# A CYTOLOGICAL STUDY OF SWITCHGRASS, PANICUM VIRGATUM 

by

ROBERT FRANKLIN CARVER
B. S., Oklahoma Agricultural and Mechanical College, 1953

A THESIS
submitted in partial fulfiliment of the requirements for the degree MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

TABLE OF CONTENTS

INTRODUCTION $\qquad$ REVIEW OF LITERATURE $\qquad$ MATERIALS AND METHODS $\qquad$ 2

Plant Materials $\qquad$ 2 Cytological Methods $\qquad$ 3 Photomicrographs $\qquad$ EXPERIMENTAL RESULTS $\qquad$
Chromosome Complements and Morphology ........................ 5
Chromosome Pairing at Metaphase I .............................. 10
Chromosome Behavior at Anaphase I .............................. 18
Chromosome Behavior at Telophase I ............................. 21
Meiotic Irregularities at the Quartet Stage ............... 28
$\qquad$ DISCUSSION $\qquad$ 35
Chromosome Complements .......................................... 35
Meiotic Behavior ................................................... 37
Chromosome Stickiness ............................................. 40
Pollen Stainability .............................................. 40 SUMMARY ......................................................................... 41 ACKNOWLEDGMENTS $\qquad$ 43 LITERATURE CITED $\qquad$

## INTRODUCTION

Many agronomists belleve that switchgrass is one of the most promising of the warm season grasses for the Great Plains area. It is used for hay, grazing, and soll-conservation purposes. The species is readily adaptable to domestication, exhibiting none of the undesireble seed and/or seed setting characteristics oommon to many native grasses. It has good seedling vigor, and is adapted to a wide range of soils and climates.

Recent establishment of a plant introduction nursery provides a wealth of material for breeding work at this station. A wide occurrence of polyploidy and a great range in morphological characters has been reported by Nielsen (1944). It therefore seemed desirable to study the population cytologically and describe the plants at least according to chromosome numbers. It also seemed advisable to include a study of meiotic behavior as this aspect of the species' cytology appeared to heve been unstudied. An attempt was made to combine these two objectives in the present study.

## REVIEW OF LITERATURE

Available literature on the eytological aspects of switchgrass is limited. A basio chromosome number of 9 in the genus, Panicum, was reported by Church (1929). Church (1940) reported a polyploid condition in switchgrass. Plants grown from seed from Oklahoma yielded mostly individuals with 36 chromosomes, the tetraploid number for this genus. A few of the plants were noticeably different, being smaller and very pilose in contrast to
the rest of the group. These smaller individuals proved to be octoploids with 72 chromosomes. An octoploid from Kansas gave rise to plants of the same average height but not so pilose as the octoploid type from Oklahoma. In the same paper Church reported the tetraploid number 36 for $\underline{P}$. Virgatum var. spissum Linder which was collected in Massachusetts. This subspecies was quite glabrous, had short spikelets, and was intermediate in height between the western tetraploids and octoploids.

A cytological study by Burton (1942) on the tribe, Panicese, further substantiated a basic chromosome number of 9 for the Panicum species. In this study Burton reported a plant from Gainesville, Florida having 72 chromosomes.

A more complete polyploid series was reported by Nielsen (1944) who studied collections from a large area comprising a number of states. He found, in addition to tetraploid and octoploid forms, plants with $18,54,90$, and 108 chromosomes, but concluded that there was no regional segregation of chromosome races. He also found a great deal of morphological variations in the species, this variation being slightly greater among than within chromosome races. In a later paper (1947) Nielson reported no correlation between winterhardiness and chromosome numbers in $\underline{P}_{\text {. virgatum. }}$

## MATERIALS AND METHODS

## Plant Materials

Sporocyte materials used for this study were obtained from plants growing in a plant introduction nursery at the Ashland

Agronomy farm of Kansas State College or from open-pollinated seed progeny of these plants. These introductions had been collected previously as seed from their native habitats in the states of Kansas, Oklahoma, Arkansas, and Texas (Table l). The plants were classifled in the fleld as lowland or upland types. Hughes, et al. (1952) p. 514 stated "Two native types are recognized, the lowland and the upland types. The lowland type is much taller and coarser stemmed than the upland type." All plants were readily classified according to this distinction.

## Cytological Methods

Parts of panicles for melotic study were collected in the field and fixed in the following Carnoy's solution:

6 parts 100 percent ethanol.
3 parts chloroform,
1 part glacial acetic acid.
Materials not immediately examined were stored in a refrigerator at approximately $4^{\circ} \mathrm{C}$. The anthers were smeared in iron acetocarmine according to the method described by Smith (1947). Satisfactory smears were immediately studied or made semipermanent by sealing with clear fingernail polish as described by Barnett (1955). Chromosome counts were made on all of the plants, and the following aspects of melotic behavior were studied:
(1) The nature of chromosome pairing and the number of off-plate figures present at metaphase $I$,
(2) The nature and frequency of irregularities at anaphase $I$ and telophase $I$,
(3) The frequency of quartet micronuclei.

Parts of panicles with mature pollen were collected and fixed in the Carnoy's solution described above. The pollen was subsequently evaluated on the basis of its stainability in the following solution:
potassium iodide . . . . 1
lodine . . . . . . . .
gm.
ethanol . . . . . . . . 100 ml

Pollen grains were classified $A, B$, or $C$ depending upon their individual staining reactions. Grains representative of each of these classes may be described as follows:

Class A: Non-shrivelled grains with 90 percent or more of their contents intensely and uniformly stained,

Class B: Grains exhibiting some stain but considered abnormal due to shrivelling, mottling, partial staining (less than 90 percent), and/ or low intensity of stain,
Class C: Grains exhibiting no stain.

## Photomicrographs

Photomicrographs were taken through a Bausch and Lomb mioroscope with a 93X oil immersion lens (N. A. 1.25) and a 10 X ocular. The figures were photographed with a 35 mm . Exakta camera on mierofile film. Final magnirication was 915 X for all figures except Fig. 4, Plate V, which was 800X and Pig. 2, Plate I, which was 88X.

## EXPERIMENTAL RESULTS

Chromosome Complements and Morphology

In this study only tetraploid (36), hexaploid (54), octoploid (72), and aneuploid plants were found (Table 1). The aneuploids occurred at the octoploid level. Of the 56 plants for which chromosome numbers were determined, 18 had 36 chromosomes, one had 54, and 32 had 72, while four were aneuploids, with 68 , 70, 76, and 78 chromosomes. Cells showing 36,72,76, and 78 chromosomes can be seen in the figures respectively: Pig. 1, Plate II; Fig. 1, Plate III; Fig. 1, Plate V; F1g. I, Plate IV; and Fig. 6, Plate VI. The chromosome number of plant 46 was somewhat questionable. Some cells of this plant had 72 chromosomes (Fig. 4. Plate IV), one appeared to have 72 bivalents, a few seemed to have in exeess of 108 , while others appeared to have more than 200 chromosomes or fragments (P1g. 6, Plate IV). These cells were difficult to interpret, because they stained very poorly.

Counts of up to and including 54 may be considered to be acourate. Some bias in favor of euploid counts probably existed, since a count was considered to be an even multiple of 9 unless aneuploidy was definitely apparent.

Chromosome counts were determined in the pollen mother cells at whatever stage was the most desirable. Anaphase I cells were very helpful in many cases, but cells at diakinesis were very difficult to interpret. Counts were determined at metaphese I when possible.

Table 1. Chromosome numbers and sources of plants studied.

| Code | Kansas State | Chromosome | : |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| No. | No. | No. | Nource |  |

Lowland

1
2
3
4
5
6
7
8
9
10
11
12

51047-1
51047-3-2
51048-1-2
36
36
51049-1-2
36
51050-1 36
51051-4 36
51216-1-2
36
6332-3
36
6336-2
36
51254-1-2
36
51048-1-2
36
51041-1-2

Treece, Kans.
Treece, Kans.
Treece, Kans.
Treece, Kans.
Treece, Kans.
Treece, Kans.
Fort Scott, Kans.
Treece, Kans.
Treece, Kans.
Arkansas University
Treece, Kans.
Iola, Kans.

