrmann et al. 1997).

MEASUREMENTS. The mapped plants were compared for clone area, plant production as indicated by height and leaf size, and seed production (Tables 2-3). Clone area and change in clone area were determined digitized maps (ArcView (ESRI 1997). Foliage height and width were measured on the largest dimension available.

For seed mass, all caryopses were weighed to the nearest 0.01 g. Good seed was determined from a sample of 100 (or counted were fewer) where seed coat was removed to see if a filled seed was inside. Virtually all full sized filled seeds will germinate. For large seed biomasses the percent good seed was calculated from the sample.

Statistical analysis used PC-SAS (1996) GLM program.

RESULTS

TABLE 1: Distribution of Cytotypes. Natural populations varied from a majority of 60 chromosome cytotypes to a majority of 90 's. Intermediate values were rare.

TABLE 2: Clones. Size: Hexaploid (60) clones were smaller than enneaploids (90s) but not significantly (Wilcoxon signed rank for hexaploids vs enneaploids, $Z=1.70$, $p = 0.089$. Intermediate cytotypes are significantly different, van der Waerden $p = 0.02$).
Change in Clone Size: Changes between 1996-8 did not differ significantly between cytotypes (Kruskal-Wallis test (with intermediates), chisq approx = 0.28, p =0.87, Wilcoxon of 60 vs 90, p =0.5). Dividing change in size for initial sizewas also not significant (data not shown, p=0.94)

TABLE 3. Comparisons. Seed Production: Hexaploids (60s) produced fewer seeds / plant but not significantly (repeated measures anova: cytotype not significant, alone or in relation to plot or year (p's 0.39 - 0.84)).
Viable Seed Production: Differences between cytotypes were not significant (repeated measures anova: p's > 0.21). Seed production/area likewise was not significantly different (not shown).
Seedlings: Mean number of seedlings/gram of caryopsis biomass is much higher for hexaploids (60s). In 5 samples of 1 gm caryopses from 6 hexaploids, mean # seedlings = 35.7 (se 35.7) for 8 enneaploids = 8.7 (se = 8.2). These means are significantly different, Mann-Whitney U, p = 0.0011. However, when a good seed was present, germination rates did not differ: 57 of 101 good (round, brown, smooth) seeds from hexaploids germinated, 6 of 11 good seeds of enneaploids germinated ($X^2 = 0.23$, df = 110, ns.)

Contrary to expectations from meiotic difficulties, enneaploids are often large individuals producing numerous seeds.
Leaf Characters. Hexaploids (60s) were significantly smaller than enneaploids in every test (t-test, p<0.011).

TABLE 4. Cytotypes of Progeny. In these mixed populations, seeds have varied cytotypes. In a sample from 1998, while hexaploid "mothers" produced progeny of which a majority were hexaploid, enneaploid "mothers" produced only 1 enneaploid in 10 germinating seedlings. Distribution of cytotypes in the population is not at equilibrium.

Table 1. Distribution of *Andropogon gerardii* Cytotypes in Boulder CO Plots

Plot		Hexaploid (60 chromosomes)	Enneaploid (90)	Intermediate (61-89)	Total
36	wet	21	14	1	36
58	wet	13	7	1	21
45	mesic	50	13	8	71
102	mesic	1	17	0	18
28	dry	17	7	0	24
52	dry	18	5	2	25
57	dry	8	9	0	17
61	dry	30	8	2	40
	Totals (%)	158 (62.7)	80 (31.7)	14 (5.6)	252

Table 2. Comparison of *Andropogon gerardii* Clones
See Results for Statistics

	Hexaploid (60)			Enneaploid (90)			Intermediate (61-89)		
	Mean	SD	N	Mean	SD	N	Mean	SD	
Initial Clone Size	2365.5	8082.5	152	2798.7	5988.4	88	2766.8	6678.6	
Change in Clone Area 1996-8	765.1	2161.5	151	497.3	3224.0	87	451.8	2600.0	

Table 3. Comparison of Cytotypes: Seed Production, Leaf Characters.
See Results for Statistics.

