

REPRODUCTIVE BIOLOGY OF SEVERAL BROMEGRASSES
(BROMUS): BREEDING SYSTEM, PATTERN OF
FRUIT MATURATION, AND SEED SET¹

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ABSTRACT

Five species of *Bromus* were tested for self-fertility when bagged. *Bromus inermis* was self-incompatible. *Bromus tectorum*, *B. kalmii*, *B. ciliatus*, and *B. latiglumis* were capable of self-fertilization. Further evidence from flowering behavior suggested that *B. tectorum* almost always self-pollinated and that the remaining self-fertile species sometimes outcrossed. Florets in different positions on a spikelet varied in the proportion that set seed. Open-pollinated *B. inermis* plants had lower seed set than the self-fertile species, in agreement with the pattern in a variety of hermaphroditic plants.

THE RATE of self-pollination can have a profound effect on the reproductive and population biology of hermaphroditic plants. In comparison with closely related outcrossing taxa, plants that have high rates of self-fertilization can be expected to have lower rates of gene flow via pollen, smaller neighborhood size, more homozygosity, and greater genetic differentiation and ecotypic specialization among populations (Stebbins, 1957; Allard, Jain and Workman, 1968; Schoen, 1982; Layton and Ganders, 1984). Ornduff (1969) has listed many other correlates of breeding system. In addition, Sutherland and Delph (1984) have recently shown a relationship between the breeding system and the rate of seed set in many different plant species.

To test the generality of these patterns and as part of a study of the reproductive biology of several species of bromegrass (*Bromus* L.), I investigated the breeding system and pattern of seed set in five congeneric species that show wide variation in breeding system.

Like most grasses, species of the genus *Bromus* are wind pollinated. The flower is much reduced and, with the two subtending bracts, is referred to as a floret; florets are grouped together on the plant into spikelets. Each floret

contains a single ovule and so can produce only one seed. The fruit, consisting of the single seed fused to the pericarp, is technically a caryopsis, but herein will be referred to interchangeably as "seed" or "fruit."

Bromus tectorum L. is an annual, weedy species introduced into North America from Eurasia in the late 1800's (Mack, 1981). In Minnesota, *B. tectorum* grows as a winter annual (Hulbert, 1955) and blooms in late May. *Bromus inermis* Leyss. is also native to Eurasia but is now widely cultivated and escaped in North America. It is perennial and strongly rhizomatous; flowering occurs in late June. *Bromus kalmii* Gray, *B. ciliatus* L., and *B. latiglumis* (Shear) Hitchc. are all native, non-rhizomatous perennials that grow in wet woods and prairie. In Minnesota, *B. kalmii* and *B. ciliatus* bloom in early July, *B. latiglumis* in early August.

Bromus tectorum, *B. kalmii*, and *B. latiglumis* are diploid, $2n = 14$ (Hulbert, 1955; Armstrong, 1981). Armstrong (1981) also reports that *B. ciliatus* is diploid, but Elliott (1949) found both diploid and tetraploid forms. *Bromus inermis* is usually octoploid, $2n = 56$ (Hill and Myers, 1948), but tetraploids are found occasionally (Armstrong, 1981).

STUDY SITES AND METHODS—The study population of *B. tectorum* was located on the Minneapolis campus of the University of Minnesota, on a disturbed site near the Botany Greenhouse. *Bromus inermis*, *B. kalmii*, and *B. ciliatus* were studied at Cedar Creek Natural History Area in Anoka and Isanti Counties, Minnesota, about 50 km north of Minneapolis. The *B. latiglumis* study site was on the banks of the Minnesota River near its confluence with

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the Mississippi River in Fort Snelling State Park, St. Paul, MN.

