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COMPARISON OF COMMON CYTOTYPES OF *ANDROPOGON GERARDII* (ANDROPOGONEAE, POACEAE)¹

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Many plant species contain populations with more than one polyploid cytotype, but little is known of the mechanisms maintaining several cytotypes in a population. *Andropogon gerardii* cytotypes were compared to evaluate different models of autopolyploid cytotype coexistence. The enneaploid (90 chromosome, 9x) cytotype was found to be larger and taller than the hexaploid (60 chromosome, 6x) cytotype. Seed production is significantly more efficient in hexaploids, but seed production per area was not significantly different. The two cytotypes are not exomorphologically separable in the field because of great plasticity in response to environmental variation and wide variation within each cytotype. These data suggest cytotypic variation is maintained by natural selection.

Key words: *Andropogon gerardii*; cytotype; enneaploid; hexaploid; Poaceae; polyploidy.

Polyploidy is a common phenomenon among plants, and although generally ignored, presence of plants of several ploidy levels within local populations is widespread (Stebbins, 1971; Lewis, 1980; Lumaret 1988a; Thompson and Lumaret, 1992; Keeler, 1997). A number of authors have pointed out the difficulties in establishing a polyploid mutant in a diploid, or lower polyploid, population (Stebbins, 1971; Grant, 1981; Levin, 1983; Fowler and Levin, 1984; Felber, 1991; Bever and Felber, 1993; Rodríguez, 1996a, b). At the same time, it is obvious that this step must have repeatedly occurred to produce existing patterns of polyploidy and intrapopulation polyploidy.

Autopolyploids, plants with a shared genome, but varying in the number of copies of that genome, are also relatively common (Lewis, 1980; Jackson, 1982; Lumaret, 1988a, b; Thompson and Lumaret, 1992; Keeler, 1997). They are believed to result from nonreduction of the genome during reproduction (Stebbins, 1947; Jackson, 1976, 1982; Bretagnolle and Thompson, 1995).

Levin (1975, 1983) and Fowler and Levin (1984) showed that a new autopolyploid will be at a significant disadvantage as a result of frequency-dependent minority status, and, even if it has the same fitness as the previous cytotype, is likely to be lost. Survival of the polyploid is enhanced by selective (competitive) superiority (Levin, 1983; Fowler and Levin, 1984; Felber, 1991; Rodríguez, 1996a, b). New polyploid establishment is also assisted if genetic drift renders the new polyploid locally dominant, reversing the rare cytotype disadvantages (Levin

1983; Fowler and Levin, 1984; Felber, 1991; Rodríguez, 1996b) or if the species is iteroparous or autogamous (Rodríguez, 1996b).

Models of establishment of polyploids resulting from selection (Levin, 1983; Fowler and Levin, 1984; Rodríguez, 1996a, b) appear to have assumed directional selection favoring the higher polyploid. The widespread occurrence of populations containing several polyploid cytotypes (see reviews by Lewis, 1980; Keeler, 1997) suggests intraspecific polyploid variation may be stable rather than transitory. Much work is needed on polyploid population genetics generally (Thompson and Lumaret, 1992; Bever and Felber, 1993) and on the dynamics of autopolyploidy within a population in particular (e.g., Felber, 1991). Lacking theoretical analysis of the conditions for stable intraspecific polyploid variation, in this paper we consider the possibility that balanced rather than directional selection may operate in polyploid complexes. We present data that compares the fitness of cytotypes of a grass species with widespread intraspecific polyploidy to test the hypothesis that selection is favoring replacement of the lower polyploids by the higher. The simplest alternative model was that higher polyploids represent unfit mutants and are rapidly eliminated. As the data below indicate, we find the need for alternate models that would address the maintenance of intraspecific autopolyploidy.

Andropogon gerardii Vitman (big bluestem) is one of the dominant grasses of the tallgrass prairie, comprising up to 80% of the biomass on favorable sites (Weaver, 1954). Populations across its range contain two cytotypes, hexaploid ($2n = 6x = 60$) and enneaploid ($2n = 9x = 90$) (Gould, 1965, 1967; Norrmann, Quafm, and Keeler, 1997). In Nebraska, Kansas, and Colorado prairies, these two cytotypes are often in nearly equal proportions (Keeler et al., 1987; Keeler, 1990, 1992, and unpublished data). In these populations, other cytotypes are rare (Keeler, 1992, and unpublished data). Meiosis in the hexaploid is regular and seed set can be high; meiosis in the enneaploid is irregular with a high frequency of gametic loss resulting from unbalanced genomes (No-

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TABLE 1. Size comparisons between common *Andropogon gerardii* cytotypes.