## Upland

13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39

51034-2 72
51096-1 72
51086-1 72
51083-1 72
51077-2 72
51116-1 72
6186-11 72
51082-1 72
6166-6 72
51135-1 72
51034-1 72
51314-1 72
2172-15 72
51098-2 72
1412-1 72
1431-16 72
1428-4 72
51074-1 72
51003-2 72
51085-1-2 72
51068-1 72
51095-2 72
1425-11 72
51071-1 72
51081-3 72
51141-2 72
51024-2 72
51027-1 72
51246-1-2 72

Welda, Kans.
Purcell, Okla.
Perkins, Okla.
Cushing, Okla.
Watova, Okla.
Kinsley, Kans.
Arisansas University
Hallett, Okla.
Unknown
Bonham, Tex.
Welda, Kans.
Drummond, Okla.
Unknown
Pauls Valley, Okla. Unknown
Blackwell Selection
Blackwell Selection
Pawhuska, Okla.
Turon, Kans.
St1llwater, Okla.
Earlton, Kans.
Asher, Okla.
Blackwell Selection
Alma, Kans.
Ponca city, Okla.
Red River, Okla.
Osawatomie, Kans.
Osawatomie, Kans.
Lake Comanche, Okla.

Table 1 (concl.).

| Code No. | : | Kansas State No. | : | $\begin{gathered} \text { Chromos ome } \\ \text { No. } \\ \hline \end{gathered}$ | : | Source |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 42 |  | 51223-3 |  | 72 |  | Yale, Okla. |
| 43 |  | 51242-1 |  | 72 |  | Ryan, Okla. |
| 44 |  | 51291-19 |  | 72 |  | Blackwell Selection |
| 45 |  | 51087-2 |  | 54 |  | Perkins, Okla. |
| 46 |  | 51153-2-2 |  | ? |  | Hutchinson, Kans. |
| 47 |  | 2130-19 |  | 76 |  | W2 Okla. Selection |
| 48 |  | 51090-2 |  | 70 |  | Bristow, Okla. |
| 49 |  | 51235-1 |  | 78 |  | Frederiok, Okla. |
| 50 |  | 51232-1-2 |  | 68 |  | Manitou, Okla. |
|  |  |  |  | Lowland ${ }^{\text {4 }}$ |  |  |
| 51 |  | 6341-8 |  | 36 |  | Cleo Springs, Okla. |
| 52 |  | 6341-2 |  | 36 |  | Cleo Springs, Okla. |
| 53 |  | 6349-5 |  | 36 |  | Arkansas University |
| 54 |  | 6349-8 |  | 36 |  | Arkansas University |
| 55 |  | 6337-1 |  | 36 |  | Treece, Kans. |
| 56 |  | 51058-1 |  | 36 |  | Treece, Kans. |

* Only chromosome numbers determined for these plents.

All 18 of the plants that were of the gigas or lowland type proved to have 36 chromosomes. Plants classifled as upland, or possibly intermediate between lowland and upland, were found to be mostly octoploids with one hexaploid, four aneuploids, and one plant (number 46) with a questionable chromosome number.

Little can be said about chromosome morphology, since no enumeration data were taken. The chromosomes were small and appeared to vary in size within each comploment. No distinctly identifying characters were noted.

## EXPLANATION OP PLATE I

Fig. 1. Comparison of lowland and upland switchgrass, lowland on the right and upland on the left. Fig. 2. Well-stained pollen. 88X

PLATE I


PIg. 1


FIg. 2

## Chromosome Pairing at Metaphase I

A total of 39 of the plants were analyzed for chromosome pairing at metaphase I (Table 2). It was very difficult to find this stage, and some of the plants were not analyzed.

In the lowland plants chromosome pairing was very regular. Six of the 12 plants showed complete bivalent pairing (Fig. 1 , Plate II). There were no trivalent or quadrivalent configurations in this type. The other six had a few cells with univalents, but no cell exhibited more than two unpaired chromosomes.

Chromosome pairing at metaphase I was strikingly different in the upland type. There was a great deal of variation in the frequencies of univalent, bivalent, and quadrivalent configurations. There were no trivalent configurations present in any of the plants studied. Relatively few quadrivalent configurations were found although six plants showed some quadrivalent configurations with plant 41 having one in 20 cells and plant 50 ( $2 n=68$ ) having five cells out of 12 with quadrivalents. Quadrivalents as rings can be seen in Fig. 2, Plate III, and Fig. 2, Plate V. The variation in univalent and bivalent occurrence was the most significant feature at metaphase 1 . The average frequencies of univalents and bivalents varied from 36 bivalents and 0 univalents in five plants to an average of 18.5 bivalents and 35 univalents in plant $35(2 n=72)$. In this plant none of the pollen mother cells examined had more than 26 bivalents. A fow cells had as few as 12 and 13 bivalents. Out of 48 cells analyzed, plant 49 $(2 n=78)$ had only five pollen mother cells with all chromosomes

Table 2. Chromosome pairing in metaphase I cells.


## Lowland

| 1 | 6 | 0.00 | 18.00 | 0.00 | 0.00 |
| ---: | ---: | ---: | ---: | ---: | ---: |
| 2 | 7 | 0.00 | 18.00 | 0.00 | 0.00 |
| 3 | 2 | 0.00 | 18.00 | 0.00 | 0.00 |
| 4 | 4 | 0.50 | 17.75 | 0.00 | 0.00 |
| 5 | 11 | 0.20 | 17.91 | 0.00 | 0.00 |
| 6 | 8 | 0.00 | 18.00 | 0.00 | 0.00 |
| 7 | 4 | 0.50 | 17.75 | 0.00 | 0.00 |
| 8 | 8 | 0.00 | 18.00 | 0.00 | 0.00 |
| 9 | 12 | 0.17 | 17.91 | 0.00 | 0.00 |
| 10 | 34 | 0.12 | 17.94 | 0.00 | 0.00 |
| 11 | 5 | 0.00 | 18.00 | 0.00 | 0.00 |
| 12 | 11 | 0.18 | 17.91 | 0.00 | 0.00 |

Upland

| 15 | 5 | 0.00 | 36.00 | 0.00 | 0.00 |
| :--- | ---: | ---: | ---: | ---: | ---: |
| 16 | 5 | 0.00 | 36.00 | 0.00 | 0.00 |
| 17 | 2 | 0.00 | 36.00 | 0.00 | 0.00 |
| 20 | 8 | 0.50 | 35.00 | 0.00 | 0.38 |
| 21 | 10 | 1.60 | 35.20 | 0.00 | 0.00 |
| 23 | 3 | 0.00 | 36.00 | 0.00 | 0.00 |
| 24 | 15 | 0.75 | 35.60 | 0.00 | 0.00 |
| 25 | 17 | 1.88 | 34.70 | 0.00 | 0.18 |
| 27 | 8 | 2.00 | 35.00 | 0.00 | 0.00 |
| 28 | 6 | 2.70 | 34.00 | 0.00 | 0.00 |
| 30 | 9 | 0.67 | 35.66 | 0.00 | 0.00 |
| 32 | 2 | 5.00 | 31.50 | 0.00 | 1.00 |
| 34 | 6 | 2.67 | 34.67 | 0.00 | 0.00 |
| 35 | 20 | 35.00 | 18.50 | 0.00 | 0.00 |
| 36 | 2 | 1.00 | 35.50 | 0.00 | 0.00 |
| 37 | 6 | 1.50 | 35.00 | 0.00 | 0.17 |
| 38 | 1 | 0.00 | 36.00 | 0.00 | 0.00 |
| 39 | 8 | 1.00 | 35.00 | 0.00 | 0.25 |
| 40 | 19 | 1.00 | 35.50 | 0.00 | 0.00 |
| 41 | 13 | 0 | 0.96 | 34.26 | 0.00 |
| 42 | 2.00 | 35.50 | 0.00 | 0.05 |  |
| 43 | 12 | 2.33 | 35.00 | 0.00 | 0.00 |
| 44 | 1 | 1.00 | 34.83 | 0.00 | 0.00 |
| 45 | 2.00 | 0.00 |  |  |  |
| 48 | 12 | 2.58 | 34.00 | 0.00 | 0.00 |
| 49 | 1.00 | 37.70 | 0.00 | 0.00 |  |
| 50 | 12 | 1.17 | 31.75 | 0.00 | 0.00 |
|  |  |  |  |  | 0.75 |

## EXPLANATION OF PLATE II

Meiotic behavior of Lowland switchgrass.