In order to determine self-fertility, I measured seed set of inflorescences bagged in parchment "Pollen-tector" bags (Carpenter Paper Company, Des Moines, IA 50302). In the days prior to anthesis, I periodically checked anthers to determine their maturity (immature anthers are translucent to green, mature anthers are bright yellow). When the population approached flowering, budding culms ("plants") were chosen haphazardly and then randomly assigned to be either open-pollinated or bagged plants. Bags were placed over the entire inflorescence, stapled shut at the bottom, and either taped or tied to a supporting stake so that the weight of the bags would not collapse the shoot. When fruits were mature, but before any dispersal, all aboveground parts of bagged and open-pollinated plants were collected and stored at room temperature until they could be counted. These experiments were performed successfully on *B. tectorum*, *B. kalmii*, and *B. latiglumis* in 1982, and on *B. inermis*, *B. kalmii*, and *B. ciliatus* in 1983.

Using a dissecting microscope, I checked each floret of each plant for the presence of a seed, recording also the location of the floret within its spikelet. In most cases it was obvious if a seed had developed within a floret. Approximately 3% of the florets of *B. kalmii* and *B. ciliatus* had seeds that were smaller than usual and seemed arrested in their development. In these cases, I counted the seed as present if the length was greater than half the length of the subtending lemma.

There is a gradual reduction in floret size toward the tops of the spikelets. At some point along a spikelet, the florets are clearly too small to be functional and have no anthers or seeds. To obtain a total of the florets present for calculation of percent seed set, it was necessary to determine the lower size limit for a functional floret. I did this by measuring the length (excluding awns) of the upper florets of each spikelet and determining for each species the smallest floret size that ever produced seed; this was then used as the minimum size for a functional floret. All smaller florets were excluded from further analysis.

I visited the experimental populations at anthesis to observe the way in which florets opened and the extent of anther exertion. Voucher specimens of the five experimental species were placed in the University of Minnesota Herbarium, St. Paul.

RESULTS—All experimental species but *B. inermis* were able to produce significant

TABLE 1. The effect of bagging on percent seed set in the five experimental species

Species	Bagged		Open-pollinated		Significance*
	Mean % seed set	N	Mean % seed set	N	
<i>B. tectorum</i>	56.3	4	79.0	6	$P = .04$
<i>B. inermis</i>	0.3	19	29.9	18	$P < .0001$
<i>B. kalmii</i>	38.6	14	72.2	30	$P < .0001$
<i>B. ciliatus</i>	48.9	15	69.6	19	$P = .0003$
<i>B. latiglumis</i>	43.3	13	64.8	14	$P = .001$

* P values from Mann-Whitney U -test for differences between bagged and open-pollinated plants.

amounts of seed when only self-pollen was available (Table 1), though all species had lower seed set when bagged. Bagged *B. tectorum*, *B. ciliatus*, and *B. latiglumis* set about 70% as much seed as open-pollinated plants. Bagged *B. kalmii* plants set about 53% as much seed as open-pollinated plants. *Bromus inermis* was essentially sterile when bagged; only four florets set seed out of 1,284 examined from bagged plants.

Nonbagged *B. inermis* plants had low seed set; most florets did not produce a fruit. Seed set of open-pollinated plants was significantly higher in the four self-fertile species than in *B. inermis* (Table 2). The annual *B. tectorum* had the most florets, spikelets, and seeds per shoot. The number of florets that made up a spikelet varied significantly among the species in a way not obviously related to other reproductive variables.

Except in *B. inermis*, fruit production was not randomly distributed among florets with respect to spikelet position (Table 3). *Bromus kalmii*, *B. ciliatus*, and *B. latiglumis* had peak seed set in the second or third floret from the glumes; there was a large drop in seed set in the upper florets of *B. kalmii* and *B. latiglumis*. Seed set fell consistently with floret position in *B. tectorum*.

All of the populations were observed during anthesis. I visited the *B. tectorum* population fairly infrequently but never found anthers completely exerted from the florets. Rarely, part of an anther was just visible protruding from between the palea and lemma. In contrast, flowering *B. inermis* had florets opened widely (i.e., lemma and palea widely separated), anthers dangled in the wind free from the floret, and stigmas were conspicuously exposed. Often, a large proportion of the florets of a *B. inermis* shoot were open synchronously.