Trait	Location (year)	Hexaploid			Enneaploid			Test
		Mean	SD	N	Mean	SD	N	
Flowering Stalk Height (cm)	LG (1988)	94.6	49.3	32	134.3	29.5	18	<i>t</i> ***
	LG (1989)	134.2	61.0	41	188.8	23.9	22	<i>t</i> ***
	LG (1990)	148.7	62.6	40	204.2	24.8	22	<i>t</i> ***
	MG (1991)	159.1	51.1	151	176.4	47.2	34	<i>t</i> ns
	B (1995)	25.57	37.96	58	93.80	34.96	15	<i>U</i> ***
Leaf length (cm)	B (1996)	28.13	8.48	77	39.82	11.46	28	<i>U</i> ***
Leaf width (mm)	B (1996)	6.28	1.96	54	8.13	1.73	15	<i>U</i> ***
Vegetative canopy height (cm)	K (1989)	25.1	11.5	172	35.8	11.1	176	<i>t</i> *
	K (1990)	44.5	15.9	84	55.0	19.7	123	<i>t</i> ***
	K (1991)	42.5	17.0	225	47.3	28.0	193	<i>t</i> ns
	K (1992)	24.9	23.8	67	26.3	35.7	43	<i>t</i> ns
	B (1995)	34.66	41.61	90	69.52	50.08	50	<i>t</i> ***

LG = Lincoln common garden, MG = Mead common garden, K = Konza Prairie B = Boulder native prairie; Statistical tests: *t* = Student's *t* test, *U* = Mann-Whitney *U* test; *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significantly different.

rmann, Quarín, and Keeler, 1997). Both cytotypes are obligately outbreeding and when crossed, produce viable offspring of intermediate ploidy level, which vary in fertility and vigor (Norrman, Quarín, and Keeler, 1997; Norrman and Keeler, unpublished data).

The two cytotypes cannot readily be distinguished in the field (Keeler et al., 1987; Norrman, Quarín, and Keeler, 1997), as is often the case for intraspecific polyploids (Lumaret, 1988a; Keeler, 1997). This paper reports the results of detailed comparisons looking for differences between the cytotypes that might produce a selective advantage for one or the other of a sort that would result in directional selection. Such a comparison is critical for understanding whether the one polyploid cytotype can be expected to replace the other or whether the intraspecific variation in polyploidy is being maintained within the population.

MATERIALS AND METHODS

Cytotypes of individual plants were determined by chromosome counting on root tip smears and flow cytometry (Keeler et al., 1987; Norrman, Quarín, and Keeler, 1997). Plants compared in this study were collected as rhizomes from sites where both hexaploids and enneaploids were abundant, i.e., western prairies (see Keeler, 1990). Where native populations have been analyzed in detail, cytotypes other than hexaploid and enneaploid occur with a frequency under 10% (Keeler, 1992; Norrman, Quarín, and Keeler, 1997; Keeler, unpublished data). This paper focuses on the two common cytotypes of mixed populations of *A. gerardii* (hexaploids and enneaploids) because we had too few observations of other cytotypes to analyze. These intermediate ploidy levels are the subject of ongoing work.

The plants originated at Konza Prairie Research Natural Area, Manhattan, Kansas; Pawnee Prairie, Beatrice, Nebraska; Nine-Mile Prairie, Lincoln, Nebraska (sites described in Keeler, 1990) and the City of Boulder Mountain Parks and Open Space, Boulder, Colorado (descriptions in Bock, Bennett, and Bock, 1995; Bock et al., 1995). All four prairies have a similar pattern: overall a slight majority of hexaploids with local areas varying from 0 to 80% enneaploids (Keeler, 1990, 1992, unpublished report to City of Boulder Open Space, 1996).