	Yr	Hexaploid (60) Mean	SD	N	Enneaploid (90) Mean	SD	N	Intermediate (61-89) Mean	SD	N
No.Seeds	96	180.5	898.0	135	1878.8	4977.3	71	77.9	141.9	11
Per	97	116.6	830.1	145	499.9	1184.9	75	39.0	86.0	14
Plant	98	148.1	665.3	157	895.0	1881.7	79	196.9	568.7	14
Good	96	27.8	188.1	134	124.8	816.9	71	12.2	35.8	11
Seeds /	97	3.7	31.9	149	1.0	3.9	75	1.0	3.9	14
Plant	98	31.2	251.1	158	20.9	100.1	79	5.5	17.2	14
Foliage	95	28.1	8.5	77	39.2	11.3	28	22.2	7.8	6
Height	96	24.3	6.8	71	28.2	8.3	46	20.3	7.4	7
Leaf Width	98	6.4	1.8	74	7.3	1.5	46	5.8	1.2	7

Table 4. Progeny Raised from Seeds Collected in Boulder Plots, 1998. Cytotype, 1998 seed crop: DNA content given, in ascending order. 60 chromosomes DNA < 6.5-7.0 picograms DNA (blue), Intermediate c. 7-8 pg DNA (purple), 90 chromosomes > 8 or 8.5 pg DNA (red).

Plant	45-144	45-037	45-115	45-119	45-136	45-248	45-137
Parental DNA (chrom #)	5.83 (60)	6.09 (60)	6.07 (60)	5.85 (60)	5.8 (60)	9.42 (90)	9.37 (90)
Progeny DNA							
	6.58	5.73	5.51	-	5.02	5.86	6.06
	6.91	5.75	5.52	5.23	5.16	5.86	6.27
	7.09	5.92	5.60	5.36	5.26	5.89	6.59
	7.19	5.94	5.64	5.40	5.29	6.26	6.63
	7.29	5.99	5.73	5.59	5.31	6.31	6.82
	7.31	6.02	5.85	5.70	5.38	7.36	7.06
	7.35	6.13	6.00	5.70	5.45	7.36	7.36
	7.50	6.19	6.00	5.78	5.46	7.64	7.57
	7.57	6.21	6.09	5.81	5.6	7.7	7.70
	8.07	6.33	6.34	6.69	6.75	8.18	8.66

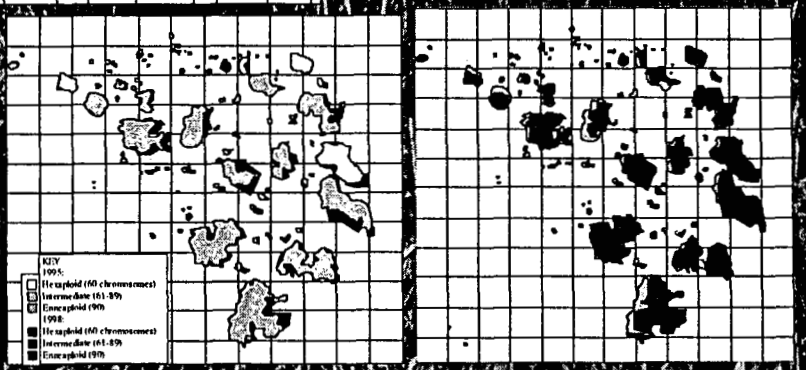

Figure 1. Plot 45 1995-1998 Light colors are 1995, dark 1998. A. Expansion. 1998 clones under 1995. B. Contraction. 1995 clones under 1998.

DISCUSSION

Enneaploids (90s) have markedly lower fertility than hexaploids but are large plants and quite numerous. Enneaploids do not spread faster than hexaploids (Table 2). They compensate for poor quality seeds by producing large numbers (Table 3). In present populations enneaploids are contributing substantially to population dynamics.

This cannot be a stable situation. 1) Relative fitness of seeds favors hexaploids dramatically. Any environmental change which decreases total seed set will favor hexaploids. 2) Hexaploids regularly produce hexaploid progeny. Enneaploids produce chiefly aneuploid progeny, with occasional euploids (Table 4). Even in an all enneaploid population, high enneaploid frequencies would not be maintained.

I hypothesize that this polyploid complex arose when the population was reduced to a few individuals e.g. during periods of drought. Isolated hexaploids produced unreduced gametes with circumvented the incompatibility system and allowed seed production. In the absence of competition (e.g., at the end of a drought) those enneaploid ($2n$ gamete (60) + n gamete (30) plants survived, and have maintained themselves vegetatively a long time. This model is consistent with the data and research to verify it is in progress.

If this model is correct, if stable conditions are maintained, the enneaploids will be gradually lost and the populations become largely or entirely hexaploid. It suggests the possibility that although he enneaploids can be considered unfit mutants that are gradually eliminated, the mechanism of producing unreduced gametes to allow isolated self-incompatible individuals to reproduce may be adaptive. It also suggests long-term disequilibrium in the dynamics of this polyploid complex.

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