Bromus kalmii, *B. ciliatus*, and *B. latiglumis* were similar in their flowering behavior. Fully open florets were common in all three species.

TABLE 2. Differences among open-pollinated plants of the five species studied

Species	Florets/plant	Spikelets/plant	Florets/spikelet	% Seed set	Seeds/plant	Height (cm)	Dry weight (g)
<i>B. tectorum</i>	327.5c ^a	108.5d	3.00a	79.0b ^b	262.3d	70.4a	ND ^c
<i>B. inermis</i>	64.2a	16.9ab	4.21ab	29.9a	17.2a	68.4a	.74a
<i>B. kalmii</i>	95.2a	13.6a	6.77d	72.2b	64.1ab	72.2a	.66a
<i>B. ciliatus</i>	166.4b	35.0c	5.79c	69.6b	117.1c	78.9ab	.75a
<i>B. latiglumis</i>	166.9b	32.5bc	5.07bc	64.8b	103.4bc	89.9b	ND

^a Those values in a column followed by different letters are significantly different, as determined by analysis of variance followed by Tukey's test for honestly significant differences ($\alpha = .05$).

^b The arcsine square-root transformation was performed on the percent seed set before ANOVA.

^c ND indicates that the measurement was not made.

The anthers and stigmas, though exposed to the wind, frequently did not hang free from the floret but remained cupped within. A relatively small proportion of florets was found open at any one time on a particular plant.

DISCUSSION—Breeding system—The experimental species varied greatly in their ability to self-pollinate. *Bromus inermis* was self-incompatible, consistent with reports by previous workers (Beddows, 1931; Smith, 1944; Cheng, 1946; Adams, 1949; Wilsie, Ching and Hawk, 1952). Nearly all of the seed produced in a population of *B. inermis* must be the product of cross-fertilization. The typical system of incompatibility in the Poaceae is gametophytic, with two incompatibility loci each having multiple alleles (Nettancourt, 1977; Heslop-Harrison, 1982).

The other four species were clearly self-compatible. *Bromus tectorum* has previously been reported as highly self-fertile (Beddows, 1931; Hulbert, 1955). Stebbins (1957) listed *B. ciliatus* as self-compatible; I found no previous reports on the breeding systems of the other two species.

The rate of self-pollination cannot be inferred from the fact that a species is capable of self-fertilization. Depending on the behavior of the flower at the time of anthesis, a self-fertile plant could range from being completely self-pollinated to completely outcrossed.

In my limited observations of *B. tectorum*, its florets rarely (if ever) opened. Hulbert (1955) "never observed anthers of any of the annual bromegrasses to be exerted," and he suggested that fertilization routinely occurs by self-pollination. In studies of *B. tectorum* and a wide variety of related annual *Bromus* species, Beddows (1931) found anther exertion to be rare and concluded that self-pollination is the rule in *B. tectorum* in particular and in annual bromegrasses in general. This conclusion is supported by work on *B. rubens*, another annual in the same section of the genus (*Eubro-*

mus) as *B. tectorum*. Jain (1975) used genetic markers to estimate the outcrossing rate; no heterozygotes were found among 200 families of *B. rubens* from six sites, so Jain estimated the outcrossing rate to be zero.

Bromus kalmii, *B. ciliatus*, and *B. latiglumis* florets often opened widely at anthesis, exposing stigmas and anthers to the wind; thus, outcrossing could occur regularly in these species. In order to estimate the proportion of florets that certainly opened, I noted whether florets of *B. kalmii* and *B. ciliatus* contained dried anthers when seed was mature. If the anthers were missing, the floret must have opened (Harlan, 1945). There were no anthers in 57% ($N = 1,189$) of the *B. kalmii* florets and in 19% ($N = 1,302$) of the *B. ciliatus* florets. The proportion of florets that possibly could be outcrossed is higher, since a floret can open to expose its stigmas and close without the loss of its anthers (pers. obs.).