Fig. 1. Metaphase I showing 18 II. 915X
Fig. 2. Metaphase I with no off-plate figures. 915X
Fig. 3. Anaphase I showing 18-18 distribution of ohromosomes. 915X

Fig. 4. Anaphase I showing lagging univalents. 915X
Fig. 5. Late anaphase I showing lagging univalents. 915X
Fig. 6. Telophase I showing no laggards. 915X

PLATE II


Fig. 1


Fig. 3


Fig. 5


Fig. 2


F1g. 4


Pig. 6
paired (39 bivalents). The number of univalents present was either two or four. In the analysis of 12 pollen mother cells from plant $50(2 n=68)$, only two cells had all chromosomes paired. Other plants showed a lesser number of unpaired univalents with the number varying some from cell to cell. Figure 6, Plate $V$, shows a P.M.C. with 23 bivalents and 26 univalents at metaphase I. Pigure 1, Plate III, and Fig. 4, Plate IV, show 35 bivalents and two univalents, Fig. 1, Plate V, shows 33 bivalents and two univalents, and Fig. 3, Plate VI, shows 37 bivalents and four univalents at motaphase $I$.

Some stickiness was present at metaphase I in plants 24, 46, and 25. The bivalents seemed to be strung together by small bits of matrix. In one case eight bivalents appeared to be joined in this manner.

Meiotic irregularity as indicated by figures off the metaphase I plate is summarized in Table 3. The lowland type tended to have sporocytes with fewer off-plate figures at metaphase I than the upland type. Four lowland plants exhibited complete regularity in this respect, with no off-plate figures present. It is interesting to note that the occurrence of univalents seemed to be positively correlated with the frequency of off-plate figures in most cases. This was not always the case, because some of the off-plate figures were bivalents.

The frequency of off-plate figures in upland awitchgrass was variable, but generally higher than in the lowland type. None of the upland plants exhibited a complete absence of off-plate figures. It is interesting to note that, of all upland plants, the

## EXPLANATION OF PLATE III

Meiotic behavior of upland switchgrass.

P1g. 1. Metaphase I showing 35 II and $2_{I}$. 915X
Fig. 2. Netaphase I showing ${ }^{2}$ IV. 915 X
Fig. 3. Anaphase I with no lagging chromosomes. 915X
Fig. 4. Anaphase I showing 9 lagging univalents. 915X
Fig. 5. Telophase I showing bridge configurations. 915X Fig. 6. Telophase I showing lagging univalents. 915X

PLATE III


FIg. 1


Fig. 3


Pig. 5


Fig. 2


FIg. 4


Fig. 6

Table 3. Chromosome behavior at metaphase I as indicated by off-plate figures.


Lowland

| 1 | 41 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 2 | 26 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 3 | 3 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 4 | 25 | 84.0 | 12.0 | 0.0 | 4.0 | 0.0 | 0.24 |
| 5 | 23 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 6 | 42 | 88.0 | 4.8 | 4.8 | 2.4 | 0.0 | 0.21 |
| 7 | 36 | 88.9 | 8.3 | 2.8 | 0.0 | 0.0 | 0.14 |
| 8 | 27 | 96.3 | 0.0 | 0.0 | 3.7 | 0.0 | 0.11 |
| 9 | 38 | 73.7 | 13.2 | 10.5 | 0.0 | 2.6 | 0.45 |
| 10 | 73 | 71.2 | 20.6 | 2.7 | 5.5 | 0.0 | 0.42 |
| 11 | 29 | 79.3 | 13.8 | 6.9 | 0.0 | 0.0 | 0.28 |
| 12 | 41 | 90.2 | 4.9 | 4.9 | 0.0 | 0.0 | 0.15 |

## Upland

| 13 | 6 | 50.0 | 16.7 | 33.3 | 0.0 | 0.0 | 0.83 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 14 | 110 | 52.7 | 28.2 | 13.6 | 2.7 | 2.7 | 0.75 |
| 15 | 32 | 37.5 | 31.3 | 15.6 | 3.1 | 12.5 | 1.22 |
| 16 | 30 | 30.0 | 53.3 | 13.3 | 0.0 | 3.3 | 0.93 |
| 17 | 50 | 44.0 | 30.0 | 14.0 | 8.0 | 4.0 | 1.00 |
| 18 | 19 | 42.1 | 31.5 | 15.8 | 5.3 | 5.3 | 1.00 |
| 19 | 9 | 88.9 | 11.1 | 0.0 | 0.0 | 0.0 | 0.11 |
| 20 | 117 | 18.8 | 25.6 | 26.5 | 15.4 | 13.7 | 1.90 |
| 21 | 48 | 16.7 | 29.1 | 22.9 | 25.0 | 6.3 | 1.79 |
| 22 | 43 | 23.3 | 37.2 | 14.0 | 7.0 | 18.5 | 1.81 |
| 23 | 98 | 32.6 | 33.7 | 24.5 | 8.2 | 1.0 | 1.11 |
| 24 | 73 | 35.6 | 35.6 | 20.5 | 2.8 | 5.6 | 1.10 |
| 25 | 61 | 29.5 | 31.1 | 27.9 | 8.1 | 3.2 | 1.26 |
| 26 | 22 | 27.3 | 27.3 | 31.8 | 0.0 | 9.2 | 2.33 |
| 27 | 57 | 24.6 | 38.6 | 22.8 | 12.3 | 1.8 | 1.30 |
| 28 | 27 | 33.4 | 37.0 | 22.2 | 3.7 | 3.7 | 1.30 |
| 29 | 66 | 12.2 | 30.3 | 15.1 | 16.6 | 25.8 | 2.35 |
| 30 | 39 | 51.3 | 33.3 | 5.1 | 2.6 | 7.7 | 0.87 |
| 31 | 29 | 27.6 | 34.4 | 20.7 | 3.5 | 13.8 | 1.52 |
| 32 | 20 | 55.0 | 20.0 | 10.0 | 10.0 | 5.0 | 1.00 |
| 33 | 50 | 34.0 | 40.0 | 14.0 | 8.0 | 4.0 | 1.08 |
| 34 | 89 | 27.0 | 28.1 | 25.8 | 14.6 | 4.5 | 1.44 |
| 36 | 58 | 56.9 | 29.3 | 13.8 | 0.0 | 0.0 | 0.57 |
| 37 | 34 | 38.3 | 32.4 | 17.6 | 8.8 | 0.0 | 1.15 |
| 38 | 60 | 28.3 | 23.4 | 28.3 | 13.3 | 6.7 | 1.52 |
| 39 | 34 | 41.2 | 17.6 | 29.5 | 2.9 | 8.8 | 1.24 |
| 40 | 55 | 61.9 | 32.7 | 1.8 | 3.6 | 0.0 | 0.47 |

Table 3 (concl.).

| Code No. | $\vdots$ | $\begin{aligned} & \text { No. } \\ & \text { cella } \end{aligned}$ | : | Percent P.M.C. with given number off-plate figures |  |  |  |  |  |  |  |  | $\begin{aligned} & \text { : Me an No. } \\ & \text { : per cell } \\ & \hline \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 0 | : | 1 | : | 2 | : | 3 | : | 4-10 |  |
| 41 |  | 47 |  | 10.6 |  | 34.1 |  | 27.7 |  | 10.6 |  | 17.0 | 2.00 |
| 42 |  | 54 |  | 50.0 |  | 33.3 |  | 11.1 |  | 5.6 |  | 0.0 | 0.72 |
| 43 |  | 21 |  | 61.9 |  | 19.0 |  | 14.3 |  | 4.8 |  | 0.0 | 0.62 |
| 44 |  | 55 |  | 60.0 |  | 21.8 |  | 10.9 |  | 7.3 |  | 0.0 | 0.65 |
| 45 |  | 28 |  | 89.3 |  | 0.0 |  | 10.? |  | 0.0 |  | 0.0 | 0.21 |
| 46 |  | 5 |  | 20.0 |  | 0.0 |  | 20.0 |  | 20.0 |  | 40.0 | 3.00 |
| 47 |  | 46 |  | 23.9 |  | 26.0 |  | 30.4 |  | 15.2 |  | 4.4 | 1.07 |
| 48 |  | 63 |  | 60.3 |  | 28.6 |  | 9.5 |  | 1.6 |  | 0.0 | 0.52 |
| 49 |  | 47 |  | 40.4 |  | 23.3 |  | 31.9 |  | 0.0 |  | 4.4 | 1.06 |
| 50 |  | 29 |  | 20.7 |  | 48.3 |  | 17.2 |  | 13.8 |  | 0.0 | 1.24 |

hexaploid (plant 45) had the largest percentage of cells with no off-plate flgures at metaphase I. Plant 46 (chromosome number questionable) had the largest percentage of cells in the 4-10 column, but only five cells were analyzed. Only 12.2 percent of the cells of plant 29, an octoploid, showed no off-plate figures. The aneuploids exhibited about the same behavior as the 72-chromosome euploids. Plant $50(2 n=68)$ had the lowest percentage of cells with no off-plate figures, and plant $48(2 n=70)$ had the highest percentage of cells with no off-plate figures but neither fitted the extremes of the euploids.

