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Impact of Intraspecific Polyploidy in Andropogon gerardii (Poaceae) Populations

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ABSTRACT.—*Andropogon gerardii* populations are comprised of two (or more) polyploid forms over much of the range of the species. To understand the impact of intraspecific polyploidy, polyploid cytotypes were compared over 4 y in native grasslands in Boulder, Colorado. Boulder *A. gerardii* populations averaged 59.6% hexaploids (60 chromosomes), 35.3% enneaploids (90 chromosomes) and 5.1% intermediate (aneuploid) chromosome numbers using flow cytometry to infer chromosome numbers. Neither mean clone area nor mean annual change in clone area differed significantly between ploidy levels. Hexaploid clones produced significantly more viable seeds than enneaploids. Enneaploids are not replacing themselves, whether that is measured absolutely or relative to hexaploids. Enneaploid reproductive effort was greater than hexaploid reproductive effort in some years and they produce substantial numbers of good seeds, but those seeds rarely have enneaploid cytotypes. The populations should eventually become entirely hexaploid. In the current populations, however, enneaploids are big, vigorous and fertile individuals.

INTRODUCTION

Polyploidy within populations of a single species is relatively common (Lewis, 1980; Lumaret, 1988a; Keeler, 1997). Theoretical considerations suggest that mixed ploidy populations should be unstable, eventually fixing one cytotype (Fowler and Levin, 1984; Bever and Felber, 1993; Rodríguez, 1996a, b; Ramsey and Schemske, 1998). Low fertility of hybrids between the ploidy levels selects against establishment of new polyploids since potential mates for a new polyploid are not polyploid. Even when two polyploids are equally common and have equal fitness, models predict the elimination of one (Fowler and Levin, 1984; Husband, 2000). Nevertheless, species with multiple ploidy levels in the same population are not uncommon. Studies of intrapopulation polyploidy have generally, but not always, shown small-scale microhabitat differentiation of the cytotypes (Lewis, 1976; Felber-Girard *et al.*, 1996; Husband and Schemske, 1998).

The pattern in grasses is similar to the pattern in Angiosperms generally. In the best-studied system, *Dactylis glomerata*, there is gene flow between diploids and tetraploids by way of triploids (Zohary and Nur, 1959; Lumaret, 1988b), but in populations where several cytotypes were present, fine-scale habitat differentiation was detected (Lumaret and Barrientos, 1990). *Panicum virgatum*, a dominant of the tallgrass prairie, has two widespread races which usually have different ploidy levels (Porter, 1966). In addition, there is a polyploid series within each race and ploidy levels from diploid to dodecaploid ($12x$) can co-occur (Nielsen, 1944; Eberhart and Newell, 1959; McMillan, 1959; Porter, 1966; Hultquist *et al.*, 1997). An exhaustive study by Nielsen (1947) found no difference between diploids, tetraploids and hexaploids for agronomically important traits. Other grasses in which intraspecific polyploidy has been studied include *Anthoxanthum odoratum* (Hedberg, 1967), *Paspalum* spp. (Quarín and Fernández, 1982; Norrmann *et al.*, 1989) and *Deschampsia caespitosa* (Rothera and Davy, 1986).

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Andropogon gerardii Vitman, Poaceae, was the dominant plant of the tallgrass prairie region (Weaver and Fitzpatrick, 1934). It has two common cytotypes, hexaploid ($2n=6x=60$ chromosomes) and enneaploid ($2n = 9x = 90$ chromosomes). Plants are obligately out-crossing (Law and Anderson, 1940; Norrmann *et al.*, 1997; McKone *et al.*, 1998) and the cytotypes are interfertile (Norrmann *et al.*, 1997; Norrmann and Keeler, 2003). In the eastern tallgrass prairie, enneaploids are rare, but present (Keeler, 1990). In the western part of the tallgrass prairie region, the distribution of cytotypes is approximately 55% hexaploids, 40% enneaploids and 5% intermediate cytotypes (Keeler *et al.*, 1987; Keeler, 1990, 1992).

The hexaploid and enneaploid are related to each other as if they were diploid and triploid. Plants with intermediate cytotypes (aneuploids with chromosome numbers 61–89) are produced in controlled crosses between hexaploids and enneaploids (Norrmann *et al.*, 1997; Norrmann and Keeler, 2003) and occur at frequencies of 0–7% in natural populations (Keeler, 1992).