Common gardens were established in 1986–1987 on the University of Nebraska East Campus (designated Lincoln garden, LG) and at the University of Nebraska Agricultural Station in Mead, Nebraska (MG), using, in approximately equal numbers, plants taken as rhizomes from Konza, Pawnee, and Nine-Mile Prairies. Plants had been growing in 10-cm (four-inch) pots in the greenhouse for more than a year. Hexaploids

and enneaploids were alternated in a grid. Water was provided to get the plants established, but after that conditions were not managed.

At Konza Prairie Research Natural Area (Konza hereafter) individual plants were marked and cytotyped in 1988–1989, establishing 18 plots of 24–50 marked plants. Naturally occurring shoots were chosen to be at least 1 m apart. These were unlikely to be the same clone (Keeler, 1992). In Boulder, Colorado (Boulder), nine 10 × 10 m plots were established in 1995 and 1996 on Boulder Mountain Parks and Open Space land. All *A. gerardii* in the plot were mapped and more than half of the 613 clumps (plants) have been cytotyped to date.

Height was measured on the tallest flowering stalks (Table 1) and on the canopy height (Table 2). Tables 1 and 2 contain independently collected data.

Boulder data from 1995 are winter-grazed plots because only those existed in 1995; for consistency, those same plots are presented for 1996. In Boulder, winter grazing is the most favorable treatment for flowering because grazing clears off the litter, which inhibits flowering in ungrazed plots (burning is not a routine treatment) (Keeler, unpublished data).

Leaf length was measured on the longest leaf available (some potentially larger leaves were too damaged to measure). Leaf width was taken at the widest part of the widest leaf available. Biomass was determined by clipping the entire canopy at ground level after it had gone dormant in the fall and drying it 2–3 d in a plant drier at 60°C to remove any remaining moisture. Leaves and inflorescences were separately weighed to the nearest 0.1 g.

To understand the influence of the environment between cytotypes plant height was compared under natural conditions in four different sites. The sites were Osage Prairie, Tecumseh, Nebraska; Nine-Mile Prairie, Lincoln, Nebraska; Reller Natural History Study Area, 30 km southwest of Lincoln, Nebraska; and Konza. Konza and Nine-Mile Prairies are native prairies, Reller was replanted to native grass mix about 1970 (R. C. Lommason, University of Nebraska-Lincoln, personal communication) and Osage includes both native and replanted portions (Nebraska Game and Parks Commission, unpublished report). At each site, areas burned the previous May were compared to areas not burned in the previous year. Hill and low areas are relative: tops of the low hills vs. the base of the hills.

Plant sizes for LG plants were determined by photographing the basal area of the plants at the end of the growing season, projecting the slide onto paper, and mapping and calculating the area with a planimeter. Total area for Boulder plants was determined from the area on to scale maps digitized in ArcView (ESRI, 1997).

For seed mass, all caryopses on a marked plant were gathered at the end of the growing season, stored at room temperature, and weighed to the nearest 0.01 gm. For the Boulder plants, good seed was determined

TABLE 2. Plant height as function of plant origin, burning history, and cytotype (1996). Plant height was measured to the nearest centimetre in fall 1994 and compared across four prairies (sites) each with planted and replanted sections (nested within site) and burned and unburned areas (not nested). Cytotype was determined using flow cytometry.

Source	df	Sum of squares	Mean square	F	P	r ²
SITE	3	21.81	7.271	271.09	<0.001	***
BURN	1	3.68	3.677	137.10	<0.001	***
CYTO	2	0.11	0.053	1.96	0.141	ns
NR ^a (SITE)	1	0.03	0.031	1.15	0.284	ns
HILO(SITE)	4	1.86	0.466	17.37	<0.001	**
NR × HILO(SITE)	1	0.05	0.054	2.01	0.157	ns
BURN × HILO(SITE)	1	0.04	0.037	1.39	0.239	ns
HILO × CYTO(SITE)	3	0.15	0.147	1.83	0.141	ns
SITE × CYTO	2	0.199	0.199	3.71	0.025	*
BURN × CYTO	1	0.227	0.227	8.47	0.004	**
Model	20	71.57	3.579	133.43	0.0001	0.822
Error	579	15.53	0.027			

^a NR = native vs. replanted prairies.

based on individually removing the seed coat to see whether a filled seed was present in a sample of 100 caryopses (or all the caryopses if under 100). For large reproductive masses, the percentage good seed was calculated by multiplying the frequency of filled seeds in the sample of 100 caryopses by the total number of caryopses actually counted from the plant. Caryopses and seeds discussed in this paper are from sessile spikelets. While seeds from pedicellate spikelets are reported (Boe, Ross, and Wynia, 1983; Springer, 1991) seed production by pedicellate spikelets was rare to nonexistent in our data (see Discussion).

