University of Alberta Library

0 1620 3416715 3

For Reference

NOT TO BE TAKEN FROM THIS ROOM

STUDIES ON THE GENUS AGROPYRON

Frank Herbert Peto
Department of Field Crops

University of Alberta,
Edmonton, Alberta,
April, 1930.

Ex LIBRIS
UNIVERSITATIS
ALBERTAENSIS

thesis
1930
#3

STUDIES ON THE GENUS AGROPYRON.

Frank Herbert Peto
Department of Field Crops

A THESIS

submitted to the University of Alberta
in partial fulfilment of the requirements for
the degree of

MASTER OF SCIENCE.

Edmonton, Alberta.

April, 1930.

TABLE OF CONTENTS.

	Page.
INTRODUCTION	1
PART I. DISTRIBUTION AND MORPHOLOGICAL VARIABILITY.	
Collection and propagation of material	3
Distribution of the <u>Agropyrons</u> .	
General distribution	5
Distribution in Alberta	6
Morphological variability.	
Literature review	9
Observations	10
Discussion	14
PART II. CYTOLOGICAL STUDIES.	
Literature review	18
Material	19
Methods.	
Pollen-mother-cell preparations	20
Root-tip preparations	23
Formulas for reagents	24
Cytology of species	26
Discussion	
Polyploidy	32
Cytological evidence of natural hybridization.	33
GENERAL CONCLUSIONS	40
SUMMARY	42
LITERATURE CITED	44

STUDIES ON THE GENUS AGROPYRON.*

INTRODUCTION.

Preliminary investigations on the genus Agropyron have revealed many problems of a fundamental nature and the solution of these is a matter of considerable importance since the genus contains some of our most valuable native hay and pasture grasses.

The taxonomy of the Agropyrons is in a very unsatisfactory condition. Authorities differ widely in their concepts of the species within this genus. This undoubtedly is due to the wide range of variability existing within the so-called species and also to the large number of intergrading types that occur between these species. In some instances the extent of the variability has never been reported and in others some of the intermediate types have been classified as distinct species. These taxonomic difficulties extend to the seeds; analysts and seed merchants are unable to separate the desirable and undesirable forms with reasonable accuracy. Comparative morphology cannot be relied upon entirely to solve these taxonomic difficulties; additional evidence, provided by ecological, genetical and cytological studies, appears to be necessary. The information made available through the application of all these methods of study will undoubtedly be of great value to the

* This is a general project of the Department of Field Crops. The first contribution was made by W. Robinson (26) whose work covered the seasons of 1926-27.

Digitized by the Internet Archive
in 2018 with funding from
University of Alberta Libraries

taxonomist and to the plant breeder as well. A knowledge of the distribution of the various species and their adaptability to various types of soil and climate is prerequisite to the selection of types of economic value. Investigations of a genetical nature are needed to explain the wide variability found within the species and also the appearance of intermediate types. Cytological evidence such as chromosome number may assist in providing a definite basis for classification, in addition to indicating the crossability of species with each other, while chromosome behavior at reduction division is of value in detecting hybridity as well as in providing clues to the possible causes of sterility.

Certain of these modes of attack have been employed in this investigation in an endeavor to solve some of the taxonomic difficulties and to provide useful information of a fundamental nature to the plant breeder. The writer has had an opportunity during the last two years of making a general study of the distribution and morphological variability of the Agropyrons, in addition to making a more intensive cytological study of a few species of this genus.

PART I. DISTRIBUTION AND MORPHOLOGICAL VARIABILITY.

Collection and propagation of material.

A large proportion of the material used in this investigation was collected during the summer of 1929. A wide area of Alberta was covered by two automobile trips. The general route of the first was from Edmonton south as far as Medicine Hat via Hanna and Brooks, west through Lethbridge, Raymond and Cardston, and then north through Macleod and Calgary. Later another trip was made west of Edmonton through the Edson district, returning via Greencourt and Rockfort Bridge. Dr. L.E. Kirk of the University of Saskatchewan supplied specimens taken from a wide territory in Saskatchewan. Additional specimens were collected by the writer in southern Manitoba.

In collecting, the whole plant was dug up, the roots wrapped in moist cotton batting and placed in fibre cans where they would keep satisfactorily for a couple of weeks. The stems and inflorescence were pressed for herbarial purposes. Complete information as to locality, soil type, and plant associations was recorded. On returning to the university the roots were planted either in the grass-garden or in the greenhouse. This procedure makes possible a study of the influence of environment on the morphological characters of these plants by comparing the plants produced at the university under uniform conditions with herbarium specimens

which had grown in variable native habitats. About one hundred native plants were collected in the above manner during the summer of 1929.

Seed of the various Agropyron species was collected wherever possible. Seventy-five samples of seed of native species were procured. Additional seed samples of both native and introduced species were obtained from the Universities of Manitoba, Saskatchewan and California. It was felt that an attempt should be made to obtain seed of the Agropyrons from European countries where conditions are similar to our own, and consequently the following species were introduced.

Botanical Gardens of Tiflis, U.S.S.R. Caucase, Georgie.

- A. repens (L.) Beauv.
- A. dagnae Grossh.
- A. repens P.B. var glaucescens
- A. orientale R. & S.
- A. cristatum Schrb. R.B.
- A. sibiricum W. Eichw.

Experimental Station, Omsk, Siberia.

- A. sibiricum
- A. cristatum
- A. repens

Experimental Station, Krasnyi Kut (gov. Saratov).

A. desertorum

A. cristatum

A. tenerum

Botanical Gardens of Copenhagen, Denmark.

A. caninum (L.) R. & S.

A. " R. & S.

A. glaucum R. & S.

A. junceum (L.) Beauv.

A. obtusiusculum Lange.

A. orientale

A. repens (*Triticum repens* L.)

A. sibiricum var. *desertorum*

A. repens (L.) Beauv.

A. villosum Link.

Distribution of the Agropyrons.

General Distribution.— There are about sixty species in this genus, which are widely distributed over the temperate regions of the northern hemisphere. Approximately thirty-five species occur in Canada and the United States, and of these about ten are native to Alberta. All of the native species observed in Alberta are valuable as forage plants, the two most important being western-rye grass (*A. tenerum* Vasey) and western-wheat grass (*A. Smithii* Rydb.). The former has been

successfully grown under cultivation in western Canada since 1885. The latter is extremely drought hardy and is a very important constituent of the range grasses of the western plains.

Distribution in Alberta-- The distribution of the common native species was studied in a general manner from information obtained while on field trips. The points at which the various species had been collected were marked on a map, and it was observed that, in general, various species groups seemed to be confined largely to the soil types and vegetative zones to which they were best adapted. This is illustrated in the map of southern Alberta, Plate I. The four major soil types are marked off on the map by single lines. The triple line marks the northern and western limits of the prairie zones, while the double line indicates the western border of the parkland. West of this zone are the wooded areas.

The most common species on the typical grey-wooded and black soils are A. Richardsonii and A. tenerum. These grasses are generally found in the same associations. Robinson (26) reports A. tenerum growing in Stipa-Bouteloua associations near Macleod, frequently with the "prairie wool" of the plains. The observations made by the writer indicate that A. tenerum and A. Richardsonii are not common in the typical Stipa-Bouteloua associations of the south-eastern part of the province, except in unusual associations where the moisture supply is abundant, such as moist ravines, shaded hillsides, etc.