Chromosome Behavior at Anaphase I

Chromosome behavior at anaphase I is sumnarized in Table 4. In all of the lowland plants, anaphase I irregularities were very rare. They consisted of a few lagging univalents with some of these dividing into chromotids (Fig. 4, Plate II). Most of the cells were regular as shown in P1g. 3, Plate II. There were no

Table 4. Chromosome behavior at anaphase I.


Lowland

| 1 | 3 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 2 | 5 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 3 | 2 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 4 | 5 | 80.0 | 0.0 | 0.0 | 20.0 | 0.0 | 0.0 | 0.0 |
| 5 | 5 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 6 | 6 | 83.3 | 16.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 7 | 14 | 78.6 | 14.3 | 7.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| 8 | 2 | 50.0 | 0.0 | 50.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 9 | 5 | 60.0 | 40.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 11 | 2 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 12 | 18 | 66.6 | 0.0 | 16.7 | 11.1 | 5.6 | 0.0 | 0.0 |

Upland

| 13 | 6 | 0.0 | 0.0 | 33.3 | 0.0 | 66.7 | 0.0 | 0.0 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 14 | 20 | 10.0 | 0.0 | 25.0 | 35.0 | 30.0 | 0.0 | 0.0 |
| 15 | 4 | 0.0 | 25.0 | 0.0 | 25.0 | 50.0 | 0.0 | 0.0 |
| 16 | 7 | 14.3 | 0.0 | 57.1 | 0.0 | 28.6 | 0.0 | 0.0 |
| 17 | 6 | 0.0 | 16.7 | 16.7 | 16.7 | 49.9 | 0.0 | 0.0 |
| 18 | 6 | 0.0 | 0.0 | 33.3 | 0.0 | 0.0 | 66.7 | 50.0 |
| 19 | 2 | 0.0 | 0.0 | 50.0 | 50.0 | 0.0 | 0.0 | 0.0 |
| 20 | 10 | 0.0 | 10.0 | 0.0 | 10.0 | 80.0 | 0.0 | 20.0 |
| 21 | 13 | 0.0 | 7.7 | 0.0 | 7.7 | 84.6 | 0.0 | 0.0 |
| 22 | 1 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 |
| 23 | 12 | 0.0 | 16.7 | 33.3 | 0.0 | 50.0 | 0.0 | 0.0 |
| 24 | 8 | 50.0 | 12.5 | 12.5 | 12.5 | 12.5 | 0.0 | 50.0 |
| 25 | 2 | 50.0 | 50.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 26 | 4 | 0.0 | 0.0 | 25.0 | 50.0 | 25.0 | 0.0 | 75.0 |
| 27 | 14 | 0.0 | 0.0 | 35.7 | 28.6 | 35.7 | 0.0 | 0.0 |
| 28 | 9 | 22.2 | 11.1 | 33.4 | 11.1 | 22.2 | 0.0 | 0.0 |
| 29 | 11 | 18.2 | 9.1 | 27.3 | 0.0 | 45.4 | 0.0 | 36.4 |
| 30 | 9 | 22.2 | 66.7 | 0.0 | 0.0 | 11.1 | 0.0 | 0.0 |
| 31 | 20 | 25.0 | 15.0 | 5.0 | 20.0 | 35.0 | 0.0 | 5.0 |
| 32 | 1 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 33 | 4 | 25.0 | 0.0 | 0.0 | 25.0 | 50.0 | 0.0 | 50.0 |
| 34 | 11 | 9.1 | 0.0 | 0.0 | 18.2 | 72.7 | 0.0 | 63.6 |
| 36 | 7 | 0.0 | 14.3 | 14.3 | 14.3 | 57.1 | 0.0 | 0.0 |
| 37 | 4 | 50.0 | 25.0 | 25.0 | 0.0 | 0.0 | 0.0 | 75.0 |
| 39 | 6 | 16.7 | 0.0 | 16.7 | 16.7 | 16.7 | 0.0 | 0.0 |
| 40 | 14 | 21.4 | 14.4 | 21.4 | 21.4 | 21.4 | 0.0 | 0.0 |
| 41 | 7 | 14.3 | 0.0 | 14.3 | 28.6 | 42.8 | 0.0 | 37.5 |
| 42 | 9 | 66.7 | 33.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

Table 4 (concl.).

bridge configurations present in any of the cells studied. Five of the lowland plants had no cells with lagging chromosomes.

Anaphase I irregularities were much more common in the upland plants as indicated in Table 4. They consisted of lagging univalents, late-dividing bivalents, the occasional occurrence of bridges, and chromosome stickiness.

Lagging univalents were common in the upland pollen mother cells. Of the 38 upland plants none was completoly lacking in anaphase I laggards, but the frequency of lagging bodies varied considerably from plant to plant. One sell of plant 46 (chromosome number questionable) had 33 laggards, but not enough cella of this plant were examined to establish this as a general rule. Plant 18 ( $2 n=72$ ) also showed an extremely high frequency of laggards. The aneuploids showed no more irregularity in melotic behavior than the euploids. Other plants exhibited considerable lagging, but no definite pattern seemed to be followed.

Some bridges were observed at anaphase I (Fig. 3, Plate IV), with 12 plants showing this type of irregularity. Bridge-fragment conflgurations were fairly common, but bridges were frequently unaccompanied by fragments. The largest number of bridges found in a single cell was five (plants 26 and 50 ). No plants exhibited bridges in all cells oxamined. Plants 26 and $37(2 n=72)$ showed high frequencies of bridges, but for each of these plants, only four cells were examined.

Chromosome stickiness was quite prevalent in the upland plants, but was completely absent in the lowland type. Stickiness (P1g. 5, Plate IV) presented a problem in the analysis of some cells. Plants $18,24,26,31$, and 46 exhibited extreme stickiness at anaphase I. In plants 24 and 31 this phenomenon was so pronounced that individual chromosomes could scarcely be distinguished. Some sticky configurations bore considerable resemblance to multivalents.

Chromosome Behavior at Telophase I

Chromosome behavior at telophase I is summarized in Table 5. In all lowland plants telophase I irregularities were rare. Seven of the plants showed no lagging chromosomes (Fig. 6, Plate II), and other plants exhibited very few (P1g. 5, Plate II). One bridge was found out of 510 cells examined.

Telophase I irregularities were more frequent in upland switchgrass. These abnormalities consisted of laggards, bridges, and the formation of visibly abnormal daughter nuclei. Laggards frequently appeared to be univalents, but smaller fragmentary

## EXPLANATION OF PLATE IV

Meiotic behavior of upland switchgrass.

Fig. 1. Anaphase I of plant 47 showing 76 chromosomes. 915X Pig. 2. Anaphase I of plant 47 showing 5 lagging univalents. 915X

Plg. 3. Early anaphase I of plant 46 (chromosome number questionable) showing bridge configurations. 915X

Fig. 4. Metaphase $I$ of plant 46 showing $35 I I$ and $2_{I}$. 915 X
Fig. 5. Anaphase I of plant 46 showing sticky chromosomes. 915X

Fig. 6. Anaphase I of plant 46 showing over 200 ohromosomes and/or fragments. 915X

PLATE IV

Fig. 1


FIg. 3


Fig. 5


FIg. 2


P1g. 4

Fig. 6

## EXPLANATION OF PLATE V

Meiotic behavior of upland awitchgrass.