Seed viability was determined by planting standard masses or counts of caryopses gathered from the plants of known cytotype at LG and MG, in individual vermiculite-filled 10-cm (four-inch) clay pots in the greenhouse. The number of seedlings emerging were recorded and compared as percentage germinating using ANOVA and a repeated-measures ANOVA. Plant (genotype) was treated as a random variable.

Total annual seed production by a cytotype was estimated by summing the total good seed production for a plot by cytotype.

Statistical significance was determined with Student's *t* test where a normal distribution was evident and using Mann-Whitney *U* test where normality could not be assumed, especially in flowering-related char-

acters, which had a high frequency of zeros. The impact of a variety of variables on height was tested using mixed-model analysis of variance. Repeated-measures statistics were used for data sets involving the same plants sampled in different years. Programs used were Statview (1994) and SAS (1996).

RESULTS

Enneaploids were consistently taller than hexaploids with longer and wider leaves, whether flowering or vegetative (Table 1). These data are from both common gardens and native prairies.

In common gardens, total biomass produced in a season was compared and found to be greater in enneaploids. This was significantly related to time in the Lincoln common garden: enneaploids increased more than that of hexaploids between 1987 and 1988 (the first year after transplanting into the garden) so that subsequent differences are a result of a difference established by 1988 (Fig. 1). At MG, hexaploids transplanted in 1989 averaged 145.9 and 572.2 g dry mass in 1990 and 1992, respectively ($N = 66, 64$), and enneaploids averaged 171.4 g dry mass and 845.4 ($N = 72, 71$), respectively. The former is not significantly different, but the latter is ($P < 0.001$, Student's *t* test). Total biomass production was thus variable and greater in enneaploids, sometimes significantly.

While we can demonstrate replicable differences between the two cytotypes, these are not readily detected in natural populations because of the responsiveness of *A. gerardii* to a variety of environmental variables. To illustrate this, we measured canopy heights from both native and replanted prairies in 1996. Height varied significantly with location (SITE), recent burning history (BURN), and elevation (location within a site, contrasting hilltops to low areas just higher than streams or ponds, HILO) (Table 2). Cytotype was not significant in this test. Thus, although we find cytotype a significant variable when other variables are controlled, it is only one of a series of variables that significantly determine *A. gerardii* exomorphology.

Clone areas were not significantly different in transplants in LG after 3 yr (hexaploid mean area ± 1 SD 1001.8 ± 633 cm², enneaploid mean ± 1 SD = 1662.8 ± 1289 cm², $N = 23$, *t* test). In MG after 7 and 8 yr,

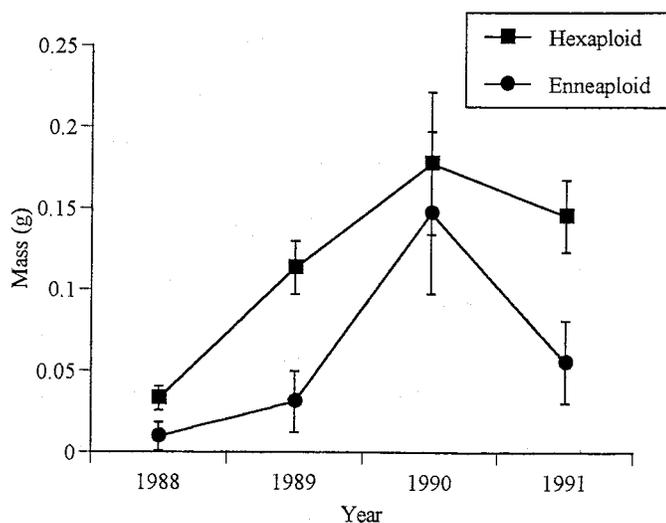


Fig. 1. Comparison of biomass per plant, by cytotype, in Lincoln common garden plants 1987–1990. End of season total aboveground dry mass (g) (± 1 SE) per plant. Repeated-measures analysis of variance: comparison of cytotypes $P < 0.0001$ in 1987–1988, ns in 1988–1989 and 1989–1990.

