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Virus Diseases of Cereal Crops in South Dakota

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of
Cereal Crops
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PLANT PATHOLOGY
DEPARTMENT

AGRICULTURAL EXPERIMENT STATION
South Dakota State College of Agriculture and Mechanic Arts
Brookings, South Dakota

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Virus Diseases

of Cereal Crops in South Dakota

J. T. SLYKHUIS¹

Introduction

Virus diseases of wheat, oats and barley have been reported from various parts of the world during the last three decades. In some instances viruses have proven to be the real causes of diseases formerly attributed to other agents.

The earliest reports of a virus disease of wheat concerned a mosaic-roseette disease first observed in southeastern Illinois in 1919 (7). This disease, caused by a soil-borne virus, was later found in a number of localities in the eastern half of the United States (8), but to date it has not been reported west of the Mississippi River. However, other mosaic diseases of wheat have been observed in the Great Plains region since 1922 (4, 8). Recently a similar mosaic disease was found on wheat in California (5). Reports from foreign countries indicate the occurrence of soil-borne mosaics in Japan (6) and Egypt (15), and a leafhopper-transmitted virus causing a mosaic of wheat in western Russia (20).

The virus diseases reported on

oats include a soil-borne mosaic of winter oats in Alabama and the Carolinas (1, 10), and a leafhopper-transmitted virus in Siberia (19).

Barley has also been infected with certain viruses. False stripe, which has long been considered a non-parasitic disease of barley, was recently shown to be caused by a virus which is seed-borne (11). In 1951 an aphid-transmitted disease of barley named "yellow dwarf" was discovered in California (16).

In the fall of 1949 experimental work was begun on virus diseases affecting cereal crops in South Dakota. The diseases that have been studied so far include wheat streak mosaic, wheat striate mosaic, barley false stripe, and *Agropyron* streak mosaic. The results of investigations on the distribution, transmission and host range of these diseases are presented.

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The author wishes to acknowledge the helpful suggestions given by Dr. C. M. Nagel, Head, Plant Pathology Department.

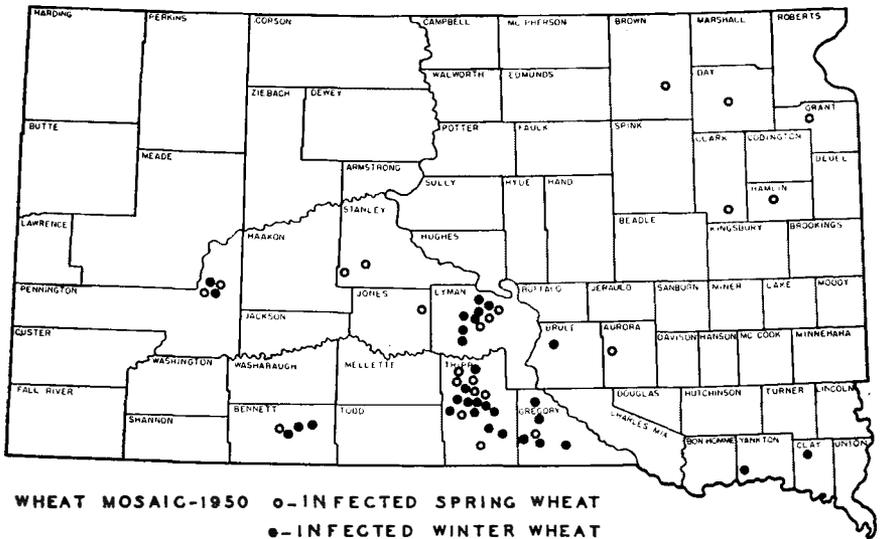


Fig. 1. Map of South Dakota showing the locations of spring wheat (durum and hard red spring) and winter wheat fields in which mosaic was found in 1950