Plate I

Distribution of the Agropyron species in southern Alberta.

In the brown soil zone which corresponds roughly to the short grass plains, A. Smithii and A. dasystachyum are very common and are frequently observed in the same associations. A. Smithii is perhaps the more abundant. Large areas of pure stands are found scattered throughout the dry range country. It seems to thrive particularly well on abandoned farms in this area.

In the transitional belt between the brown and black soils there exists an intermediate condition both in soil and vegetation. In the northern part of the belt of which Wainwright is the centre, there are localized areas of very light typical prairie soil dispersed among patches of heavier soil which is more typical of the parkland. Naturally in this area species representative of both soil types were observed. This district was not visited by the writer but conclusions were largely based on observations made by Dr. E.H. Moss and on herbarium specimens collected from that district by the Botany Department, University of Alberta. In the typical prairie associations in this region A. Smithii and A. dasystachyum are found while in the typical park-land associations A. tenerum and A. Richardsonii are common.

On the open prairie in the southern part of this transition soil zone A. tenerum and A. Richardsonii were not frequently observed, whereas A. Smithii and A. dasystachyum were quite common. A. Griffithsii was also an important species in this region and was often found associated with A. Smithii

and A. dasystachyum especially in the western part of this zone extending from Didsbury to Cardston. The distribution of A. spicatum is very uncertain. Dr. S.E. Clarke of the Dominion Range Experiment Station reports this species in the south-western part of the province. Sampson (28) states that this species has a very wide distribution and that it occurs from northern Michigan and central Alberta to Alaska. However in a reply to a personal letter in this regard Dr. Sampson states that he made no collections of this species in Alberta, but relied on herbarium specimens at the National Herbarium at Washington. He states (28)

"As this is a highly drought enduring grass, the best growth is made on well-drained lands, particularly on light sandy loam soils. In the north-west at medium elevations it often constitutes the controlling type of plant growth. It is often the chief grass species on scab-lands, bench-lands, and on gritty poorly disintegrated soils of low water content."

The uncertainty which exists in regard to the occurrence and distribution of A. spicatum is probably due to its similarity to A. Griffithsii in all but root characters. One of the plants in a collection made by W. Robinson (26) was first identified as A. Griffithsii and was later identified as A. spicatum. Dr. R. Newton and Dr. O.S. Aamodt of the Department of Field Crops collected specimens at Waterton Lakes Park which were typical A. spicatum in spike characters but their identification was uncertain since the roots were not collected.

This general study of the distribution seems to indicate that the species groups are in general largely confined to definite soil types or vegetation zones, but there are many

exceptions in so far as these zones contain localized areas on which the vegetation is not typical of the zone as a whole. Small associations may be observed in the wooded area, which are typically xerophytic in character and may closely resemble the typical dry plains associations in both soil type and vegetation.

Morphological Variability.

Literature review.- The morphological variability in A. tenerum was recognized by Malte (22) who states,

"This species occurs in a tremendously large number of forms in Canada."

His observations were made at Edmonton, Alberta, where a large number of western-rye grass forms occur in great profusion. Kirk (17) collected seed of 150 individual plants of A. tenerum within a radius of ten miles of Saskatoon and remarks that one is impressed with the variability exhibited in this material. He states,

"Some of the more obvious characters in which the strains differ are color; width and texture of leaf; fineness, height and strength of stem; length and density of spike; earliness and productivity."

Raunkiaer (25) made a detailed morphological study of the native species of Agropyron from different localities in Denmark. He differentiated between the various forms by means of small morphological characters which he called "isoreagents." He studied 12,000 plants of A. repens from different localities, and observed especially the pubescence, color, etc. He found that there seemed to be no definite relation existing between these different characters and the environment. He studied

similarly A. junceum (L.) Beauv., A. litorale (Host) Dum. and interspecific crosses between the three species.

The seed characteristics of A. tenerum, A. repens and A. Smithii have been thoroughly studied by Dalberg (6), Foulds (10) and Henry (13). Foulds' paper describes the seeds of the three species mentioned above and also those of A. cristatum, A. Richardsonii and A. divergens, and deals more briefly with seeds from herbarium specimens of five less common species. Foulds also noticed distinct seed types within A. tenerum, A. Smithii and A. dasystachyum. Miss Henry's paper presents in an especially lucid manner the distinguishing characteristics of the typical seeds of A. repens, A. Richardsonii and A. tenerum, which are well illustrated by drawings.

Observations.- A study of the native species of Agropyron growing in Alberta indicated a wider range of variability than hitherto reported in the literature. This was especially true of A. tenerum and A. Richardsonii. There appeared in nature such a complete gradation of forms between these two species that it was nearly impossible to determine which species certain of these intermediate forms more nearly resembled. Plate III, illustrates this condition. These spikes were collected in Alberta in 1929 from native plants. Spikes Nos. 1 to 5 are typical A. Richardsonii and correspond with a few minor exceptions to Rydberg's (27) description:

"spikes 7-10 cm. long, one-sided; spikelets 3-4 flowered; empty glumes 12-16 mm. long, short-awned or awn-pointed; lemma 10-15 mm. long, scabrous on the margins."

Plate III.

Spikes Nos. 1- 5 typical A. Richardsonii.

" " 25-28 " A. tenerum.

" " 6-24 intermediate forms.

These five spikes vary in color of empty glumes, Nos. 1 to 3 being a dark purple. The spikes are longer than the limits given by Rydberg. The remainder of the A. Richardsonii-like spikes differ in many respects. The awns vary in length from 1.5 to 30 mm. The length of the awns in these cases was not considered by the writer to be a satisfactory criterion of species. Spikes Nos. 7 to 13 have very short awns but they closely resemble typical A. Richardsonii in the other spike characteristics such as density, one-sidedness of the spikes, etc. Dr. J.R. Swallen of the Grass Herbarium, United States Department of Agriculture, identified specimens with this form of spike as A. tenerum. He evidently considered that the awns on these spikes were not of sufficient length to allow the plants to be classified as A. Richardsonii. This illustrates the difficulties encountered in attempting to identify these intermediate forms.

Spikes Nos. 25 to 28 are typical A. tenerum, according to Rydberg (27). He describes this species as follows:

"Spikes slender, 1-1.5 dm. long, lax; spikelets 3-5 flowered; empty glumes 10-12 mm. long, acute to awn-pointed, 5 nerved; lemma 8-10 mm. long, smooth often mucronate or with short awned tip."

The remainder of the tenerum-like spikes vary from the normal in many respects. Length of spike varies from 8 dm. in No. 14 to 32 dm. in No. 29. The awns on the lemmas of seven of these spikes are very short, less than 1.5 mm.; the remaining four have awns from 5 to 16 mm. long. The density of spike varies

between the short dense spike in No. 22 to the very lax spike in No. 29. Some of the tenerum-like spikes show a distinct unilateral condition which is more typical of A. Richardsonii; this condition is very marked in Nos. 20, 21, 22 and 24. A careful examination of this plate discloses a complete gradation of spike forms between these two species, the typical members of which are very distinct. It is however practically impossible to determine the limits of these two species when this multiplicity of intergrading forms is taken into consideration.