Meiosis is regular in hexaploids and highly irregular in enneaploids and aneuploids (Riley and Vogel, 1982; Norrmann *et al.*, 1997; Norrmann and Keeler, 2003). Consequently, hexaploids produce a higher frequency of viable seeds. Under common garden conditions, enneaploid plants grow bigger than hexaploids, although visual identification of ploidy is unreliable (Keeler and Davis, 1999). Populations frequently include numerous plants of both common cytotypes (Keeler, 1992). No statistically significant relationship to environment or microhabitat has been detected (Keeler, 1990, 1992).

This study was undertaken to compare *Andropogon gerardii* cytotypes under natural conditions, as advocated by Lumaret (1988a). Flow cytometry allows determining cytotypes of plants in situ (Keeler *et al.*, 1987; Michaelson *et al.*, 1991). The study was conducted in the City of Boulder Open Space and Mountain Parks because in these tallgrass prairies, on some sites, *A. gerardii* plants are sufficiently scattered to allow distinguishing individuals. Initially, hexaploids were expected to be so much more fit than enneaploids that the question was whether enneaploids made any contribution at all to the population. Thus, this study was initiated to determine if enneaploid plants had increased growth or survival in situ that would explain their presence despite their low viable seed production.

MATERIALS AND METHODS

The plants studied are in permanent plots on City of Boulder Open Space and Mountain Parks land in Boulder, Colorado. The plots are in tallgrass prairie (Livingston, 1952; Branson *et al.*, 1965; Bock and Bock, 1998). Plots were located on or near Jane and Carl Bock's permanent markers: my plot numbers conform to their system. Additional information is available from the City of Boulder Open Space and Mountain Parks and in Bennett (1997). The plots include a range of soil types and management treatments. Since *Andropogon* is very responsive to growing conditions (*e.g.,* Svejcar, 1990), diverse sites allow comparison of the cytotypes, not the land management. Four plots were established in 1995, the remainder in 1996: data reported here are from 1996–1999.

Plots were originally 10×10 m in area and contained from 22 to 268 plants of *Andropogon gerardii*. To improve comparisons between plots, plot 45, the densest population, was reduced in area to 80 sq. m., the rest remained at 100 sq. m.

Plants were defined based on gaps separating clumps of *Andropogon gerardii*. In the populations studied, *A. gerardii* forms distinct patches and interpatch distances are in most cases several times the average annual clone expansion distance (0.33 cm^2, Fig. 1). Comparison of the height, color, shape and phenology of plants confirmed assignment to a clone.

Cytotypes were determined using flow cytometry: fresh leaves were sent to the Flow Cytometry Facility at the University of Nebraska-Lincoln where total nuclear DNA content
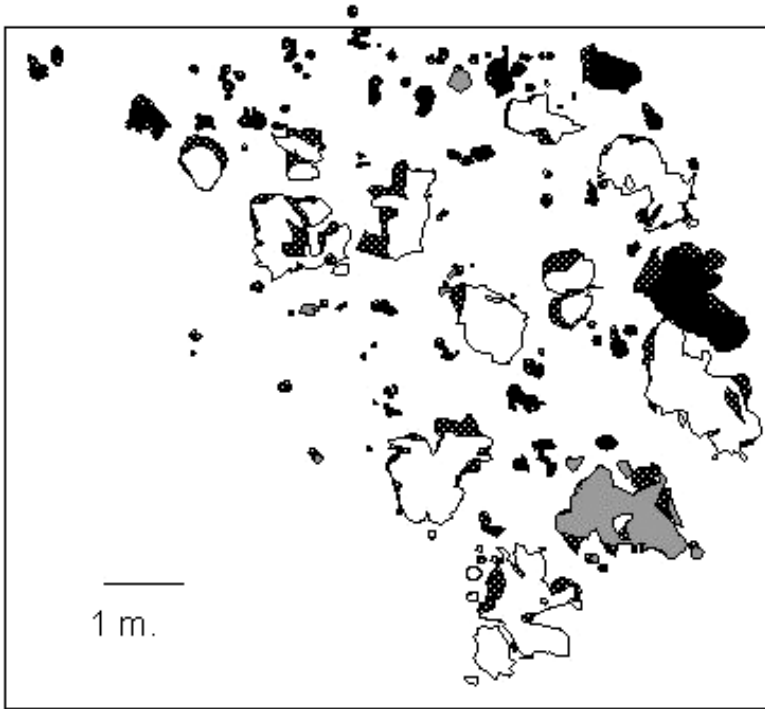
FIG. 1.—Map of Plot 45, highest density plot, showing natural gaps between plants and change between 1995 (dark stipple) and 1999 (black/gray/white). 60 chromosomes: black, intermediate: gray, 90 chromosomes, white