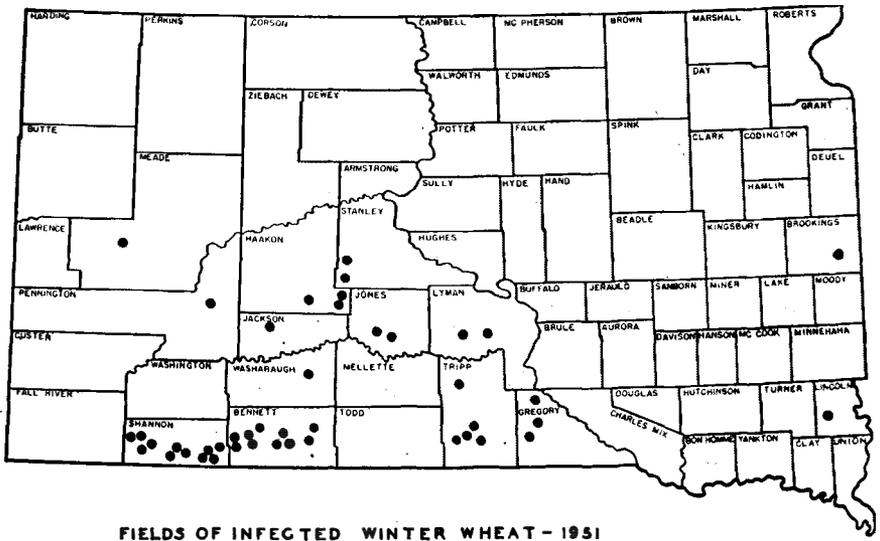


Fig. 2. Map of South Dakota showing the locations of fields in which mosaic was found in 1951 (Mosaic was not found in spring wheat)

Wheat Streak Mosaic

In 1949 wheat streak mosaic was brought to the attention of agriculturists throughout the Great Plains region because of its destructive occurrence in western Kansas (4). It was first recognized in South Dakota in June 1949² but, according to symptoms described by farmers, it appears likely that the same disease affected wheat in certain areas of the state several years earlier. In October 1949 this mosaic was found on volunteer and fall-sown wheat in Gregory, Tripp and Bennett counties. It occurred in amounts varying

from a trace to an abundance in 16 counties in 1950, and in 14 counties in 1951. (Figs. 1 and 2 show its distribution in South Dakota.) Serious crop losses were observed in isolated fields located in Bennett, Gregory, Lyman, Pennington and Tripp counties where grain yields in some winter wheat fields were reduced 35 to 75 percent. In 1950, streak mosaic infected, and in some instances caused serious losses, in spring as well as in winter wheat, but in 1951

²Mr. D. G. Fletcher, Secretary, Rust Prevention Association, reported finding this disease in Bennett and Tripp counties in June 1949.

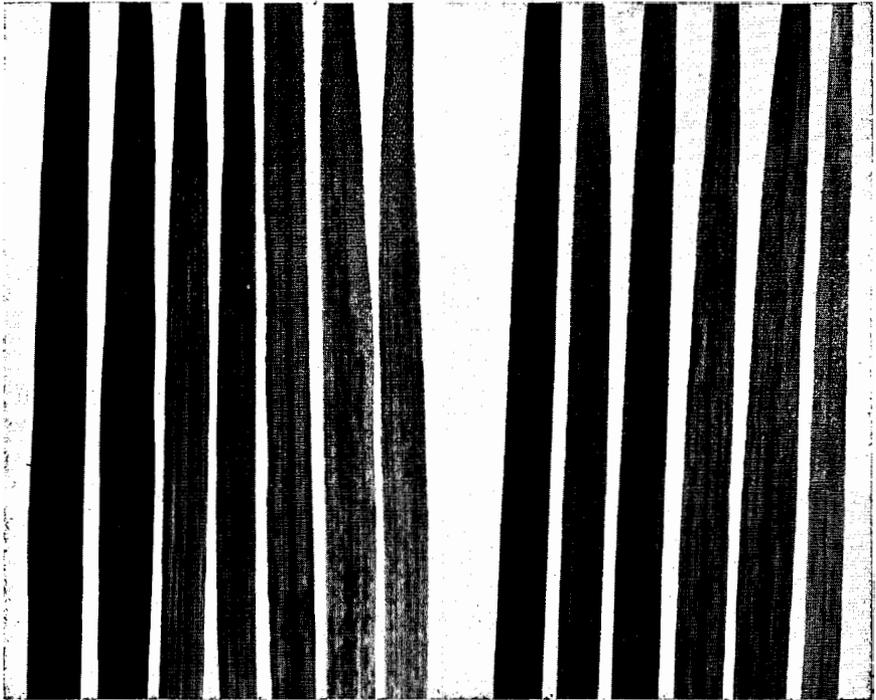


Fig. 3. Leaves of Minter wheat (left) and Mindum wheat (right), illustrating the foliage symptoms of wheat streak mosaic. For each variety, the leaves on the left are healthy, the others show symptoms varying from the early, mild streaks to severe chlorosis

the disease was not found on spring wheat except in the experimental plots.

