



Ecological, biosystematic and biochemical studies of species in the genus *Agropyron* Gaertn. native to Montana
by Don Desmond Collins

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Genetics
Montana State University
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Abstract:

Eleven species and one naturally-occurring hybrid in the genus *Agropyron* that are native to Montana were investigated using ecological, morphological, histological, cytogenetical and serological methods to determine their biosystematic relationships. All of the species showed variations of the basic chromosome number of 7, ranging from the diploid to the octoploid level between species with the majority being tetraploid.

One species (*A. spicatum*) was found to exist at two levels, diploid and tetraploid, the tetraploid form being apparently of an allopolyploid origin. Six species were found to be allotetraploids; *A. albicans*, *A. latiglume*, *A. scribneri*, *A. subsecundum*, *A. trachycaulum*, and *A. dasystachyum*.

One taxon, *A. inerme*, is considered to be a variety of *A. spicatum*. There are some indications that *A. albicans* is a varietal form of *A. dasystachyum*; while *A. subsecundum*, which is often considered a variety of *A. trachycaulum*, is a distinct species.

Two taxa, *A. griffithsii* and *A. saxicola*, were found to be sterile hybrids probably of intergeneric origin. Original chromosome counts were determined for *A. saxicola* from root tip material, as plants of this species failed to undergo meiosis. One natural hybrid of the putative parentage *A. latiglume* x *A. scribneri* was discovered which proved to be a tetraploid. Meiotic examination of the hybrid disclosed that a high degree of genome homology exists between the two parental species.

Detailed morphological information including leaf epidermal features is given for all of the species.

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DON DESMOND COLLINS

A thesis submitted to the Graduate Faculty in partial
fulfillment of the requirements for the degree

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in

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ABSTRACT

Eleven species and one naturally-occurring hybrid in the genus Agropyron that are native to Montana were investigated using ecological, morphological, histological, cytogenetical and serological methods to determine their biosystematic relationships. All of the species showed variations of the basic chromosome number of 7, ranging from the diploid to the octoploid level between species with the majority being tetraploid.

One species (A. spicatum) was found to exist at two levels, diploid and tetraploid, the tetraploid form being apparently of an allopolyploid origin. Six species were found to be allotetraploids; A. albicans, A. latiglume, A. scribneri, A. subsecundum, A. trachycaulum, and A. dasystachyum.

One taxon, A. inerme, is considered to be a variety of A. spicatum. There are some indications that A. albicans is a varietal form of A. dasystachyum; while A. subsecundum, which is often considered a variety of A. trachycaulum, is a distinct species.

Two taxa, A. griffithsii and A. saxicola, were found to be sterile hybrids probably of intergeneric origin. Original chromosome counts were determined for A. saxicola from root tip material, as plants of this species failed to undergo meiosis.

One natural hybrid of the putative parentage A. latiglume x A. scribneri was discovered which proved to be a tetraploid. Meiotic examination of the hybrid disclosed that a high degree of genome homology exists between the two parental species.

Detailed morphological information including leaf epidermal features is given for all of the species.

INTRODUCTION

Agropyron is the largest of twelve genera recognized by Hitchcock (1950) as comprising the tribe Hordeae, one of ten tribes forming the subfamily Festucoideae, which, together with the subfamily Panicoideae, forms the family Gramineae. Linnaeus (1753), recognized five genera that were later included in the tribe Hordeae: Lolium, Elymus, Secale, Hordeum and Triticum. The genus Agropyron was erected in 1770 by Gaertner (Nov. Comm. Acad. Petrop. XIV, 1770, p. 531) who described two species: A. cristatum, based on the perennial Bromus cristatus L., and A. triticeum, a then new annual species which was illustrated in detail. The first typification of the genus was made by Britton and Brown (1913) who chose the perennial A. cristatum (L.) Gaertn. as the type species. Hitchcock (1920), apparently unaware of the earlier selection, chose the annual A. triticeum Gaertn. as the generic type. According to Jones (1960) this selection is in direct conflict with the International Rules of Botanical Nomenclature, which state that the first choice of a lectotype shall be followed by subsequent workers unless there are good grounds for disagreement. As the description of the genus is such that it does not apply more suitably to one species than to the other, it would appear that the selection of A. cristatum by Britton and Brown is the proper one on the basis of priority. Agropyron has since been amended by Nevski (1934) who chose A. cristatum (L.) Gaertn. as the type species.

The five original genera of the tribe Hordeae were increased to twelve by Bentham and Hooker (1883) who treated Agropyron, Triticum, Elymus and Hystrix as separate genera but still included Sitanion as a

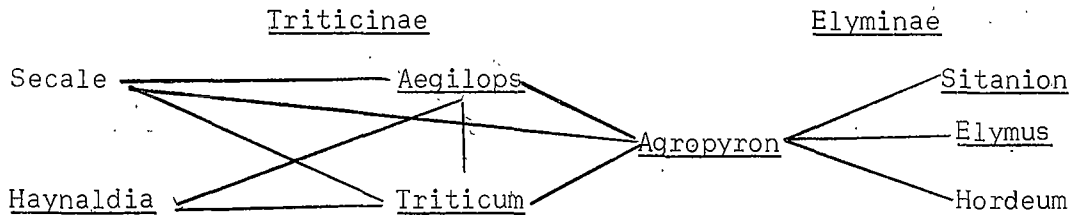
section of Elymus. In North American grass classifications Beal (1896) and Hitchcock (1950) follow essentially the same classification, but Hitchcock recognizes Sitanion as a genus distinct from Elymus.

Bentham and Hooker (1883) also proposed that the Agropyrons be divided into two sections: Agropyron proper, which would contain the perennial species, and Eremopyrum (Ledeb.) Jaub. and Spach., which would contain the annual species. In 1926 Holmberg divided the genus into four sections: 1) Goulardia (Husnot) Holmberg, 2) Holopyron Holmberg, 3) Agropyron Gaertn., and 4) Eremopyrum (Ledeb.) Jaub. and Spach. Nevski (1934) also claimed that the genus is artificial and split it into four independent genera, but his interpretation is not widely followed by other workers in the field.

The name Gramineae was given to the grass family by Jussieu (Jackson, 1893) based on the ancient term Gramina which was used but not originated by Linnaeus (1753). The tribal name Hordeae (sic) was originated by Lindley (Jackson, 1893), based on the term Hordeaceae proposed by Kunth (Jackson, 1893).

Pilger (Bowden, 1959) has shown that the earliest valid name for the tribe is Triticeae Dumort., published in 1823 by Dumortier, rather than the commonly accepted name Hordeae. Because of the derivation of the tribe name, the genus Triticum L. is automatically the type genus of the tribe. The typical subtribe is Triticinae, which included Triticum, Aegilops, Secale, and others. Other subtribes listed include Hordeinae Nevski, composed of two genera, Hordeum and Agropyron.

Godley (1951) diagrammed a comparium of the Hordeae based on relationships outlined by Clausen, Keck and Hiesey (1945). The eight genera comprising the comparium are all connected either directly or indirectly with each other by the various intergeneric hybrids which have been formed artificially or found to occur naturally. Based on a classification by Hubbard (Hutchinson 1934) the tribe is divided into two subfamilies: 1) Elyminae, having two to three spikelets per node, and 2) Triticinae, which have one spikelet per node. The genus Agropyron serves as a connecting link between the two subfamilies in the following manner:



Hordeae comparium (Godley, 1951)

Based on the available evidence, Godley suggested as a general rule that no hybrids can be produced by normal methods between the two subtribes except through the genus Agropyron. Godley also felt that should members of the genus Agropyron differentiate such that crossing between the subtribes was no longer possible, the Hordeae comparium would be split and two intersterile groups would be formed.

Parodi (cited by Connor, 1954) considered the genus Agropyron partly artificial, as separation of South American representatives of Elymus and Agropyron on the basis of morphological characteristics could not be achieved.

Classically, Elymus and Agropyron are separated on the basis of the number of spikelets occurring at each node of the rachis, the former having two and the latter one. Also, in Elymus the florets are oriented more or less dorsiventrally to the rachis while in Agropyron they are lateral. These characteristics are easily recognized in some species, but are not uniformly evident throughout the two groups. Such inconsistencies have led Gould (1947) to transfer the California species of Agropyron together with members of Sitanion and Hystrix to the genus Elymus. However, such a classification contributes very little to clearing up the confusion surrounding the complex and therefore has not received widespread favor. Stebbins and Walters (1949) concluded that there was not enough evidence to determine accurately the boundaries of the genus Agropyron but felt that further attempts of classification should await the development of a more natural system, based on cytological as well as morphological characteristics.

Currently there are approximately 150 recognized species of Agropyron. The genus is cosmopolitan; about 30 species are native to North America, 100 occurring in Eurasia, and the rest indigenous to South America or Australia. Since 1900 several exotic species have been introduced into the United States. Some, notably the Agropyron cristatum complex ("Crested wheatgrasses"), have been widely used in efforts to

rehabilitate depleted rangelands. Many have been used in breeding programs with the goal of incorporating desirable genes into the closely related domestic wheats.

In 1960 a research program was initiated at Montana State College, primarily concerned with the biosystematics of the genus Agropyron. The program involves morphological, cytological, ecological, genetic, chromatographic and serological studies of existing species and interspecific hybrids. The present study, a part of this program, is focused upon the Agropyron species native to Montana, selected as a workable group, even though artificially delimited.

A. MORPHOLOGICAL AND ECOLOGICAL STUDIES

I. GENERAL DISCUSSION

Booth (1950) listed fourteen species of Agropyron indigenous to Montana. Eleven of these, A. albicans, A. inerme, A. dasystachyum, A. griffithsii, A. smithii, A. saxicola, A. subsecundum, A. scribneri, A. spicatum, A. latiglume and A. trachycaulum were located during an extensive statewide survey. Herbarium collections at Montana State College, Montana State University, and the U. S. Forest Service, at Missoula, were examined and locations recorded for all of the Agropyron specimens available. Three supposed species (A. pseudorepens, A. bakeri and A. riparium) that are listed as occurring within the state could not be located by the author and no valid herbarium specimens were found. A. pseudorepens is listed by Beetle (1952) as a rhizomatous form of A. trachycaulum. Sterile hybrids apparently resulting from crosses of A. smithii and A. trachycaulum were found that fit the morphological descriptions of A. pseudorepens given by Hitchcock (1950) and Beetle (1952). Also, certain specimens of A. trachycaulum were collected that exhibit weakly developed rhizomes and could be misidentified as A. pseudorepens unless closely examined. Specimens representing either situation could explain the listed occurrence of this species within the state. A. bakeri and A. riparium, listed as resembling A. subsecundum and A. dasystachyum respectively (Hitchcock, 1950) may have been either overlooked, or if observed, considered as merely ecotypes of the latter two species and hence not collected. Herbarium specimens identified

as A. riparium were found actually to be representatives of A. dasystachyum grown under low moisture conditions.

One of the Agropyron species (A. griffithsii) while thought to occur within the state (Booth, 1950) was not represented in the collections studied. Another species (A. saxicola) had not been collected since 1914 (Hawkins, MONT. 31918). Both of these species were located and collected in the present study.

In order to avoid the problems involved in collecting specimens for conducting a study on such a group and to attempt to standardize procedures, it is a customary practice to utilize seed collections that are available from various supply sources. Such seed collections are subject to several sources of error. Natural hybridization is common in the wheatgrasses, related to their proximity, similar phenologies, profuse amounts of wind-borne pollen, self-incompatibility of some species and similarity of reproductive organs. These factors are compounded by the complexity of the species relationships within the group due to the large infraspecific variation that is prevalent in many of its members. For these reasons, a seed collection may not only be misidentified, but even if correctly identified as to species, may actually represent just a biotype within the broad range of variation included within that species. Therefore, original collections representing large, relatively pure populations are needed to represent adequately the species involved. No seed collections were used in this study, instead mature plants of each species were collected from such representative populations.

It is frequently noted that herbarium specimens are not truly representative of a species, their inclusion depending more upon ease of collection than upon taxonomic representation. There is also a tendency for herbarium collections to have an unusual number of unique ecotypes rather than those that are widespread throughout populations. By limiting collections to large, relatively pure populations, both the most prevalent biotypes and the range of variation within the species can be evaluated.

Ten plants of each species, in each case considered to represent adequately, the population sampled, were potted in eight-inch pots and transferred to the Montana State College Greenhouses in the summer and fall of 1962. Pertinent habitat information, including soil type, slope, exposure, associated species, and general climatic data (prevailing winds, precipitation, temperature) was recorded for each of the species. Herbarium samples of each were prepared and sent to the Smithsonian Institute, U. S. National Herbarium for verification. Voucher specimens were placed in both the National Herbarium and the Montana State College Herbarium at Bozeman. Whenever possible, pollen mother cell material was taken for cytological evaluation (Sec. D). Morphological measurements (Sec. B) were also made on a number of typical specimens of each of the species at the time of collection.

Each taxon is discussed in the following manner; (1) name and list of synonymy, (2) history of nomenclature, (3) ecological information, and (4) morphological description. The locations of the

populations selected for this study, together with the herbarium numbers assigned to the specimens placed in the Montana State College Herbarium, are summarized at the end of this section (Table I).

Associated species names are those used by Booth (1950).

Agropyron spicatum (Pursh) Scribn. & Smith

Agropyron spicatum (Pursh) Scribn. & Smith, U. S. Department Agr., Div. Agros., Bul. 4:33. 1897.

Festuca spicata Pursh, Fl. Amer. Sept. 1:83. 1814.

Schedonorus spicatus Roem. & Schult., Syst. Veg. 2:707. 1817.

Triticum divergens Nees ex Steud., Syn. Pl. Glum. 1:347. 1854.

Agropyron divergens Vasey, Desc. Cat. Grasses U. S. 96, 1885.

Agropyron divergens var. tenuis Vasey, Desc. Cat. Grasses U. S. 96. 1885.

Agropyron divergens var. tenuispicum Scribn. & Smith, U. S. Dept. Agr., Div. Agros. Bul. 4:37. 1897.

Agropyron vaseyi Scribn. & Smith, U. S. Dept. Agr., Div. Agros. Bul. 4:27. 1897.

Agropyron spicatum var. tenuispicum Rydb., N. Y. Bot. Gard. Mem. 1:61. 1900.

Agropyron spicatum var. vaseyi E. Nels., Bot. Gaz. 38:378, 1904.

Zeia spicata Lunell, Amer. Midl. Nat. 4:227. 1915.

Elymus spicatus Gould, Madrono 9:125. 1947.

A. spicatum was first described by Pursh in 1814 and named Festuca spicata. The type specimen was from the Lewis and Clark collection of 1806 taken along the Columbia river. It was later classified in the genera Schedonorus (Roem. and Schult., 1817) and Triticum

(Nees ex Steud, 1854). The name A. spicatum was coined and applied to what is now known as A. smithii by Scribner and Smith (1897) due to a misidentification, which was later clarified by Rydberg (1900). Pursh's original description calls for a long scabrous awn which clearly shows that a mistake was made when the name was applied to the species now known as A. smithii. Since Scribner & Smith included Festuca spicata in synonymy, they were publishing a new combination, Agropyron spicatum (Pursh) Scribner & Smith, rather than a new name. According to the Rules of International Botanical Nomenclature (Briquet, 1956) the new combination must be retained for the species to which the epithet was originally applied and attributed to the author who first published it. Scribner and Smith originally used the name A. divergens (Vasey) to describe what is now called A. spicatum. The first Montana collection was by Rydberg (No. 2299) in 1897.

A. spicatum, sometimes known as "Bluebunch Wheatgrass", is one of the most widespread wheatgrasses in the United States. Its range is from Alaska to northern California and New Mexico, including Montana and most of the western states. In the Pacific Northwest and Intermountain Region it is a dominant herbaceous species, forming up to sixty percent of foliage cover in some localities (Hoover et al. 1948). Its extensive distribution, abundance and drought resistance are directly related to its importance as a western range grass. In Montana it is found in greatest abundance in the central and western mountain regions, but it commonly occurs on hillsides in all areas of the state, chiefly on dry, gravelly soils in the open or in partial

shade.

This perennial bunchgrass often begins growth early in the spring and remains green until late in the summer. The new growth is palatable to livestock, but if unused the stem and leaf material tend to become wiry, affording little in the way of useable forage. On the bison range, at Moiese, Montana, it is utilized by buffalo chiefly as a winter feed after the snows have tended to soften the previous summer's cured foliage. It is heavily utilized by elk, whenever accessible, throughout the year.