was determined under the direction of K. Arumuganathan (method of Arumuganathan and Earle, 1991). Propidum iodide was the stain and barley the internal standard. Under these conditions hexaploid plants give a mean of 5.93 pg DNA (±0.52 95% cl) per nucleus and enneaploid plants averaged 8.92 pg DNA/nucleus (±0.48) (Keeler *et al.*, 1987; Norrmann *et al.*, 1997). Plants with DNA contents between those were taken to have intermediate chromosome numbers, as seen in crossing studies (Norrmann *et al.*, 1989; Norrmann and Keeler, 2003) and behave as aneuploids. Plants in this study that were retested 1 to 4 y apart differed in mean DNA contents by 0.08 to 0.25 pg DNA, or 1–4% (N=6), which is consistent with previous work on this species (Keeler, 1992).

A few plants in the areas studied were omitted because they were so small that removing a leaf for flow cytometry might have killed them; they are excluded from analysis.

Andropogon gerardii plants in the marked area were mapped to the nearest cm. Every year the following information was collected for each plant: map position, number of seeds produced, weight of seeds produced, number and frequency of filled seeds. Clone area and change in clone area were determined from plot maps digitized into the geographic information system program ArcView (ESRI, 1997).

Several morphological characters were compared. Plant size generally increases with ploidy level, as was previously seen in *Andropogon gerardii* (Keeler and Davis, 1999). This was considered in this population by measuring the maximum leaf length and leaf width.

To compare reproductive effort and success, the number of flowering stalks, number of racemes and number and mass of fertile and sterile spikelets (containing the single-seeded fruits and the seeds) produced were determined. These measures were found to correlate tightly to each other (see Results). All spikelets produced by marked plants were gathered at the end of the growing season and weighed to the nearest 0.01 g.

Andropogon gerardii frequently produces large numbers of fertile spikelets that do not contain a seed (Masters *et al.*, 1993). Thus, number and percent of seeds in the spikelets were carefully determined. First, fertile spikelet mass was weighed and the number of fertile spikelets counted. If there were fewer than 100 on the plant, all spikelets were checked for seeds: each was opened to see if a seed was inside. Most full-sized seeds germinate (see below). "Good seeds" are thus oval, plump and brown. For large spikelet masses, the number of seeds produced by the plant was estimated by multiplying the frequency of good seeds in the sample of 100 by the total number of fertile spikelets counted from that plant. Small or broken seeds were counted separately. Plump but short seeds were considered good, flat but long seeds were not. Seed production was low enough that when in doubt I called it good. Where kernel smuts (*Sphacelotheca occidentalis*) occurred in the seed crop, those were counted separately as well. The total number of viable seeds produced by the plant equalled the sum of good seeds plus broken seeds (presumably killed by herbivores), plus the kernel smuts, since those require seed (Snetselaar and Tiffany, 1990).

Andropogon gerardii sometimes produces seeds from the "sterile spikelets," the pedicellate spikelets, that are paired with the perfect "fertile" sessile spikelets along the raceme (Boe *et al.*, 1983; Springer, 1991). Therefore, 100 pedicellate spikelets per plant were also checked for seeds. Across all plots, seeds were present in an average of 1 in 1.6×10^4 spikelets and, of those, 3.8% were contributed by pedicellate spikelets. Because they were so rare, the few seeds in pedicellate spikelets were simply included in the number of viable seeds. Percent viable seeds, thus, represents seeds from sterile plus fertile spikelets divided by number of fertile spikelets checked, times 100.

The data do not have a normal distribution: each year many plants did not send up a flower stalk and most plants produced no viable seeds. The relationship of seed production to ploidy was tested by coding flowering attempts as 0 or 1 and comparing in a contingency table. The same approach was used to compare the incidence of successful seed production between ploidy levels: seeds in any of the 4 y was scored as 1, none at all as 0.

