Notes on Apomixis in Sideoats Grama[1]

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Bouteloua curtipendula Michx., the familiar "sideoats grama" of the western grasslands, is one of our most important and widely adapted native forage grasses. With a wide range of distribution in North, Central, and South America, this grass occurs throughout the United States except in the extreme southeast and northwest.

Sideoats grama not only has been able to compete successfully in a wide range of habitats, but also it exhibits remarkable variation in morphological characteristics. Differences in plant habit are greatest in northern Mexico, in the states of Coahuila, Chihuahua, and Durango. Here mixtures of types include low-growing, fine-bladed, stoloniferous plants intermingled with tall, coarse, broad-bladed, rhizomatous and non-rhizomatous plants. In some localities a dozen or more morphological variants may be distinguished.

Cytologically the species is equally variable. Fultz (1942) reported chromosome counts of 2n = 28, 35, 40, 42, 56, and 70. Harlan (1949) reported apomictic types with 2n = 80-101. Freter and Brown (1955) reported sexual types with 2n = 40 and 52, and apomictic types with 2n = 75-96. The writer has made chromosome counts in pollen mother cells of 2n = 20, 40, 40 plus a fragment or univalent, 42, 42 plus a univalent, 50, and presumably apomictic types with 2n = 80-102.

Until the recent discovery of a diploid (2n = 20) strain of *Bouteloua curtipendula* (Gould, 1958), it was supposed that the species arose at the tetraploid level through hybridization (Freter and Brown, 1955). Diploid chromosome counts have been reported for four closely related species, *Bouteloua uniflora* Vasey, *B. radicosa* (Fourn.) Griffiths, *B. filiformis* (Fourn.) Griffiths, and *B. heterostega* (Trin.) Griffiths. There is good reason to

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believe that the complex of plants taxonomically referred to *Bouteloua curtipendula* has arisen through a series of hybrids between species of the Chondrosium section of the genus. It is logical to assume that the crosses and backcrosses not only have involved diploids and tetraploids but aneuploids as well.

Freter and Brown concluded that all *B. curtipendula* plants with chromosome numbers higher than 2n = 52 are obligate apomicts. The absence of sexual hexaploids, octoploids, and plants of higher ploidy is in striking contrast to the situation existing in the *Andropogon* species of the Amphilophis section that are also concentrated in southwestern U. S. and northern Mexico. In the New World species of this group there are four levels of polyploidy and perhaps a complete absence of aneuploidy (Gould, 1956).

Materials and Methods

Chromosomes were counted in pollen mother cells. Bud material was fixed with the standard 3:1 absolute alcohol-glacial acetic acid solution and smears were prepared with aceto-carmine stain. Pollen diameter measurements were made on 50-grain samples taken from dried plant specimens. The pollen from one or more anthers was placed in a drop of Lugol's Solution and allowed to soak for a few minutes. Measurement of the greatest diameter of each grain was made by means of a calibrated ocular scale. Most of the live plant material was made available through the Texas Agricultural Experiment Station Hatch Projects 717 and 988. The writer is indebted to Mr. Miguel Hycka of Zaragoza, Spain, for assistance in the pollen size analysis.

Observations and Results

Freter and Brown have reported on the variability of pollen size associated with unequal distribution of chromosomes during the meiotic divisions in *Bouteloua curtipendula* plants with high chromosome numbers. Similar observations were made in the present study. The unequal distribution of chromosomes takes place in Division I (Figure 1, left) and apparently results from an extremely high percent of unpaired chromosomes. Division II is very regular (Figure 1, center) and a tetrad of two large and two small spores result (Figure 1, right). All of these spores may develop into well-rounded, apparently mature pollen grains or many may cease development and shrivel. It is generally assumed that these pollen grains with variable numbers of chromosomes are non-functional.

As all *Bouteloua curtipendula* plants with chromosome numbers higher than 2n=52 are presumed to be apomictic, they will be referred to simply as "apomicts" in this paper. Plants with chromosome numbers of 2n=52 or less are referred to as "sexual," although it is possible that some of these actually may also be apomictic. Such apomicts, however, would be inseparable from the sexual types on the basis of pollen size.

In a check on pollen size and size patterns in sexual and apomictic plants, pollen samples