Fig. 1. Metaphase $I$ of plant 50 showing $33_{I I}$ and ${ }^{2}$ I. $915 X$
Pig. 2. Metaphase I of plant 50 showing ${ }^{31}$ II, ${ }^{1}$ IV, and ${ }^{2}$ I. 915 X

Pig. 3. Anaphase I of plant 50 showing 68 chromosomes. 915X
Fig. 4. Quartet with no micronuclei. 800X
Pig. 5. Anaphase I showing 3 lagging univalents with 2 divided into chromotids. 915X

Fig. 6. Metaphase I showing 23 II and 26 I.

PLATE V


Pig. 1


FIg. 3

Fig. 5



Fig. 2


Fig. 4

F1g. 6

Table 5. Chromosome behavior at telophase I.


Lowland

| 1 | 82 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 2 | 27 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 3 | 9 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 4 | 55 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 5 | 34 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 6 | 40 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 7 | 54 | 94.4 | 3.7 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| 8 | 29 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 9 | 46 | 91.3 | 2.2 | 4.3 | 2.2 | 0.0 | 0.0 | 2.2 |
| 10 | 51 | 92.2 | 3.9 | 0.0 | 3.9 | 0.0 | 0.0 | 0.0 |
| 11 | 22 | 91.0 | 4.5 | 0.0 | 0.0 | 4.5 | 0.0 | 0.0 |
| 12 | 61 | 98.4 | 0.0 | 0.0 | 1.6 | 0.0 | 0.0 | 0.0 |

## Upland

| 13 | 79 | 24.1 | 21.5 | 26.5 | 11.4 | 16.5 | 0.0 | 0.0 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 14 | 44 | 34.1 | 20.4 | 22.7 | 11.4 | 11.4 | 0.0 | 0.0 |
| 15 | 54 | 13.0 | 20.4 | 25.9 | 27.7 | 13.0 | 0.0 | 0.0 |
| 16 | 45 | 46.7 | 28.9 | 11.1 | 4.4 | 8.9 | 0.0 | 0.0 |
| 17 | 56 | 30.4 | 39.2 | 19.7 | 3.6 | 7.1 | 0.0 | 0.0 |
| 18 | 9 | 11.1 | 11.1 | 11.1 | 22.2 | 44.4 | 0.0 | 0.0 |
| 19 | 31 | 90.4 | 3.2 | 0.0 | 3.2 | 3.2 | 0.0 | 0.0 |
| 20 | 32 | 9.4 | 28.1 | 9.4 | 25.0 | 28.1 | 0.0 | 0.0 |
| 21 | 67 | 22.4 | 16.4 | 32.8 | 19.4 | 9.0 | 0.0 | 4.5 |
| 22 | 52 | 73.1 | 21.2 | 3.8 | 0.0 | 1.9 | 0.0 | 0.0 |
| 23 | 35 | 22.9 | 17.1 | 37.2 | 17.1 | 5.7 | 0.0 | 0.0 |
| 24 | 30 | 40.0 | 30.0 | 20.0 | 10.0 | 0.0 | 0.0 | 23.3 |
| 25 | 28 | 67.9 | 21.4 | 7.1 | 3.6 | 0.0 | 0.0 | 0.0 |
| 26 | 10 | 10.0 | 40.0 | 30.0 | 10.0 | 10.0 | 0.0 | 30.0 |
| 27 | 35 | 22.9 | 28.6 | 31.4 | 11.4 | 5.7 | 0.0 | 5.7 |
| 28 | 58 | 24.1 | 38.0 | 22.4 | 10.3 | 5.2 | 0.0 | 1.7 |
| 29 | 43 | 41.8 | 41.8 | 7.0 | 7.0 | 2.2 | 0.0 | 0.0 |
| 30 | 62 | 56.4 | 32.3 | 8.1 | 1.6 | 1.6 | 0.0 | 0.0 |
| 31 | 20 | 20.0 | 20.0 | 15.0 | 20.0 | 25.0 | 0.0 | 5.0 |
| 32 | 18 | 16.7 | 50.0 | 5.6 | 0.0 | 27.7 | 0.0 | 11.1 |
| 33 | 35 | 57.1 | 31.5 | 5.7 | 5.7 | 0.0 | 0.0 | 2.9 |
| 34 | 56 | 19.6 | 28.6 | 23.2 | 10.7 | 17.9 | 0.0 | 35.7 |
| 35 | 5 | 0.0 | 0.0 | 40.0 | 40.0 | 20.0 | 0.0 | 20.0 |
| 36 | 57 | 14.0 | 35.1 | 21.1 | 19.3 | 10.5 | 0.0 | 5.3 |
| 37 | 35 | 57.2 | 25.7 | 17.1 | 0.0 | 0.0 | 0.0 | 8.6 |
| 38 | 7 | 14.3 | 14.3 | 14.3 | 28.6 | 28.6 | 0.0 | 0.0 |
| 39 | 57 | 42.1 | 10.5 | 22.8 | 12.3 | 12.3 | 0.0 | 0.0 |

Table 5 (concl.).

bodies were also common. Lagging bodies had sometimes coalesced into large masses of chromatin material. Daughter nuclei were sometimes unequal in size and occasionally failed to separate cleanly, appearing to have been formed through the "pulling apart" of the entire parent nuclei rather than the separation of individual univalents, bivalents, and multivalents.

The number of cells with laggards was definitely lower at telophase I than at anaphase $I$, but most upland plants could still be considered irregular at this stage. Plant 46 (chromosome number questionable) was the only one which had an extremely high number of laggards, but many had from four to ten per sporocyte. The 76and 78-chromosome plants had more cells with laggards than the 68and 70-chromosome aneuploids. Some bridge configurations (Pig. 5, Plate III) occurred in 13 of the 38 plants examined. Plants 24, 26, and 34 (octoploids) had the highest frequeney of bridges. Plants 24 and 31 (octoploids) formed apparently abnormal daughter
nucle1, as described above, because of the chromosome stickiness.

Table 6. Quartet micronuclei.

| Code | : | $\begin{aligned} & \text { No. } \\ & \text { cells } \end{aligned}$ | : | Percent |  |  | quartets |  |  |  |  | nur |  |  |  | Mean No |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| No. | : |  | : | 0 | : | 1 | : | 2 | : | 3 | : | 4-10 | : |  |  | quartet |

Lowland

| 2 | 111 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 3 | 32 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 4 | 19 | 84.0 | 10.0 | 5.2 | 0.0 | 0.0 | 0.0 | 0.21 |
| 5 | 5 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 6 | 25 | 96.0 | 0.0 | 4.0 | 0.0 | 0.0 | 0.0 | 0.08 |
| 7 | 37 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 8 | 2 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 9 | 56 | 91.1 | 8.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.09 |
| 10 | 73 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 11 | 7 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 12 | 47 | 89.3 | 4.3 | 2.1 | 4.3 | 0.0 | 0.0 | 0.21 |

Upland

| 14 | 11 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 15 | 56 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.00 |
| 16 | 95 | 73.7 | 26.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.26 |
| 17 | 55 | 58.2 | 29.0 | 5.5 | 7.3 | 0.0 | 0.0 | 0.62 |
| 18 | 102 | 88.2 | 11.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.12 |
| 20 | 75 | 62.7 | 28.0 | 8.0 | 1.3 | 0.0 | 0.0 | 0.48 |
| 21 | 134 | 83.6 | 15.7 | 0.7 | 0.0 | 0.0 | 0.0 | 0.17 |
| 22 | 52 | 94.2 | 5.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.06 |
| 23 | 83 | 43.4 | 32.5 | 20.5 | 2.4 | 1.2 | 0.0 | 0.87 |
| 24 | 74 | 93.2 | 6.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.07 |
| 25 | 47 | 61.7 | 34.0 | 4.3 | 0.0 | 0.0 | 0.0 | 0.43 |
| 26 | 66 | 59.0 | 28.9 | 10.6 | 1.5 | 0.0 | 0.0 | 0.55 |
| 27 | 84 | 94.0 | 6.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.06 |
| 28 | 3 | 66.7 | 33.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.33 |
| 29 | 94 | 77.7 | 22.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.31 |
| 30 | 67 | 85.1 | 13.4 | 1.5 | 0.0 | 0.0 | 0.0 | 0.16 |
| 31 | 19 | 31.6 | 42.1 | 10.5 | 10.5 | 5.3 | 0.0 | 1.16 |
| 32 | 48 | 58.3 | 25.0 | 14.6 | 2.1 | 0.0 | 0.0 | 0.60 |
| 33 | 122 | 86.9 | 11.5 | 1.6 | 0.0 | 0.0 | 0.0 | 0.15 |
| 34 | 115 | 57.4 | 29.6 | 10.4 | 1.7 | 0.9 | 0.0 | 0.60 |
| 36 | 108 | 66.7 | 22.2 | 8.3 | 1.9 | 0.9 | 0.0 | 0.48 |
| 37 | 67 | 73.1 | 23.9 | 3.0 | 0.0 | 0.0 | 0.0 | 0.30 |
| 38 | 73 | 26.0 | 21.9 | 23.3 | 17.8 | 11.0 | 0.0 | 1.71 |
| 39 | 63 | 90.4 | 4.8 | 4.8 | 0.0 | 0.0 | 0.0 | 0.14 |
| 40 | 54 | 85.2 | 11.1 | 3.7 | 0.0 | 0.0 | 0.0 | 0.19 |