Viability of seeds was tested in two ways and compared between parental ploidy levels. First, individual, apparently good, field-collected seeds were stored at room temperature all winter and planted in standard soil in the greenhouse in April 1999. Number and percent germination were compared by maternal cytotype. Second, 1 g. samples of unsorted spikelets were placed on soil in the greenhouse. The number of seedlings that emerged was compared by maternal cytotype. All available material was used and more enneaploids than hexaploids produced large numbers of spikelets that year. In 1999 seed production was too low to repeat these experiments. The distribution of cytotypes among sibships produced in the germination experiments just described was determined by measuring the nuclear DNA content using flow cytometry. I tested the first 10 seedlings in the pot, independent of seedling vigor.

Areas, change in area and seed production measures were compared between ploidy levels using repeated measures ANOVA, after square root transformation to normalize the distribution. The basic model looked at ploidy and year as fixed effects and treated plant and plot as random (SAS Mixed program SAS Institute Inc., 1999). Plant was the unit of observation and as noted above, plot was treated as random in order to focus on the effects of polyploidy. Contingency table analyses used Fisher's Exact Test. Mean number of

TABLE 1.—Distribution of *Andropogon gerardii* cytotypes in Boulder CO plots in 1996

Plot	Moisture	Grazing	Other	Hexaploid (60 chromosomes) (%)	Intermediate (61–89) (%)	Enneaploid (90) (%)	Total
36	wet	winter	Floods in spring	22 (48.9)	1 (2.2)	22 (48.9)	45
58	wet	ungrazed	Floods in spring	13 (54.2)	1 (4.1)	10 (41.7)	24
45	mesic	winter	Spring irrigated	58 (72.5)	8 (10.0)	14 (17.5)	80
102	mesic	ungrazed	Burned 96	1 (6.2)	0	15 (93.8)	16
28	dry	summer		16 (72.7)	0	6 (27.7)	22
52	dry	winter		15 (60.0)	3 (12.0)	7 (28.0)	25
57	dry	ungrazed	Burned 97	9 (40.9)	0	13 (59.1)	22
61	dry	summer		30 (73.2)	1 (2.4)	10 (24.4)	41
	Totals (%)			164 (59.6)	14 (5.1)	97 (35.3)	275

seedlings per maternal parent was compared with Mann-Whitney U test. Statistical analysis used the StatView 5.0 and PC SAS programs (SAS Institute Inc., 1999).

RESULTS

A total of 275 plants of *Andropogon gerardii* were mapped and cytotyped within eight plots in the City of Boulder Open Space and Mountain Parks, Boulder, Colorado. Of those, 164 (59.6%) were hexaploid, 14 (5.1%) had intermediate chromosome numbers and 97 (35.3%) were enneaploids (Table 1). Frequency of hexaploids within plots ranged from 6–73% (Table 1). This distribution is similar to the distribution of cytotypes at Konza Prairie, Manhattan, Kansas, both in the overall mean and in the wide range of variation between plots (Keeler, 1992).

One additional plot [Bocks' Plot 7, *see* Bennett (1997)] contained only hexaploid plants, 18 of them. It has been omitted from further analysis because it could not be used to compare response of the different ploidy levels in a shared microhabitat. With the addition of this plot, the City of Boulder Open Space and Mountain Parks have 63.9% hexaploids, 4.6% intermediate cytotypes and 31.5% enneaploids.

Intermediate cytotypes are included throughout the analysis. However, they are rarely significantly different from the other cytotypes because they are highly variable. Intermediate cytotypes produced in controlled crosses were likewise sometimes very fertile and vigorous, sometimes very weak (Norrmann *et al.*, 1997; Norrmann and Keeler, 2003).

The effect of plot management on *Andropogon gerardii* was generally statistically significant. Controlled burning, winter grazing and irrigation all improved *A. gerardii* growth and flowering. These effects have been repeatedly documented (*e.g.,* Svejcar, 1990). No significant difference between cytotypes has been detected (Keeler, 1992; Keeler and Davis, 1999). These responses to burning and grazing occurred in the plots studied here, but they were not the focus of the study.