TABLE 3. Comparison of caryopsis production (g) per plant between cytotypes. Locations defined in Table 1. Statistical test is Student's *t* or Mann-Whitney *U* test.

Year	Location	Hexaploids			Enneaploids			Test
		X	SD	N	X	SD	N	
1992	MG	6.1	9.1	61	21.2	20.9	71	<i>t</i> ***
1995	B	1.10	3.74	77	4.75	7.90	40	<i>U</i> ***
1996	B	2.90	14.79	55	15.36	23.16	31	<i>U</i> **

area was significantly greater, mean ± 1 SD for hexaploids = 208.7 ± 2.4 cm², mean for enneaploids = 279.0 ± 15.8 cm², N = 260, P < 0.001, ANOVA). In native prairie in Boulder, the mean area of enneaploids was also larger (hexaploid mean ± 1 SD = 1584.7 ± 3547.2 cm², enneaploid = 4072.6 ± 5661.3 cm², N = 108, P < 0.01, Mann Whitney *U* test).

Total reproductive effort per plant, measured as mass, was significantly greater for enneaploids (Table 3). Good seed, per plant or per square centimetre, was not statistically significantly different. In Boulder in 1995, for hexaploids X ± 1 SD = 18.04 ± 89.3 seeds/plant, enneaploids X ± 1 SD = 38.25 ± 109.14 seeds/plant, df = 107, and in 1996 X ± 1 SD for hexaploids = 88.39 ± 427.2 seeds/plant and X ± 1 SD for enneaploids = 144.10 ± 320.7 seeds/plant, df = 86. Recalculated on a per square centimetre basis the results are not statistically significant either: a mean of 0.018 seeds/cm² and 0.145 seeds/cm² for hexaploids in 1995 and 1996, respectively, and 0.013 seeds/cm² and 0.037 seeds/cm², respectively, for enneaploids. For the plants at LG, repeated-measures analysis indicates a significantly different effect of time on the plants: change in seed production of the two cytotypes was significantly different in 1987–1988 and 1988–1989 but not 1989–1990 (Fig. 2).

For a standard number of seeds, germination of open-pollinated seeds from plants of known cytotype (therefore, one parent known) was significantly greater for hexaploids (Table 4). There were also significant effects

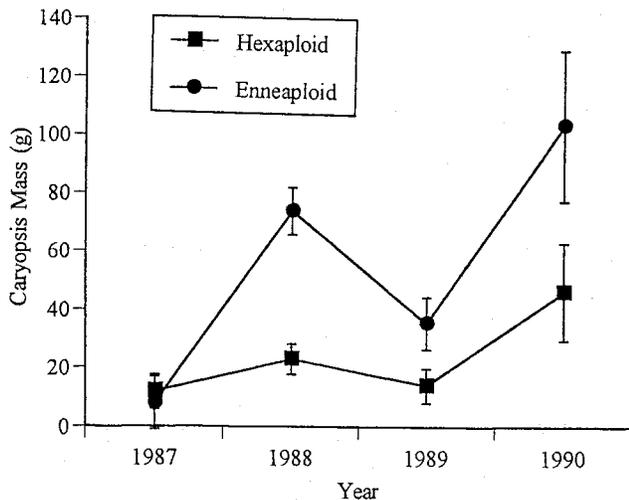


Fig. 2. Comparison of total caryopsis production per plant (g) (± 1 SE) in Lincoln common garden plants 1987–1990. Repeated measures analysis of variance: comparison of cytotypes 1987–1988 P < 0.0017, 1988–1989 P < 0.0037, 1988–1990 P = 0.22.

TABLE 4. (A) Comparison of percentage germination by maternal cytotype. Samples of caryopses taken from plants of known cytotype and germinated in vermiculite (B) ANOVA of (A), log transformed. Studies done in Lincoln Garden.