The same degree of variability can be observed between the species A. Smithii and A. dasystachyum. This is illustrated in Plate IV. Spike No. 2 is typical of A. Smithii, while spikes Nos. 10, 11 and 12 are typical A. dasystachyum. Rydberg's description for the spike characters of A. Smithii is as follows:

"Spikes 7-18 cm. long; spikelets much flattened, spreading, 7-13 flowered, sometimes in pairs; lemma 8-12 mm. long, lanceolate, acute or acuminate, seldom awn-pointed, smooth or nearly so."

Spike No. 1 differs in having 2 spikelets at each node. No. 3 has awns 2 mm. long. No. 4 is a dense spike with light purple lemmas and glumes. No. 5 is a short dense spike, with dark purple lemmas and glumes, the lemmas being minutely pubescent with hispidulous margins.

Spikes Nos. 6 and 7 were identified at the Grass Herbarium, United States Department of Agriculture, as A. Smithii molle

Plate IV.

Spike No. 1 A. Smithii; note two spikelets at each node.

" " 2 typical A. Smithii.

Spikes Nos. 3-5 forms of A. Smithii.

" " 6-7 typical A. Smithii molle.

" " 8-14 forms of A. dasystachyum.

S.S. Jones. These spikes differ from typical A. Smithii by the presence of fine pubescence on the rachis glumes and lemmas.

The spikes of A. dasystachyum are described by Rydberg as follows:

"Spike 6-18 cm. long; spikelets slightly compressed, 4-8 flowered; lemma long, villose, broadly lanceolate, 10-12 mm. long, acute or rarely short awned."

The variation in density of the spikes is very marked, Nos. 13 and 14 being very lax, while Nos. 8, 9 and 10 are dense. Spikes Nos. 9, 13 and 14 are faintly pubescent, while those of Nos. 8, 10, 11 and 12 are villose. In general form, spikes Nos. 13 and 14 are quite distinct. The latter was identified by the writer as A. Griffithsii on account of its divergent awns, subterete spikelets and faintly pubescent lemmas. However both these plants were identified at the Grass Herbarium, United States Department of Agriculture, as A. dasystachyum. Individual spikelets of these two plants are shown on Plate II, Figs. 11 and 12.

The gradation between A. Smithii and A. dasystachyum is further illustrated in Plate II showing individual spikelets of these forms. Nos. 1 to 3 are A. Smithii forms and vary in color, size, length of awn and pubescence. Nos. 4 to 6 are A. Smithii molle and differ from typical A. Smithii in being faintly pubescent. Nos. 7 to 12 illustrate various spikelet forms of A. dasystachyum. No. 9 is nearest the typical. Nos. 11 and 12 show two forms which closely resemble A. Griffithsii.

Plate II.

Fig. 1-3 - Spikelet forms of A. Smithii.

" 4-6 - " " " A. Smithii molle.

" 7-12- " " " A. dasystachyum.

A. repens is a species introduced from Europe which has become well established, especially in the older settled districts, where it has become a very serious weed. The variability found in this species is illustrated in Plate V. The first four spikes represent forms found growing under similar conditions near Emerson, Manitoba, within a mile of each other, so that the differences noted in this case are not likely attributable to environment. The remainder were collected in various parts of Alberta and represent a wide variation in length and density of spike, number of florets per spikelet, pubescence of the rachis, and color of the lemma and palea. Spikes Nos. 2, 5 and 6 were identified at the Grass Herbarium, United States Department of Agriculture.

The species, A. cristatum was introduced from Russia and is becoming recognized as a forage crop of some merit. This species also exhibits considerable variability in spike form, as illustrated by Plate VI. These spikes were collected in a small plot at the Dominion Experimental Station at Lethbridge, Alberta. The most variable characteristics are length, density, spreading condition of the spike, length of awns and number of florets per spikelet.

Discussion.— The foregoing evidence indicates a wide range of variability within all the species of Agropyron studied, and in two cases an intergrading series was observed between the species. In attempting to explain this condition

Plate V.

Spike forms of A. repens.

PLATE VI.

Spike forms of *A. cristatum*.

the effect of environment must not be overlooked. Some of the variation observed is likely due to the specimens being grown under varying conditions of soil and climate. An estimation of the extent to which this is true awaits the results that may be obtained from growing this apparently variable material in the same environmental conditions. However many cases have been observed where widely different forms were growing side by side.

These intergrading forms may be genetically pure lines and may therefore breed true on further test. Malte (22) found this to be the case in A. tenerum. He used nine individual plants representing nine widely different types. The progeny of each of these plants did not exhibit the slightest observable morphological variation. Kirk (17) obtained the same results in the main but he states that some degree of self-pollination takes place, since he found by observing large numbers of individual plant progenies that occasional families showed segregation for one or more characters. Further breeding work is needed on a large number of forms of all the species to determine adequately what proportion of the native forms are genetically pure lines.

Interspecific hybridization may be responsible for the appearance of these intermediate forms. If there is a high percentage of self-fertilization, and sufficient time has elapsed since the cross occurred, many of the segregates may breed true. However if the cross is of recent origin,

segregation for the various characters would be expected. Numerous indications of interspecific hybridization in this genus have been observed in European countries. Troitzky (32) states that in the steppe Haredja (Central Transcaucasia) in places where A. cristatum J. Gaerfn. grows along with A. repens (L.) P.B. var. glaucescens. Engl., specimens were observed transitional in all their recognizable characters between the two above-mentioned species and forming moreover, a series of very gradual transition from A. repens to A. cristatum. Of these specimens, those occupying an intermediate position between A. repens and A. cristatum cannot be distinguished morphologically from A. sibiricum Eichw. Hitherto the latter species has not been met with in Transcaucasia. It is however scattered over south-eastern Russia, western Siberia and Turkestan. Troitzky concludes that this phenomenon may be attributed to a secondary formation of A. sibiricum through hybridization or it is a convergent formation identical to the existing species.

Raunkiaer (25) reports that in Denmark many types were found which he believed to be hybrids between A. junceum and A. repens and which were very similar to A. obtusiusculum Lange. He further reports forms some of which he believes to be hybrids between A. junceum and A. litorale, and others of which he regards as hybrids between A. repens and A. litorale.

The findings of these two workers are of great interest to us since it appears that we have a very similar situation

in the occurrence of intergrading series between A. Richardsonii and A. tenerum, and also between A. Smithii and A. dasystachyum.

It was noted above that A. Smithii molle appears to occupy an intermediate position between A. Smithii and A. dasystachyum. This condition parallels identically that reported by Troitzky for the Russian species, especially when we consider that the species which show the intermediate forms are always found closely associated in the same community under ideal conditions for natural hybridization. The evidence presented so far seems to point strongly to natural hybridization as being responsible for the appearance of these intermediate forms. The cytological data presented in Part II of this paper provides further evidence in support of this hypothesis.

PART II. CYTOLOGICAL STUDIES.

Literature review.

The chromosome numbers of a great many species of Gramineae have been established during the last twelve years. The counts for the principal cereal crops were listed by Stolze (30) in 1925 and by Aase and Powers (1) in 1926. In the last four years a mass of cytological data has been accumulated on the cereals, so that in this group of plants our knowledge of the chromosome numbers is fairly complete.