Plant material was collected from a dominant population occurring west of the C. A. A. transmission tower located east of Belgrade, Montana, in an enclosed area that is leased by the Animal and Range Sciences Department and used for ecological investigations by the Botany Department of Montana State College. It has been subjected to only occasional accidental use since 1936 and is in excellent condition. Located at an altitude of 4450 feet, the area is subjected to frequent winds. Precipitation in the area is approximately thirteen inches, with eight inches falling between April and October. Soils are Beaverton gravelly loam (De Young and Smith, 1931) with underlying gravels. Associated species are Koeleria cristata, Poa secunda, Carex spp., and forbs such as Phlox hoodii, Lupinus sericius and Delphinium bicolor. In this area A. spicatum begins growth in late May, heads in mid-June and is fully mature by the middle of July. Between late July and September it is relatively dormant. With the advent of fall moisture a certain amount of regrowth is realized.

Seed set in the area is excellent. This population is uniform, upon analysis all specimens showing a chromosome number of $2n=14$.

A second population containing the chromosome complement of $2n=28$ was discovered near Whitehall, Montana in a Deer Lodge National Forest grazing area known as Wilson Park. This population is located along a hillside of moderate slope bordering a mountain meadow, exposed to fairly constant winds, at an elevation of approximately 5,200 feet. Precipitation figures for the area are not available, but a majority of the moisture falls in the form of a heavy snow cover during the winter months.

Associated species are Poa secunda, Stipa columbiana, and Koeleria cristata. The population appears to be uniform, all specimens collected showing the same chromosome number ($2n=28$).

A. spicatum is commonly found at altitudes ranging up to seven thousand feet, but one population comprised of a few low-stature individuals was located on a chromium mine dump in the Beartooth Plateau at an altitude of 10,200 feet. These specimens showed a distinct reddish tinge in the vegetative organs as well as in the inflorescence. In this population, as well as in several others observed, awn length was extremely variable, ranging from awn-tipped to long-awned.

Agropyron spicatum (Pursh) Scribn. & Smith ("Bluebunch wheatgrass")
The following description is based on the population occurring near Belgrade, Montana ($2n=14$).

General Characteristics: Perennial bunch grass, bluish to light green in color. Leaves mostly basal. Divergent awns of variable length, spikelets distant.

Culms: Slender, erect, 61-78 cm. tall, smooth, devoid of hairs. Internodes 10-16 cm. long, nodes smooth, dark, vernation rolled.

Blades: Leaves mostly basal, flat to tightly rolled when dry, 15 to 30 cm. long, 2 to 5 mm. wide. Sometimes hairy on upper surface, without hairs on lower surface. Upper surface prominently veined, scabrous, midrib prominent on lower surface. Auricles absent to rudimentary.

Sheath: Round, split with overlapping scarious margins, smooth veins, indistinct, often reddish below ground. Collar continuous to sometimes divided by midrib, glabrous, light green.

Ligule: Short, 1/2 mm wide, membranous, lacerate, truncate.

Inflorescence: Terminal, 2 sided spikes 8-20 cm. long. Spikelets distant, overlap 1/3 to 1/2. Spike slender, divergent awns. Rachis smooth.

Spikelets: 6 to 8 flowered, 1-2 cm. long, disarticulating above the glumes.

Glumes: 5 to 7 mm. long, about 1/2 as long as spikelet, 3 to 4 nerved. Narrow, 1 mm. wide, pointed but not awned, equal.

Lemma: About 9 mm. long, the awn strongly divergent, usually 10-17 mm. long. Rounded to keeled above, 4 to 5 nerved, faintly nerved, smooth, scarious margins.

Palea: Slightly longer than lemma, scabrous on 2 keels.

Fruit: Grain enclosed in lemma, adherent to palea.

Location and Abundance: Dry plains and foothills across the state; common.

Agropyron inerme (Scribn. & Smith) Rydb.

Agropyron inerme (Scribn & Smith) Rydb., Torrey Bot. Club
Bul. 36:539. 1909.

Agropyron divergens var. *inerme* Scribn. & Smith, U. S. Dept.
Agr., Div. Agrost. Bul. 4:27. 1897.

Agropyron spicatum inerme Heller, N. Amer. Pl. Cat. ed.
2. 3. 1900.

A. inerme was first named *A. divergens* var. *inerme* and described by Scribner & Smith in 1897 as a variety of what is now known as *A. spicatum*. The type specimen was collected by Henderson (No. 3058) in Idaho. The name *A. inerme* was applied by Rydberg (1909) based on Scribner and Smith's type description.

Known in vernacular as "Beardless Bluebunch Wheatgrass" it is taxonomically differentiated from *A. spicatum* only upon the basis of the absence of awns. The validity of separating these apparently closely related taxa into species has been questioned by some who regard *A. inerme* as only a variety of *A. spicatum* (Daubenmire 1939, Beetle 1952).

A. inerme is rare in Montana, the only previously recorded specimens from Montana occurring in the Polson region. Another population was located by the author in an area known as Pleasant Valley, near Libby, which furnished the specimens used in the present study. Approximately one acre in size, it was located on a slight slope with a southern exposure. Elevation is approximately 4,400 feet. Soil is a silty loam underlain by gravel. Although plants of *A. spicatum* in

the vicinity showed gradations in awn length, the population was uniformly awnless. Associated species are A. spicatum, Stipa columbiana, Koeleria cristata and Poa secunda. The habitat is characteristic of A. spicatum, so it does not appear that the two could be separated on the basis of their ecological requirements. Heading dates and other vegetative stages of maturity are identical for the two species based on their growth in the field plot. Chromosome counts for all specimens examined were $2n=14$.

Agropyron inerme (Scribn. & Smith) Rydb. (Beardless Bluebunch Wheatgrass)

The following description is based on the population occurring at Pleasant Valley, located near Libby, Montana ($2n=14$).

Perennial bunch grass resembling A. spicatum (Pursh.) Scribn. & Smith but lacking awns.

General Characteristics: Perennial bunchgrass, poor seed former. Many sterile florets.

Culms: 45-78 cm. tall, erect, often bent upward at node. Internodes 12 to 17 cm. long. Culms slender, smooth, devoid of hairs. Nodes conspicuous, smooth.

Blades: Leaves mostly basal. Basal leaves 15-30 cm. long. Upper leaf 6 to 10 cm. long. Blades 1-4mm. wide, flat or rolled inward. Upper surface with or without hairs, prominently herved above, without hairs on lower surface. Auricles are rudimentary.

Sheath: Split, margins overlapping, smooth, membraneous on edges, not hairy, round. Collar smooth, divided by midrib. Vernation rolled.

Ligule: Extremely short, less than 1/2 mm. membraneous, truncate.

Inflorescence: Terminal, 2 sided spikes 8-20 cm. long. Spike-

lets overlapping $1/3$ to $1/2$, 15 to 22 spikelets. Rachis scabrous.

Spikelets: 1 to 2 cm. long, 6-8 flowered, many sterile florets. Usually single at each node, side of spikelet toward rachis, rachilla disarticulating above the glumes and between the florets.

Glumes: 6 to 9 mm. long, $1/3$ to $1/2$ as long as spikelet, equal, acute, strongly nerved, 4-5 nerves, nerves often scabrous, usually pubescent on inner surface of glume.

Lemma: 5 to 10 mm. long, narrowing from the base, 5 to 7 faintly nerved, rounded on the back to slightly keeled above.

Palea: As long or longer than lemma, bifid at apex, 2 keels toothed.

Fruit: Grain enclosed in lemma adherent to palea.

Location and Abundance: Dry foothills and plains in western Montana. Rare.

Agropyron scribneri Vasey

Agropyron scribneri Vasey, Torrey Bot. Club Bul. 10:128. 1883.

Elymus scribneri Jones, West. Bot. Contrib. 14:20. 1912.

A. scribneri was named and described by Vasey (1883). It was named in honor of F. L. Scribner who collected it on Lone Mountain in the Gallatin Range in 1883. However, Vasey mentions a previous collection by C. G. Pringle in the Sierras in 1882 which was distributed as Triticum caninum L.

One of the rarest of the Montana wheatgrasses is A. scribneri, called "Scribner's Wheatgrass" or "Spreading Wheatgrass". Restricted to the alpine zone, it has been collected in three localities in Montana; the Beartooth Plateau near Red Lodge, Lone Mountain

in the Gallatin Range near Bozeman, and Fairy Lake near Bozeman. It may well occur in many remote alpine areas but has not been widely collected.

A large population scattered over an area of several miles was located in the Beartooth Plateau near the Montana-Wyoming border. It is one of the dominant grasses in the region that is geographically centered around Boundary Lake. Representative samples were collected on a south slope at an elevation of 10,500 feet. Associated species include Carex spp., Trifolium spp., Deschampsia caespitosa, Trisetum spicatum, Artemisia scopulorum and Antennaria spp. The soil would be classified as an alpine meadow type (Retzer, 1956). These soils are highly organic, being black to dark brown in color. The texture is a loamy sand, with a rocky subsoil. Subsoil temperatures are comparatively low, even in the summer months. Afternoon showers are a daily occurrence during the summer. No precipitation records are available for the region, but the entire area is under snow from early September until mid-July. Date of maturity is approximately mid-August, with seed production being profuse.

Variation in growth habit is readily apparent. On fine textured soils composed of primarily organic matter plants are three to five inches in diameter with from one to three seed heads. Wherever small sand pockets occur the plants are much larger, the bunches being up to ten inches in diameter and having from eight to fifteen seed heads. This difference may be due to the higher soil temperatures that are characteristic of the coarser textured soils. A. scribneri is also

common in the vicinity of lava outcrops in the Beartooth region.

Johnson (1962) found A. scribneri to be most abundant on soils derived from redeposited volcanic material in alpine regions in Wyoming.

Agropyron scribneri Vasey (Scribner wheatgrass)

The following description is based on the population occurring near Boundary Lake in the Beartooth Plateau ($2n=28$).

General Characteristics: Low-stature alpine perennial bunchgrass without rhizomes.

Culms: 20 to 40 cm. long, reclining or spreading along the ground, usually abruptly bent upward, round, smooth, faintly nerved; nodes dark, glabrous.

Blades: Mostly basal, 2 to 5 mm. wide, rigid, pubescent on both surfaces, flat or rolled tightly when dry, blades short, 5 to 10 cm. long, usually 2 to 3 blades per stem, midrib prominent, margins very narrow, auricles less than 1mm., not clasping, whitish in color.

Sheath: Round, split with overlapping scarious margins, retrorsely short pubescent, especially on the lower sheaths, old sheaths very persistent, often pinkish at the base. Vernation rolled, collar divided, very faint.

Ligule: Membranous, short, 5 mm. long, truncate, ciliate.

Inflorescence: Terminal, 2 sided spikes, flexuous, dense, 3 to 8 cm. long, closely overlapping $1/2$ to $3/4$, entire head easily broken from stalk when dry, awns very divergent, rachis scabrous on margins, often purple where florets attach.

Spikelets: 10 to 15 mm. long, 2 to 5 flowered, rachilla scabrous on margins, disarticulating readily between florets and above glumes.

Glumes: 4 to 8 mm. long, narrow, 1mm. wide, keeled, 1 slightly longer having more pronounced nerves, 3 to 5 nerves, both having scarious margins, scabrous on margins and keel, tapering into a divergent awn, 10 to 15 mm. long, the longer glume often having a bifid apex, the shorter awn being 1 to 3 mm.

Lemma: 7 to 10 mm. long, keeled, 4 to 5 faint nerves, scabrous on the outer side, scarious margins, tapering into an awn 15 to 25 mm. long, the awns very divergent when dry.

Palea: Slightly longer than the lemma, scabrous-short pubescent on both surfaces, especially the margins of the 2 keels, the apex with 2 short teeth, also scabrous.

Fruit: Grain enclosed in lemma, adherent to palea.

Location and Abundance: Alpine areas. Not widely collected.

Agropyron latiglume (Scribn. & Smith) Rydb.

Agropyron latiglume (Scribn. & Smith) Rydb., Torrey Bot. Club Bul. 36:539, 1909.

Agropyron violaceum var. *latiglume* Scribn. & Smith, U. S. Dept. Agri., Div. Agros. Bul. 4:30. 1897.

Agropyron biflorum *latiglume* Piper, Torrey Bot. Club Bul. 32:547. 1905.

Agropyron caninum var. *latiglume* Pease and Moore, Rhodora 12:73. 1910.

Roegneria latiglumis Nevski, Akad. Nauk U.S.S.R. Bot. Inst. Trudy I. 2:55. 1936.

A. latiglume was first described by Scribner & Smith (1897) and named *A. violaceum* var. *latiglume*. The type specimen was one collected by Tweedy (No. 1011) on Lone Mountain in Gallatin County, Montana, in 1886. The name *A. latiglume* was applied by Rydberg (1909) based on this specimen.

Sometimes called "Subalpine Wheatgrass", it and *A. scribneri* are the only alpine species of *Agropyron* native to Montana. Although often classed as an alpine species, a large population was found well below timberline at 8000 feet at the head of the Stillwater River

near Cooke City. In this area it tends to assume a sod-forming habit instead of the usual bunch type of growth. Two other distinct ecotype populations were found within the state. One of these populations was located in the vicinity of Logan Pass in Glacier National Park. It occurs at 6,000 feet on a talus slope. Large forbs, sedges, and grasses such as Trisetum spicatum and Bromus marginatus occur in the area. Collections were made the latter part of August at which time seed had set. This ecotype is much larger and not as leafy as the second ecotype, which occurs in the Beartooth Plateau. The Beartooth collection was made at 10,000 feet on a south-facing slope of 10°. A. latiglume occurs in scattered populations at the higher elevations across the Beartooths. It is restricted to rocky outcrops in the area, seldom occurring on the alpine turf. The soils in these outcrops are of decomposed granite with little to no organic matter present. Soil temperature appears to be a major factor, as the most vigorous plants grow adjacent to granite boulders, their matted roots completely exposed to the rock surface. Plant material was collected in early September, at which time seed had matured, and the plants showed the effect of frost. It does not appear to be as well adapted to the alpine zone as A. scribneri, but instead better suited to the sub-alpine zone. In the Stillwater area, which would be classified as subalpine, it makes up ten to twenty percent of the vegetation on the slopes about dwarf willow bottoms. These plants are much more vigorous than the alpine type, reaching heights of 14-18 inches as compared to the 8-10 inch ecotype of the alpine region. The alpine plants are

also leaflier than the subalpine form.

Agropyron latiglume (Scribn. & Smith) Rydb. (Subalpine Wheatgrass)

The following description is based on the population occurring in the Beartooth Plateau ($2n=28$).

General Characteristics: Perennial without creeping rhizomes, bright green, leafy, alpine or subalpine species, forming leafy bunches, distinctive ecotypes in Montana.

Culms: 20 to 50 cm. tall, loosely tufted, curved or bent upward at the base, smooth to distinctively nerved, glabrous, nodes glabrous, culms slender, somewhat flattened.

Blades: Bright green, numerous, 3 to 8 mm. wide, flat, 10 to 20 cm. long, lax, scabrous to short pubescent on both surfaces, conspicuously veined, midrib prominent towards base, narrow, scarious scabrous margins, tips boatshaped. Auricles small to rudimentary.

Sheaths: Round, smooth to ribbed with overlapping scarious margins, glabrous to lightly pubescent, old sheaths persistent, bases often purplish, sheaths often largely enclosing inflorescence at maturity with upper flag leaf extending vertically from the tip. Vernation rolled. Collar divided, not distinct.

Ligule: Membraneous, .5 to 1 mm. long, obtuse, ciliate.

Inflorescence: Terminal, 2 sided spikes, very compact, 5 to 10 cm. long, erect, rachis smooth, margins scabrous, spikelets sometimes in pairs.

Spikelets: 8 to 15 mm. long, overlapping $1/2$ to $2/3$, 2 to 4 mm. wide, 3 to 5 flowered, rachilla pubescent, disarticulating above the glumes and between the florets.

Glumes: 6 to 10 mm. long, almost as long as the spikelet, broad, 1.5 to 2.5 mm. wide, rounded, 3 to 5 prominent nerves, smooth to scabrous, with broad hyaline margins, margins smooth, wider on one side than the other, awn tipped, awn 1 to 2 mm. in length, tending to extend from side with narrower margin.

Lemmas: 4 to 6 nerved, the nerves becoming more prominent at tip, 2 extending out to form 2 short teeth, lemmas 8 to 10 mm. long, 2 mm. wide, rounded, scabrous to short pubescent, with scarious margins. Some ecotypes show broad hyaline margins with short awn tip 1 to 2 mm. long.

Palea: About as long as the lemma, scabrous on the margins of the 2 keels, short pubescent near the tip. Apex sometimes bifid.