A) Year	Site ^a	Hexaploid			Enneaploid		
		X	SD	N ^b	X	SD	N ^b
1988	LC	4.1	6.3	28	1.1	1.5	23
1989	LC	12.0	12.3	33	3.1	4.8	27
1990	LC	28.3	26.1	22	15.9	28.2	25
1991	LC	18.2	16.3	28	5.6	7.5	27

B) Source CHROM	df	Type III sum of squares	Mean square	F	P
1988	1	0.0071870	0.0071870	4.32	0.0419 *
1989	1	0.0794821	0.0794821	11.80	0.0011 **
1990	1	0.0124524	0.0124524	0.35	0.5570 ns
1991	1	0.0863761	0.0863761	7.30	0.0090 **

^a Legend as in Table 1.

^b N refers to number of parents; 200 seeds were tested if available, and the minimum was 20 seeds.

of genotype and year and the interaction of genotype, but not cytotype, with year. Wilks' Lambda was significant (P < 0.001) in the repeated-measures ANOVA: since the complete seed crop was removed each year, we take this to mean that individual ramets were consistent in their percent germinating seeds (previous year a significant predictor), a product of both clone vigor and reception of pollen from neighbors.

Taking the results all together, these effects seem to balance: for the Boulder plots number of viable seeds contributed by the two cytotypes were not distinguishable (Table 5).

DISCUSSION

This study compared the two dominant *Andropogon gerardii* cytotypes found in native tallgrass prairies. Although crosses between these cytotypes usually result in aneuploids (Norrman, Quarin, and Keeler, 1997), those are uncommon in the field (e.g., Keeler, 1992, and unpublished data). This study looks at fitnesses of the two cytotypes that make up the bulk of the plants in natural populations of *A. gerardii*, a necessary but not sufficient step for understanding this polyploid complex.

TABLE 5. Comparison of mean number of filled seeds per plant, by cytotype, Boulder native prairies. Comparison of cytotypes is within plot and year only. An identical letter indicates P > 0.05 (t test).

Plot	Hexaploid			Enneaploid		
	1995	1996	1997	1995	1996	1997
36						
Mean	2.8a	58.6a	na	1.0a	34.5a	na
SD	7.6	73.5		7.6	79.7	
N	25	12		25	16	
45						
Mean	16.7a	22.9a	1.3a	112.3b	485.6b	0.1b
SD	101.8	66.9	2.2	164.2	819.1	0.3
N	48	55	19	15	16	16
52						
Mean	8.2a	0.2a	0.2a	4.4a	0.0a	0.0a
SD	18.0	0.6	0.4	9.8	0.0	0.0
N	16	15	8	5	5	5

The hexaploid and enneaploid cytotypes differed in most of the characters measured. Because they produce unequal frequencies of good seed (Norrmann, Quarín, and Keeler, 1997), the initial expectation was that the enneaploid cytotype was less fit than the hexaploid cytotype. That being the case, enneaploid establishment seemed improbable. However, the widespread existence of enneaploids (Keeler et al., 1987; Keeler, 1990, 1992, and unpublished data) either demonstrates that enneaploid establishment happens or represents a mutation: selection balance with a long time frame. By the time the enneaploid has persisted for more than a decade or reached a metre in diameter, it is reasonable to describe it as "established" and consider the intrapopulation dynamics and consequences resulting from intrapopulation cytotypic variation. Where there are data on plant size in natural populations (Boulder), enneaploids are demonstrated to be big, productive plants.

Enneaploid *A. gerardii* produce markedly poorer quality seeds than hexaploids (Norrmann, Quarín and Keeler, 1997; Table 5), but they are bigger plants (Fig. 1, Results), producing more seeds overall (Table 3) and so, on a per plant basis, more good seeds (see Results). The outcome is similar contributions of the two cytotypes to good seed production at a site (Table 5).

Variation is striking (e.g., for flowering stalk height, Table 1). Because there is dramatic between-year variation at a site (Table 1), we attribute this to the plasticity of the species in response to the environment. This is supported by Table 2 and studies of response of *A. gerardii* to fire (e.g., Collins and Wallace, 1987).