There is relatively little information available on the cytology of native and cultivated grasses. Evans (9) in 1926 reported counts in various species of Lolium and Festuca. Davies (7) a year later announced counts for Dactylis glomerata. Church (4) and (5) published in 1929 the results of extensive cytological studies in 31 species of the tribes, Festuceae, Aveneae, Agrostideae, Chlorideae, Phalarideae, Paniceae, and Andropogoneae.

A review of the literature revealed only one instance where any cytological work had been done on the Agropyrons. Stolze (30) included in the Triticum group the counts of Triticum (Agropyron) repens L. and reported 21 chromosomes in pollen-mother cells and 42 in somatic cells.

The early cytological findings in this investigation

THE JOURNAL OF THE
ROYAL ANTHROPOLOGICAL INSTITUTE

The following account of the recent work of the
Institute is given in the first part of the
Journal. The second part contains the report of the
Committee on the Anthropology of the British Isles
in 1901. In the third part there is a short account of the
work of the Institute in the year 1902. The fourth part
contains the report of the Committee on the Anthropology of the
British Isles in 1903.

There is a special issue of the Journal devoted to
the subject of the British Isles. The first part of this
issue contains the report of the Committee on the
Anthropology of the British Isles in 1901. The second part
contains the report of the Committee on the Anthropology of the
British Isles in 1902. The third part contains the report of the
Committee on the Anthropology of the British Isles in 1903.

The following account of the recent work of the
Institute is given in the first part of the
Journal. The second part contains the report of the
Committee on the Anthropology of the British Isles
in 1901. In the third part there is a short account of the
work of the Institute in the year 1902. The fourth part
contains the report of the Committee on the Anthropology of the
British Isles in 1903.

were reported by the writer (24) in a short article in which the chromosome counts of six species of Agropyron were given. These species were found to fall into three groups with haploid chromosome numbers of 7, 14 and 21.

Material.

Most of the cytological preparations were made from material that had been grown in the greenhouse during the winters of 1928-29 and 1929-30. This was made possible by the use of artificial lighting for a part of the night. The greenhouse was essential for this work, since the material for root-tip study had to be grown in pots. For chromosome counts in pollen-mother cells material grown in the greenhouse was found superior to that grown in the field, because of the difficulty of getting the material at the correct stage. The plants in the field developed very uniformly and all the spikes on the plant reached the stage about the same time, which allowed only a short time in which it was possible to get anthers at the correct stage. It was found that this difficulty could be overcome to some extent in the greenhouse by controlling the growing conditions and cutting back the plants.

The plants were grown in either pots or wooden boxes. The latter, being larger, were most satisfactory for growing pollen-mother-cell material, since more spikes usually developed. The plants used for root-tip study were grown in pots. The young growing root-tips were easily collected after carefully removing the plants from the pots.

There has been as yet no opportunity to check the identity of some of the plants reported in this investigation.

Methods.

Pollen-mother-cell preparations.- The anthers were killed and fixed when the majority of pollen-mother cells were undergoing either the heterotypic or homotypic divisions. This stage is reached at widely varying times in different species. In A. tenerum the proper time to examine the plants is when the tip of the spike is still 1 or 1.5 inches below the point of emergence from the leaf-sheath, while in A. cristatum this stage is not reached until the spike has emerged 2 or 3 inches. The proper stage was quickly ascertained by preparing temporary mounts by Belling's (2) aceto-carmin method. One or two stamens were placed on a slide and covered with a few drops of strong aceto-carmin solution which contained a trace of ferric hydrate. A cover glass was placed over them and gently tapped sufficiently to burst the anthers and allow the pollen-mother cells to exude. These were stained sufficiently in a minute or two, so that the chromosomes could be distinguished. When the proper stage was observed, the florets from the same position of adjacent spikelets were used for making permanent mounts.

For the preparation of permanent mounts, the anthers with the enclosing lemma and palea were fixed in Carnoy's 6-3-1

solution for two minutes and then for twenty-four hours in Zenker's fluid, Lee (19). The material was then washed in running water over night, after which it was dehydrated by treatment for 30 minutes in each of the following alcoholic solutions: 5, 10, 20, 30, 40, 50, 70, 85 and 95% and three changes of absolute alcohol. Xylol and chloroform were both used as clearing agents with satisfactory results. The following proportions of these with absolute alcohol were used, and changes were made every hour:

- 1 chloroform (or xylol) - 3 absolute alcohol
- 1 " " " - 1 " "
- 3 " " " - 1 " "

This was followed by two changes of pure chloroform or xylol. The only advantage chloroform has over xylol is that the paraffin does not need to be changed in the oven during infiltration when the former is used. The xylol has the advantage of being cheaper and not so unpleasant to handle.

Cold paraffin was added to the clearing solution and allowed to infiltrate slowly into the material for 24 hours with the vials corked, another 24 hours with the vials uncorked and 6 - 12 hours in the oven.

The sections were cut 20 u. thick, attached to the slide with Mayer's fixative, and allowed to dry on the warming plate over-night. The slides were then handled according to the following schedule:

Washed with xylol using dropper.

Xylol - 5 minutes.

$\frac{1}{2}$ xylol $\frac{1}{2}$ abs. alcohol - 2 minutes.

Washed with abs. alcohol using dropper.

Abs. alcohol - 2 minutes.

95% alcohol - 2 minutes.

50% " - 2 "

Washed in running water - 15 minutes.

Stained in 1% solution of gentian-violet - 5-7 minutes.

Rinsed rapidly in water.

Iodine solution - 30 seconds.

Passed rapidly through 2 jars of absolute alcohol.

Differentiated in clove oil.

Xylol 1 - 2 minutes.

" 2 - 5 "

" 3 - 10 "

Mounted in Canada balsam.

The iodine-gentian-violet method as described above proved very valuable for pollen-mother-cell preparations, especially in conjunction with Zenker's killing and fixing agent. It seemed particularly well suited for studying the various prophase stages in addition to giving excellent chromosome counts in the heterotypic metaphase. It had the advantage of being quicker than Heidenhein's Iron-Haematoxylin method, and gave better results with the Agropyrons. W.C.F. Newton of John Innes Horticultural Institution devised this

Shower with light rain.

Clear - 2 minutes.

Light rain - 2 minutes.

Shower with light rain.

Clear - 2 minutes.

Light rain - 2 minutes.

Clear - 2 minutes.

Shower in passing rain - 2 minutes.

Shower in light rain of passing rain - 2 minutes.

Shower rapidly in rain.

Light rain - 2 minutes.

Shower rapidly in rain - 2 minutes.

Shower rapidly in rain.

Light rain - 2 minutes.

Clear - 2 minutes.

Clear - 2 minutes.

Shower in passing rain.

The light rain - 2 minutes.

Shower very rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

Shower rapidly in light rain - 2 minutes.

adaptation of the Gram method, Huskins (14).

Root-tip preparations.- The root-tips were taken from young vigorously growing plants. It was found advisable to water the plants the night before fixing in order to enlarge the cells.

The root-tips were fixed in Karpetschenko's solution for 24 hours. The procedure followed from this point until the sections were ready for staining was the same as that given for the pollen-mother-cell method, except that the sections were cut to 10 u. thick instead of 20 u. The iodine-gentian-violet method was found unsatisfactory for root-tip work and Heidenhein's iron-haematoxylin was used with excellent results. The slides after being passed through the alcohols and washed in water for 15 minutes were treated in the following manner:

Hydrogen peroxide 25% solution	- 1 hour.
Washed in running water	- 15 min.
Iron alum 4%	- 2 hours.
Washed in running water	- 15 min.
Haematoxylin $\frac{1}{2}$ % solution	- over night.
Washed in running water	- 15 min.
Destained in 2% iron alum, watching process under microscope.	
Washed in running water	- 1 hour.
50% alcohol	- 2 min.
95% "	- 2 "

Washed with abs. alcohol using dropper.