Table 6 (concl.).

| Code No. | ! | No. cells | ! | Percent |  | quartets with given number of micronuclei |  |  |  |  |  |  |  |  | :Mean No. <br> : per <br> :quartet |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 0 | : | 1 | : | 2 | : | 3 | : | 4-10 | : | $10+$ |  |
| 41 |  | 29 |  | 75.9 |  | 24.1 |  | 0.0 |  | 0.0 |  | 0.0 |  | 0.0 | 0.24 |
| 42 |  | 115 |  | 95.8 |  | 2.6 |  | 0.8 |  | 0.8 |  | 0.0 |  | 0.0 | 0.07 |
| 43 |  | 64 |  | 48.3 |  | 21.9 |  | 21.9 |  | 6.3 |  | 1.6 |  | 0.0 | 0.91 |
| 44 |  | 47 |  | 83.0 |  | 17.0 |  | 0.0 |  | 0.0 |  | 0.0 |  | 0.0 | 0.17 |
| 45 |  | 77 |  | 92.2 |  | 3.9 |  | 3.9 |  | 0.0 |  | 0.0 |  | 0.0 | 0.12 |
| 46 |  | 30 |  | 3.3 |  | 3.3 |  | 6.7 |  | 20.0 |  | 53.4 |  | 13.3 | 5.60 |
| 47 |  | 119 |  | 41.2 |  | 38.7 |  | 14.3 |  | 5.9 |  | 0.0 |  | 0.0 | 0.85 |
| 48 |  | 94 |  | 70.2 |  | 21.3 |  | 7.4 |  | 1.1 |  | 0.0 |  | 0.0 | 0.39 |
| 49 |  | 3 |  | 0.0 |  | 0.0 |  | 33.3 |  | 66.7 |  | 0.0 |  | 0.0 | 2.67 |
| 50 |  | 55 |  | 74.6 |  | 21.8 |  | 3.6 |  | 0.0 |  | 0.0 |  | 0.0 | 0.29 |

Meiotio Irregularities at the Quartet Stage

Meiotic irregularities at the quartet stage are sumarized in Table 6. Irregularities consisted of micronuclei and formation of Visibly abnommal nuclei (Pigs. 1, 2, and 4, Plate VI). Occasional micronuclei were found in lowland plants, but the frequencies were very low. Seven of 11 lowland plants showed no micronucle1 (Fig. 4, Plate V).

Micronuclei frequency was much higher in the upland switchgrass, but varied considerably among plants. Two of 38 upland plants exhibited no micronuclei.

One evident fact was that the number of micronuclel was not in agreement with the number of laggards at anaphase I or telophase I, the number of laggards at telophase I being greater then the number of micronuclei observed. Thus in plant 15, an octoploid, only 13 percent of the telophase figures were without laggards while 100 percent of the quartets showed no mieronuclei. A similar

## EXPLANATION OF PLATE VI

Melotic behavior of plant $49(2 n=78)$.

Fig. 1. Abnormal quartet. 915X
P1g. 2. Abnormal quartet. 915X
Fig. 3. Metaphase I showing 37 II and ${ }^{4}$ I. $915 X$
Fig. 4. Abnormal quartets. 915X
Fig. 5. Metaphase I showing 38II and 2I. 915X
Fig. 6. Motaphase I showing 39II. 915X


Fig. 1


Fig. 3


Fig. 5
$\qquad$


Fig. 2


Fig. 4


Fig. 6
relationship was found in many other upland plants.
Apparently abnormal nuclei formation was exhibited in plant $49(2 \mathrm{n}=78)$. More than four spores were sometimes formed from each microsporocyte, but when only four resulted, many were multinucleate.

## Pollen Stainability

Pollen stainability is summarized in Table 7. Well-stained grains are shown in Fig. 2, Plate I. The lowland plants gave a high percentage of pollen grains in Class A with very little variation among plants.

In upland type plants pollen stainability was quite variable although many of the plants had a large percentage of grains in class A. It is interesting to note that the hexaploid ( $2 n=54$ ) had the highest percentage of well-stained grains of any plant observed in the entire study. With the exception of plant 49 $(2 n=78)$ the aneuploids were below average in pollen stainability. Plants 46 (chromosome number questionable) and 31 (sticky) had below the average percentage of class A pollen.

For the purpose of statistical analysis, the entire experimental population was divided into four groups on the basis of chromosome number: tetraploids (i.e. lowland plants); hexaploid; octoploids; and aneuploids. Homogeneity within each group was tested by contingency chi-square. The 36 -chromosome group was surprisingly homogeneous with a nonsignificant ohi-square of 21.227 (with 16 degrees of freedom, $0.10<P<0.25$ ). A oh1-square of 1788.93 was highly significant for the 72 -chromosome group

Table 7. Pollen grain stainability.

|  | : | Percentage ${ }^{\text {\% }}$ of grains classified as |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Code No. | : | A | : | B | : | C |

## Lowland

| 97.4 | 1.6 | 1.0 |
| :--- | :--- | :--- |
| 97.0 | 1.6 | 1.4 |
| 96.6 | 2.4 | 1.0 |
| 96.4 | 1.2 | 2.4 |
| 95.8 | 1.8 | 2.4 |
| 97.0 | 2.8 | 0.2 |
| 97.6 | 1.2 | 1.2 |
| 96.6 | 1.8 | 1.6 |
| 97.4 | 1.2 | 1.4 |

## Upland

| 13 | 83.6 | 15.0 | 1.4 |
| ---: | ---: | ---: | ---: |
| 14 | 93.6 | 5.0 | 1.4 |
| 15 | 88.6 | 9.2 | 2.2 |
| 16 | 85.2 | 13.0 | 1.8 |
| 17 | 82.6 | 15.2 | 2.2 |
| 18 | 78.0 | 18.6 | 3.4 |
| 19 | 97.2 | 0.4 | 2.4 |
| 20 | 97.4 | 0.2 | 2.4 |
| 21 | 90.4 | 9.2 | 0.4 |
| 22 | 94.0 | 2.4 | 3.6 |
| 24 | 94.0 | 3.2 | 2.8 |
| 25 | 98.8 | 0.6 | 0.6 |
| 26 | 80.6 | 1.4 | 18.0 |
| 27 | 98.8 | 0.8 | 0.4 |
| 28 | 96.4 | 0.2 | 3.4 |
| 29 | 87.0 | 7.6 | 5.4 |
| 30 | 86.4 | 8.8 | 4.8 |
| 31 | 78.0 | 17.6 | 4.4 |
| 32 | 91.9 | 4.0 | 4.1 |
| 33 | 84.2 | 2.0 | 0.8 |
| 34 | 97.6 | 9.4 | 5.8 |
| 36 | 98.8 | 0.6 | 1.8 |
| 37 | 90.8 | 3.8 | 1.8 |
| 38 | 93.8 | 7.8 | 2.8 |
| 39 | 93.0 | 2.0 | 1.4 |
| 41 | 99.0 | 2.2 | 4.2 |
| 44 | 81.4 | 0.4 | 4.8 |
| 45 | 65.0 | 2.0 | 0.6 |
| 46 | 74.8 | 15.0 | 16.6 |
| 47 | 92.8 | 20.0 | 20.0 |
| 48 | 80.4 | 3.2 | 5.2 |
| 49 | 11.6 | 4.0 |  |
| 50 |  |  | 8.0 |

(with 52 degrees of freedom, P<<.001). The aneuploids were also heterogenous with a highly signifioant ohi-square of 127.86 (with alx degrees of freedom, $\mathrm{P} \ll .001$ ).

