CHROMOSOME NUMBERS IN THE ANNUAL *MUHLENBERGIA* (POACEAE)

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ABSTRACT

Chromosome numbers were obtained from field-collected microsporocytes and root-tip preparations from greenhouse-grown specimens for 25 species of annual *Muhlenbergia* sensu lato. Nine of these counts are first reports: *M. annua* ($2n=20$), *M. biloba* ($n=8$), *M. eludens* ($n=20$), *M. fragilis* ($n=10$), *M. pectinata* ($n=10$), *M. schmitzii* ($n=20$), *M. shepherdii* ($n=8$), *M. sinuosa* ($n=10$, 12), and *M. tenuissima* ($n=10$). Besides sharing a haploid number of $n=8$, *M. biloba* and *M. shepherdii* also have large chromosomes unlike those of the other species. Both appear to be misplaced in *Muhlenbergia*: *M. biloba* is better treated as *Bealia mexicana* and *M. shepherdii* probably should be transferred to *Blepharoneuron*.

RESUMEN

El número de cromosomas de 25 especies de *Muhlenbergia* sensu lato se obtuvieron de muestras obtenidas de esporócitos recogidos en el campo o de preparaciones de ápices de la raíces de ejemplares cultivados en invernaderos. Se reporta por primera ves el número de cromosomas de 9 especies diferentes. Estas son las siguientes: *M. annua* ($2n=20$), *M. biloba* ($n=8$), *M. eludens* ($2n=20$), *M. fragilis* ($n=10$), *M. pectinata* ($n=10$), *M. schmitzii* ($2n=20$), *M. shepherdii* ($n=8$), *M. sinuosa* ($n=10$, 12), y *M. tenuissima* ($n=10$). *Muhlenbergia biloba* y *M. shepherdii* se destacan de otras especies al tener un número haploide de 8 cromosomas y al tener cromosomas de tamaño mayor. Parece ser que ninguna de estas dos últimas especies pertenecen en el género *Muhlenbergia*: *M. biloba* se debe condiderar como *Bealia mexicana* y *M. shepherdii* se debe transferir al género *Blepharoneuron*.

Muhlenbergia Schreb. (Chloridoideae: Eragrostideae) comprises over 160 species (Clayton and Renvoize 1986), most of which occur in arid lands of the New World. Of the 32 annual species, 31 taxa occur in Mexico, 14 of which also occur in the southwestern United States, and a single species is restricted to Guatemala. Although several alliances within the annuals are apparent, some groups appear to be paraphyletic and closely related to several perennial *Muhlenbergia*.

Chromosome counts reported here are part of a long-range systematic study on the annual species of *Muhlenbergia* (Peterson and Rieseberg 1987, Peterson et al. 1988, Peterson 1989). Chromosome counts for only 16 species had been reported (Myers 1947, Tateoka

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MADROÑO, Vol. 35, No. 4, pp. 320–324, 1988

1962, Gould 1965, 1966, Reeder 1967, 1968, Gould and Soderstrom 1970, Pohl and Davidse 1971, Davidse and Pohl 1974, Hatch 1980). I determined additional chromosome counts to help provide baseline data for a systematic study of the group. Chromosome data may also be valuable for inferring phylogeny and interpreting patterns of evolution (Clausen et al. 1945).

Materials and Methods

Floral buds were field collected and fixed in ethanol-acetic acid (3:1, V:V) prior to storage under refrigeration in 70% ethanol. Meiotic chromosome counts were obtained from aceto-carmine squashes of pollen mother cells. Root tips were collected from greenhouse-grown specimens and subsequently treated in 0.002 M 8-hydroxyquinoline (4 hr), ethanol-acetic acid fixative (2 hr), glusulase (45 min), and 0.2 N hydrochloric acid (2 min) before being squashed in aceto-carmine (Soltis 1980). Representative cells were recorded with sketches and photographed using a Nikon Biophot, phase-contrast microscope, using 35 mm Kodak technical pan 2415 film. Chromosome number determinations were based on observations of 15 or more cells from at least three individuals per population. Vouchers of the plants counted are deposited in WS.