Fruit: Grain, light colored, short pilose at upper tip, grain enclosed in lemma, adherent to palea.

Location and Abundance: Alpine to subalpine areas across the state. Scattered around boulders and lava outcrops.

Agropyron trachycaulum (Link) Malte

Agropyron trachycaulum (Link) Malte, Canada Natl. Mus. Ann. Rpt. 1930. (Bul. 68): 42: 1932.

Triticum pauciflorum Schwein., in Keat., Marr. Exped. St. Peters River, 2:383. 1824.

Triticum missuricum Spreng., Syst. Veg. 1:325. 1825.

Triticum trachycaulum Link, Hort. Berol. 2:189. 1833.

Agropyron trachycaulon Steud., Syn. Pl. Glum. 1:344. 1854.

Crithopyrum trachycaulon Steud., Syn. Pl. Glum. 1:344. 1854.

Agropyron tenerum Vasey, Bot. Gaz. 10:258. 1885.

Agropyron violaceum var. majus Vasey, U. S. Natl. Herb. Contrib. 1:280. 1893.

Agropyron repens var. tenerum Beal, Grasses N. Amer. 2:637. 1896.

Agropyron tenerum var. longifolium Scribn. & Smith, U. S. Dept. Agr., Div. Agrost. Bul. 4:30. 1897.

Agropyron tenerum var. ciliatum Scribn. & Smith, U. S. Dept. Agr., Div. Agrost. Bul. 4:30, 1897.

Agropyron novae-angliae Scribn. in Brain., Jones, and Eggl., Fl. Vt. 103. 1900.

Agropyron tenerum var. majus Piper, Torrey Bot. Club Bul. 32:543. 1905.

Agropyron tenerum var. trichocoleum Piper, Torrey Bot. Club Bul. 32:546. 1905.

Agropyron caninum var. tenerum Pease & Moore, Rhodora 12: 71. 1910.

Agropyron caninum var. tenerum forma ciliatum Pease & Moore, Rhodora 12: 72. 1910.

Agropyron caninum var. tenerum forma fernaldii Pease and Moore, Rhodora 12: 73. 1910.

Agropyron caninum var. hornemanni forma pilosifolium Pease and Moore, Rhodora 12: 75. 1910.

Zeia tenera Lunell, Amer. Midl. Natl. 4: 227. 1915.

Agropyron tenerum var. novae-angliae Farwell, Mich. Acad. Sci. Rpt. 21: 355. 1920.

Agropyron missuricum Farwell, Amer. Midl. Natl. 12: 48. 1930.

Agropyron trachycaulum var. tenerum Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 44. 1932.

Agropyron trachycaulum var. glaucescens Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 45. 1932.

Agropyron trachycaulum var. trichocoleum Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 45. 1932.

Agropyron trachycaulum var. fernaldii Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 46. 1932.

Agropyron trachycaulum var. majus Fernald, Rhodora 35: 171. 1933.

Agropyron trachycaulum var. novae-angliae Fernald, Rhodora 35: 174. 1933.

Agropyron pauciflorum Hitchc., Amer. Jour. Bot. 21:132. 1934.

Roegneria trachycaulon Nevski in Komarov, Fl. U.R.S.S. 2:599. 1934.

Roegneria pauciflora Hylander, Uppsala Univ. Årsk. 7: 36, 89. 1945.

Elymus pauciflorus Gould, Madrono 9: 126. 1947.

A. trachycaulum was apparently first collected in 1824 in Minnesota and given the name Triticum pauciflorum Schwein. Another possible collection was made in 1825 along the Missouri and given the name T. missuricum Spreng.. In 1833 Link gave the name T.

trachycaulum to specimens grown from seed collected by Richardson in "North America". A. trachycaulum Steud. was applied as a synonym to this material. The name A. tenerum, still used by many workers, was applied by Vasey in 1885. Malte (1932), in an intensive taxonomic study of this species, applied the name A. trachycaulum to the type known as I. trachycaulum Link and used varietal names to distinguish other types previously collected. The name A. violaceum (Hornem.) Lange is often applied to alpine forms of this species.

A. trachycaulum, known as "Slender Wheatgrass", is the most widely distributed of all the native wheatgrasses, ranging from Newfoundland to California. In Montana it is common on most of the well drained slopes and river bottoms across the state. It occurs mostly on light, sand-loam soils, but it is also found in dry mountain valleys, meadows and open timberlands up to and including the alpine zone. It has a fairly high drought resistance and is exceeded in alkali tolerance among the native wheatgrasses only by A. smithii.

A. trachycaulum is the largest of the native wheatgrasses, ranging up to four feet in height with some bunches reaching a foot in diameter. It is often cut for hay in the mountain valleys, being highly palatable to livestock. On winter game ranges that are not overused it is a major source of nutrition of big game populations.

Representative plant samples were selected from a large population located on the slopes of the Bridger Range bordering Reese Creek in the Gallatin Valley near Bozeman. Slopes are variable,

ranging from five to fifteen degrees with southerly exposure. Soils range from a silty loam along the stream to coarse-textured decomposed granite on the slopes above. Associated species include Bromus marginatus, Poa secunda, Phleum alpinum and Spiraea spp. Plants are of the typical lowland type, having broad glumes with the spikelets well separated. Seed matures in August, and seed production is excellent in the area, which receives little to no grazing use by domestic animals. In this area A. trachycaulum commences growth in June and remains green until damaged by frost in late fall.

Agropyron trachycaulum (Link) Malte. (Slender wheatgrass)

The following description is based on the population occurring at Reese Creek near Bozeman, Montana ($2n=28$).

General Characteristics: Perennial, without rhizomes, often forming large leafy bunches.

Culms: 50 to 100 cm. tall, dark green, round, smooth, faintly nerved, nodes glabrous, culms erect.

Blades: Leaves mostly basal, tufted, 3 to 10 mm. wide, 10 to 30 cm. long, flat to loosely rolled when dry, upper and lower surface smooth to scabrous, narrow margins scarious, somewhat scabrous, blades hairless. Auricles small, 1 mm. long and less, sometimes missing clawlike and loosely clasping if present, whitish to purplish in color.

Sheath: Smooth, round, split with overlapping scarious margins, margins smooth, usually hairless but lower ones sometimes short pubescent, often pinkish at base. Midrib white rather prominent. Vernation rolled. Collar divided, not too distinct.

Ligule: .5 to 1 mm. long, membranous, obtuse, ciliate.

Inflorescence: Terminal, 2 sided spikes 10 to 25 cm. long, spikelets distant to closely overlapping, spike slender, erect to somewhat nodding, rachis smooth, scabrous on margin.

Spikelet: 10 to 18 mm. long, 3 to 7 flowered, rachilla margins scarious and scabrous, disarticulating above the glume and between the florets.

Glumes: Broad, rounded, "Beetle backed", almost as long as the spikelets, ridges, 4 to 7 prominent nerves, fairly wide, scarious margins, glumes equal, acuminate, often awn tipped.

Lemma: 8 to 12 mm. long, scarious margins somewhat scabrous, 4 to 6 faint nerves, rounded, smooth, acuminate to awn tipped.

Palea: Somewhat shorter than the lemma, scabrous on the margins of the keels, glabrous.

Fruit: Grain enclosed in lemma, adherent to palea.

Location and Abundance: Common along mountain streams, valleys, parks and all areas of moderate moisture across the state.

Agropyron subsecundum (Link) Hitchc.

Agropyron subsecundum (Link) Hitchc., Amer. Jour. Bot. 21:131. 1934.

Triticum subsecundum Link, Hort. Berol. 2:190. 1833.

Triticum richardsoni Schrad., Linnaea 12: 467. 1838.

Agropyron richardsoni Schrad., Linnaea 12:467. 1838.

Cryptopyrum richardsoni Heynh., Nom. 2:174. 1846.

Agropyron unilaterale Cassidy, Colo. Agr. Expt. Sta. Bul. 12: 63. 1890.

Agropyron caninum var. unilaterale Vasey, U. S. Natl. Herb. Contrib. 1:279. 1893.

Agropyron violaceum forma caninoides Ramaley, Minn. Bot. Studies 1:108. 1894.

Agropyron caninum forma violacescens Ramaley, Minn. Bot. Studies 1:107. 1894.

Agropyron violacescens Beal, Grasses N. Amer. 2:635. 1896.

Agropyron caninoides Beal, Grasses N. Amer. 2: 640. 1896.

Agropyron caninum var. pubescens Scribn. & Smith, U.S. Dept. Agr., Div. Agrost. Bul. 4:29. 1897.

Agropyron richardsoni var. ciliatum Scribn. & Smith, U.S. Dept. Agr., Div. Agrost. Bul. 4: 29. 1897.

Agropyron caninum forma glaucum Pease & Moore, Rhodora 12: 71. 1910.

Agropyron caninum var. unilaterale forma ciliatum Pease & Moore, Rhodora 12: 76. 1910.

Agropyron caninum var. richardsoni Jones, West. Bot. Contrib. 14: 18. 1912.

Zeia richardsoni Lunell, Amer. Midl. Nat. 4: 227. 1915.

Agropyron trachycaulum var. unilaterale Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 46. 1932.

Agropyron trachycaulum var. ciliatum Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 47. 1932.

Agropyron trachycaulum var. caerulescens Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 47. 1932.

Agropyron trachycaulum var. glaucum Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 47. 1932.

Agropyron trachycaulum var. pilosiglume Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 48. 1932.

Agropyron trachycaulum var. hirsutum Malte, Canada Natl. Mus. Ann. Rpt. 1930 (Bul. 68): 48. 1932.

Elymus pauciflorus subsp. subsecundus Gould, Madrono 9: 126. 1947.

A. subsecundum was first named Triticum subsecundum by Link in 1883, based on a garden plant raised from seed collected by

Richardson in "Western North America". It was later thought to be the same species as A. caninum (L.) Beauv., an Old World species which it closely resembles. However, an intensive taxonomic study by Malte (1932) resulted in clearly showing the two to be distinct species. The name A. subsecundum was applied by Hitchcock (1934) based on the type I. subsecundum Link. It is often referred to in the older literature as A. unilaterale Cassidy. It was first collected in Montana by F. L. Scribner in 1883 (No. 422) under the name A. caninum var. unilaterale Vasey.

An apparently closely related species to A. trachycaulum is the lesser known A. subsecundum, known as "Bearded Wheatgrass". Some authorities (Beetle 1952) classify it as being an awned variety of A. trachycaulum. Although an abundance of awned A. trachycaulum was observed throughout the state, the author considers that A. subsecundum is a separate species, as its growth habit and appearance in this region readily distinguish it from A. trachycaulum.

A. subsecundum is common on the north slopes of the Bridger Range in Gallatin County at approximately 7,000 feet. It apparently has a high moisture requirement and seldom if ever occurs on dry southern slopes in the area. Representative samples were selected from a large population on Flathead Pass of the Bridger Range at 7,000 feet. The population occurs on a north slope of approximately eight percent. The soil is a deep silty loam, showing a high moisture content. Associated species include Phleum alpinum, Bromus marginatus and scattered plants of Koeleria cristata. Little domestic grazing

pressure is evident, but pocket gophers, numerous in the area, utilize a considerable amount of the available forage.

The area is subjected to relatively constant southwesterly winds. Growth habit is distinct, the plants being more or less single stalked, with two or three leaves scattered along the stalk, the sheaths highly pubescent. Upon maturity the spikelets twist to one side of the rachis, giving a definite "flagged" appearance to the plant. This does not seem to be a response to some environmental factor because of the apparent randomness of the twisting. The same characteristic is shown by plants in the field plot.

Agropyron subsecundum (Link) Hitch. (Bearded wheatgrass)

The following description is based on the population occurring on Flathead Pass in the Bridger Range in Gallatin County, Montana (2n=28).

General Characteristics: Green or glaucous perennial, without rhizomes, long awned. The spikelets commonly twist to one side giving a "flagged" appearance.

Culms: 30 to 70 cm. tall, erect, smooth, nodes glabrous, seed stalks conspicuous, often solitary with 2-4 flag leaves. Internodes short, 6 to 10 cm. Vernation rolled.

Blades: Leaves mostly basal, 15 to 25 cm. long, 3 to 8 mm. wide, flat, tapering to a boat-tailed sharp point. Upper surface ridged, scabrous to pubescent, hairs 1 to 2 mm. long, margins white, densely scabrous. Lower surface scabrous to densely pubescent. Upper flag leaf at base of inflorescence.

Sheaths: Round, split with overlapping scarious margins. Sheaths glabrous but often heavily retrorsely pubescent on primary basal sheath. Collar divided by midrib, glabrous, well defined, light green. Auricles if present clawlike, clasping, 1 mm. long, whitish in color.

Ligule: Membraneous, 1 mm. long, obtuse, lacerate, brownish when mature.

Inflorescence: Terminal, 2 sided spike, unilateral when mature due to twisting of the spikelets to one side of the rachis resulting in "flagged" appearance. Spike 10 to 25 cm. long, erect to slightly nodding, dense head, long awned, rachis scabrous margined.

Spikelets: Rather closely imbricate, 1 to 2 cm. long, 4 to 8 flowered. Rachilla densely long hairy, disarticulating above glumes and between florets. Callus of the florets short-pilose.

Glumes: Broad, 2-3 mm. wide, equal, 7-15 mm. long, rigid, rounded, 4 to 6 prominent nerves, glumes almost as long as spikelet, tapering into an awn 6-10 mm. long.

Lemmas: 6 to 10 mm. long, shorter than glumes, margins scarious, 5 nerved, rounded, awns over twice as long as lemma, awns straight, densely scabrous.

Palea: Slightly shorter than lemma, densely scabrous on margins of 2 keels.

Fruit: Grain enclosed in lemma, adherent to the palea.

Location and Abundance: North slopes in the higher mountain areas of southwestern Montana. Limited occurrence within the state.

Agropyron smithii Rydb.

Agropyron smithii Rydb., N. Y. Bot. Gard. Mem. 1:64. 1900.

Agropyron glaucum var. occidentale Scribn., Kans. Acad. Trans. 9: 119. 1885.

Agropyron occidentale Scribn., U. S. Dept. Agr., Div. Agrost. Circ. 27: 9. 1900.

Zeia occidentalis Lunell, Amer. Midl. Nat. 4: 226. 1915.

Zeia smithii Lunell, Amer. Midl. Nat. 4: 227. 1915.

Agropyron spicatum var viride Farwell, Mich. Acad. Sci. Rpt. 21: 356. 1920.

Elymus smithii Gould, Madrono 9: 127. 1947.

Agropyron smithii var. typica Waterf., Rhodora 51: 21.
1949.

Agropyron smithii var. molle (Scribn. & Smith) Jones,
West. Bot. Contrib. 14: 18. 1912.

Agropyron spicatum var. molle Scribn. & Smith, U. S. Dept.
Agr., Div. Agrost. Bul. 4: 33. 1897.

Agropyron molle Rydb., N. Y. Bot. Gard. Mem. 1: 65. 1900.

Agropyron occidentale var. molle Scribn., U. S. Dept.
Agri., Div. Agros. Circ. 27: 9. 1900.

Zeia mollis Lunell, Amer. Midl. Nat. 4: 226. 1915.

Agropyron smithii var. palmeri Heller, N. Amer. Pl. Cat.
ed. 2: 3. 1900.

Agropyron spicatum var. palmeri Scribn. & Smith, U.S.
Dept. Agri., Div. Agrost. Bul. 4: 33. 1897.

Agropyron occidentale var. palmeri Scribn., U.S. Dept.
Agri., Div. Agrost. Cir. 27: 9. 1900.

Agropyron palmeri Rydb., Colo. Agr. Expt. Sta. Bul. 100:
55. 1906.

A. smithii was originally described by Scribner and Smith (1897) and given the name A. spicatum. Scribner and Smith included Festuca spicata Pursh (1814), Triticum missuricum Sprengel and A. glaucum occidentale Vasey in synonymy. The type specimen was given as Geyer, "Upper Missouri". However, as they included F. spicata Pursh in synonymy they were publishing a new combination rather than a new name, and therefore the new combination was retained for the original species described by Pursh. Rydberg (1900) was the first to notice that Scribner and Smith had confused two species and therefore renamed the one they described A. smithii.

The pubescent form, *A. smithii* var. *molle* (Scribn. and Smith) Jones is based on *A. spicatum* var. *molle* Scribn. and Smith (1897). The type specimen is one collected by Rydberg in Montana. (No. 3193).