CLONE SIZE COMPARISONS

Clones ranged in area from 4.5 cm^2 to 99,380 cm^2. The mean clone area of hexaploid plants was 2910 cm^2 (SE 692), of intermediate cytotypes 2450 (SE 1302) and of enneaploids 3191 (SE 528). The mean areas of the different ploidy levels are not significantly different (repeated measures anova, including plot as a random variable $F = 1.37$, $P = 0.25$) and there was no significant effect of year or year*ploidy ($F = 0.06$, $P = 0.99$).
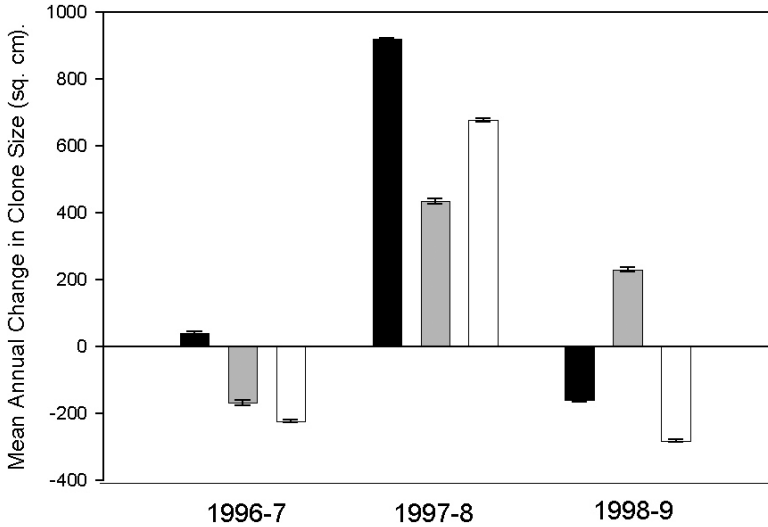
FIG. 2.—Mean annual change in area, in sq. cm. Hexaploid black (N = 146, 145, 143), intermediate gray (N = 12), enneaploid white (N = 91, 91, 90). Error bar is 1 SE

Mean annual change in area for hexaploids was 278 cm^2 (SE 137), intermediates 166 (SE 72) and enneaploids 69 (SE 54) (Fig. 2). Repeated measures ANOVA, including plot as a random variable, showed no significant effect of ploidy (F = 0.81, P = 0.47). Year had a significant effect of the size change (F = 13.4, P < 0.001), but the interaction with ploidy was not significant (F = 0.89, P = 0.47). When mean clone expansion was corrected for area of clone (Fig. 3), there was no significant effect of ploidy (ANOVA of normalized data, using plot as
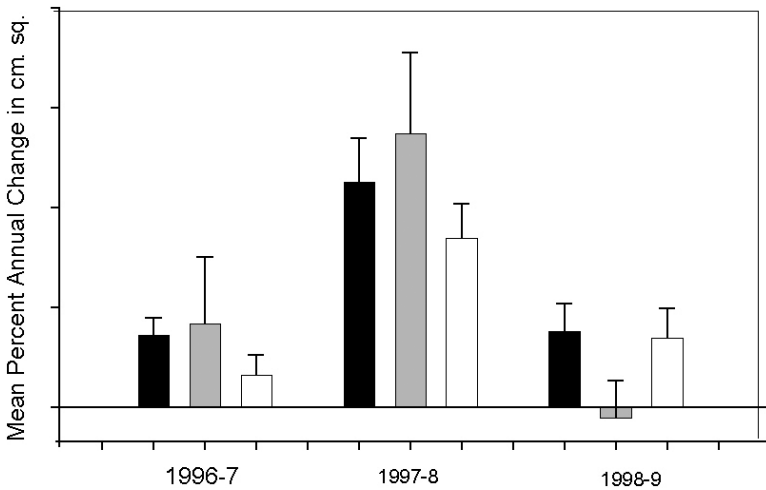

FIG. 3.—Mean percent change in clone size, as a function of initial clone size. Hexaploid black (N = 147), intermediate gray (N = 12), enneaploid white (N = 93). Error bar is 1 SE

a random variable) ($F_{ploidy} = 2.53$, P = 0.08, df = 2, 236, $F_{year} = 2.03$, $P_{year} = 0.13$, $F_{ploidy \times year} = 1.57$, P = 0.18).