Results

A total of 67 chromosome counts were made, representing 25 species of annual *Muhlenbergia* sensu lato. Chromosome number, locations, and collection numbers are listed in Table 1 for each of the 25 species. Chromosome numbers for the following nine species are first reports: *M. annua* ($2n=20$), *M. biloba* ($n=8$), *M. eludens* ($n=20$), *M. fragilis* ($n=10$), *M. pectinata* ($n=10$), *M. schmitzii* ($n=20$), *M. shepherdii* ($n=8$), *M. sinuosa* ($n=10$, 12), and *M. tenuissima* ($n=10$). The chromosome numbers of *M. brevis* ($n=10$), *M. ciliata* ($n=10$), *M. minutissima* ($n=30$), *M. crispiseta* ($n=10$), *M. depauperata* ($n=10$), *M. diversiglumis* ($n=10$), *M. filiformis* ($n=9$), *M. implicata* ($n=10$), *M. microsperma* ($n=10$), *M. ramulosa* ($n=10$), *M. strictior* ($n=10$), *M. tenella* ($n=10$), *M. tenuifolia* ($n=20$), *M. texana* ($n=20$), and *M. vaginata* ($n=9$) are concordant with previous reported counts (Meyers 1947, Tateoka 1962, Gould 1965, 1966, Reeder 1967, 1968, Gould and Soderstrom 1970, Pohl and Davidse 1971, Davidse and Pohl 1974, Hatch 1980). *Muhlenbergia sinuosa* has two different chromosome races with two $n=12$ populations from Cochise and Santa Cruz counties, Arizona and two $n=10$ populations from Grant County, New Mexico and Chihuahua, Mexico. The meiotic chromosome count for *M. pusilla* ($n=15$) substantiated a previous somatic count of $2n=30$ for the same species (Reeder 1968). Some microsporocytes of three populations of *M. strictior*

TABLE 1. CHROMOSOME COUNTS IN THE ANNUAL *Muhlenbergia* SENSU LATO. Populations are arranged alphabetically by species and locality. All collections are those of the author and C. R. Annable. Vouchers are deposited in WS. Unless otherwise noted, all counts were obtained from microsporocytes.

M. annua (Vasey) Swallen $2n=20$. Mexico, Chihuahua, nw. of Hernandez Javales, *4053*; Durango, w. of Navios, *4582* (root tip count).

M. biloba A. S. Hitchc. $n=8$. Mexico, Durango, sw. of El Ojito, *4570*.

M. brevis C. Goodding $n=10$. Mexico, Chihuahua, s. of Hernandez Javales, *4041*; n. of Cuesta Blanca, *4047*; sw. of Madera, *4051*; ne. of El Vergel, *4061*; Durango, w. of Río Chico Crossing, *4094*.

M. ciliata (H.B.K.) Kunth $n=10$. Mexico, Chihuahua, ne. of El Vergel, *4080* (some cells at $n=9$); Durango, w. of Río Chico Crossing, *4093*; e. of El Salto, *4119*; Michoacán, s. of Uruapan, *4619*; Sinaloa, nw. of Surutato, *4165*.

M. crispiseta A. S. Hitchc. $n=10$. Mexico, Durango, sw. of El Ojito, *4571*.

M. depauperata Scribn. $n=10$. Mexico, Chihuahua, n. of Villa Matamoros, *4082*; s. of Villa Matamoros, *4083*; Zacatecas, nw. of Fresnillo, *4596*.

M. diversiglumis Trin. $n=10$. Mexico, Sinaloa, e. of Santa Lucia, *4147*.

M. eludens C. Reeder $n=20$. Mexico, Durango, w. of Río Chico Crossing, *4096*. USA, AZ, Santa Cruz Co., sw. of Canelo, *4018*.

M. filiformis (Thurb.) Rydb. $n=9$. USA, AZ, Apache Co., e. of McNary, *3994*; Washington, Klickitat Co., Wash. St. Salmon Hatchery, *3987*.

M. fragilis Swallen $n=10$. Mexico, Chihuahua, w. of Parral, *4554*. USA, AZ, Santa Cruz Co., Sycamore Canyon, *4024*.

M. implicata (H.B.K.) Kunth $n=10$. Mexico, Chihuahua, ne. of El Vergel, *4079*; Durango, s. of El Ojito, *4566*; Oaxaca, se. of Sinaxtla, *4670*.

M. microsperma (DC.) Kunth. $n=10$. USA, AZ, Santa Cruz Co., Sycamore Canyon, *4023*; NV, Clark Co., Lake Mead, *3067*.

M. minutissima (Steud.) Swallen [incl. *M. confusa* (Fourn.) Swallen] $n=30$. Mexico, Chihuahua, sw. of Colonia Juarez, *4037*; Durango, w. of Río Chico Crossing, *4097*; Mexico, w. of Toluca, *4634*. USA, AZ, Apache Co., n. of Sunrise Lake, *3998*.

M. pectinata C. Goodding $n=10$. Mexico, Durango, s. of Durango, *4089*; w. of El Salto, *4132*; w. of La Ciudad, *4135, 4139, 4141*; Sinaloa, s. of Surutato, *4151, 4152*.

M. pusilla Steud. [incl. *M. pulcherrima* Scribn.] $n=15$. Mexico, Chiapas, nw. of Motozintla de Mendoza, *4712*; Chihuahua, sw. of El Vergel, *4073*.

M. ramulosa (H.B.K.) Swallen [incl. *M. wolfii* (Vasey) Rydb.] $n=10$. Mexico, Chihuahua, ne. of El Vergel, *4064*. USA, AZ, Cochise Co., Rustler Campground, *4011*.