A. smithii, known as "Western Wheatgrass", ranges in western North America from Canada to Texas, being one of the commonest of the wheat-grasses in the Great Plains. Its distinctive bluish color and rigid, upright growth habit are well known in Montana. Most abundant on well drained bottom lands, it is also common on open plains, hillsides and benchlands throughout the state. It is often found on overflow areas along streams, being able to withstand up to a foot of soil deposition and still survive (Mueller, 1941). Although it produces an abundance of seed its major means of propagation is by rhizomes which reach six to eight feet in length in favorable overflow areas.

It is one of the first grasses to populate abandoned fields. According to Weaver and Clements (1938) this is the result of shallow tillage practices, which break up but do not destroy the hardy rhizomes. Under such circumstances complete revegetation occurs in 3 to 5 years. Where the rhizomes have been destroyed or colonization is initiated, the process may take from 20 to 40 years.

Representative collections were made from two areas. A large, pure population was found growing on an overflow area on Slim Sam Creek near Radersburg. This area is a level outwash fan composed of a deep deposition of heavy, clayey soil overlying the normal silt found in the area. On the fan, scattered plants of *Stipa viridula* and *Opuntia polyacantha* were present while on the neighboring non-

alluvial areas A. spicatum was the dominant species. Precipitation is approximately eight inches in the area with little to no grazing use. Many of the plants show heavy infestations of ergot and nematodes (Collins, 1965). Plants having two spikelets per node are common in the population.

The second collection was made in the Belgrade area from a population growing in the bottom of a swale. Both the typical A. smithii and the pubescent type known as A. smithii var. molle occur in the population. The soil tends to be alkaline in nature and is subjected to periodic runoff from the surrounding area. Growth begins in May with seed maturing in August in this area, with the plants remaining in a green growing condition until late fall.

Agropyron smithii - Rydberg (Western Wheatgrass)

The following description is based on the population occurring at Slim Sam Creek near Radersburg, Montana ($2n=56$).

General Characteristics: Glaucous perennial with strong, extensively creeping rhizomes and a deep fibrous root system.

Culms: 26 to 80 cm. tall, striate when dry, smooth, rigid, erect, glabrous with two to five glabrous, yellowish-brown nodes. Offshoot leaves in loose tufts, smaller than those of the culm, culm leaves 3 to 5, decreasing in size upwards, with sterile shoots from the very base.

Blades: 5 to 25 cm. long, bluish green, 3 to 5 mm. wide, rigid and spreading, flat or involute, prominently ridged and scabrous on upper surface, glaucous. Margin finely barbed, lower surface smooth. Auricles .2 to 1.0 mm. long, acute, clawlike and clasping, often purplish.

Sheath: Striate when dry, smooth, glabrous, rarely pilose, round, split with scarious margins, veins fairly distinct,

white at the base. Collar continuous, not distinct, glabrous, light green.

Ligule: Membraneous, very short, .5 mm. long, glabrous, lacerate to ciliate.

Inflorescence: Terminal, stiffly erect, 2 sided spike, 7-15 cm. long, exserted, lower four rachis nodes often sterile, spikelets rather closely overlapping, rachis scabrous on the margins.

Spikelets: 1 to 2 cm. long, sometimes two at a node, 2 to 12 flowered, glabrous, acute compressed, divergent when mature. Rachilla scabrous to short pubescent, disarticulating above the glumes and between the florets.

Glumes: 6 to 12 mm. long, acuminate or awn tipped from below the middle, $1/2$ to $2/3$ as long as the spikelet, the first glume slightly longer than the second, 3 to 5 nerved, keeled, subcoriaceous and rigid, scabrous on margins and keel, margins scarious, tapering into a short awn, glabrous or variously pubescent, blue green.

Lemma: 8 to 12 mm. long, including the awn, lanceolate, acuminate to short awn tipped, smooth with scabrous scarious margins, broad, rounded rigid, often pubescent at the base, obscurely nerved.

Palea: As long as or slightly shorter than the lemma, scabrous to pubescent on the two keels, veins finely ciliate.

Fruit: Grain enclosed in lemma, adherent to palea, densely pilose on the callus, purple-brown in color.

Location and Abundance: Common on overflow areas and heavier soils throughout the state.

Agropyron griffithsii Scribn. & Smith

Agropyron griffithsii Scribn. & Smith ex Piper, Biol. Soc. Wash. Proc. 18: 148. 1905.

Agropyron albicans var. griffithsii (Scribn. & Smith) Beetle, Wyo. Ag. Expt. Sta. Bul. 312: 13. 1952.

A. griffithsii was first named by Scribner and Smith but described by Piper in 1905. The type specimen was collected by

Williams and Griffiths in Wyoming. Piper notes that "the species is near A. albicans but readily separable by its nearly smooth flowering glume".

A. griffithsii, sometimes known as "Griffiths' Wheatgrass", is a little known species that has never before been reported in Montana. Sometimes classified as a variety of A. albicans (Beetle 1952) it differs chiefly in having glabrous lemmas. However, several populations of A. albicans were located that were varied in the amount of pubescence they exhibited, often being completely glabrous, but still definitely identifiable as A. albicans. A small population of wheatgrasses was found in the vicinity of the Deep Creek Canyon near Townsend that was observed to be a different species. The area is approximately 6,000 feet in elevation. The population occurs in an old stream bed or overflow area that has since been revegetated. Soil is a sandy-silt of two to three feet in depth underlain by shale. Vegetational cover is excellent, with associated species predominantly A. trachycaulum, Phleum alpinum, Poa pratense and numerous forbs. Precipitation is approximately twelve inches in the region, however the area receives a large amount of runoff from the upper slopes. The habitat is definitely not typical for wheatgrass species other than A. trachycaulum. Herbarium specimens were confirmed by Dr. J. R. Swallen as being A. griffithsii. Chromosome number, determined by the author, was found to be $2n=28$ for all specimens.

Agropyron griffithsii Scribn. & Smith (Griffiths' Wheatgrass)

The following description is based on the population occurring at Deep Creek near Townsend, Montana ($2n=28$).

General Characteristics: Perennial, with creeping rhizomes, tends to form open tufts, leaves mostly basal, tall, robust seed stalks, long awned.

Culms: 35 to 90 cm. tall, dark green, round, smooth but becoming short-scabrous just below inflorescence, thick, rigid, often bent upward at the nodes, nodes glabrous, quite pronounced, stems erect but bending at maturity.

Blades: Mostly basal, flat to rolled inward when dry, 15 to 40 cm. long, 2 to 7 mm. wide, upper surface ridged, scabrous, lower surface smooth to slightly scabrous, midrib prominent towards base, margins scarious, scabrous, tips boatshaped, blades hairless. Auricles variable, from rudimentary to 1.5 mm. long, clawlike and clasping if present, whitish.

Sheath: Smooth, hairless, round, split with broad overlapping scarious margins, margins smooth, prominent midrib. Vernation rolled. Collar divided, not too distinct.

Ligule: Membraneous, short, .5 mm. to 1 mm. long, truncate, ciliate.

Inflorescence: Terminal, 2 sided spikes, 10 to 25 cm. long, spikelets overlapping $1/3$ to $1/2$, erect to nodding, rachis smooth with scabrous margins.

Spikelets: 10 to 20 mm. long, narrow, 3 to 5 mm. wide, 4 to 7 flowered, rachilla scabrous to short pubescent, disarticulating above the glumes and between the florets.

Glumes: $1/2$ to $2/3$ length of spikelet, 7 to 10 mm. long, 1.5 to 3 mm. wide, unequal, ridged, 4 to 6 prominent nerves, smooth to scabrous, scarious margins, acuminate, tapering into an awn 1 to 3 mm. long.

Lemma: 8 to 12 mm. long, 1.5 to 3 mm. wide, 4 to 6 faint nerves, smooth to scabrous, scarious, faintly scabrous margins, lemmas rounded, tapering into an awn 6 to 14 mm. long, the awn straight, diverging somewhat when dry.

Palea: As long as to slightly longer than the lemma, densely scabrous on the margins of the 2 keels.

Fruit: Sterile.

Location and Abundance: The only population known to occur in Montana was found along a revegetated watercourse.

Agropyron saxicola (Scribn. & Smith) Piper

Agropyron saxicola (Scribn. & Smith) Piper, U. S. Natl. Herb. Contrib. 11: 148. 1906.

Elymus saxicola Scribn. & Smith, U. S. Dept. Agr., Div. Agrost. Bul. 11: 56. 1898.

Sitanion flexuosum Piper, Erythea 7: 99. 1899.

Sitanion lanceolatum J. G. Smith, U. S. Dept. Agr., Div. Agrost. Bul. 18: 20. 1899.

Agropyron flexuosum Piper, Wash. Biol. Soc. Proc. 18: 149. 1905.

Agropyron sitanioides J. G. Smith in Piper, Wash. Biol. Soc. Proc. 18: 149. 1905.

Agropyron saxicola was originally described and named as Elymus saxicola by Scribner and Smith (1898). The type specimen was collected by E. Elmer (No. 554) in 1897 on Mount Chopera, Okanogan County, Washington, at 5,700 feet. Scribner and Smith (1898) mentioned that the grass was first thought to be an Agropyron, but they said, "... further examination determines its position as an Elymus. In many of the spikes the spikelets are all solitary, but the position of the first flowering glume in being slightly turned to one side in its relation to the main axis is a character of the genus Elymus". It was first collected in Montana by Rydberg in 1899 near Barker, and identified by J. G. Smith as Sitanion lanceolatum. The generic name was later changed to Agropyron by Piper (1905) after examination of the original type specimen.

One of the rarest of the native wheatgrasses in Montana is the little known A. saxicola, sometimes called "Rock Wheatgrass" or "Foftail Wheatgrass". Prior to the present study, the most recent collection from Montana was one dated 1914 (Hawkins, Mont. 31918) with the location given only as "Lake Abundance". However, there are several lakes of that name in Montana, including some which have undergone name changes in recent years.

A small population of approximately thirty plants was located near the shores of the Lake Abundance that lies at the head of the Stillwater River near Cooke City. The population occurs at 7,800 feet on a rocky knoll about 500 yards from the east end of the lake. Large boulders cover the top of the knoll where the plants occur, with the plants growing in and around the rocks. Soil depth is very thin, with the soils being largely decomposed sandstone, with minor amounts of organic matter present. Although precipitation in the area is relatively high, the substrate complex results in an extremely dry site. The knoll has an eastern exposure with a slope of approximately six degrees. Winds are infrequent in the area. The knoll shows no grazing use, although the surrounding willow bottoms are heavily utilized by moose. There is no grazing by domestic livestock in the area. The habitat is characteristic of Sitanion hystrix, which occurs in large numbers in the area. Other associated species in the area include Danthonia unispicata and Sedum spp. Somewhat removed from the immediate vicinity of the population of A. saxicola

are large populations of A. latiglume and A. trachycaulum. Reproduction of A. saxicola is accomplished by the weakly developed rhizomes that are present.

Agropyron saxicola (Scribn. & Smith) Piper. (Foxtail Wheatgrass)

The following description is based on the population occurring at Lake Abundance near Cooke City (2n=28).

General Characteristics: Perennial, leaves mostly basal, weakly rhizomatous sterile hybrid. Softly pubescent, slender divergent awns, rare.

Culms: 25 to 65 cm. tall, loosely tufted, erect, smooth, glabrous to short pubescent, nodes glabrous, culms round.

Blades: Flat, boatshaped at tip, 2-5 mm. wide, 10 to 20 cm. long, lax, short pubescent on both sides, margins narrow, scarios, scabrous, blades smooth, somewhat ridged above, midvein prominent on lower surface. Auricles clawlike and clasping, 1 to 1.5 mm. long, whitish.

Sheaths: Round, pubescent, split with overlapping scarios margins, bases often pinkish, vernation rolled. Collar divided, somewhat pubescent, not distinct.

Ligule: Membraneous, short, .5 mm. long, truncate to obtuse, ciliate.

Inflorescence: Terminal, 2 sided spike, spikelets often in pairs, dense, overlapping 1/2 to 2/3, erect, rachis scabrous at margins, disarticulating when mature, spike 5 to 10 cm. long.

Spikelets: 12 to 17 mm. long, about twice as long as the internodes of the rachis, narrow, 3 to 4 mm. wide, 4 to 6 flowered, rachilla densely pubescent, spikelets disarticulating below the glumes, falling entire.

Glumes: 6 to 9 mm. long, narrow, 1 to 1.5 mm. wide, tapering into an awn, the awn 5 to 12 mm. long, divergent, scabrous, 3 conspicuous nerves, glumes scabrous, margins scarios, very narrow, smooth.

Lemmas: 7 to 10 mm. long, 1 1/2 times as wide as glumes, awned, the awn 4 to 8 mm. long, awn divergent, lemma short-pubescent, 5 to 6 faint nerves, scarious margins, smooth, the awn minutely scabrous.

Palea: About as long as the lemma, scarious margins, scabrous on the 2 keels.

Fruit: Sterile.

Location and Abundance: Among boulders and rocky crevices on dry, sandy soils. Extremely rare.

Agropyron dasystachyum (Hook) Scribn.

Agropyron dasystachyum (Hook.) Scribn. Torrey Bot. Club Bul. 10: 78. 1883.

Triticum repens var. dasystachyum Hook., Fl. Bor. Amer. 2: 254. 1840.

Triticum repens var. subvillosum Hook., Fl. Bor. Amer. 2: 254. 1840.

Triticum dasystachyum A. Gray, Man. 602. 1848.

Agropyron dasystachyum var. subvillosum Scribn. & Smith, U. S. Dept. Agr., Div. Agrost. Bul. 4: 33. 1897.

Agropyron lanceolatum Scribn. & Smith, U. S. Dept. Agr., Div. Agrost. Bul. 4: 34. 1897.

Triticum repens var. acutum Vasey ex Scribn. & Smith, U. S. Dept. Agr., Div. Agrost. Bul. 4: 34. 1897.

Agropyron subvillosum E. Nels., Bot. Gaz. 38: 378. 1904.

Zeia dasystachyum Lunell, Amer. Midl. Nat. 4: 226. 1915.

Elymus subvillosus Gould, Madrono 9: 127. 1947.

Elymus lanceolatus Gould, Madrono 10: 94. 1949.

A. dasystachyum was originally named Triticum repens var.

dasystachyum by Hooker in 1840. It was later raised to the level of

species by Gray who named it Triticum dasystachyum in 1848. In 1883 Scribner gave it the name A. dasystachyum based on Hooker's original type specimen, collected by Richardson in Saskatchewan, Canada. Recently, Gould (1947) has given it the name Elymus subvillosus, based on a synonym used by Hooker, T. repens var. subvillosum, in 1840.

A. dasystachyum, commonly known as "Thickspike Wheatgrass", ranges from Alaska to northern California and across the Great Basin to the Lake States. It is widely distributed across Montana occurring in a variety of habitats. Somewhat resembling A. smithii, it is the author's opinion that much of the wide distribution attributed to A. smithii is due to observers confusing these two species. A. smithii is found predominantly on the heavier soils in the state, and is not common on the lighter soils of the hillsides. A. dasystachyum, however, ranges from all but the heaviest of soils well into the dry, rocky, thin soils of the foothills across the state. It is found in great abundance on the sand dunes in the Red Rock Refuge in southwestern Montana where it contributes to the stabilization of the area. Commonly a sod-former in the heavier soils, in foothill areas it assumes a bunch type of habit with clumps up to ten inches in diameter being formed.

In altitudinal distribution it compared favorably with A. trachycaulum. Two distinct phenotypes are located in a limited area above 10,000 feet on Mt. Washburn in Yellowstone National Park. One exhibits typical alpine characteristics; low growth with single

scattered seed stalks and weak rhizomes. This type is distributed across the alpine sod in the area. The other grows on the disturbed sandy roadside that leads up to the lookout tower; it forms bunches up to two feet in diameter and one to two feet tall with masses of rhizomes extending outwards from the bunches.

The population selected for collecting was located in the Bear Paw Mountains near Havre on the North Montana Branch Station grazing allotment. It is widely distributed in the area, occurring at approximately 6,000 feet on the south slopes. Soils in the area are lithosols, with A. dasystachyum occupying the deep sandy loams. Associated species include Festuca scabrella, Festuca idahoensis, Koeleria cristata and A. albicans. Winds are fairly constant, with precipitation between twenty to twenty-five inches in the area. Growth begins in May in this region with seed maturing in late July to early August. Several of the plants show a lavender tinge with red glumes that are distinct from the normal light-green coloration that is typical for the species.

Agropyron dasystachyum (Hook) Scribn. (Thickspike Wheatgrass)

The following description is based on the population occurring in the Bear Paw Mountains near Havre, Montana (2n=28).

General Characteristics: Perennial, green or glaucous, strong creeping rhizomes.