VEGETATIVE COMPARISONS

Maximum leaf length and width of hexaploids were significantly smaller than those of enneaploids. Mean leaf length in 1995 was 28.1 cm (SE 0.3, N = 77) for hexaploids, for intermediates 22.2 (SE 1.1, N = 6) and for enneaploids 39.2 (SE 0.6, N = 28). The first two are significantly different from the last, but not from each other (*t*-test, P < 0.05). Repeating the comparison of leaf length in 1996 gave the same pattern, hexaploids 24.2 (SE 0.3, N = 72), intermediates 20.3 (SE 1.0, N = 7) and enneaploids 28.1 (SE 0.4, N = 47), hexaploids and intermediates significantly different from the enneaploids (and smaller), but not significantly different from each other (*t*-test, P < 0.05). Leaf widths likewise were smaller in hexaploids and intermediates, (hexaploid 6.3 mm, SE 0.2, N = 75, intermediates 5.9 SE 2.6, N = 7; enneaploids 7.2 SE 0.2, N = 47), significantly less than enneaploids, but not different from each other (*t*-test, P < 0.05).

REPRODUCTIVE COMPARISONS

Reproduction depends on both the effort invested in flowering and the viability of each seed and seedling.

The number of plants that produced a flower stalk at least once in the 4 y of observation did not differ significantly between cytotypes (Fisher's Exact Test, P = 0.27, N = 224).

Measures of flowering effort were tightly correlated. The number of flower stalks correlated positively and significantly to spikelet biomass ($r^2 = 0.86$, 0.98 and 0.91, for 1996, 1998 and 1999, respectively, in all cases P < 0.001). Likewise, number of spikelets counted per plant correlated significantly with the weight of the spikelet biomass ($r^2 = 0.96$, 0.94, 0.98 and 0.96 for 1996-9, P < 0.001 in all cases). Consequently, spikelet number is used in further analysis.

There was no significant effect of ploidy on number of spikelets per plant, after normalizing (Fig. 4, $F_{ploidy} = 2.16$, P = 0.12, df = 2, 365, $F_{ploidy \times year} = 1.09$, P = 0.41) although there is a significant effect of year on seed production ($F_{year} = 4.71$, P = 0.003).

Since many spikelets were empty (2.7% were filled, SD 4.0), and bigger plants tended to produce more spikelets ($r^2 = 0.39$, P < 0.001, N = 225), seeds (not spikelets) was compared between plants (Figs. 4, 5). Ploidy had a significant impact on percent good seeds (P < 0.001) as did year (P < 0.001). The ploidy × year interaction was nonsignificant (P = 0.81). Eliminating the zeros, the relationships were similar but weaker ($P_{ploidy} = 0.01$, $P_{year} = 0.01$, $P_{ploidy \times year} = 0.86$). (Correcting for area of each plant gave the same pattern $P_{ploidy} = 0.02$, $P_{year} < 0.001$, $P_{ploidy \times year} = 0.51$).

Some spikelets contained seed fragments. Broken seeds could be a result of herbivory or could represent seeds spontaneously aborted due to unbalanced genomes. Frequency of broken seeds was significantly associated with cytotype (repeated measures ANOVA, F = 4.75, P = 0.009). Hexaploids had the highest frequency of broken seeds (mean percent broken: hexaploids 1.07, SD 3.0, intermediate cytotypes 0.77, SD 2.1, enneaploids 0.49, SD 1.6). Since hexaploids have regular meiosis and usually the highest frequency of good seeds (Fig. 5), this is more likely due to herbivory than chromosomal abnormalities.

A few of the plants had kernel smuts during study period: 4, 4 and 5 in 1997–9, different plants each year. Thirteen were hexaploids and four enneaploids. The occurrence of kernel smuts did not differ between ploidy levels (Fisher's Exact Test, P > 0.99).