Boe, Ross, and Wynia (1983) and Springer (1991) compare the fertility of seeds from pedicellate and sessile spikelets. They find both to have 70–80% germinable pedicellate and sessile spikelet seeds/caryopsis. This is in strong contrast to a maximum of 28% germinable seeds/caryopsis found here (Table 4). We believe that the difference between their results and ours is that we are working in populations of mixed cytotypes. The common garden planting scheme alternated cytotypes, and intermingling occurs naturally in the native prairies studied. Boe, Ross, and Wynia (1983) used wild-collected seed, which, given the poor fertility of enneaploids, selects strongly for seed quality and therefore for hexaploidy (Norrmann, Quarín, and Keeler 1997; see also Table 4). Springer (1991) used USDA-Soil Conservation Service seed (PI 483446). Since USDA plant breeders generally gather seed from wild populations and propagate plants via seed, those populations too are generally hexaploid, with better seed set. In contrast, mixed populations with high frequencies of aborted pollen and ovules would be expected to have much lower frequencies of good seed. Very low seed production is observed in wild populations (e.g., Masters et al., 1993; L. Reidel, City of Boulder Open Space, personal communication).

The observations of fertile pedicellate spikelets of Boe, Ross, and Wynia (1983) and Springer (1991) also do not match ours. We have only very rarely observed fertile pedicellate spikelets. Filled seeds from pedicellate spikelets were included in total seed counts when observed, but they were rare. At present, we can only ascribe this to the highly significant effect of sites on fertile pedicel-

late spikelet seed yields found by Boe, Ross, and Wynia (1991).

Effects resulting from cytotype are always confounded by genotypic effects, because a particular genotype always has the same cytotype. Where we have looked at genotype, it is a more important determinant of response in *A. gerardii* than cytotype (Davis, unpublished data) as might be expected. Within a site, significant effects of cytotype may result from significant effects of genotype. In this study, that was controlled for by using samples of both cytotypes combined in a garden from a series of sites or replicate plots within prairies. There is no reason to expect replicate plots or several prairies to differ in a systematic way based on genotype: the emergent effects can thus be attributed to cytotype. For any particular trait, we do not doubt that genotype is the most important variable, but there are consistent effects of cytotype as well.

The absence of the aneuploids that result from crossing hexaploid and enneaploid *A. gerardii* remains a problematic factor for understanding this system. Since enneaploids would have lower fitness if they crossed with each other rather than with hexaploids (Norrmann, Quarín, and Keeler, 1997), it seems unlikely that the populations are reproductively isolated. The most likely situation is that strong selection is removing most hybrid seedlings and the realized fitness of enneaploids—number of reproducing progeny—is lower than the data on seed production and germination suggest. Ongoing research is addressing the absence of aneuploids.

Thus, while alternative hypotheses cannot be eliminated at this time, from the data gathered to date, the best explanation is that offsetting selection in *A. gerardii* appears to be maintaining the two cytotypes, with the hexaploid having more efficient seed set and the enneaploid greater vegetative vigor and so greater total reproduction. Consequently, analysis of selective mechanisms that might be responsible seems appropriate. Because existing theory addresses establishment and appears to assume replacement not polymorphism, we can find little applicable theory.

The distribution of cytotypes in western prairies as compared to eastern prairies (Keeler, 1990, 1992) suggests important regional differences, probably in relative cytotype fitness. However, in the populations of mixed cytotypes, maintenance by balanced selection seems the most likely at this time. In other taxa, habitat and flowering time differ among *Claytonia virginica* cytotypes (Lewis, Suda, and MacBryde, 1967; Lewis and Suda, 1976), *Dactylis glomerata* diploids and tetraploids showed slight habitat preferences (Lumaret et al., 1987; Lumaret and Barrientos, 1990), and cytotype is one of the determinants of variation in *Panicum virgatum* (McMillan and Weiler, 1959; Porter, 1966; Hultquist, Vogel, and Kaeppler, 1997) and *Paspalum* (Norrmann, Quarín, and Burson, 1987). Thus *A. gerardii* is one of an array of autopolyploid complexes with significant differences between co-occurring cytotypes. An obvious conclusion is that balanced polymorphism may be adaptive because it can extend the range of tolerance of the species. Intraspecific polyploidy, as a form of genetic variation that may expand environmental tolerance in plant species, requires serious future theoretical and field analysis.

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