Pollen of the different groups was compared by means of analysia of variance (Table 8).

Table 8. Analysis of variance on class A pollen stainability.

| Sources of varlation | D.P. | S.S. | : | M.S. | P |
| :--- | ---: | ---: | ---: | ---: | ---: |
| Between groups | 2 | 960.62 | 480.31 | $11.76^{\text {m/4 }}$ |  |
| Plants within groups | 37 | 1510.82 | 40.83 |  |  |
| Total | 39 | 2471.44 |  |  |  |

* 

Significant at the . 01 level.

Mean frequencies of class $A$ pollen for the tetraploid, ootoploid, and aneuploid groups were compared by L.S.D. (Table 9).

Table 9. Class a pollen stainability comparisons by L.S.D.

| Oroups | \% | $\bar{x}$ | : | $\bar{x}-78.25$ | : | $\bar{x}-90.83$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tetraploids |  | 96.87 |  | $\begin{gathered} 18.62^{m \pi} \\ (\text { L.S.D. } 11.06) \end{gathered}$ |  | $\begin{gathered} 6.04 \\ (L . S . D \cdot 7.08) \end{gathered}$ |
| Octoploids |  | 90.83 |  | $\begin{gathered} 12.58^{*} \\ (\text { L.S.D. } 9.85) \end{gathered}$ |  |  |
| Aneuploids |  | 78.25 |  |  |  |  |

[^0]
## DISCUSSION

## Chromosome Complements

The range of chromosome numbers found in this study (2n=36, $54,72,68,70,76$, and 78 ) is not in complete agreement with that reported by Nielsen (1944) $(18,36,54,72,90$, and 108). The greater range of polyploidy Cound by Nielsen may be due to the fact that he studied plants from a larger area than that sampled in this study. Also, chromosome counts in this study were determined in sporocytes, while the counts by Nielsen were determined in root t1ps.

Separation of switchgrass into two separate types by morphological and oytological characters should be of considerable importance in plant breeding. All plants designated as lowland type proved to have 36 chromosomes, while those designated as upland were found to have $54,72,68,70,76$, and 78 chromosomes, with most of the latter having 72 chromosomes. Plant $45(2 n=54)$ could conceivably be a hybrid between a 72-chromosome and a 36-chromosome plant, although its cytological behavior and morphological appearance did not substantiate this hypothesis. It was relatively regular at meiosis, had mostly paired chromosomes at metaphase $I$, very few quartet micronuclei, and exhibited the highest percentage of well-stained pollen in the study.

If difference in chromosome number furnishes a basis for distinction of species, the lowland and upland types might well be different species. They do not seem to cross readily in the field, but available ilterature contains no reports of attempts to cross
them artificially. Certainly, it would seem desirable to attempt controlled crosses between the two types and to study the morphology and breeding behavior of any hybrids which might be produced.

The occurrence of aneuploidy in the octoploids is not surprising considering the frequency of irregularity at melosis. A higher frequency of aneuploidy might in fact be expected in view of the extreme irregularity of some plants. Evidently, gametes with 36 chromosomes are favored in competition with those of abnormal chromosome complements.

The different chromosome numbers found in sporocytes of plant 46 is puzzling. Sporocytes with a large number of chromosomes were reported by Barnett (1955) who suggested spontaneous chromosome doubling in the floret or spikelet initials as a possible cause. The appearance of cells with an excess of 108 and 200 chromosomes or fragments could possibly be an artifact, but there certainly appeared to be many stained bodies in these sporocytes. Several cells could have been stuck together, but it seoms unlikely that this would have occurred repeatedly as observed. Further, only one cell appeared to be involved in each case. Another possible explanation is the presence of genetic control (Smith, 1942). Smith found pollen mother cells with $14,21,28,56,112$, and higher numbers of bivalents in barley. It would be desirable to study plant 46 further in order to establish its karyological status.

## Meiotic Behavior

Meiotically, the extremely regular lowland switchgrass is in strange contrast with its upland counterpart where, although there is a generally-high frequency of bivalents, meiotic behavior is variable with some plants being highly irregular. Whether this distinction reflects some fundamental phylogenetic differences or whether it is entirely associated with chromosome number differences is a matter of speculation. Certainly lowland switchgrass would be expeoted to be more stable karyologically than the upland population so that the range of chromosome numbers exhibited by the latter is in this respect not surprising. Variation in the meiotic behavior of upland switchgrass might be explained by a genetic factor as found in maize by Beadle (1930, 1933). Beadle reported the factor, "asynaptio," which affected bivalent formation in such a way that most of the chromosomes arrived on the metaphase plate as univalents rather than bivalents. It was determined later by Rhoades (1947) that orossing over in the asynaptio plants occurred, but that ohiasmata falled to form.

In the present case, however, the occurrence of karyotypio differences among plants of upland switchgrass seems to be a more satisfactory explanation of the observed meiotic variability and irregularity. Considerable modirioation of the Beadle-Rhoades hypothesis would be required to explain the facts thet pairing fallure was never complete and that multivalent formation was occasionally observed in the present material. Some degree of karyotypic variation is of course already established by the
occurrence of the hexaploid plant and the existence of aneuploidy at the octoploid level. If differences in chromosome number occur, it is ressonable to suspect that karyotypic differences also exist among plants of the same chromosome number. Such differences might involve whole chromosomes and/or parts of chromosomes. Hybrid karyotypes resulting from hybridizations among plants of different karyological constitutions would augment the meiotic variability of the upland population. Karyological dif ferences of this nature would almost undoubtedly prevent random recombination of germ plasm, and it is quite possible that genetic barriers exist even among plants of the same chromosome number. Such barriers would obviously complicate the problem of improving upland switchgrass through breeding.

Complete bivalent chromosome pairing in a polyploid is generally considered to be indicative of allopolyploid origin (Riley, 1949), p. 596. Scarcity of quadrivalent configurations in awitchgrass auggests that both lowland and upland forms may be of allopolyploid origin. This is especially true with respect to lowland switchgrass which exhibited almost complete bivalent pairing. Bivalent chromosome pairing can not, however, be taken as conclusive evidence of allopolyploidy. Selection toward a bivalent, and hence a more regular type of melosis, may have occurred in many autopolyploids. Thus Lotus corniculatus L., which might have been considered an allotetraploid because of its bivalent chromosome pairing, was found by Dawson (1941) to exhibit tetrasomic inheritance. In Dactylis glomerata L. a considerable proportion of the chromosomes pair bivalently (Meyers and H111, 1942),
although this species is considered by most authorities to be an autotetraploid. Therefore, it would not be advisable to consider switchgrass an allopolyploid until this aspect has been more thoroughly investigated. In view of the karyological status of upland switchgrass it seems that the origin of this population probably involved more than simple allopolyploidy.

Discrepaney between quartet mieronuclei frequency and the occurrence of laggards at telophase $I$ is difficult to explain. The laggards may eventually become included in the nuelei at anaphase II. Another possibility is that the micronuclei are obscured by the main nuclei of the quartets. Perhaps the most likely explanation would be that the chromosomes lose their matrix in the cytoplasm and do not stain sufficiently to be visible. Analysis of irregularities at telophase $I$ or dyad stage would probably be more reliable than analysis of quartet micronuclei in critical evaluation of plants for meiotic regularity. The telophase I stage is more readily obtained than quartet figures, and the scarcity of micronuclei might give a false impression of meiotic regularity.

Abnormal quartet formation in plant $49(2 n=78)$ is an interesting feature. This type of abnormality was reported in a hybrid between Triticum vulgare and Agropyron elongatum by Marghall and Schmidt (1954). Clark (1940) reported a genetic change in maize which caused changes in the structure of the spindle and resulted in abnormalities similar to those observed here. In the present study it is possible that a genic unbalance resulting from the presence of six extra chromosomes is responsible for the production of aberrant quartets in plant 49.

## Chromosome Stickiness

Some of the plants exhibited considerable chromosome stickiness at metaphase $I$, anaphase $I$, and telophase I. Chromosome stickiness resulted in configurations which were difficult to interpret and which, in some respeots, were suggestive of multivalency. It seems possible that such stickiness could prevent cells from completing cell division.