All species studied had reduced seed set when bagged. This could be due to lower fertilization rates by self-pollen, to higher abortion rates of fruits produced by self-pollination, to insufficient pollen transfer within bags (though this appears rare: Beddows, 1931; Keller, 1945), or to reduced photosynthetic rates because of lower light levels within bags.

Apomixis is an alternative mechanism by which bagged plants could produce seeds. Apomixis occurs widely in the Poaceae, but it has not been reported in *Bromus* (Connor, 1981), even though the cytogenetics of the genus has been well studied.

Several species of *Bromus* produce cleistogamous flowers (Campbell et al., 1983). If cleistogamy is defined broadly to include self-fertilization in any flower that does not open, *B. tectorum* produces mostly cleistogamous flowers (cleistogamy Type IVb of Campbell et al., 1983). Cleistogamy cannot be ruled out in the other three self-fertile species investigated. Near the time of anthesis I examined many florets of all five species. I found no evidence of cleis-

TABLE 3. Percent seed set in florets at different positions within the spikelet

Species	Floret position ^a								Chi-square	Significance
	1	2	3	4	5	6	7	8		
<i>B. tectorum</i>	85.4	82.1	77.8	43.3 ^b					62.6	$P < .005$
<i>B. inermis</i>	33.0	28.7	29.4	23.7	25.9				4.0	.25 < $P < .50$
<i>B. kalmii</i>	77.3	77.0	82.8	82.2	77.7	77.0	48.2	40.9	144.6	$P < .005$
<i>B. ciliatus</i>	73.6	78.4	76.8	73.1	68.2	67.4	65.3	66.7	18.1	$P < .01$
<i>B. latiglumis</i>	67.8	71.4	70.7	67.1	66.7	65.8	40.5		16.4	$P < .025$

^a Position numbers are counted from the glumes up.

^b The highest position column for each species is a composite of all florets at that position and higher, lumped together for chi-square analysis when higher positions had too few entries

to gamous florets that were morphologically differentiated from chasmogamous florets, as occurs in *B. carinatus* (Harlan, 1945) and *B. unioides* (Langer and Wilson, 1965).

In short, *B. inermis* rarely self-pollinates, *B. tectorum* rarely cross-pollinates, and *B. kalmii*, *B. ciliatus*, and *B. latiglumis* probably have intermediate levels of self-pollination. These differences are likely to be associated with differences among these species in their population and genetic structure (see Introduction).

Pattern of fruit maturation—The way in which the florets on a plant are divided among spikelets varied among species (Table 2). In turn, the placement of a floret within its spikelet had a significant effect on the probability that a particular floret would produce a fruit (Table 3). There was a strong tendency for the upper florets in a spikelet to produce less seed than lower florets. This is similar to the pattern observed in oat (*Avena sativa*) cultivars (Takeida and Frey, 1980).

In *Bromus* species, anthesis occurs over several days with the florets near the base of the spikelet blooming first and the uppermost blooming last (Harlan, 1945; pers. obs.). Spikelet position therefore is correlated with the relative flowering time of the florets. Differences in seed set among florets could be due to changes in the availability of nonself-pollen as the flowering period progresses. Alternatively, upper florets may respond to variation among years and among plants in resource availability; resources might be allocated first to lower florets, and to upper florets only when resources are unusually abundant (Lloyd, 1979; Lee and Bazzaz, 1982).