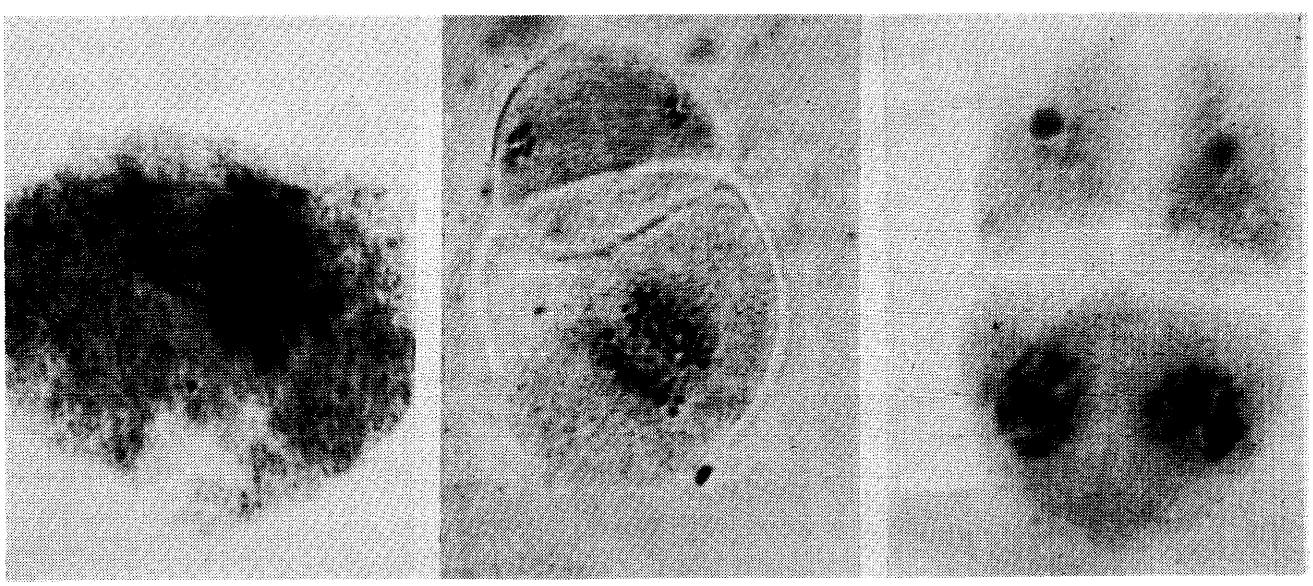

FIGURE 1. Photomicrographs (x1100) of *Bouteloua curtipendula* pollen mother cell divisions in clone 7491 from seed collected at Zimipan, Mexico. Somatic chromosome number ca. 2n=94, with only about 10 bivalents at metaphase. Left, anaphase of division I, with about 10 chromosomes going to one pole and 84 to the other. Center, division II, chromosomes at early anaphase in the large cell and at late anaphase or telophase in the small cell. Note the lack of lagging or excluded chromosomes. Right, spore tetrad showing unequal size of nuclei. From this tetrad will develop two large and two small pollen grains, all presumably non-functional. Usually one-fourth to one-half of the spores shrivel and do not complete their development.

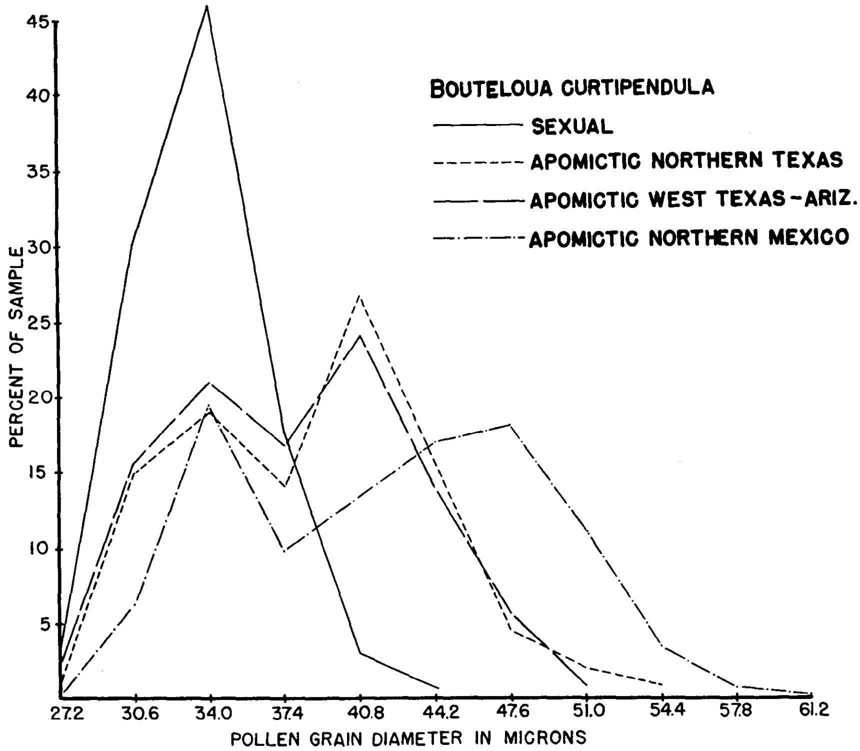

FIGURE 2. Graph of pollen size in samples from 26 sexual and 40 apomictic *B. cu.* plants. The apomictic plants are treated in 3 groups, north-central Texas (8 plants), western Texas to Arizona (22 plants) and northern Mexico (10 plants).

were taken from 66 *Bouteloua curtipendula* plants grown in the greenhouse. These plants were grown from seed collected in widely separated localities in Texas, New Mexico, Arizona, and Mexico. Twenty-six of the plants were sexual types with chromosome numbers from 2n=40 to 2n=52, and the remaining plants were apomictic strains with chromosome numbers over 2n=80.