Absolute alcohol - 2 min.

$\frac{1}{2}$ abs. alcohol $\frac{1}{2}$ xylol - 2 "

Washed with xylol using dropper.

Xylol - 10 "

Washed with xylol using dropper.

Mounted in Canada balsam.

Formulas for reagents.- Belling's Iron-Aceto-Carmine,
Belling (2).

Heat a 45 per cent. aqueous solution of glacial acetic acid to the boiling point with an excess of powdered carmine. Cool and filter. Add trace of ferric hydrate dissolved in 45 per cent. acetic acid to the acetic carmine until the liquid becomes bluish red, but no precipitate forms.

2. Carnoy's fixing agent.

Absolute alcohol - 6 parts.

Chloroform - 3 "

Glacial acetic - 1 "

3. Zenker's fixing agent. Lee (19). 5 per cent. of corrosive sublimate (Bichloride of mercury) and 1 or 2 per cent. of glacial acetic acid dissolved in a Müller's solution (acetic acid to be added just before using).

Müller's Solution.

Potassium bichromate - 2 - 2.5 parts.

Sodium sulphate - 1 "

Water - 100 "

4. Karpetschenko's fixing agent.

Solution A.

Distilled water	- 65 c.c.
Glacial acetic	- 10 c.c.
CrO_3	- 1 gram.

Solution B.

Distilled water	- 35 c.c.
Commercial formalin	- 40 c.c.

The two solutions are mixed in equal proportions just before putting in the fresh material to be fixed.

5. Mayer's fixative. Chamberlain (3).

White of egg	- 50 c.c.
Glycerine	- 50 c.c.
Salicylate of soda	- 1 gram.

6. Iodine Solution. Huskins (14).

1 per cent. iodine.	
1 " " potassium iodide.	
80 " " alcohol.	

Cytology of Species.

A. tenerum Vasey. A large number of counts were made on eight plants representing two cultivated strains and six native plants from widely different sources. Seven of these plants had 14 bivalent chromosomes in the heterotypic metaphase (Plate VIII, Fig. 1), and meiosis appeared to be normal with the exception that slight lagging of one or two chromosome pairs was observed in the heterotypic anaphase in a few cases. This lagging did not appear to be sufficient to prevent these chromosomes being included in the daughter nuclei.

The root-tips of these plants had 28 chromosomes (Plate VII, Fig. 1). The shape of these chromosomes was characteristic of all the species. They were very long with single or double bends. The extent of flexure in individual chromosomes did not appear to be constant and there were no marked differences in size and shape of any of the chromosomes that would be of value in identifying the species.

One plant studied was abnormal both in chromosome number and behavior at reduction division. In external appearance the plant differed from typical A. tenerum in having awns 5 mm. long. Twenty-two chromosomes were observed in root-tip cells of this plant, (Plate VII, Fig. 3) and somatic mitosis appeared to be normal. The behavior during meiosis was extremely irregular. The chromosomes evidently failed to pair normally in the prophase, since from 14 to 18 univalents and from 2 to 4 bivalents with occasional trivalents were observed at the

heterotypic metaphase. These bivalents and trivalents appeared to exhibit very weak end to end synapsis (telosynapsis), which was quite distinct from the appearance of the normal bivalents in normal plants. In Plate VII, Fig. 4 there appears to be one bivalent and one trivalent chromosome. These are very weakly conjugated. In the heterotypic division the univalents wandered presumably at random to the poles while the bivalents aligned themselves at the equatorial plate. The condition is shown in Plate VII, Fig. 2. The resulting daughter cells of such a division were often of unequal size and contained varying numbers of chromosomes. In the homotypic division the chromosomes apparently divided equationally. The resulting tetrads are very abnormal and are probably sterile since this plant produced no seed.

A. Richardsonii Schrad. The meiotic divisions in all the plants examined were normal; very clear counts of 14 chromosomes were obtained in both the heterotypic and homotypic divisions (Plate VIII, Fig. 2). The morphology of the chromosomes in somatic tissue is illustrated in Plate XII, Fig. 3. This represents the late metaphase since the chromosomes are just beginning to split. A number of distinct forms within this species which showed variation in spike density and length of awn were examined cytologically but no abnormalities could be noted in chromosome behavior.

Hybrids between A. Richardsonii and A. tenerum. Crosses

were made between these species during the summer of 1926 by W. Robinson (26). The F. 1 plants were sterile which indicated that the cross had been effected. These plants resembled the A. tenerum parent and were more vigorous than either parent. The examination of the pollen-mother cells proved to be very interesting, since they did not show any of the irregularities such as incomplete synapsis or lagging chromosomes which are typical of hybrids. The appearance of the bivalent chromosomes in the heterotypic metaphase is illustrated in Plate XII, Fig. 1. In contrast to this, Fig. 2 of the same plate shows the chromosomes in the homotypic metaphase. These chromosomes more closely resemble those in somatic tissue. The bivalent chromosomes of the heterotypic metaphase differ in being much thicker; they are rectangular in general outline and show the indentations initial to the disjunction of the synaptic mates.

A. Smithii mobilis (S. & S.) Jones. A study was made of two plants of this species which were collected in adjacent districts at Granum and Claresholm, Alberta. These plants were very similar and were identified at the Grass Herbarium, United States Department of Agriculture. In view of this it was surprising to find that they had different chromosome numbers. Plate X, Fig. 2 shows 28 chromosomes in a root-tip cell of one plant, while Fig. 4 of the same plate shows 56 chromosomes in a root-tip cell of the other plant. Root-tip cells of the latter plant were slightly larger, but contained smaller chromosomes of the same general shape as the 28-chromosome form.

A. Smithii Rydb. Definite counts of 56 were obtained from root-tips of one plant, (Plate X, Fig. 3). Several other plants were examined. The chromosome number could not be accurately established but it appeared to be about 56. This species flowers so sparingly that it has been difficult to obtain material for pollen-mother-cell counts.

A. dasystachyum (Hook.) Scribn. Root-tip counts were made for plants collected at Hanna, Medicine Hat and Lethbridge, Alberta. All these plants had 28 chromosomes. (Plate X, Fig. 1)

A. Griffithsii Scribn. & Smith. Pollen-mother-cell counts of 14 bivalent chromosomes were made on one plant. (Plate VIII, Fig. 4). Twenty-eight somatic chromosomes were observed in the root-tips of two other plants. (Plate XII Fig. 4). The writer in a previous publication (24) reported a plant of this species to have 7 bivalent chromosomes at the heterotypic metaphase of pollen-mother cells. This plant was later identified at the Grass Herbarium, United States Department of Agriculture, to be A. spicatum.

A. spicatum (Pursh.) Scribn. & Smith. Only one plant of this species has been studied cytologically. However, a large number of counts have been made on this plant and it was observed to have 7 haploid and 14 diploid chromosomes. (Plate VIII, Fig. 7 and Plate IX, Fig. 3).