Culms: 35 to 72 cm. tall, light green to glaucous, smooth, nodes glabrous, fairly wide, culms erect.

Blades: Leaves mostly basal, 1-5 mm. wide, flat to tightly in-rolled when dry, 10 to 25 cm. long, strongly ridged, very

scabrous on upper surface, margins scabrous, lower surface smooth to slightly scabrous, more so towards base, hairless. Auricles clawlike, clasping, 1-2 mm. long, rather slender, whitish to light green.

Sheath: Smooth, round, split with overlapping scarious margins, white to pinkish at ground level, basal sheath sometimes retrosely short pubescent, smooth or slightly scabrous on margins. Vernation rolled. Collar divided, not distinct.

Ligule: Membraneous, obtuse, lacerate, very distinct, 1 to 1.5 mm. long.

Inflorescence: Terminal, 2 sided spike, 5 to 14 cm. long, lightly to densely pubescent, often reddish or purplish tinged, rachis scabrous-pubescent on margins.

Spikelets: Rather closely overlapping, 10-18 mm. long, 5 to 8 flowered, rachilla densely pubescent, disarticulating above glumes and between the florets.

Glumes: Small, usually light green, acute to awn tipped glumes 4 to 7 mm. long, rounded, fairly equal, 3-4 prominent ridges, wide scarious margins that are pubescent but not as heavily as the lemmas.

Lemmas: 7-10 mm. long, 1 1/2 times as large as glumes, lightly to densely pubescent, 4 to 5 nerved, faintly nerved, acute to awn tipped, margin scarious.

Palea: About as long as lemma, sparingly to densely pubescent over entire outer surface, especially on margins of 2 keels.

Fruit: Grain, small, light color, often heavily plumose, enclosed in lemma, adherent to palea.

Location and Abundance: Foothills and mountain slopes across the state. Common on most soils ranging from heavier soils along streams to the dry, rocky soils of the foothills.

Agropyron albicans Scribn. and Smith

Agropyron albicans Scribn. and Smith, U. S. Dept. Agr., Div. Agrest. Bul. 4: 32. 1897.

A. albicans was first described and named by Scribner and Smith (1897). The type specimen was collected by P. A. Rydberg (No. 3405) at Yogo Gulch, Montana in August, 1896. The species epithet was given to denote the characteristic whitish appearance of the spike which is due to the pubescence.

A seldom collected, apparently close relative of A. dasystachyum is A. albicans, known as "Montana Wheatgrass". This species occurs in limited areas east of the continental divide in Montana and may occur on the western side, although it is unreported. It closely resembles A. dasystachyum, the main difference being the presence of awns, which vary greatly in length. Near Francis, north of Belgrade, both of these species occur in a small area with all gradations of awns being present.

A. albicans appear to be restricted to the dry, low foothills and plains where it occurs chiefly on thin, rocky soils. The degree of pubescence is variable, apparently being correlated with the vigor of the plant. In areas of low moisture and rocky soil where the plants show little vigor, pubescence is largely lacking, while in areas more favorable to growth, profuse pubescence is common. The length of awn also tends to follow a moisture gradient, being short in sites of low moisture and longer in mesic areas.

The most vigorous population was found in the same general area that was used for the collection of A. dasystachyum in the Bear Paw Mountains near Havre. Collections were made at 5,800 feet on a 20° south-facing slope. Associated species are Festuca idahoensis,

F. scabrella, A. spicatum and Koeleria cristata. The only habitat difference between A. albicans and A. dasystachyum is the occurrence of A. dasystachyum on the heavier soils while A. albicans is more or less restricted to the drier rocky areas. Soils are lithosols, the upper portion being a grayish-brown sandy loam that varies in depth with an underlying stratum of rocks and gravel. The growing season pattern is similar to that of A. dasystachyum, with seed set occurring in early August.

Agropyron albicans Scribn. & Smith (Montana Wheatgrass)

The following description is based on the population occurring in the Bear Paw Mountains near Havre, Montana (2n=28).

General Characteristics: Perennial, slender creeping rhizomes.
Not a strong sod former.

Culms: Spikelets pubescent with long, divergent awns. 25-60 cm. tall, erect, whitish to pale green, often pinkish at ground level.

Blades: 18-40 cm. long, mostly 3-6 mm. wide, tapering into boat-shaped tips. Blades fairly lax, not stiff, sometimes heavily pubescent on the upper surface with hairs up to 1 mm. in length. Blades flat to tightly rolled when dry, margins scabrous, scabrous and ridged on the upper surface. Nerves conspicuously raised on upper surface. Auricles whitish to purplish, 1-2 mm. long, not clasping, flattened.

Sheath: Smooth, round, split with overlapping scarious margins. Old sheaths persistent. Collar smooth, divided by midribs. Vernation rolled.

Ligule: Short, 1 mm. long, membraneous obtuse, lacerate.

Inflorescence: Terminal, 2 sided spike, sparingly to densely pubescent. Rachis short pubescent, spike 7-15 cm. long, spikelets overlapping 1/3, slender, erect heads.

Spikelets: 1-2 cm. long, 4-7 flowered, rachilla sparingly to densely pubescent, disarticulating above the glumes and between florets, callus of florets pilose.

Glumes: Green, small, 1-1.5 mm. wide, 3-7 mm. long, acuminate, tapering into an awn 3-4 mm. long, glumes equal, pubescent, scarious, margins 4-5 nerved, rounded, awn scabrous.

Lemma: 7 to 10 mm. long, 1.5-2.5 mm. wide, 1 1/2 times the size of the glumes, rounded, densely pubescent, 4-5 faint nerves, acuminate, tapering into an awn 1-2 cm. long, awn scabrous, divergent when mature.

Palea: About as large as the lemma, scabrous-pubescent on the margins of the two keels and on the upper portion of the palea.

Fruit: Grain, light colored, densely pilose on upper end, enclosed in the lemma and adherent to the palea.

Location and Abundance: Dry foothills and mountain slopes in eastern Montana on rocky, thin soils. Limited occurrence in the state.

Agropyron scribneri Vasey x Agropyron latiglume (Scribn. & Smith) Rydb.

Interspecific and intergeneric hybridization has furnished important evidence in the study of systematic and phylogenetic relationships within the Gramineae. Hybridization, both natural and controlled, is much more common in the Gramineae than in most of the other plant families. The determination of parentage in cases involving natural hybrids is usually based on morphological similarities and proximity of occurrence of the species in question. Meiotic examination of all the species concerned is also useful in final determinations of such cases.

In 1963, Dr. E. Booth, of the Montana State College Botany Department, discovered a number of plants growing in the Bridger

Mountain Range north of Bozeman that exhibited morphological characteristics intermediate to the two alpine species, A. scribneri and A. latiglume, both of which were also present. He informed the author of the location and hypothesized that these plants were natural interspecific hybrids of A. scribneri and A. latiglume. The area, a pass west of Sacajawea Peak, was visited and several specimens of the suspected hybrid as well as the putative parents were collected by the author. The population is predominantly A. scribneri, with lesser amounts of A. latiglume and the suspected hybrid being present.

The population occurs on a pass above a large, boulder-filled cirque that marks the upper limits of the subalpine zone. The population also extends down the south side of the pass for approximately 50 yards on slopes that vary from 5% to 30% in inclination. Elevation is approximately 9,500 feet at the pass. Soils are of the alpine meadow type (Retzer, 1956) consisting of a shallow layer of mixed organic material and sand underlain by gravel. No precipitation figures are available for the area. The area is subjected to constant winds of frequently high velocity. Associated species consist of a mixture of sedges (Carex) and grasses such as Trisetum spicatum, Deschampsia caespitosa, Danthonia unispicata, and several species of Poa.

The specimens of both A. latiglume and A. scribneri closely resemble the ecotypes found in the Beartooth Plateau. The suspected hybrid is intermediate to A. scribneri and A. latiglume in most of its morphological characteristics, although it bears a closer re-

semblance to A. latiglume except for the awned nature of the inflorescence. All are similar in over-all size, varying from 15-30 cm. in height. In growth habit the hybrid resembles A. scribneri, the culms being noticeably decumbent. Leaf characteristics of the hybrid and A. latiglume are similar, both having predominantly basal leaves with the old leaves persisting. The hybrid and A. latiglume are also similar in spike characteristics, except for the presence of awns. Both have a compact spike of a sometimes purplish nature which is often enclosed by the sheath upon maturity. Both the glumes and lemmas are awned in the hybrid as well as in A. scribneri, although the awns in the hybrid are only approximately 1/4 as long as those found in the supposed parent. The divergent characteristic of the awns that is pronounced in A. scribneri is exhibited only slightly by the hybrid.

Agropyron scribneri Vasey x A. latiglume (Scribn. & Smith) Rydb.

The following description is based on the population occurring near Sacajawea Peak in the Bridger Mountains, north of Bozeman (2n=28).

General Characteristics: Perennial, without creeping rhizomes, stems spreading, inflorescence compact, awned, purplish, often enclosed in a sheath upon maturity, mostly basal leaves, old leaves persistent.

Culms: 15 to 30 cm. tall, often pinkish near base, stems spreading, geniculate, sharply bent at the nodes, nodes smooth, thickened, dark, prominent, internodes 5-15 cm. long.

Blades: Leaves mostly basal, flat, 4-7 mm. wide, 10-20 cm. long, heavily ribbed on upper surface, medium to heavy pubescence, margins short toothed. Underside of leaf short pubescent, prominent midrib, rib continuous, leaf tips boatshaped. Stem blades flat, 3-7 mm. wide, 5-8 cm. long, usually 3 blades per stem, boatshaped at tip. Underside of stem blade smooth, sometimes short haired with scattered long hairs intermixed, prominent midrib. Upper surface of stem blade heavily ribbed, ribs hairy, leaf margins serrate. Old basal leaves persistent.

Sheaths: Split, overlapping, strongly nerved, margins entire, translucent. Vernation rolled. Collar divided, not distinct.

Ligule: Thin, membranous, flat topped, entire, less than 1/2 mm. long.

Inflorescence: Terminal, 2 sided spike, 18-22 spikelets, spike 7-10 cm. long, compressed, spikelets overlapping 1/2 to 3/4. Rachis smooth, pubescent on margins. Inflorescence often largely enclosed in the sheath upon maturity. Usually purplish tinged.

Spikelets: 8-15 mm. long, 5-7 flowered, rachilla heavily pubescent, disarticulating above the glumes and between the florets.

Glumes: 6 to 9 mm. long excluding awn, 3/4 length of spikelet, bifid near apex on lower spikelets, margins entire, translucent, 4 prominent nerves, mid-nerve tapering into an awn 3-5 mm. long, awn barbed, divergent when dry.

Lemmas: 3 to 6 nerved, nerves faint, midrib prominent, ending in an awn 2-4 mm. long. Lemmas 7-9 mm. long excluding awn, broad, 2 1/2 - 3 1/2 mm. wide, pubescent, the pubescence lessening towards the tip. Lemmas keeled from upper end to 1/2 the length, apex bifid on lower spikelets.

Palea: Almost as long as the lemma, smooth, toothed on the margins.

Fruit: Sterile.

Location and Abundance: Only known location is near Sacajawea Peak in the Bridger Mountains north of Bozeman.

Table I. Locations of the species collected for biosystematic investigations.

Species	MSC Herbarium No.	Source
<u>A. albicans</u>	MONT 58,689	Collected in Bear Paw Mountains, near Havre, Montana, in the Montana State College grazing allotment on August 8, 1962. Widespread along hillsides at 6,000 feet elevation.
<u>A. dasystachyum</u> (Hook) Scribn.	MONT 58,690	Collected in Bear Paw Mountains, near Havre, Montana, in the Montana State College grazing allotment on August 8, 1962. Widespread along hillsides at 6,000 feet elevation.
<u>A. griffithsii</u> Scribn. et Smith	MONT 58,688	Collected 3 1/2 miles west of Deep Creek Section house East of Townsend, Montana, along highway on August 2, 1962. Scattered along moist, silty bottom.
<u>A. inerme</u> (Scribn. et Smith) Rydb.	MONT 60,564	Collected at Pleasant Valley near Libby, on August 22, 1962. Scattered along south slopes at 4,400 feet on thin, silty soils.
<u>A. latiglume</u> (Scribn. et Smith) Rydb.	MONT 58,679	Collected at Beartooth Pass, between Cooke City and Red Lodge, Montana, above Boundary Lake, on July 26, 1962. Abundant around rocky outcrops at 10,000 feet elevation.
<u>A. saxicola</u> (Scribn. et Smith) Piper	MONT 60,565	Collected at Lake Abundance near Cooke City, on rocky knoll 500 yards from the east end of the lake, on September 6, 1962. Population of thirty plants, 7,800 feet.
<u>A. scribneri</u> Vasey	MONT 58,684	Collected along Boundary Lake at Beartooth Pass, between Cooke City and Red Lodge, Montana, on July 26, 1962. Widespread over alpine slopes at 10,000 feet elevation.

Table I. Locations of the species collected for biosystematic investigations (cont'd)

Species	MSC Herbarium No.	Source
<u>A. smithii</u>	MONT 58,683	Collected in Slim Sam Creek area, 4 miles north of Radersburg, Montana, on June 26, 1962. Large population over wide overflow bench.
<u>A. spicatum</u> (Pursh) Scribn. et Smith	MONT 58,686	Collected at the Belgrade transmission tower, Belgrade, Gallatin Co., Montana, on July 28, 1962. Large population over gravelly bench.
<u>A. subsecundum</u> (Link) Hitch.	MONT 58,687	Collected at Flathead Pass, Bridger Mountains, near Bozeman, Gallatin County, Montana, on September 10, 1962. Widespread on north slopes at 7,200 feet elevation.
<u>A. trachycaulum</u> (Link) Malte	MONT 58,685	Collected at Reese Creek, Bridger Mountains, near Bozeman, Gallatin County, Montana, on September 11, 1962. Widespread along slopes above creek.
<u>A. scribneri</u> Vasey x <u>A.</u> <u>latiglume</u> (Scribn. et Smith) Rydb.	MONT 60,563	Collected in alpine pass west of Sacajawea Peak in the Bridger Range north of Bozeman on August 8, 1963. Intermingled with populations of <u>A. scribneri</u> and <u>A. latiglume</u> at 9,500 feet elevation in alpine sod.

B. HISTOLOGICAL STUDIES

Although floral morphology is emphasized in traditional taxonomic classifications, in recent years attempts have been made to utilize characteristics of leaf epidermal tissue in plant classifications. Duval-Jouve (1875) found that the diversity of the structure of the grass leaf together with the distribution of the chloroplasts paralleled morphological differences between species. Simmonds (1949) working with Musa, found the stomata to be larger and less numerous in species of higher ploidy level, the relationships being approximately linear. Mochizuki and Sueka (1955) in a comparison involving three ploidy levels in sugar beets, found the average number of chloroplasts per guard cell to be 12.4 in the tetraploid, 10.07 for the triploid and 7.27 for the diploid specimens. Dudley (1958) confirmed these findings and suggested the procedure as a rapid means of determining ploidy level in other genera. However, Brown (1962) in an electron microscope study of 16 species of grasses involving 10 tribes, found plastids but no developed chloroplasts present in the guard cells. One member of the Hordeae (Elymus virginicus) was included in this study.

METHODS

Epidermal surfaces of the eleven species of Agropyron native to Montana together with one naturally-occurring hybrid were investigated for: (1) the occurrence of chloroplasts in their guard cells, (2) sizes of guard cells, (3) density and pattern of stomata on the lower and upper epidermal surfaces of the leaves, and (4) the sizes of

epidermal cells other than the guard cells. Photographs were made of the epidermal surfaces of each species.

Leaf sections of approximately 4 inches in length were removed from the center of mature, green leaves. These were then placed in water for 3-4 minutes to soften the tissue. In some species such as A. smithii a mild detergent (Vel) was added to facilitate the softening. The tissue sections were then placed under a dissecting scope on a glass plate and carefully scraped with a scalpel. When the desired thickness was reached, the specimens were mounted in a drop of water and covered with glass cover slips.

Stomatal density was determined by counting the number in each of ten randomly selected fields, averaging, and multiplying by an appropriate factor of 1300 to give the concentration per square centimeter. Cell measurements were made by the use of an ocular micrometer. Measurements of long epidermal cells were made of the longest one observed for each species.