Symptoms of streak mosaic were sometimes found on young winter wheat plants in late fall, but in many instances definite symptoms were not observed until spring. In the 1950 season, mosaic was found on spring wheat as early as June. The first symptoms on both winter and spring wheat consisted of faint chlorotic dashes or streaks which ran parallel with the leaf veins and appeared to be associated with the mesophyll tissues (Fig. 3). The streak-type symptom frequently gave rise to a general mottling and eventually to complete necrosis. Diseased plants were usually stunted and often the tillers on the same plant varied considerably in height (Fig. 4). It was not uncommon to find stunted plants with sterile heads still standing after harvest just the height, or shorter than the stubble. In occasional fields severe reduction in the yield and grade of grain resulted from diseased plants because of complete or partial sterility of the heads and poor filling of the kernels. Although streak mosaic seldom caused premature death of plants under favorable growing conditions in the greenhouse, the death of immature plants was observed frequently under field conditions, apparently as a result of mosaic.

Both a mild and a severe type of wheat streak mosaic were found in a number of wheat fields. According to the identifications made by H. H. McKinney, the severe type is identical with the yellow streak-mosaic



Fig. 4. Stunting effect of streak mosaic on winter wheat (Nebred). The plants were collected from a farmer's field two weeks before harvest. Damage ranged from slight to severe stunting of some of the tillers and prevention of heading

virus (*Marmor virgatum* var. *typicum* McKinney, or wheat virus 7) and the milder type is identical with the green streak-mosaic virus (*M. virgatum* var. *viride* McKinney, or wheat virus 6), both of which occur in Kansas and other areas of the Great Plains region (8, 9). The more severe strain was used in the experiments reported here.

Extreme abnormalities occasionally occurred on mosaic-infected wheat plants grown in the greenhouse. Distorted leaves, incomplete head emergence, brittle, crooked,



Fig. 5. Vegetative malformations of mosaic-diseased wheat grown in the greenhouse. A: Rushmore with aerial tillering. Note also the Crown roots emerging from two nodes above the normal crown. B: Rushmore with deformed heading of an extremely stunted plant. C: Rival with constricted sheaths. D: Rushmore with brittle, bent culm. E: A normal head of Kubanka. F and G: Kubanka with branches bearing spikelets

and sometimes branched culms with distorted heads have developed (Fig. 5). Some of the less extreme abnormalities of the leaves and culms have been observed in the field, but the more extreme abnormalities including branched culms and multiple heads have not been observed under natural conditions. These extreme abnormalities appear to occur as a result of virus-infected plants growing under abnormal conditions of light, temperature, and moisture which are conducive to prolonged vegetative growth. It is interesting to note the similarity between these abnormalities and those produced by 2,4-D weed killers on cereal crops (3).

Transmission Studies

The inoculum used for experiments in the greenhouse consisted of sap extracted from diseased plants and was usually obtained either from leaves of diseased plants transplanted from the field into pots and kept in a cool greenhouse, or from diseased leaves collected in the field and stored in a dry condition in a refrigerator.

Manual transmission was successfully accomplished by the carborun-

dum-rub method by mixing a fine grade of carborundum powder (320 grain) with the diluted sap from diseased leaves. This inoculum was then applied to the leaves of the plants according to the technique developed by McKinney (8).

Although a high proportion of plants could usually be infected when carborundum powder was omitted from the inoculum, tests showed that the addition of about 3 parts of a fine abrasive to 100 parts of inoculum usually increased the proportion of plants infected. Three grades of carborundum powder were compared including 320, 400 and 600 grain and all gave good results. In addition, Celite Filter-Cel and other grades of Celite³ were found to be equally effective.

Occasionally variations in methods of inoculation were desirable (13), hence several methods were compared using the same inoculum diluted 1:20. The efficiency of the methods is indicated in Table 1. A small number of plants became infected as a result of inoculation by all of the methods tested including spraying the inoculum on the leaves. However, the only reliable methods

³Manufactured by Johns-Manville.

Table 1. Comparison of Methods of Inoculating Wheat with Yellow Streak Mosaic

Method of Inoculation	Number of Plants	
	Inoculated	Diseased
Pricking of leaves with needle dipped in inoculum	18	2
Hypodermic (injection into leaves)	21	12
Hypodermic (injection into leaf whorl)	20	14
Spray (forceful watersoaking of leaves)	19	7
Spray (gentle)*	18	3
Spray, then rub*	19	19
Carborundum-rub method*	20	20
Check	20	0

*2 percent of 320-grain carborundum powder added to inoculum.

included the rubbing of the leaves either after they had been dipped in the inoculum or after the inoculum had been sprayed on the leaves.

Virus strains were isolated by manual inoculation of healthy wheat plants in the three- to four-leaf stage under a greenhouse temperature ranging from 16 to 22° C. Symptoms appeared in 7 to 12 days, and nearly all of the inoculated plants usually developed symptoms of mosaic. During the earlier tests three varieties of wheat, Mindum (durum), Rushmore or Marquis (hard red spring) and Minter (hard red winter) were used simultaneously. Since it was found that these varieties were equally susceptible, Minter was used in most of the later studies.