Seed set—The four self-fertile species had relatively high seed set (Table 2). *Bromus inermis* had significantly lower seed set; less than a third of the florets of *B. inermis* produced a fruit. Predation of maturing seed by insects can be important in *B. inermis* (Nielsen and Burks, 1958) and could reduce apparent seed set. In

1982 there was a very heavy insect infestation in my experimental population; at the time of fruit maturity it was difficult to find one intact seed among hundreds of florets. In 1983 the external signs of insect damage were much reduced; yet even plants that showed no signs of insect attack had levels of seed set below those of the other four species. Although seed predation could have reduced the apparent level of seed set in some plants in 1983, it seems an insufficient explanation for the generally low seed set in *B. inermis*.

Since *B. inermis* was the only self-incompatible species examined, it is possible that the number of fruits produced was limited by the availability of nonself pollen. Pollen limitation would occur if clones of *B. inermis* were sparse enough and pollen flow restricted enough to prevent fertilization of some ovules in the population. My study was carried out in a field that was cultivated until 1955, then seeded to *B. inermis* and abandoned. Since the field remains essentially a monoculture of *B. inermis*, I could not easily determine the size of individual clones; at least initially the clone density must have been high. Knowles and Ghosh (1968) suggested a minimum distance of 50 m to insure isolation of *B. inermis* from conspecific pollen, and my study population was in an open field that allowed ample air flow for transport of pollen by wind. On days when anthesis occurs, florets open throughout the population within minutes of each other (Jones and Newell, 1946; pers. obs.) so that pollen is available simultaneously to the newly exerted stigmas. Under these circumstances pollen limitation is unlikely.

Low seed set has been found in other investigations of *B. inermis*, even in nursery plantings when pollen limitation is unlikely and seed predation unmentioned. For instance, Nielsen (1951) reports $37.4 \pm 3.4\%$ ($\bar{x} \pm SE$; $N = 56$) seed set, and Lowe and Murphy (1955) report $35.9 \pm 4.7\%$ ($N = 30$) seed set. These figures are slightly higher than those reported here, but still well below those for the self-

compatible species. A more general explanation for the consistently low seed set in *B. inermis* is necessary.

Irregularities in chromosome behavior during meiosis are found in *B. inermis* (Elliott and Love, 1948) and have been suggested as a cause for low seed set (Nielsen and Smith, 1968). Elliott (1949) found that seed set was reduced in lines previously selected for the presence of micronuclei (a correlate of meiotic irregularities). However, in nonselected lines, no correlation was found between meiotic irregularities and seed set (Hanna, 1961; Hill and Hovin, 1964), suggesting that such irregularities are an insufficient explanation for *B. inermis*'s low seed set.

The correlation between compatibility and fruit set reported here is consistent with the general pattern in a wide variety of seed plants. In a literature review of fruit set in 316 hermaphroditic plants, Sutherland and Delph (1984) report that fruit set was $22.1 \pm 13.6\%$ ($\bar{x} \pm SD$) for self-incompatible species and $72.5 \pm 12.5\%$ for self-compatible species. In this context, *B. inermis* has rather high fruit set for a self-incompatible hermaphrodite.

The theory of sex allocation (Charnov, 1982) offers a hypothesis for the relationship between breeding system and seed set in general and for *Bromus* in particular. Hermaphrodites reproduce as both males and females; the flowers that do not set seed are still able to act as pollen donors (unless flowers are strictly cleistogamous). The "extra" flowers that do not produce fruits are functionally male (Willson and Rathcke, 1974; Willson and Price, 1977; Sutherland and Delph, 1984). Relative to outcrossing species, those that frequently self-pollinate are expected to have lower relative allocation to male function (Charlesworth and Charlesworth, 1981; Ross and Gregorius, 1983). One way to accomplish relatively less male reproductive effort would be to produce few flowers that are exclusively male (i.e., produce no fruit). The pattern of seed set in *Bromus* species is consistent with this hypothesis.

Of course, there can be differences in the amount of pollen produced per floret, and this too could lead to differences in gender. Further studies are underway to document variation in pollen production among *Bromus* species, among individuals within species, and among florets within spikelets.

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