RESULTS AND DISCUSSION

No plastids identifiable as chloroplasts could be detected in the guard cells of the Agropyron species that were investigated in this study. Table I presents a summary of the results of the epidermal investigation. Guard cell lengths varied from a mean of 35.0 microns in A. spicatum ($2n=14$) to a mean of 72.5 microns in A. smithii ($2n=56$). Thus, on the basis of this limited study, there appears to be a definite increase in guard cell size associated with the higher ploidy species. A. smithii, the only native octoploid species, has a

considerably greater guard cell length than any of the other species, while the two diploid species, A. spicatum and A. inerme, have the smallest guard cells. The tetraploid form of A. spicatum has a guard cell length of 43.0 microns as compared to the diploid A. spicatum form which has guard cells averaging 35.0 microns. The hybrid, A. scribneri x latiglume, has a noticeably larger guard cell than either of its parents.

The concentration of stomata on the lower epidermis varied from 780/cm² in A. inerme to a high of 6890/cm² in the hybrid A. scribneri x latiglume. Stomata were lacking on the lower epidermis of A. saxicola. It is seen from the table that there is no correlation between stomatal size and concentration. Upper epidermal concentrations of stomata were usually 2-3 times as high as lower epidermal concentrations for all species except the hybrid. The highest concentration of stomata in the upper epidermis was found in A. inerme, which had 12,610 stomata/cm², as compared to only 780/cm² in its lower epidermal tissue.

The longest epidermal cell observed in each species varied greatly from a high of 1,084 microns in A. latiglume to 230 microns in A. smithii. No correlation can be made between ploidy level and maximum epidermal cell size.

One noticeable morphological feature of the epidermis is the interdigitate appearance of the cell walls of many of the species (Fig. 1). Interdigitate cell wall structure was observed in A. spicatum, A. inerme, A. saxicola, A. smithii, A. griffithsii and

Table II. Compiled data on the 11 species and 1 hybrid of Agropyron investigated in this study. All the data is from lower epidermal tissue, with measurements in microns. Chromosome numbers are shown to the left.

Species	Chromosome No.	Stomatal Placement	Guard Cell Length	Stomata/cm	Size Of Large Epidermal Cell
<u>A. inerme</u>	n= 7	1 row on each side of midrib	37.0	780	255 x 12
<u>A. spicatum</u>	n= 7	1 row between veins	35.0	2080	280 x 14
<u>A. spicatum</u>	n=14	2 rows between veins	43.0	1720	300 x 25
<u>A. albicans</u>	n=14	1 row between veins	43.0	2015	305 x 18
<u>A. dasystachyum</u>	n=14	2 rows between veins	50.0	2925	475 x 21
<u>A. griffithsii</u>	n=14	1 row between veins	43.0	3640	731 x 26
<u>A. latiglume</u>	n=14	1 & 2 rows, variable	47.0	1430	1084 x 18
<u>A. saxicola</u>		Lacking on lower epidermis	37.0***		260 x 30
<u>A. scribneri</u>	n=14	Scattered rows, random	42.0	4030	312 x 15
<u>A. subsecundum</u>	n=14	Variable, 1 & 2 rows	41.0	4120	408 x 14
<u>A. trachycaulum</u>	n=14	Variable, 1 & 2 rows	39.0	4810	468 x 17
<u>A. scribneri-latiglume</u>	n=14	2 rows between veins with alternate individual stomates offset	56.0	6890	143 x 19
<u>A. smithii</u>	n=28	2 rows between veins	72.5	3250	230 x 25

*** Upper epidermis

A. albicans. A. saxicola also exhibits distinctive "bone-shaped" short cells over the veins of the lower epidermis (Fig. 2). All of the species except the diploid and tetraploid forms of A. spicatum exhibit single celled hairs called short cells on both epidermal surfaces. A. spicatum and A. inerme, which are very similar in epidermal morphology, can be differentiated on this basis; A. inerme has a number of short cells on the lower epidermis while A. spicatum has none.

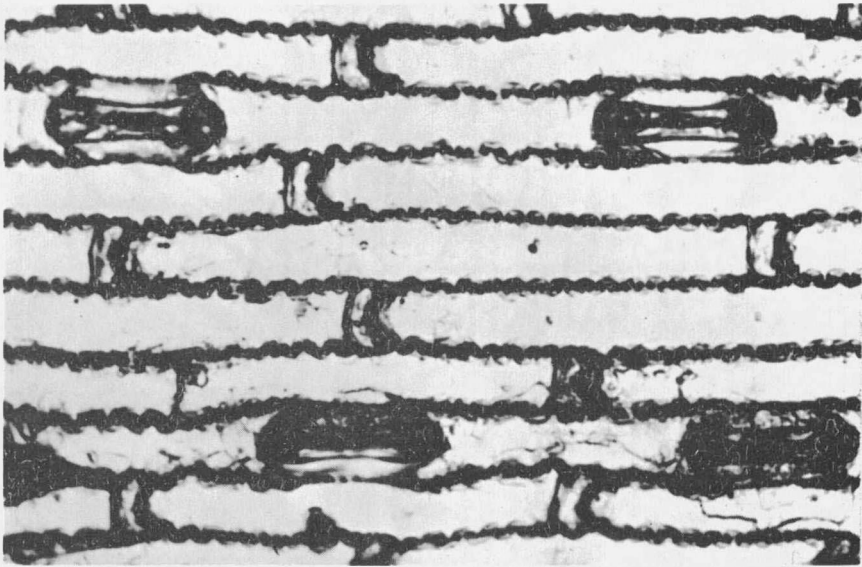


Fig. 1 Lower epidermal cells of *A. smithii* showing interdigitate cell walls. Note guard cells.

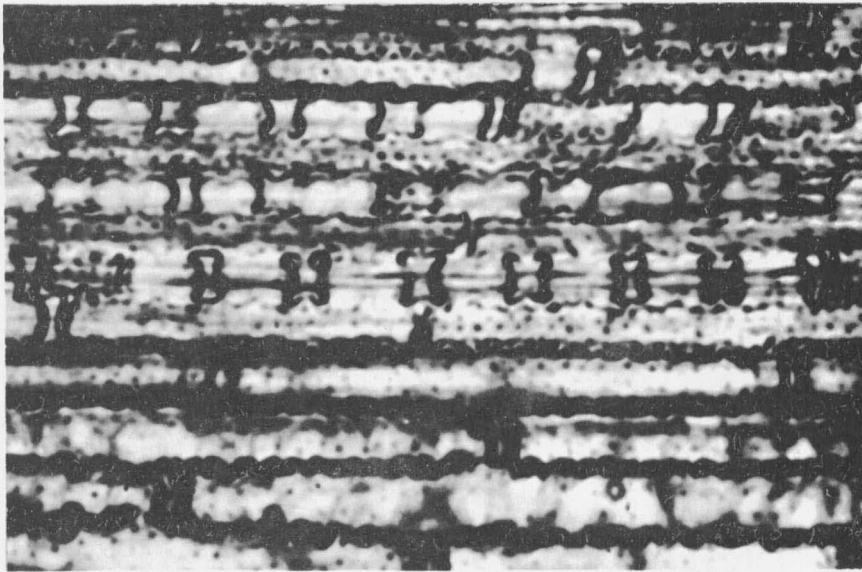


Fig. 2 Lower epidermal cells of *A. saxicola* showing distinctive "bone-shaped" cells and interdigitate cell walls.

C. CYTOGENETIC STUDIES

I. REVIEW OF THE LITERATURE

The field of cytogenetics, developed since the beginning of this century, has markedly affected the systematics of the Gramineae by offering a new approach to problems of phylogenetic relationships. When cytogenetical studies support previous classic studies based on morphological characteristics they supply confirming evidence. But, in cases where cytogenetical evidence conflicts with morphological classifications, new concepts leading to a more thorough understanding of the group in question may be formed.

The first work on the cytogenetics of the Gramineae dealt largely with cultivated crops such as the cereals. Kuwarda's (1919) work with Zea mays and Bremer's (1923) work on Saccharum are two early studies. Eyan (1926) first reported on other grasses, giving a few chromosome counts in Lolium and one in Festuca. Within a few years a multitude of papers dealing with the cytogenetics of the non-cultivated grasses were published. For excellent reviews of these works the reader is referred to Myers (1947), Tateoka (1960), or Carnahan and Hill (1961).

The genus Agropyron has been the subject of considerable cytogenetic work, primarily because of its close relationship to economically important species of wheat. Early workers suggested that A. triticeum was the source of the B-genome of the tetraploid and hexaploid wheats; a hypothesis which has since been disproven. However, the possibility of incorporating desirable characteristics from wheat-grasses, such as a perennial habit and drought resistance into a wheat

breeding program is currently a goal of a number of plant breeders throughout the world. Almost all of the species that have been successfully used in such breeding programs have been from areas other than North America; therefore the native species have received little attention other than the recording of their chromosome numbers.

Peto (1929, 1930) published the first cytogenetic treatment of the Agropyrons, giving the chromosome counts for eighteen species occurring in Western Canada, Russia and Denmark. He found the eighteen species investigated formed a polyploid series with a basic number of seven chromosomes. The entire series ranged from diploids to decaploids, although the species from Canada were found to be only diploid, triploid, tetraploid or octoploid. The only triploid was thought to be a hybrid, although it was morphologically similar to A. trachycaulum. Meiosis was very irregular, with thirteen to seventeen univalents commonly observed. Original counts were given for A. smithii ($2n=56$), A. dasystachyum ($2n=28$), A. griffithsii ($2n=28$), A. spicatum ($2n=14$), A. subsecundum ($2n=28$), and A. trachycaulum ($2n=28$). One species, A. smithii var. molle was found to have both tetraploid and octoploid forms, but later investigators have failed to verify the tetraploid count. Root tip studies of A. spicatum revealed satellite chromosomes, chromosome constrictions, and chromosome segmentations to be common. The presence or absence of satellite chromosomes was found to be variable even in the same plant.

Robertson and Weaver (1942) discovered and collected a tetraploid form of A. spicatum in Nevada that was almost twice the size of normal

diploid plants in the area. Hartung (1946) considered the distribution of the tetraploid form of A. spicatum to be limited to eastern Washington and the adjacent area of northwestern Idaho, while the diploid type was widespread. The Robertson and Weaver (1942) collection was felt to be an isolated colony of local origin and of no widespread significance. A. inerme was also found to have both the diploid and tetraploid chromosome complements, and was felt to be nothing more than a variety of A. spicatum. A. dasystachyum and A. subsecundum were both found only in the tetraploid form, while one plant of tetraploid A. smithii was found as well as the usual octoploids. Senn et al. (1947) in a study of the chromosome numbers of Canadian Agropyrons found A. spicatum to have triploid as well as diploid and tetraploid chromosome complements. They also listed A. smithii as having triploid and tetraploid complements as well as the usual octoploid number. However, in a later publication (Gillett and Senn, 1960) the tetraploid count is listed as a misidentification, the actual plant being a specimen of A. dasystachyum. No mention is made of the triploid count, although the authors doubt the existence of any form except the octoploid. This study is based on 62 cultures of A. smithii collected from throughout western North America. Mention is also made of a count by Myers (1947) based on an unpublished report by Stebbins giving a count of $2n=42$ for A. smithii. A plant of this material was obtained by Bowden and found to have a somatic chromosome number of $2n=56$ (cited by Gillett and Senn, 1960):

In a study extending over a period of several years, Stebbins has

investigated genome relationships in a number of species of Agropyron, with particular emphasis on A. spicatum. Stebbins and Singh (1950) found A. inerme to be very regular in meiosis, with 98% of the cells showing seven closed bivalents. First anaphase was nearly always normal, although cells with laggards and bridges were occasionally found. They concluded that A. spicatum and A. inerme have similar genome formulas, which they designated as A_1A_1 . On the basis of pairing configurations involving hybrids they also felt that Elymus glaucus had a more or less homologous genome, designated as A_2A_2 . They also agreed with Hartung (1947), who concluded that A. inerme should be regarded as an awnless variety of A. spicatum. To further clarify this relationship, Stebbins and Pun (1953) crossed A. inerme and A. spicatum and observed the meiotic configurations of the resulting hybrid. Using A. inerme as the female parent 59 florets gave 3 viable seeds, while the reciprocal cross yielded 9 seeds out of a total of 75 florets. The parent A. spicatum showed 97% of the meiotic cells with seven closed bivalents, with the remainder having six bivalents and two univalents. Using A. spicatum as the male parent, the resulting hybrid showed almost identical pairing. When the reciprocal cross was made only 78% of the cells showed seven bivalents; the rest of the cells having from two to four univalents present. Although the second combination had a higher number of univalents, later stages showed no more abnormalities than the parent; with pollen and seed fertility comparably high in all cases. It was concluded that separation of the two entities into species was not justified upon the basis of this cytological evidence.

A high degree of homology was also found between A. spicatum and a species from southwestern Asia, A. caespitosum. From this and the preceding study Stebbins concluded that the A. spicatum genome (A_1A_1) is widespread throughout the diploid, non-rhizomatous species of Agropyron and has also played an important role in the formation of many of the polyploid species of Agropyron and related genera. Schulz-Schaeffer and Jurasits (1962) in a karyological study of the genus involving 25 species typified the genus Agropyron on the basis of satellite chromosomes. They found 15 of the 25 species to have satellite chromosomes of the type which they designated as F-1 or F-2. This type was thought by the authors to be the indicator chromosome for the A. spicatum genome designated as A_1A_1 by Stebbins.

Stebbins and Snyder (1956) continued the investigation into the distribution of the A. spicatum genome among other species by the use of triploid hybrids. In the triploid hybrid resulting from the cross A. trachycaulum x A. spicatum 16% of the cells showed pairing in excess of 7 bivalents, with 3 to 4 of these being of the closed type. A similar situation was found to exist in hybrids resulting from the cross A. caninum x A. spicatum. On the basis of this and prior work they concluded that the genetic and phylogenetic relationships between the species of the tribe Triticeae could be most easily represented if all were placed in a single large genus. Such a drastic revision, however, should await a more thorough understanding of these relationships in the opinion of the authors. The tendency of some workers to split the conventional genera into smaller sections was felt to be

detrimental.

Another native species of Agropyron that has been utilized in crossing programs is A. trachycaulum. Stebbins and Love (1941) concluded that A. trachycaulum was an allopolyploid. In a study on California range grasses they found an increase in heat and drought tolerance associated with increased ploidy levels. Other workers have found a similar correlation between cold tolerance and ploidy level, all of which may be a result of the effects of allopolyploidy. Stebbins et al. (1946) in a study involving a natural hybrid between A. trachycaulum and Hordeum nodosum found a surprising amount of pairing in meiosis. It was believed such pairing was related to the basic number (7) of the parents, resulting in autosyndetic pairing. In autosyndetic pairing the pairing is between two genomes of one parent, rather than pairing between one genome of each parent. As all of the species involved were tetraploids, homology could well be due to the parents having two genomes of seven chromosomes each in their haploid complement.

Boyle and Holmgren (1954) found Elymus macounii Vasey to be an F₁ sterile hybrid between A. trachycaulum and Hordeum jubatum. They also found A. trachycaulum to be highly self-fertile and without meiotic abnormalities. They concluded that, in all probability, A. trachycaulum is an allotetraploid. Nielsen (1961) thought the parentage of the putative hybrid Agroelymus turneri to be A. dasystachyum and Elymus innovatus but it is not clearly proven. Boyle (1963) in a study of a controlled hybrid between A. trachycaulum and Sitanion hystrix

found a high degree of quadrivalent pairing, indicating that homologies exist between the parental species resulting in allosyndetic pairing. The hybrid was completely sterile, however. In another recent study, Dewey (1963) investigated a naturally occurring hybrid with the suspected parentage being: A. trachycaulum x A. scribneri. Meiotic chromosome behaviour of the parents was consistent with the hypothesis that both are strict allotetraploids. Chromosome pairing relationships in the hybrid suggest that 10 or 11 of the chromosomes of A. trachycaulum and A. scribneri are completely homologous. The major differences between the parental genomes apparently consist of structural rearrangements of the component chromosomes. Dewey also mentions the apparent close relationship existing between A. scribneri and A. latiglume, a possibility which is borne out in this thesis.

Lastly, Dewey, in a recent article (1964), reported on a synthetic hybrid involving the Old-World A. cristatum and the New-World A. spicatum in the tetraploid form. In the tetraploid A. spicatum every cell examined at diakinesis and metaphase I contained 1-5 quadrivalents, the average being 2.98 per cell. On the basis of this multivalent pairing, Dewey considered A. spicatum to be an autotetraploid arising from the occurring diploid form. The triploid hybrid arising from diploid A. cristatum and the tetraploid A. spicatum indicated virtually complete homology between the A. spicatum genomes, with 99% of the cells showing complete pairing between the A. spicatum chromosomes. No pairing was found between the A. spicatum and the A. cristatum chromosomes, with 7 bivalents and 7 univalents being the most common chromosome

association found in the hybrid. Lagging chromosomes, common in every cell of the hybrid, were attributed to the A. cristatum parent. Dewey suggested genome formulas for the two parents A. spicatum and A. cristatum to be BBBB and AA respectively, while their hybrid was designated ABB. Mention was also made of the successful hybridization of A. spicatum with A. repens, A. riparium, A. dasystachyum, and Sitanion hystrix. No information on these is available at the present time, however, and it is not known whether the diploid or the tetraploid strain of A. spicatum was used.