The mean number of seedlings emerging from a gram of spikelets was higher for hexaploids. In lots of 1 g of unsorted spikelets (thus, containing good and empty spikelets)
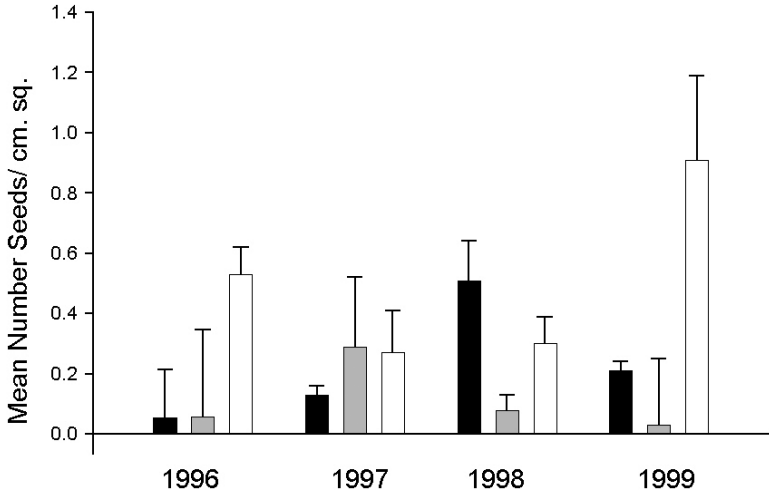
Fig. 4.—Mean number of seeds produced per sq. cm. per clone (±se). Hexaploid black (N = 147), intermediate gray (N = 12), enneaploid white (N = 93)

from 6 hexaploids (3–5 lots per plant), the mean number of seedlings was 35.7 (se 35.7), while for 8 enneaploids (5 lots per plant) mean = 8.7 (se 8.2). These means are significantly different, Mann-Whitney U, P = 0.001. Except for one family, all the enneaploids had lower frequencies of seedlings than all hexaploids.

When a good (plump, oval, brown) seed was present, there was no significant difference between parents of different cytotypes. In the greenhouse, from 127 apparently filled and healthy seeds, 55 of 105 seeds from hexaploid plants germinated, 4 of 9 seeds from
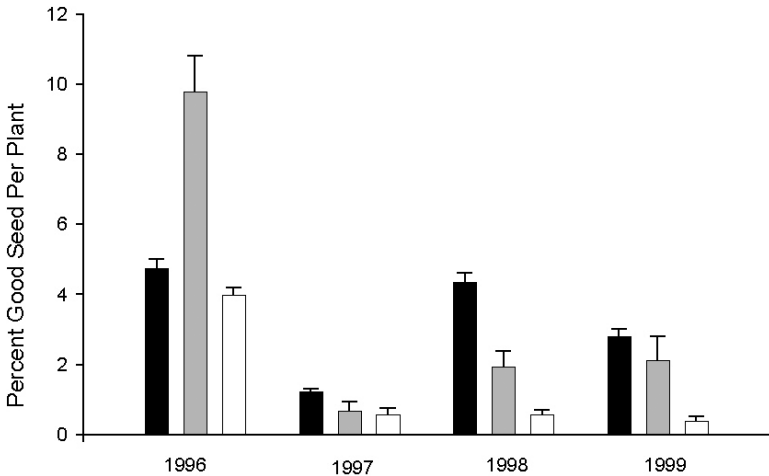

Fig. 5.—Mean percent good seeds per clone. Hexaploid black (N = 136), intermediate gray (N = 9), enneaploid white (N = 88). Error bar is 1 se

intermediate cytotypes and 8 of 13 seeds from enneaploid plants. These numbers are not significantly different (Fisher's Exact Test P > 0.14 for all pairwise comparisons).

Considering good seed production by all cytotypes in a year across plots, enneaploids contributed 68.0% of the good seeds in 1996, 14.1% in 1997, 26.4% in 1998 and 16.3% in 1999. Enneaploids are certainly part of the breeding population.

Testing the cytotypes of seedlings in comparison to the parent plant, seeds from plants of known cytotype were gathered in 1998 from the Boulder populations and germinated in the greenhouse. Ploidy was determined using flow cytometry, using the definitions (as above, Norrmann *et al.*, 1997): 5.41–6.45 pg DNA/nucleus (97% cl): hexaploids; enneaploids 8.44–9.50 pg DNA (95% cl), intermediates falling between. The progeny of seven hexaploid mothers were 52 hexaploid (78.8%), 13 intermediate (19.7%) and 1 enneaploid (1.5%) seedlings. The progeny of the one intermediate tested (maternal DNA = 7.22) were 10 hexaploids (91%) and 1 intermediate (9%). Four enneaploid plants produced 13 hexaploid seeds (25%), 37 intermediate DNA seeds (71%) and 2 enneaploid seeds (3.8%). Thus, the hexaploid mothers had hexaploid seeds 78.8% of the time, intermediate DNA mothers had intermediate seeds 9% of the time and enneaploid mothers had enneaploid seeds 3.8% of the time. Overall this sample of 10 (and in 1 case 11) seeds from each of 12 plants (parental ratio 58: 8: 33) in the natural populations yielded 75 (58.2%) hexaploid, 51 intermediate (39.5%) and 3 (2.3%) enneaploid seedlings. Since the distribution of cytotypes in the plots studied was 63: 5: 32, this small study of seedling cytotype is consistent with the idea that cytotype ratio is not stable and is changing toward hexaploid.