A. dagnae Grossh.- Only one plant grew from the seed of this species which was obtained from Caucase, Georgie, U.S.S.R. The root-tip cells of this plant were examined and gave clear counts of 14 chromosomes. (Plate IX, Fig. 4).

A. repens (L.) Beauv.- This species was studied extensively. All the native plants investigated gave clear counts of 21 bivalents in pollen-mother cells. Slight lagging of one pair of chromosomes at the heterotypic anaphase was observed in a few cells of all the plants studied. Root-tip counts were made of 5 distinct types of A. repens collected in western Canada and they all had 42 chromosomes.

Four plants of A. repens (L.) Beauv. introduced from Caucase, Georgie, U.S.S.R. were studied. Three of these plants gave counts of 42 somatic chromosomes (Plate XI, Fig. 2), while the other gave clear counts of 35 (Plate XI, Fig. 3). This latter count was checked very carefully since it is unusual to have root-tip counts of uneven numbers.

A. repens (L.) var. glaucescens was also introduced from Caucase, Georgie. Root-tip counts for four of these plants showed 42 chromosomes.

A. cristatum.- Pollen-mother-cell preparations of three plants gave counts of 14 bivalent chromosomes in the heterotypic metaphase. (Plate VIII, Fig. 3). Root-tip counts on one plant gave a count of 28 chromosomes. (Plate XI, Fig. 4).

A. sibiricum (W.) Eichw.- Root-tip preparations of this species introduced from Caucase, Georgie and the University of Saskatchewan gave counts of 28 chromosomes. (Plate XI, Fig. 1).

A. desertorum.- Only one plant was studied which was obtained from the Manitoba Agricultural College. Pollen-mother-cell preparations showed 14 bivalents in the heterotypic metaphase, (Plate VIII, Fig. 5) and the root-tips gave counts of 28 chromosomes.

A. pungens (Pers.) R. and S.- This species was introduced from Sutton & Sons, Reading, England. Pollen-mother-cell preparations were made from three plants and 21 bivalent chromosomes were observed in the heterotypic metaphase. (Plate IX, Fig. 2). Slight lagging of two or three pairs of chromosomes was frequently observed in the heterotypic anaphase.

Plate VII.

- Fig. 1. Somatic metaphase of typical A. tenerum; 28 chromosomes.
- " 2. Heterotypic anaphase of abnormal A. tenerum; note univalents at the poles and lagging bivalents at the equatorial plate.
- " 3. Somatic metaphase of abnormal A. tenerum; 22 chromosomes.
- " 4. Heterotypic metaphase of abnormal A. tenerum; note 1 bivalent and 1 trivalent chromosome.

Plate VIII.

1

2

3

4

5

6

Fig. 1 Heterotypic metaphase of A. tenerum; 14 bivalent chromosome

"	2	"	"	"	<u>A. Richardsonii</u> ; 14	"	"
"	3	"	"	"	<u>A. cristatum</u> ; 14	"	"
"	4	"	"	"	<u>A. Griffithsii</u> ; 14	"	"
"	5	"	"	"	<u>A. desertorum</u> ; 14	"	"
"	6	"	"	"	<u>A. spicatum</u> ; 7	"	"

Plate IX.

1

2

3

4

Fig. 1. Heterotypic metaphase of A. repens; 21 bivalent chromosomes.

" 2. " " " A. pungens; 21 " "

" 3. Somatic " " A. spicatum; 14 chromosomes.

" 4. " " " A. dagnae; 14 "

Plate X.

Fig. 1. Somatic metaphase of A. dasystachyum; 28 chromosomes.

"	2.	"	"	"	<u>A. Smithii molle</u> ; 28	"
"	3.	"	"	"	<u>A. Smithii</u> ; 56	"
"	4.	"	"	"	<u>A. Smithii molle</u> ; 56	"

Plate XI.

1

2

3

4

Fig. 1. Somatic metaphase of A. sibiricum; 28 chromosomes.
 " 2. " " " A. repens ; 42 "
 " 3. " " " A. repens ; 35 "
 " 4. " " " A. cristatum; 28 "

Plate XII.

1

2

3

4

Fig. 1. Heterotypic metaphase of F. hybrid (A. Richardsonii
x A. tenerum); 14 bivalent chromosomes.

" 2. Homotypic metaphase of F. hybrid (A. Richardsonii
x A. tenerum); 14 univalent chromosomes.

" 3. Somatic metaphase of A. Richardsonii; 28 chromosomes.

" 4. " " " " A. Griffithsii; 28 "

Discussion.

Polyploidy.- The chromosome numbers in the Agropyrons form a polyploid series with a base number of seven. Four groups are found with diploid, tetraploid, hexaploid and octoploid numbers. The following list summarizes the chromosome numbers as found for the species studied in this investigation.

	n.	2n.
A. spicatum	7	14
A. dagnae	-	14
A. tenerum	14	28
* A. "	22 (univalents)	22
A. Richardsonii	14	28
A. dasystachyum	-	28
A. Griffithsii	14	28
A. cristatum	14	28
A. sibiricum	-	28
A. desertorum	14	28
A. Smithii molle	-	28
* A. repens	-	35
A. "	21	42
A. " var. glaucescens	-	42
A. pungens	21	-
A. Smithii	-	56
A. " molle	-	56

* Plants having counts which did not fit into any of the four polyploid groups.

The polyploid series reported in this investigation is very similar to that found in most of the genera of Gramineae which have been studied. Sax (29) found the wheats to fall into three definite polyploid groups - diploid, tetraploid and hexaploid. Tschermak and Bleier (3) produced an octoploid form from crosses between Aegilops ovata with Triticum dicoccoides and T. durum. Griffiee (11) reported the groups in the genus Hordeum with 7, 14 and 21 haploid chromosomes. Kihara (16) reported the same series in Avena. Church (4) studied the meiotic phenomena in a number of species of the tribes, Festuceae, Aveneae, Agrostideae, Chlorideae and Phalarideae and obtained with few exceptions counts which showed the same polyploid series as reported for the cereals. Evans (9) found haploid chromosome numbers of 7 and 21 for species of Festuca and of 7 for Lolium perenne. The tribes, Paniceae and Andropogoneae were studied by Church (5). The species fell into the same series of multiples with the exception of Andropogon scoparius, which gave a decaploid count of 35 haploid chromosomes, which is the highest number reported for any species of Gramineae. The basic number varied somewhat, however, in these tribes, since five species were reported with haploid chromosome counts of 9, and fifteen species with haploid counts of 10 or multiples of 10.

Cytological evidence of natural hybridization.- The hybrid origin of many of our cereals has already been demonstrated by

careful genetical and cytological research. Sax (29) studied the chromosome relationships in wheat, and suggested that the 14 and 21 haploid chromosome numbers are the result of reduplication of the 7 chromosomes of the Einkorn wheat. In a paper in 1922 {reviewed by Church (4)}, Sax considers that the differential mating of chromosomes in crosses between these groups indicates the probable hybrid ancestry for the polyploid members.

Huskins (14) in his studies of fatuoid oats makes this statement:

"Probably hybridization and polyploidy are related phenomena in the origin of wheat and oats, and are equally and jointly responsible for the origin of speltoids and fatuoids as well as many of the peculiar features discovered in hybridization studies."