M. schmitzii Hack. $n=20$. Mexico, Michoacan, w. of Ciudad Hidalgo, *4631*.

M. shepherdi (Vasey) Swallen $n=8$. Mexico, Durango, w. of El Salto, *4122*, s. of El Ojito, *4561*.

M. sinuosa Swallen $n=10$, 12. Mexico, Chihuahua, w. of Tomochic, *4540* ($n=10$). USA, AZ, Cochise Co., Rucker Lake, *4013* ($n=12$); Santa Cruz Co., sw. of Canelo, *4020* ($n=12$); NM, Grant Co., San Lorenzo, *4008* ($n=10$).

M. strictior Scribn. $n=10$. Mexico, Chihuahua, s. of Hernandez Javales, *4039* (some cells at $n=9$), *4043*; w. of Tomochic, *4553*; w. of La Junta, *4054* (some cells at $n=9$); Durango, s. of El Ojito, *4563* (some cells at $n=9$); w. of Navios, *4584*.

M. tenella (H.B.K.) Trin. $n=10$. Mexico, Chiapas, s. of Frontera Comalapa, *4704*.

M. tenuifolia (H.B.K.) Trin. $n=20$. Mexico, Chihuahua, ne. of Parral, *4059*; s. of Villa Matamoros, *4085*.

M. tenuissima (Presl) Kunth $n=10$. Mexico, Jalisco, s. of Yahualica, *4062*.

M. texana Buckl. $n=20$. Mexico, Durango, w. of Navios, *4108*. USA, AZ, Santa Cruz Co., sw. of Canelo, *4019*; Sycamore Canyon, *4028*.

M. vaginata Swallen $n=9$. Mexico, Durango, w. of El Salto, *4124, 4591*; w. of Navios, *4587*.

and one population of *M. ciliata* exhibited irregularity (n=9) suggesting facultative aneuploidy. However, most microsporocytes of these populations had normal bivalents during meiosis (n=10). The chromosomes of *M. biloba* and *M. shepherdii* were significantly larger than those of any other species in this survey.

Discussion

Twenty of the species investigated have a basic number of x=10 which is in agreement with the previously reported base number for the genus (Darlington and Wylie 1956, Pohl and Mitchell 1965). *Muhlenbergia filiformis* and *M. vaginata* have a base number of x=9 which suggests a close relationship with *Sporobolus,* also x=9. This base number is perhaps a result of stabilized aneuploidy or dysploidy. The haploid number of n=15 for *M. pusilla* is unusual in the genus. Individuals of *M. pusilla* show tremendous morphological variation within and among natural populations. Lemmas and awns vary from 2.0–4.2 mm and 0–22 m long, respectively. The chromosome number and varying morphological forms suggest that these plants may be triploid and completely apomictic (Reeder 1968).

The two counts of n=8 for *M. biloba* and *M. shepherdii,* coupled with their large chromosome size compare with other *Muhlenbergia,* suggest that these taxa are misplaced in this genus. *Muhlenbergia biloba,* originally described as *Bealia mexicana* by Scribner in Hackel (1890), is perhaps best retained in its own monotypic genus. Cytologically, *M. biloba* shows close affinities with *Dasyochloa* Rydb. and *Erioneuron* Nash, both x=8. Lemma morphology among these taxa is very similar. All possess three-nerved, emarginate to bilobed, and often awned lemmas with pilose hairs associated with either the nerves, margins, and/or lower ⅔ of the lemma. However, *M. biloba* [*Bealia mexicana*] differs from *Dasyochloa* and *Erioneuron* by being single-flowered and annual in nature.

Muhlenbergia shepherdii seems more closely related to the monotypic genus *Blepharoneuron* Nash than to other members of *Muhlenbergia.* These two taxa share the following features: chromosome number of n=8, strongly ribbed leaf blades, indistinguishable leaf anatomy, 1-flowered spikelets, subequal glumes almost as long as the floret, rounded lemmas with pilose margins and midnerve, and paleas that are densely (appressed in *M. shepherdii*) villous on and between the keel. I plan to transfer this species into *Blepharoneuron.*

The evidence from cytology, coupled with anatomy and morphology suggests that the annual species of *Muhlenbergia* sensu lato form at least three phylogenetically distinct lines. *Muhlenbergia biloba* [*Bealia mexicana*] and *M.* [*Blepharoneuron*] *shepherdii* each seem to form two distant but related lines, whereas all other members with x=9, 10 form a possible third lineage.

Acknowledgments

This study was supported by grants from the National Science Foundation to Amy Jean Gilmartin and PMP (BSR-8612611), Sigma Xi, and WSU. Special thanks are given to Carol R. Annable for assistance in the field and discussions pertinent to this manuscript. Amy Jean Gilmartin, David J. Keil, Askell Love, Douglas E. Soltis, and an anonymous reviewer are greatfully acknowledged for significantly improving this manuscript. I thank Raul Cano for preparing the Spanish abstract.

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(Received 22 Dec 1987; revision accepted 10 Aug 1988.)