Figure 2 presents a comparison of pollen size and size patterns for 26 sexual and 40 apomictic plants. The sexual plants for the most part were from north-central Texas but some were from southwestern Texas and northern Mexico. The apomictic plants were divided into three groups, north-central Texas (8 plants), western Texas, New Mexico, and Arizona (22 plants), and northern Mexico (10 plants). Each plant was represented by a sample of 50 pollen grains and the lines on the graph represent composite samples of all plants in each of the four groups.

Pollen size (greatest diameter) in the 26 sexual plants varied from 28.2 microns to 44.2 microns, with a mean size of 33.6 microns. The maximum variation in pollen grain size in a single 50 grain sample was 13.6 microns. In the apomictic plants pollen size varied from 28.2 to 61.2 microns. In this group the mean pollen size of 39.1 microns had little significance as there were two predominant pollen size groups rather than one.

The size distribution pattern of two "highs" separated by a "low" in all three groups of apomicts also was present in the individual samples of 30 of the 40 apomict plants. The consistently low frequency of apomict pollen in the 37.4 micron size group was rather surprising in view of the normal pollen size differences that might be expected for plants from widely separated localities.

To determine the relative abundance and distribution of apomictic plants with high chromosome numbers, a general survey of the pollen from North American *Bouteloua curtipendula* specimens was made. Of the 208 plants checked, 115 were sexual, 86 were apomictic and seven

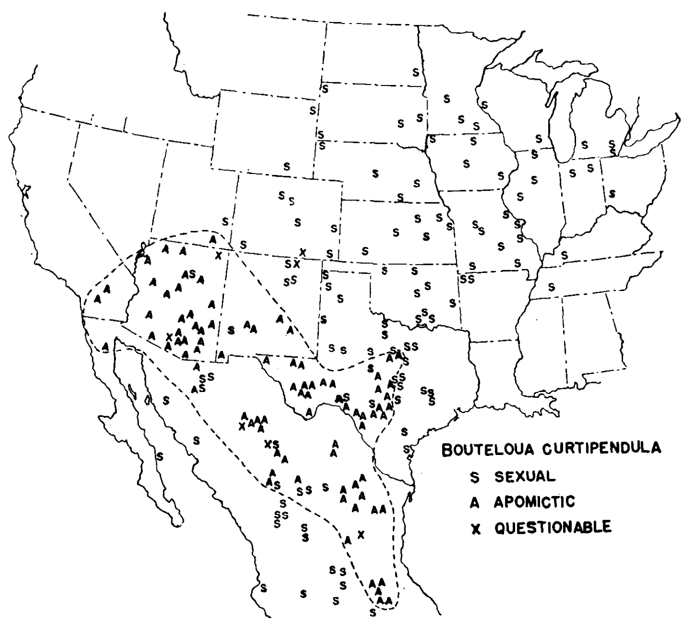

FIGURE 3. Map of North American distribution of apomicts with high chromosome numbers. The range of apomictic plants may extend further south in Mexico but this area was not sampled. Within the range of the 86 apomicts recorded, there were only 13 sexual plants and 5 undeterminable.

were undeterminable. As is shown by Figure 3, the apomictic plants are restricted to a well defined "southwestern" distribution in predominately semi-arid regions, from southern Utah and California to southwestern Texas and northern Mexico. In Texas the apomicts are restricted essentially to the Edwards Plateau and the Trans-Pecos area. Within the range of 86 apomicts, only 13 sexual plants and five undetermined plants were recorded. It is believed that the undetermined plants were sexual with chromosome numbers in the 2n=50 or 52 range.

In conclusion it should be noted that the apomicts with high chromosome numbers exhibit the same wide degree of morphological variation that occurs in the sexual types. The source of this variation and the relationships of apomictic plants with high chromosome numbers to sexual types with lower numbers are intriguing problems yet to be solved.

Summary

Extreme variation in ecological adaptation, morphological characteristics and chromosome numbers has been noted for *Bouteloua curtipendula*. Somatic (2n) chromosome numbers range from 40 (possibly 35) to over 100. It has been concluded by other workers that plants with chromosome numbers over 2n=52 are obligate apomicts, with the egg cell or some other cell of the embryo sac or nucellus developing into an embryo without fertilization.

By measurements of pollen size and variability, a survey was made of the incidence and distribution of *Bouteloua curtipendula* plants with high chromosome numbers and apomictic reproduction. These apomicts were found to occur in a broad but well defined zone from southwestern U. S. to northeastern Mexico. In southwestern U. S. the apomicts are much more frequent than are the sexual plants.

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