Jeffrey (15) believes that hybridism has clearly played a large role in the acceleration of the processes of evolution.

He states,

"Where interspecific crossing is possible, there is often clear evidence of its presence in the form of a high degree of variability, accompanying a considerable manifestation of sterility in the gametic cells, particularly the pollen."

Cytological evidence has been used in a number of instances in recent years to aid in the solution of some of the more perplexing taxonomic difficulties. This is particularly true in the genus *Rosa*. A recent paper by Erlanson (8) of the University of Michigan is worthy of careful review, since the situation found here has many points in common with

that found in the Agropyrons. They both are widely distributed and extremely variable native genera, and both contain certain wild species between which there is no clear line of morphological demarcation. Erlanson studied 107 wild roses from known stations in North America. The majority of the specimens on cytological examination fell into three classes with diploid, tetraploid and hexaploid numbers, the basic number being seven. One specimen was octoploid, two were triploid, and three aneuploid with the somatic number not a multiple of seven. Many of the diploid roses exhibited irregularities during meiosis. Incomplete pairing at diakinesis, lagging chromosomes, and polypory were frequently observed in some individuals; these were believed to be spontaneous hybrids produced by the crossing of different species.

In the aneuploid plants two contained sixteen somatic chromosomes and one fifteen. These plants appeared to be a later generation of a cross between the diploid R. blanda and the hexaploid R. acicularis. It was believed that the univalents probably lagged in the heterotypic division and gave some fertile gametes with only seven or eight chromosomes which by self-fertilization gave rise to fertile diploid and aneuploid plants.

Nearly all of the tetraploid plants examined resembled hybrid forms in their cytological behavior since they exhibited irregularities during meiosis and polypory. The tetraploid forms often exhibited some rings of four chromosomes at

diakinesis, but none were found that were completely quadri-valent. It was concluded that they originated by duplication of diploid hybrids and had hybridized with each other.

The cytological evidence presented by Erlanson certainly indicates that hybridization between many of the wild forms of Rosa is of common occurrence in nature. Other lines of evidence supporting this conclusion are based on:

- (a) the results of artificial crosses between the various species belonging to different chromosome groups;
- (b) the variation in the progeny obtained from seeds taken from individual wild plants in the field;
- (c) the large and variable percentage of sterile pollen present in many wild individuals.

Church (4) in his studies on 16 species of the tribes of Gramineae mentioned above concludes that,

"Polyploidy or cytological abnormalities of the maturation divisions or both are considered as evidence of the hybrid origin of all the species except Phalaris arundinaceae."

The cytological evidences of natural hybridization in the Agropyrons is relatively meagre. This by no means indicates that hybridization may not be responsible for a great deal of the variability. The Agropyrons are probably highly self-fertilized according to Malte (22), Robinson (26) and Kirk (17). This decreases the chances for natural hybridization and increases the homozygosity of those types that have arisen through hybridization. This inbreeding in the progeny of hybrid

plants would have the tendency to eliminate rapidly disadvantageous recessives and abnormalities in meiosis which might be perpetuated much longer in cross-fertilized populations. It might therefore be expected that the cytological evidence of hybridization would not be as plentiful in the Agropyrons as in cross-fertilized species such as Rosa.

About fifty plants representing fifteen species of Agropyrons have been carefully studied cytologically and in this limited number certain phenomena were observed that apparently can only be satisfactorily explained by assuming interspecific hybridization.

Lagging chromosomes were observed in some instances in the heterotypic anaphase in A. tenerum, A. repens and A. pungens, but other meiotic phenomena such as polypory, incomplete pairing at diakinesis, and cytomyxis were not common except in the following cases.

The abnormal plant of A. tenerum which had 22 somatic chromosomes is probably a hybrid between A. tenerum which has 14 bivalent chromosomes and some species of the 7-chromosome group. Synaptic pairing is for some reason deficient and as a result only from two to four bivalent chromosomes and an occasional trivalent are observed in the heterotypic metaphase. The unpaired univalents apparently wander to the poles at random. This is typical hybrid behavior similar to that found in hybrids arising from crosses between Zea Mays (10 pairs) and Euchlaena

perennis (20 pairs) in which Longley (20) reports the appearance of univalents, bivalents and trivalents at meiosis. The 30 chromosomes in the F. hybrid are irregularly distributed in the two maturation divisions.

The occurrence of both tetraploid and octoploid plants of A. Smithii molle may also be the result of hybridization. The fact that these 28- and 56-chromosome forms occur in a region where there appears to be a large number of intermediate forms between A. Smithii and A. dasystachyum also substantiates this hypothesis, since A. Smithii molle appears to be intermediate in morphological characters between these two species. The fact that different chromosome numbers have been observed in A. Smithii molle does not necessarily mean that these plants belong to a different species. Navashin (23) in working with Crepis states that a form arising through the duplication of chromosomes is not to be designated as a new species since the main difference between the species depends not so much upon differences of chromosome number but rather upon qualitative differences of chromosome constitution.

The plant of A. repens which has 35 somatic chromosomes is probably an F₁ hybrid of an interspecific cross between A. repens and some member of the tetraploid group. Thirty-five is the number that would be expected when gametes with 14 and 21 chromosomes were united. This explanation seems plausible since this material was obtained from Caucase, Georgie, U.S.S.R., where Trotizky (32) reports finding large numbers of native

types which are transitional in all their characters between A. repens and A. cristatum and which he believes may have arisen by hybridization between these two species.

GENERAL CONCLUSIONS.

A complete range of variability was observed between certain native species of Agropyrons in Alberta. These intermediate types were only found between species closely associated in the same environment. This was found to be particularly true in two instances:

(1) A. tenerum and A. Richardsonii were generally found growing together in the parkland and wooded areas of the province;

(2) A. Smithii and A. dasystachyum were closely associated in the open prairie of the south-eastern part of the province. Some of the intermediate types between these two species have been described as A. Smithii molle.

A similar situation was reported among the Agropyrons in Denmark by Raunkaier (25) and in Russia by Troitzky (32). They attributed the occurrence of intermediate types to natural hybridization between distinct species, and based their conclusions solely on circumstantial evidence provided by ecological and morphological observations and by analogical deductions from artificial crosses between various species of Agropyrons indigenous to the localities under consideration.

The cytological studies carried out in this investigation provide more direct evidence that natural hybridization does occur among the Agropyrons. A number of cases of abnormal chromosome number and meiotic behavior have been cited in this

paper. These can only be satisfactorily accounted for by the supposed occurrence of interspecific hybridization.

Longley (21) states,

"A review of the taxonomic, genetic and cytological findings in the genus Fragaria will demonstrate that variability is associated with polyploidy which in turn may represent a latent hybridity."

He suggested that the same conclusions could be drawn from the variability that characterizes polyploid forms of Rubus Rosa or Crataegus. It is evident that we have a very similar situation in Agropyron since the species exhibit a high degree of variability, they are closely associated in the field, and form a complete polyploid series containing species of chromosome numbers ranging from 14 to 56.

It is perhaps unsafe to draw definite conclusions until further information is available from certain other lines of investigation which have not yet been undertaken. These should include studies on: pollen sterility, the frequency of segregation in the progeny of intermediate types, and the hybrid behavior of artificial interspecific crosses. We can, however, safely conclude that natural hybridization is responsible for at least some of the variability exhibited among the Agropyrons.