II. MATERIALS AND METHODS

Plant collections consisting of ten plants of each of the eleven species and the interspecific hybrid were obtained in the field and placed in the Montana State College Greenhouse in the fall of 1962. The following spring these plants were transplanted into a prepared seedbed at the author's ranch one mile west of Bozeman. One row was used for each of the species with the rows planted three feet apart. The plot was kept cultivated and adequately watered. Care was taken so that none of the rhizomatous plants could spread out into adjacent areas.

Head samples for pollen mother cell cytological analysis were collected from each plant and recorded as to plant number and species, date and time of collection, and stage of morphological development. The heads were preserved in Newcomers solution of 6 parts acetone: 3 parts propionic acid: 1 part petroleum ether: 1 part acetone: 1 part p-dioxane. These were then stored under refrigeration at 1°C. until analyzed.

Due to the large variation among species, samples of varying stages of morphological development were collected and immediately analyzed so that maximum meiotic activity could be observed. As a general rule, maximum activity was found at the stage of growth where the spikes were either in the late "boot" stage or just beginning to emerge. However, in the two alpine species, A. latiglume and A. scribneri, maximum meiotic activity was found to occur at a much earlier stage, particularly in A. scribneri. In order to obtain maximum

activity in A. scribneri, spikes must be collected when the inflorescence swelling is first distinguishable within the sheath. The other alpine species, A. latiglume, has a more variable phenology. Although it is necessary to collect the spikes while they are still deep in the boot, the anthers can be considerably larger than those of A. scribneri and still be in the same stage of pollen development. Phenologically, A. smithii was found to be the latest of all the species, undergoing meiosis well after the head had fully emerged.

In making the collections it was found that the early morning hours just after sunrise gave the maximum meiotic activity. It seems possible that the onset of cooling temperatures in the evening resulted in a majority of the meiotic cells entering the metaphase stage, in which they remained until the temperature rose after sunrise. A similar phenomenon is observed and utilized in mitotic studies, where root tips are chilled to obtain a maximum number of metaphase configurations:

Slide preparations were made using Belling's (1926) method by placing the anthers in a drop of 5% acetocarmine and squashing with a set of dissecting needles. Heating was not required to obtain satisfactory results, and orcein (5%) was also found to give excellent staining. After squashing, excess tissue material was removed and a coverslip applied. Tapping with the blunt end of a grease pencil resulted in an increased dispersal of the chromosomes as well as removal of excess stain. The edges of the cover slip were sealed with clear fingernail polish. A modification of this technique was used to

determine rapidly which spikelets of a spike were in the desired meiotic stage. This technique consisted of squashing the anthers in the acetocarmine and immediately observing the resulting preparation under a 10X objective without applying a coverslip. If the proper stages were present, preparation of the slide was continued in the previous manner. If the desired stages were not present, the slide was wiped clean and a different spikelet selected for preparation. This method results in a considerable saving of time, which is particularly necessary at the preliminary stages of the collection, when a large amount of material must be observed rapidly and accurately. As in most of the grasses, the oldest spikelets are those in the middle of the spike, with progressively younger ones toward each of the ends. Within a spikelet the oldest florets are those at the base, the upper florets being progressively younger. Several photomicrographs were made of pollen mother cells of each species. As a general rule, photomicrographs were taken of each of the major stages of meiosis. Additional pictures were taken of cells with irregular divisions, such as those showing bridges, univalents, etc. Drawings were also made of a number of irregular cells. In most cases 200 to 300 cells were observed in each of the major stages of meiosis for each of the species. An attempt was made to study cells of as many plants as was possible for each of the species in order to get some idea of the variation within the species. Unless a particular plant showed a noticeable number of abnormalities the results were pooled. Results from highly irregular plants are reported separately.

Two species, A. smithii and A. albicans, failed to flower in 1963. Plants of both flowered in 1964, however, and cytological data was obtained at that time. All species flowered profusely in the plot regardless of their origin. Although a number of species flowered while in the greenhouse before they were transferred to the field, none of these heads were collected, as a number of workers have found meiosis to be irregular and not typical for the species while under greenhouse conditions.

One species, A. saxicola, failed to undergo meiosis. Inflorescence samples from all ten plants were collected several times at varying stages of development both in the greenhouse and the field plot with no trace of anther development observed. The somatic number of $2n=28$ was determined by root tip examination.

III. EXPERIMENTAL RESULTS

A. spicatum (Pursh) Scribn. and Smith

Meiosis in the diploid strain of A. spicatum was found to be very regular. Chromosome counts were made in the diakinesis stage from a total of 108 cells from each of the ten plants. All of them showed $2n=14$. A total of 278 cells examined at diakinesis failed to show any irregularities. At metaphase I, of 315 cells studied all had seven bivalents (Fig. 3, a & b) 307 of which were closed bivalents. Three cells had one open bivalent; 4 cells showed two and one cell three open bivalents. Anaphase I (Fig. 4a) was also regular, a total of 327 cells examined showed only one irregularity, a chromosome bridge. No irregularities were found in any of the later stages. Four pollen cells were found undergoing mitosis (Fig. 4b). The meiotic chromosomes of A. spicatum and A. inerme were found to be the smallest of all the Agropyron species examined.

The tetraploid form of A. spicatum proved to be somewhat more irregular in meiosis. Of 52 cells examined at diakinesis, 22 showed 14 closed bivalents; 17 cells had 13 closed and one open bivalent; 9 cells showed 12 closed and 2 open bivalents; and 4 cells showed 11 closed and 3 open bivalents. A study of 86 cells at metaphase I failed to show any irregularities (Fig. 5a). However, all later stages were markedly irregular. Of 164 cells observed at anaphase I (Fig. 5b) 6% (10) showed the presence of one laggard. Anaphase II showed almost 8% irregularities in 289 cells studied. The most common

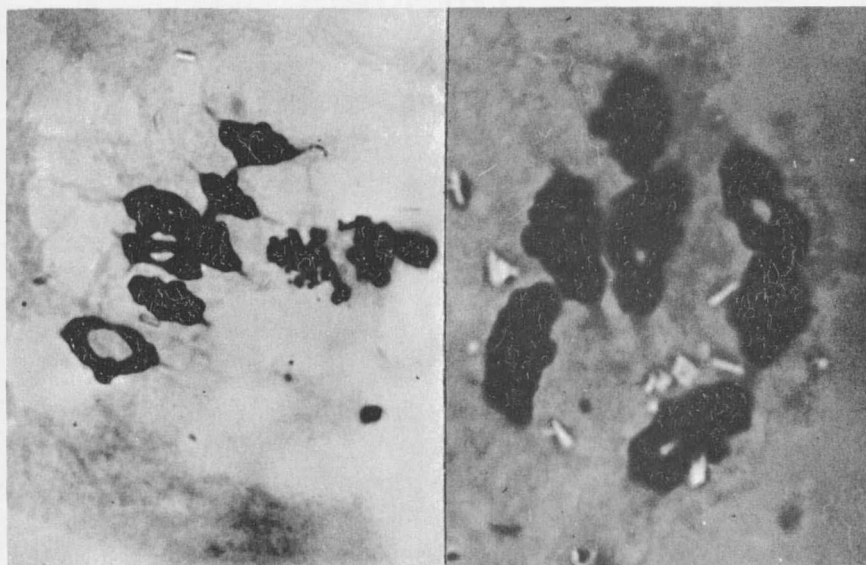


Fig. 3 Meiotic chromosomes of *A. spicatum*;
a and b) metaphase I.

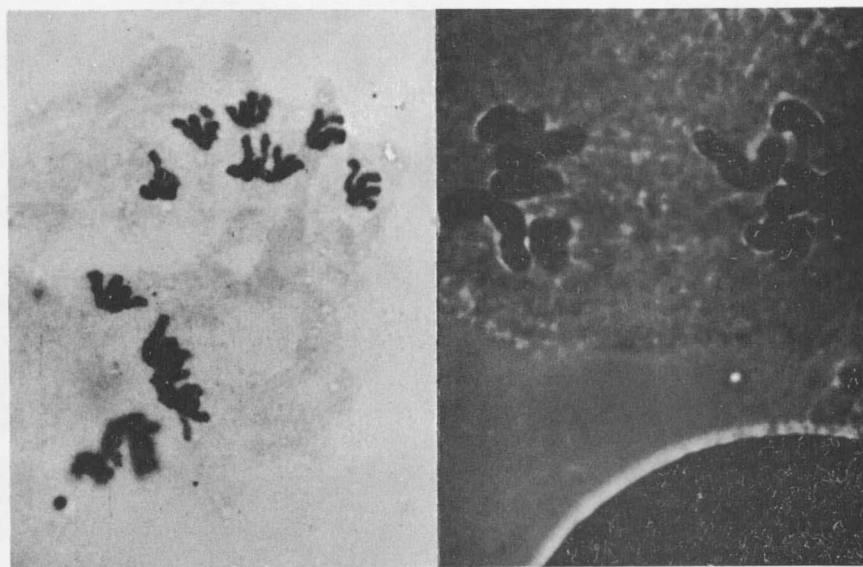


Fig. 4 Meiotic chromosomes of *A. spicatum*;
a) anaphase I and b) mitosis in pollen
cells.

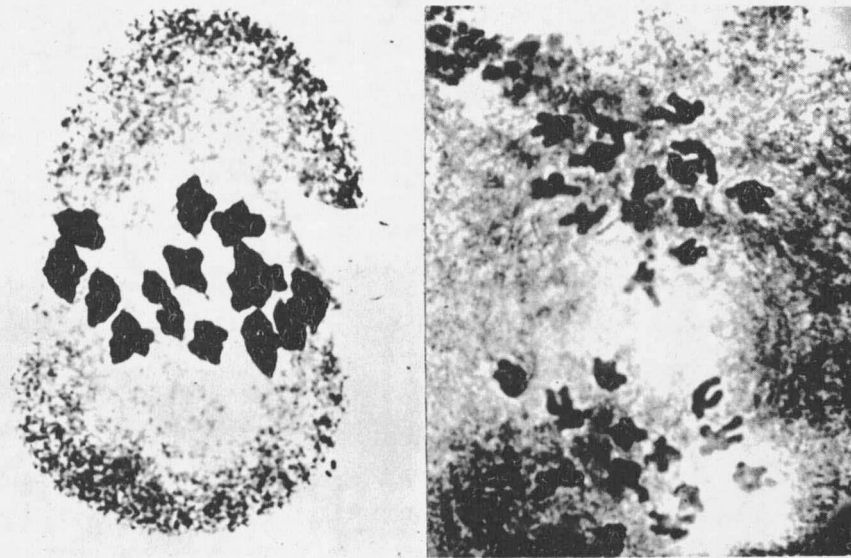


Fig. 5 Meiotic chromosomes of tetraploid A. spicatum; a) metaphase I and b) anaphase I.

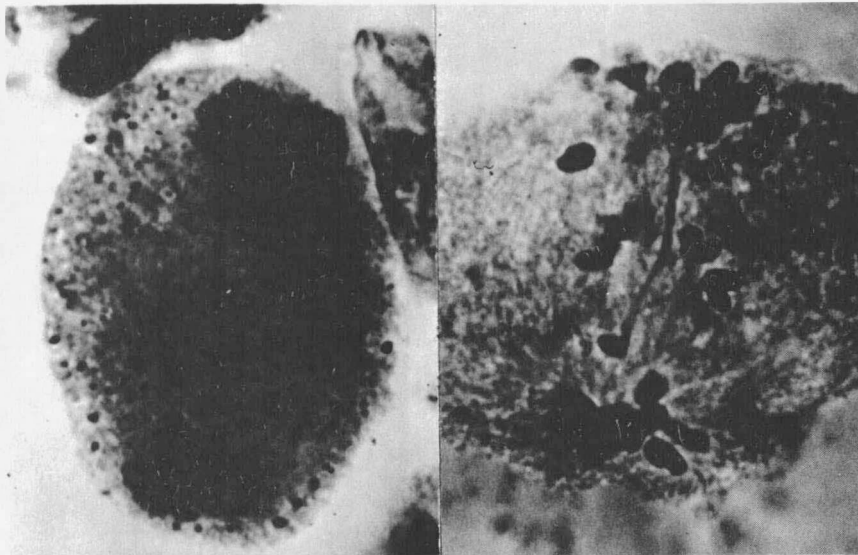


Fig. 6 Meiotic chromosomes of tetraploid A. spicatum; a) anaphase II with bridge and b) bridge and laggards.

irregularity, found in 13 cells, was one laggard, while 7 cells showed 2 laggards. Three cells showed bridges, two of which had no other abnormality (Fig. 6a). In the third cell with a bridge four laggards were also present (Fig. 6b). Micronuclei, up to 2 per quartet, were observed in 17 of 240 quartets. Multivalent associations were never observed at any stage in either the diploid or tetraploid forms of A. spicatum.

A. inerme (Scribn. and Smith) Rydb.

Meiosis in A. inerme was also regular. Eighty-nine chromosome counts were made from cells in the diakinesis stage taken from the ten plants, all of which were diploid ($2n=14$). A total of 305 cells studied in the diakinesis stage showed seven bivalents, all of which were of the closed type. Of 325 cells observed at metaphase I all showed seven bivalents, with only minor irregularities present (Fig. 7, a & b). Out of 320 cells observed at anaphase I, one showed a laggard. No irregularities were found in metaphase II. Chromosome disjunction in both anaphase I and II was consistently regular (Fig. 8a). Bridges were found in six of 300 cells observed in anaphase II, with two of the bridges occurring in the same cell (Fig. 8b). Micronuclei were not observed in 250 quartets. Although the minuteness of the meiotic cells of A. spicatum and A. inerme readily differentiate them from the remaining species of Agropyron, there are no detectable cytological differences between the two species at the diploid level.

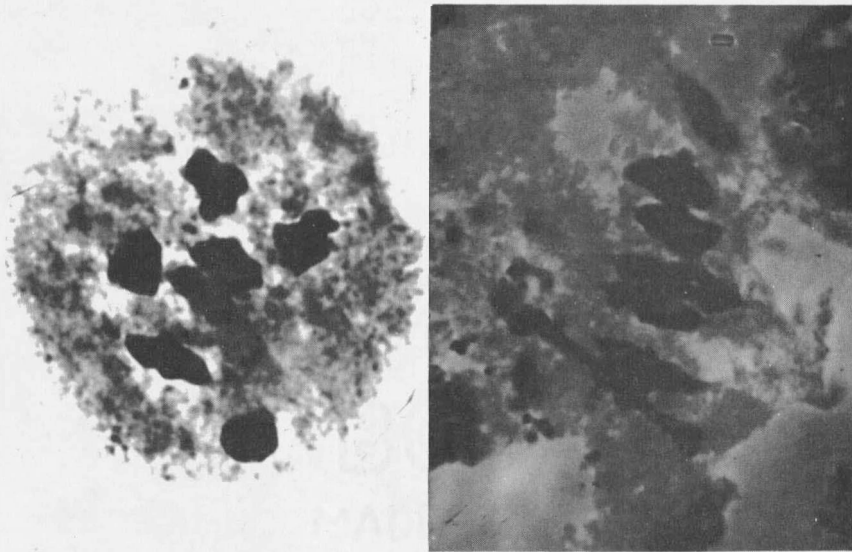


Fig. 7 Meiotic chromosomes of A. inerme; a and b) metaphase I.

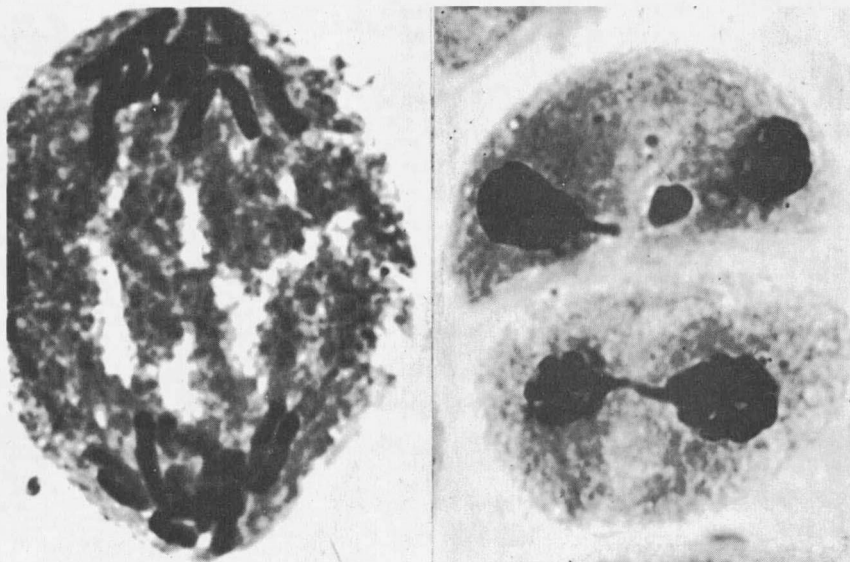


Fig. 8 Meiotic chromosomes of A. inerme: a) anaphase II and b) telophase II.