The nature and cause of this stickiness is a matter of speculation. Method of fixation may be the oause, but this seems unlikely, because all of the plants were colleoted and fired in the same manner, while only a few exhibited stickiness. It seems to be the result of simple adhesion of the matrix material. A "sticky" strain of maize has been investigated by Beadie (1932; 1937). A recessive gene, "sticky," when homozygous caused stiokiness of the chromosomes resulting in chromosome aberrations.

Pollen Stainability

The pollen-staining reaction of the lowland and upland populations is closely analogous to the meiotic behaviors of these groups. Homogensity within the lowland population is in acoord with the uniform meiotic behavior of this group while the extreme heterogeneity of the upland population corresponds nicely with the irregular and variable melotic behavior of this type. It seems likely thet pollen-staining differences are largely if not entirely the reflection of karyotypic variability.

Both tetraploid and octoploid groups had significantly better-stained pollen than the aneuploids. This is not surprising since low fertility is a common characteristic of aneuploids. Of greater interest is the fact that plant $49(2 n=78)$ had a considerably higher percentage of well-stained pollen than plant 47 ( $2 \mathrm{n}=76$ ). Since both these plants are hyperploids it would seem that "karyotypic balance" is an importance factor even at the octoploid level. It is of course also possible that plant 47 possesses karyotypic deficiencies in spite of the fact that it is a hyperploid.

## SUMOARY

Chromosome numbers of 56 plants of Panicum virgatum were determined. Seed stocks used for the study were taken from the states of Oklahoma, Arkansas, Kansas, and Texas. Counts were made from P.M.C. smear preparations. Complements of $2 n=36,54$, $72,68,70,76$, and 78 were determined. The chromosome oount for one plant was considered questionable. Some sporocytes of this plant had 72 chromosomes, one appeared to have 72 bivalents, a few seemed to have in excess of 108 chromosomes, and two appeared to have more than 200 chromosomes or fragments.

Chromosome numbers for 16 lowland type plants were determined, and all these plants proved to have 36 chromosomes. Plants classified as upland were found to have counts of $2 n=54,72,68$, 70,76 , and 78.

Lowland switchgrass was quite regular at melosis. It showed nearly complete bivalent chromosome pairing at metaphase $I$, had
few laggards at anaphase I and telophase $I$, and a negligible number of quartet mioronuclei. Upland switchgrass was quite variable in meiotic behavior. Many plants showed complete or nearly complete bivelent pairing at metaphase $I$, while others exhibited a varying number of univalents. One plant had as low as 12 bivalents out of a possible 36 at metaphase I. Some quadrivalents, but no trivalents, were found at metaphase I. Most of the plants orhibited lagging chromosomes and occasional bridges at anaphase I and telophase I. Quartet micronuclei were relatively frequent, but their total number was less than the total number of laggards at telophase $I$.

Apparent chromosome stickiness was observed in metaphase $I$, anaphase $I$, and telophase $I$ cells of some of the upland plants. Pormation of abnomal quartets was observed in one plant.

Pollon stainability was consistently high in the lowland switchgrass, but was quite variable in the upland plants. Euploid plants exhibited a higher frequency of well-stained pollen than the aneuploids.

## ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation to Dostor F. L. Barmett, me for instructor, who suggested the problem, for valuable guidance and counsel throughout the investigation, and for aid in preparation of the manusoript.

Grateful aoknowledgment is extended to Doctor Elizabeth MoCracken, Associate Professor of Botany, for helpful advice during the study.

Purther aoknowledgment is extended to Doctor Holly C. Fryer, Professor of Mathematios, for suggestions in the statistical analyses.

The study was made possible by a research assistantship granted by the Kansas State College of Agriculture and Applied Science in cooperation with the United States Department of Agriculture.

## LITERATURE CITED

Barnett, F. L.
A karyological survey of several Bromus species. Agron. Jour. 47:88-91. 1955.

Beadle, C. W.
Genetical and cytological studies of Mendelian asynapsis in Zea mars. Cornell Univ. Exp. Sta. Mem. 129:1-23. 1930.

Further studies in asynaptic maize. Cytologia 4:269-287. 1933.
Chromosome aberration and gene mutation in sticky chromosome plants of Zoa mays. Cytologia Fujil Job Vol. 43-56. 1937.

Burton, Glenn W.
A cytological study of some species in the tribe Panicoae. Amer. Jour. of Bot. 29:355-359. 1942.

Church, George L.
Meiotic phenomena in certain Gramineas. II. Paniceae and Andropogoneae. Bot. Gaz. 88:63-84. 1929.

```
Cytotaxonomic atudies in the Graminere Spartina, Andropogon and Panioum. Amer. Jour of Bot. \(27: 263-271.1940\).
Clark, F. J.
Cytogenetic studies of divergent meiotic spindie formation in Zea mays. Amer. Jour. Bot. \(27: 547-559.1940\).
Dawson, C. D. R. Tetrasomic inheritance in Lotus cornioulatus L. Gen. 42:49-72. 1941.
```

Hughes, H. D., Maurice E. Heath, and Darrel S. Metcalfe. Porages. Ames, Iowa: Iowa State College Press, 1952. 724 p.

Marshall, Harold G., and John W. Sohmidt. A study of the meiotic stability of certain Agrotricum hybrids. Agron. Jour. 46:383-387. 1954.

Myers, W. M., and Helen D. Hill. Variations in meiotio bohavior among plants of Dactylis glomerata L. (Abs.) Gen. 26:162. 1942.

Nielsen, Etlar L. Analysis of variation in Panicum virgatum. Jour. Agr. Res. 69:327-353. 1944.

Nielsen, Etlar L.
Polyploidy and winter survival in Panicum virgatum L. Jour. Amer. Soc. Agron. 39:822-827. 1947.

Rhoades, M. M.
Crossover chromosomes in unreduced gametes of asynaptic maize. Gen. 32:101. 1947.

Riley, H. P.
Genetics and oytogenetics. New York: John Wiley \& Sons. 596 p. 1949.

Smith, L.
Cytogenetics of a factor for multiploid sporocytes in barley. Amer. Jour. Bot. 29:189-191. 1942.

The acetocarmine smear technic. Stain Tech. 22:17-31. 1947.

# ROBERT FRANKLIN CARVER 

B. S., Oklahoma Agricultural and Mechanical College, 1953

## AN ABSTRACT OF A THESIS

submitted in partial fulfillment of the
requirements for the degree

MASTER OP SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE OP AGRICULTURE AND APPLIED SCIENCE

A plant introduction nursery of Panicum virgatum, composed of seed stocks collected from Oklahoma, Kansas, Arkansas, and Texas, provided the source of plant materials for this study. The purpose of the study was to investigate the karyological status of this species. Plants were classified in the field as lowland or upland types. Parts of panicles with sporocytes and matured pollen were collected in the field and fixed in Carnoy's solution for eytological study. Chromosome counts and other cytological observations were based on pollen mother cell smear preparations. Pollon fertility was ovaluated by its staining reaction in potassium iodide solution.

Chromosome counts of 56 plants are reported. Counts of $2 n=36,54,72,68,70,76$, and 78 were determined. One plant had a questionable chromosome number. Some sporocytes of this plant had 72 chromosomes while one appeared to have 72 bivalents, a few seemed to have in excess of 108, and two appeared to have more than 200 ohromosomes or fragments.

Chromosome numbers of 16 lowland plants were determined and all of these plants proved to have 36 chromosomes. Plants classifled as upland had complements of $2 \mathrm{n}=54,72,68,70,76$, and 78 .

Lowland and upland switchgrass were found to be quite different in moiotic behavior. Melotic behavior in the lowland type was quite regular with nearly complete bivalent pairing at metaphase $I$, only a few lagging chromosomes at anaphase $I$ and telophase $I$, and a negligible number of quartet micronuclel. On the other hand, melotic behavior in the upland type was quite variable.

Many upland plants were found to have some univalents at metaphase I and high frequencies of lagging chromosomes at anaphase I and telophase I. Quartet micronuclei were found in many of the upland plants, but their total was not as high as the number of laggards round at telophase I. Possible causes for this were discussed.

Apparent chromosome stickiness was found in some of the upland plants at metaphase $I$, anaphase $I$, and telophase $I$. $A b-$ normal quartet formation was observed in one plant.

Pollen stainability was consistently high in the lowland switchgrass but quite variable in the upland plants. Buploid plants exhibited a higher frequeney of well-stained pollen than the anouploids.


[^0]:    * Significant at the . 05 level.
    ** Significant at the . 01 level.