This experiment provided the only data I have comparing the contribution of the cytotypes to the next generation as male parents. The 131 seedlings above appear to have received pollen from hexaploids (and/or pollen with a hexaploid cytotype) in 113 cases (87%). This is substantially higher than the frequency of hexaploids in the population and suggests an advantage in male fitness by hexaploids as well.

<center>DISCUSSION</center>

This is the first study to compare individual plants of *Andropogon gerardii* within natural populations. Across most of the tallgrass prairie, plants are so numerous that individuals are indistinguishable. Most of eastern Colorado is too dry to support tallgrass prairie plants such as *A. gerardii*, but moisture increases in the foothills of the Rocky Mountains, providing the conditions for a band of tallgrass prairie (Livingston, 1952; Branson *et al.*, 1965; Bock and Bock, 1998). In this tallgrass ecosystem, this study exploited sites where gaps in the cover of *A. gerardii* allow distinguishing and following individuals to compare individuals with hexaploid and enneaploid chromosome complements.

Hexaploids produced a significantly higher frequency of viable seeds (Figs. 4, 5). Furthermore they reproduced their own cytotype. Enneaploids had lower fertility and rarely produced seeds with their own cytotype. Contrary to my initial expectations, however, many enneaploids were large individuals that produced numerous viable seeds. Clone size and expansion rates did not differ from those of hexaploids. As a group, enneaploids were abundant: they were 35% of the *Andropogon gerardii* plants in these plots and provided 31% of the plant cover by *A. gerardii*.

Two important conclusions emerged. First, higher polyploids contributed genes and individuals to the next generation.

Second, hexaploids were more fit than enneaploids and aneuploids. This has several aspects: (1) hexaploids produced a higher frequency of good seeds. Hexaploids had 4.5 times as many seedlings as enneaploids, from the same spikelet biomass and (2) only hexaploids

bred true: the seeds produced by enneaploids were rarely enneaploid. Taken together, this indicates that within a few generations, hexaploids will eliminate the other cytotypes.

This conclusion is complicated by the fact that the length of a generation for *Andropogon gerardii* is unknown. During this four year study a few plants appear to have been recruited into the population (1%). Of the cytotyped plants, there were 22 deaths in 1199 plant-years of observations, or 1.8%. If this turnover rate is representative and stable, generation time is 50–100 y. Clone areas changed very little over the 4 y (Fig. 1). Elimination of enneaploids and intermediates will probably require decades.

How and when so many enneaploids and intermediates were recruited into the population is also unknown. I hypothesize that when populations are reduced to a few isolated individuals, for example after drought, conditions may permit recruitment odd ploidy levels. Once established, they persist well.

Many grasses contain polyploid series (*e.g.*, Keeler, 1997). No overall theory explains this genetic variation. In some cases, it is certainly a stage in increasing ploidy level and in others a consequence of meiotic errors. Some grasses breed across ploidy levels and the uneven ploidy levels need not be sterile (*e.g.*, Zohary and Nur, 1959; Lumaret, 1988a; Ramsey and Schemske, 1998). Most of the grasses of North American prairie are polyploid (Keeler *et al.*, 1987; Keeler and Kwankin, 1989; Keeler, 1997) and many have intraspecific polyploid cytotypes (Keeler, 1997). *Andropogon gerardii* is a highly successful species: it dominated the tallgrass prairie ecosystem and beyond that its range extends from the Atlantic Ocean to the Rocky Mountains, from southern Canada to northern Mexico. Odd ploidy levels occurred at least occassionally whereever *A. gerardii* grows (Keeler, 1990, 1992). This study confirmed that polyploids with low fertility can be big healthy individuals that contribute to the area dominated by the species and to its gene pool.

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