A. scribneri Vasey

Chromosome pairing relationships were observed in 264 cells at diakinesis, all of which showed A. scribneri to be a tetraploid ($2n=28$). Pairing was complete in every cell with 14 bivalents formed in all cases, 93% of which were closed at both ends. The remaining bivalents were open at one end. One noticeable feature of meiotic prophase is the large nucleolus (Fig. 9a). At metaphase I, of 282 cells examined, 14 bivalents were regularly formed and no irregularities were observed (Fig. 9b). A study of 307 cells at anaphase I revealed 14 cells with a single laggard and one cell with two laggards. One cell was found in which 13 tetrads and a fragment moved to one pole and 14 tetrads and a fragment moved to the other (Fig. 10a). No irregularities were found in metaphase II. Examination of 259 cells at anaphase II showed 15 with a single laggard. Bridge formations or multivalent configurations were not observed at any stage. Micro-nuclei were observed in 14 quartets out of 315 examined.

A. latiglume (Scribn. and Smith) Rydb.

The other alpine species, A. latiglume, also proved to be a tetraploid, with a $2n=28$ chromosome complement. The meiotic cells of this species were the largest meiotic cells observed in the native Agropyrons. The meiotic divisions are also apparently unsynchronized, as stages varying from diakinesis to anaphase II can be found in a single floret in many of the plants. Another distinguishing feature is the large, persistent nucleolus (Fig. 10), which is also noticeable

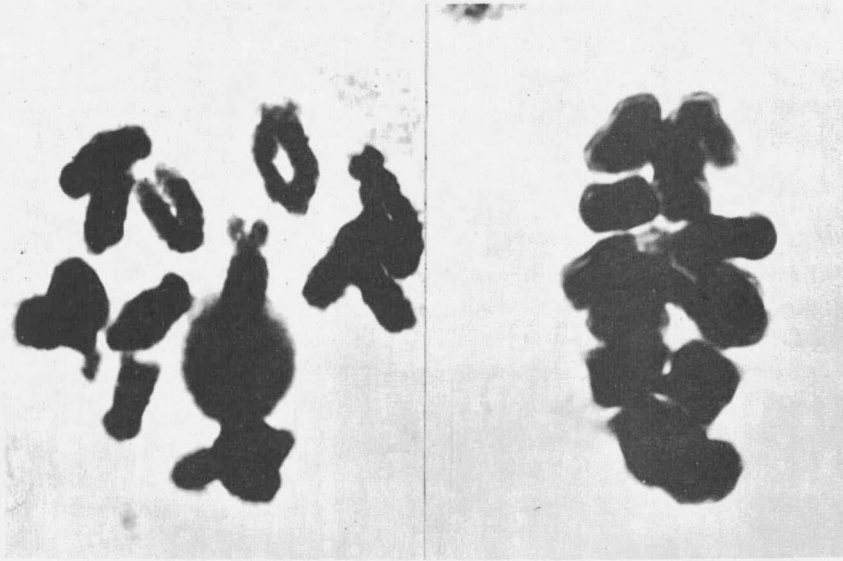


Fig. 9 Meiotic chromosomes of A. scribneri;
a) diakinesis and b) metaphase I.

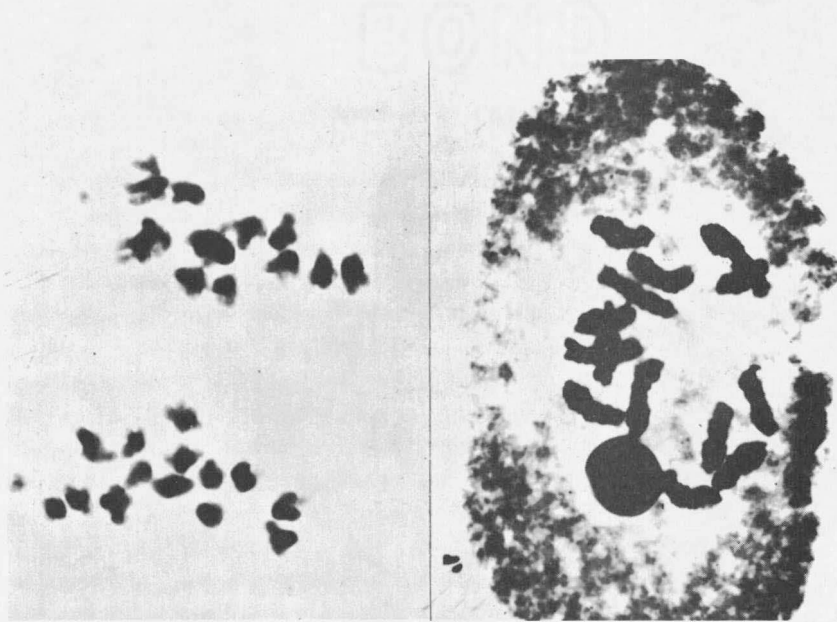


Fig. 10 a) A. scribneri, anaphase I and b)
A. latiglume, diplotene.

in the other alpine species, A. scribneri.

Meiosis was found to be regular in this species. A study of 325 cells at diakinesis revealed that 14 bivalents were regularly formed, almost all of which were closed bivalents. Figure 10b shows a cell in the diplotene stage which clearly shows the number of bivalents formed. Metaphase I was also regular, with 14 bivalents regularly formed, 92% of which were closed rings. Chromosome disjunction was normal at anaphase I and telophase I (Fig. 11a & b) with no laggards or other irregularities observed in the 295 cells examined. Metaphase II also proceeded normally, with 188 cells observed showing no irregularities. However, of 289 cells examined at anaphase II, 11 cells showed single laggards, the only type of irregularity found in this species. No irregularities were observed in the quartets examined.

A. trachycaulum (Link) Malte

A. trachycaulum proved to be a tetraploid, with a count of 347 cells at diakinesis showing 14 bivalents, almost all closed at both ends (Fig. 12a). Multivalents were never observed. In one cell (Fig. 12b) 7 bivalents in the metaphase I stage are clearly visible, all of which are closed at both ends. The rest of the cell is still in pachytene with the nucleolus and chromatin threads readily apparent. Several early prophase cells showed 2 nucleoli present which failed to fuse to form one as is normal in early prophase. Almost one-third (103 of 316) of the cells in metaphase I showed the presence of a single fragment, while 9 cells had 2 fragments present (Fig. 13a).

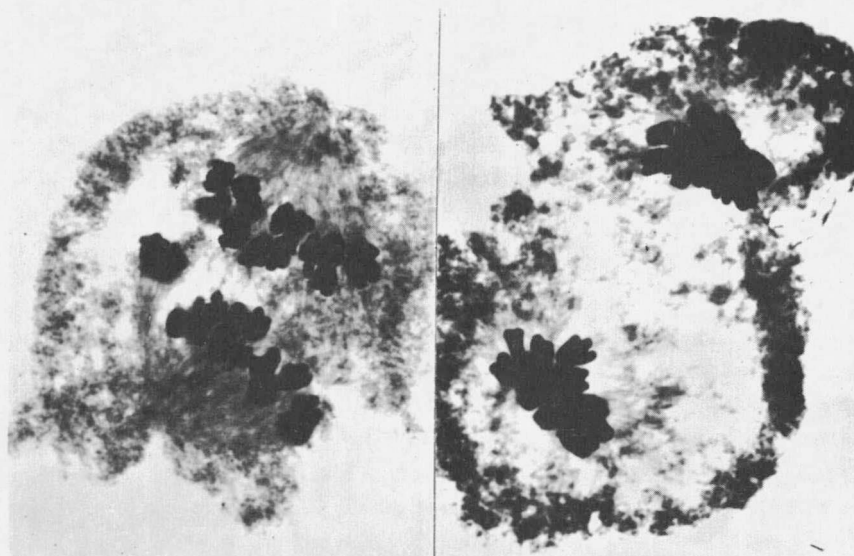


Fig. 11 Meiotic chromosomes of *A. latiglume*;
a) anaphase I and b) telophase I.

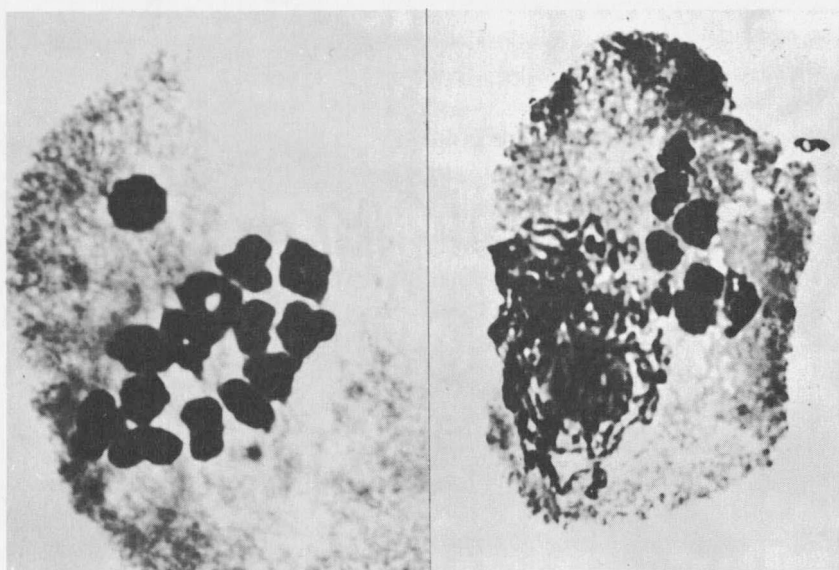


Fig. 12 Meiotic chromosomes of *A. trachycaulum*;
a) metaphase I and b) cell showing both
metaphase I and early prophase stages.

Anaphase I, however, showed less than 10% of the cells (29 of 324) with laggard fragments. Three cells were found with non-disjunction, 15 tetrads moving to one pole while 12 tetrads and one chromatid moved to the other, the remaining chromatid lagging at the equator of the cell. (Fig. 13b). Of 189 cells in anaphase II only 11 showed a single laggard. No other irregularities were found. Chromatin bridges were not observed in any stage. Micronuclei were found in 11 of 216 quartets.

A. subsecundum (Link) Hitch.

A. subsecundum is also of a tetraploid nature, with 229 cells studied in diakinesis all showing 14 bivalents, almost all of them closed. However, in metaphase I, 3 cells were found with 1 quadri-valent each, out of a total of 307 observed. One cell was found which showed 6 closed bivalents, 3 open bivalents, two univalents and one octivalent (Fig. 14a). Metaphase I showed a high number of open bivalents with 89 of the 307 exhibiting some degree of open pairing. Twenty-three cells showed 10 closed and 4 open bivalents (Fig. 14b) which was the highest number found. Anaphase I was markedly irregular with 16% (49) of 315 cells observed containing laggards. Those with two laggards were the most common, occurring in 10% of the cells (31). Six cells showed 1 laggard, 3 cells 3 laggards, 7 cells 4 laggards, and 2 cells 7 laggards. An irregular cell is shown in Figure 15a, with 6 univalents and 2 open bivalents lagging in the equatorial plate of telophase I. Anaphase II also exhibited laggards,

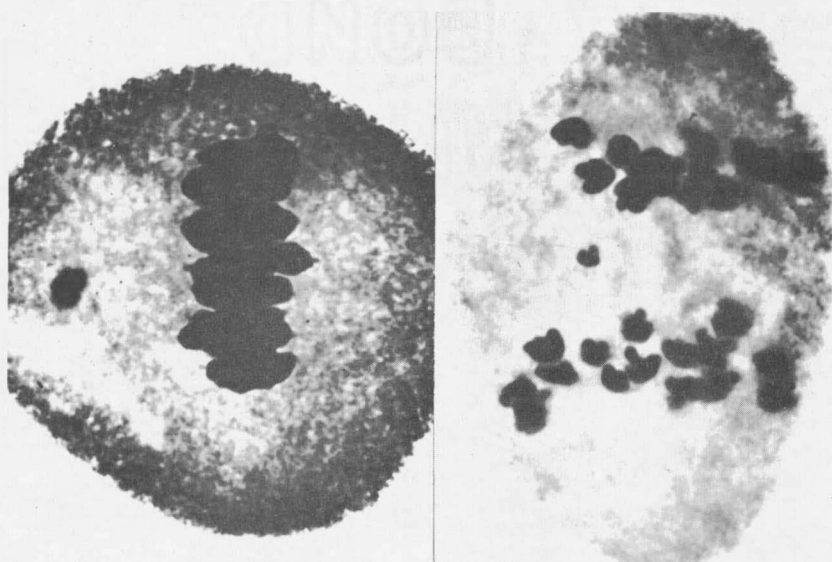


Fig. 13 Meiotic chromosomes of A. trachycaulum; a) metaphase I and b) anaphase I showing unequal disjunction.

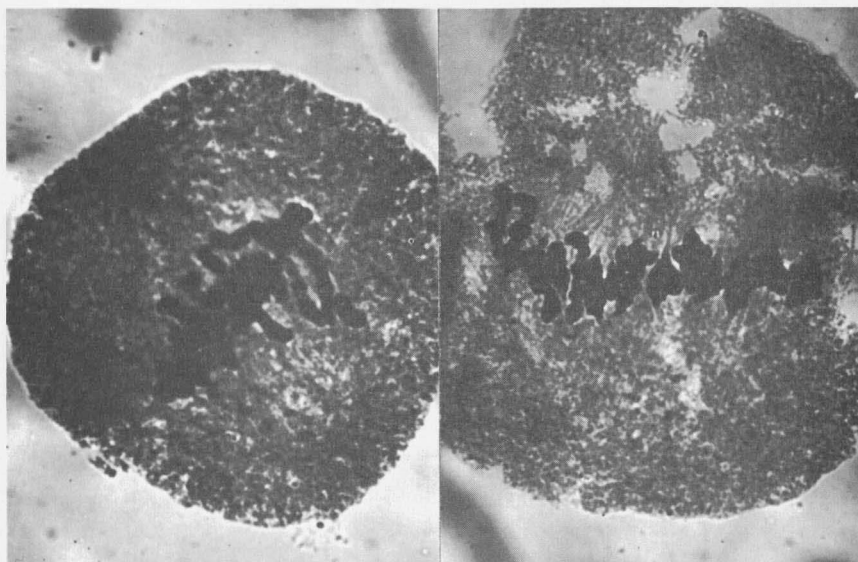


Fig. 14 Meiotic chromosomes of A. subsecundum; a and b) metaphase I.

with 1 to 3 occurring in 9 cells of 123 observed. Of 484 quartets observed, 174 showed one nucleolus, 291 showed 2 and 19 had 3 nucleoli. Figure 15b shows a quartet where three of the four cells show 2 nucleoli. One plant had over 25% of the cells showing some type of irregularity and was not included in the above results. Although A. subsecundum is markedly irregular compared to A. trachycaulum, in its general cell and chromosome size, it is very similar.

A. smithii Rydb.

A. smithii was found to have the highest ploidy level of all the species, being an octoploid with a $2n=56$ complement. A study of 58 cells at diakinesis showed 28 closed bivalents to be the most common situation, but occasionally 1 open bivalent was found (Fig. 16a). Normal pairing was exhibited in all of the 162 cells observed at metaphase I. In anaphase I, chromosome disjunction was very regular (Fig. 16b) with univalents observed in less than 3% of the cells (4 cells of 156 examined). Of 128 cells observed at metaphase II no irregularities could be detected. In anaphase II 86 cells were examined, three of which showed the presence of a single laggard (Fig. 17a). Chromatin bridges were not observed in any of the stages. A few cells were observed in the second meiotic division with the two haploid sister nuclei in different meiotic stages. In these cells one of the nuclei was found to be in the metaphase II stage while the other nucleus was in the telophase II stage (Fig. 17b). A study of 62 quartets revealed 16 with 2 micronuclei and 3 with 3 micronuclei.