SUMMARY.

1. The distribution in Alberta of the native species of Agropyron was studied in relation to the various soil and vegetative zones. The members of the various species groups were only commonly observed within the soil type and vegetative zone to which they were apparently best adapted.
2. A wide range of variability was observed both within and between the native species of Agropyron. Complete series of intergrading types were found between certain species growing together in the same regions.
3. Cytological studies were made on fifteen species. The chromosome numbers formed a polyploid series with two diploid, eight tetraploid, three hexaploid, and two octoploid species.
4. The polyploid series found in the Agropyrons is typical of the Gramineae in general.
5. The species could not be distinguished on chromosome morphology since no striking differences were noted between the chromosomes of the various species.
6. A plant resembling A. tenerum was observed with only 22 somatic chromosomes while the normal number is 28. Its

abnormal behavior at reduction division suggested hybrid origin.

7. Two plants which were collected in the same region and identified as A. Smithii molle were found to have different chromosome numbers. One had 28 and the other 56 chromosomes.
8. A number of plants introduced from Russia as A. repens were studied. One of these had 35 chromosomes while the remainder had the normal number of 42. This plant probably represented the F_1 of a cross between A. repens and some member of the 28 chromosome group.
9. The F_1 plants of artificially produced hybrids between A. tenerum and A. Richardsonii did not exhibit any meiotic abnormalities which would indicate hybridity.
10. The combined results obtained from distributional, morphological and cytological studies indicate that interspecific hybridization is responsible for some of the intermediate forms which have been found growing in the same region with the typical species.

ACKNOWLEDGMENTS.

The writer wishes to make grateful acknowledgment to all those who have given help in this investigation, especially to the following persons:

To Dr. J.R. Fryer for suggesting the problem and making available the collection of Agropyrons brought together by W. Robinson, and for critising the manuscript;

To Dr. O.S. Aamodt, for helpful suggestions in developing the plan of the work;

To Mr. A.E. Clarke for assistance in cytological methods;

To Dr. E.H. Moss for information on the distribution of Agropyrons in certain sections of Alberta;

To the following persons who supplied seed of the various species of Agropyron: Dr. L.E. Kirk, University of Saskatchewan; Mr. P. Gussew, U.S.S.R. Institute of Applied Botany and New Cultures, Leningrad; The Secretary, Botanical Gardens of Tiflis, Caucase, Georgie, U.S.S.R.; Mr. A. Lange, Botanical Gardens of Copenhagen, Denmark; the late Dr. P.B. Kennedy, University of California.

LITERATURE CITED.

- (1) AASE, H.C., and POWERS, L. Chromosome numbers in crop plants. *Amer. J. Bot.* 13:367-372. 1926.
- (2) BELLING, JOHN. On counting chromosomes in pollen mother cells. *Amer. Naturalist.* 55:573-574. 1921.
- (3) CHAMBERLAIN, C.J. *Methods in Plant Histology.* The University of Chicago Press, Chicago, Ill. 1924.
- (4) CHURCH, G.L. Meiotic phenomena in certain Gramineae, I. *Bot. Gaz.* 87:608-629. 1929.
- (5) _____ Meiotic phenomena in certain Gramineae, II. *Bot. Gaz.* 88:63-84. 1929.
- (6) DALBERG, R.C. Identification of seeds of species of Agropyron. *J. Agr. Res.* 3:275-282. 1914.
- (7) DAVIES, J.G. The chromosome number in Dactylis glomerata. *Nature*, 119:236-237. 1927.
- (8) ERLANSON, E.H. Cytological contributions and evidences for hybridity in North American wild roses. *Bot. Gaz.* 87:443-506. 1929.
- (9) EVANS, G. Chromosome complements in grasses. *Nature*, 118:841. 1926.
- (10) FOULDS, F.E. A study of the comparative morphology of the seeds of Agropyron. *Scient. Agr.* 10:200-219. 1929.
- (11) GRIFFEE, FRED. Chromosome number in species of Hordeum. *J. Series Minn. Agr. Exp. Sta.* No. 534:319-331. 1928.
- (12) HAYES, H.K. and GARBER, R.J. *Breeding Crop Plants.* McGraw Hill Book Co., Inc., New York. 1927.
- (13) HENRY, HELEN H. Seeds of quack grass and certain wheat grasses compared. *J. Agr. Res.* 35:537-546. 1927.
- (14) HUSKINS, C.L. On the genetics and cytology of fatuoid or false wild oats. *J. Genetics.* 18:315-364. 1927.
- (15) JEFFREY, E.C. Hybridization and the rate of evolution in Angiosperms. *Amer. Naturalist.* 50:129-143. 1916.
- (16) KIHARA, H. *Über cytologische Studien bei einigen Getreidearten: II Chromosomenzahlen und Verwandtschaftsverhältnisse unter Avena-Arten.* *Bot. Mag.* 33:95-98. 1919. (Rev. by Huskins in M.Sc. thesis).

- (17) KIRK, L.E. The improvement of western rye grass, Agropyron tenerum, Vasey. *Scient. Agr.* 10:239-250. 1929.
- (18) LA-COUR, L. New fixatives for plant cytology. *Nature*, 124:127. 1929.
- (19) LEE, A.B. The Microtometist's Vade-Mecum. J. & A. Churchill, 7 Great Marlborough St., London. 1924.
- (20) LONGLEY, A.E. Chromosomes in maize and maize hybrids. *J. Agr. Res.* 28:673-682. 1924.
- (21) _____ Chromosomes and their significance in strawberry classification. *J. Agr. Res.* 32:559-568. 1926.
- (22) MALTE, M.O. Breeding methods in forage plants. *Proc. Western Can. Soc. Agron.* 1:64-75. 1920.
- (23) NAVASHIN, M.S. On the variation of the number and morphological characters of the chromosomes in interspecific hybrids. *Bul. of App. Bot., of Gen. & Plant Breed.* 17:147-150. 1927.
- (24) PETO, F.H. Chromosome numbers in the Agropyrons. *Nature*, 124:181-182. 1929.
- (25) RAUNKIAER, C. Om danske Agropyrum-Arter. (Isoreagent-Studier II). *Bot. Tedsskrift* 39:329-347. 1926.
- (26) ROBINSON, W. Studies on the genus Agropyron. Unpublished M.Sc. thesis. 1928.
- (27) RYDBERG, P.A. Flora of the Rocky Mountains and adjacent plains. Pub. by the author, N.Y. Bot. Gardens, N.Y. 1922.
- (28) SAMPSON, A.W. Native American Forage Plants. John Wiley and Sons, New York. 1924.
- (29) SAX, KARL. Chromosome relationship in wheat. *Science N.S.* 54:413-415. 1921.
- (30) STOLZE, K.Y. Die Chromosomenzahlen der hauptsächlichen Getriedearten. *Bibliotheca Genetica*, 8:1-71. 1925.
- (31) TSCHERMAK, E. and BLEIER, H. Über fruchtbare Aegilops-Weizenbastarde. *Ber. Deut. Botan. Gesell.* 44:110-132. 1926. [Rev. by Hayes & Garber (12)].
- (32) TROITZKY, N. A contribution to the question of the role played by hybridization in the formation of species. *Bul. of App. Bot., of Gen. & Plant Breed.* 19(2):213-231. 1928.

829739