In working with this particular virus it was found that contamination could be virtually eliminated by washing the hands thoroughly in water or by rubbing them with 70 percent alcohol. For added safety, the practice adopted was a combination of these methods. Similar tests showed that the mortar and pestle used for macerating diseased leaves could be freed of the virus by a thorough washing in water, then a 10 minute soaking in 70 percent ethyl alcohol, or in water heated above 60° C.

There was little danger of accidentally infecting plants in the greenhouse with ordinary gentle handling of the leaves unless the hands had become contaminated with juices from crushed or bruised diseased plants. Similarly the virus did not spread when the leaves of

healthy and diseased plants touched occasionally, but if the leaves of such plants mingled excessively there was some chance for infection to spread.

Tests were made repeatedly of seed and soil as agents of transmission, but all results were negative.

Plant Tissues as Carriers of Streak Mosaic

Although leaves were usually used to prepare inoculum, tests showed that roots, stems and even heads of diseased plants likewise carried the virus when still green and succulent. However, all plant parts lost infectivity after maturity, or after death. Usually it was not possible to obtain infection from leaves that had been killed by the virus even though the remainder of the plant was still alive. Loss of infectivity of dead or mature tissues was especially rapid under moist conditions conducive to mold and decay.

Virus dilution studies showed that when succulent tissue carried symptoms of streak mosaic, dilutions of 1 gram of macerated leaf to 100 ml. of water induced good infection by the carborundum-rub method. However, lower dilutions that were tested, including 1:1, 1:5, 1:25 and 1:50, were more reliable in insuring a high percentage of infected plants. A dilution of 1:25 appeared to be optimum for most of the investigations with this virus.

It was often desirable to store mosaic-infected leaves for long periods. Although green diseased leaves remained infectious for several

months when stored in a dry condition under refrigeration at 10° C., infectivity was greatly reduced. Comparisons were made of different conditions of moisture and temperature in relation to the maintenance of the infectivity of the virus in stored leaves.

Succulent Minter wheat leaves infected with streak mosaic were cut into 1-inch lengths. The entire sample was mixed and divided into nine portions which were put into envelopes. Three of these packaged samples were placed over calcium chloride in a small desiccator, three were wrapped in moist paper and placed in waxed cartons, and three were placed in open cartons. One of the samples from each of the above groups was stored under laboratory conditions, another in a refrigerator at about 10° C., and the other in cold storage at approximately -23° C. Following various intervals of time, tests for infectivity were made on portions of each sample by inoculating Minter wheat plants. Two sets of plants were treated as checks at each test date. One set was inoculat-

ed with sap from living diseased plants; the other was rubbed with sterile carborundum and water.

The results of inoculations following different periods of storage under varied conditions of moisture and temperature are presented in Table 2. Both the moisture relations at the beginning of storage, and the temperature conditions during storage appeared to have an important influence on the survival of streak mosaic in leaves. Infectivity was reduced rapidly when the leaves were moistened before storage either at room temperature or in the refrigerator, but they still retained some infectivity after 82 days in an air dry condition. However, leaves stored in desiccators at all of the storage temperatures, and those stored at -23° C., regardless of the moisture condition of the containers, remained viable after 350 days.

The Relation of Age to Susceptibility

It appeared from field observation that wheat could become infected with streak mosaic at various

Table 2. Effect of Moisture and Temperature on the Survival of Streak Mosaic in Stored Leaves

Temperature °C.	Storage Conditions	Days in Storage									
		5	13	20	34	50	65	82	278	350	
18-24	Desiccated	+	*	+	+	+	+	+	+	+	+
	Air Dry	+	+	+	+	+	+	+	0	0	
	Moist	+	0+	0	0	0	0	0	0	0	
10	Desiccated	+	+	+	+	+	+	+	+	+	
	Air dry	+	+	+	+	+	+	+	0	0	
	Moist	+	+	0	0	0	0	0	0	0	
-23	Desiccated	+	+	+	+	+	+	+	+	+	
	Air dry	+	+	+	+	+	+	+	+	+	
	Moist	+	+	+	+	+	+	+	+	+	
Fresh leaves	+	+	+	+	+	+	+	+	+	+	
Sterile carborundum + water	0	0	0	0	0	0	0	0	0	0	

*+ indicates infection of test plants.
 0 indicates the absence of infection.

Table 3. Relation of Age to the Susceptibility of Mindum, Marquis and Minter Wheat to Streak Mosaic

Age Days	Growth Stage	Mindum Plants	Marquis Plants	Minter Plants	
		Showing Mosaic	Showing Mosaic	Growth Stage	Showing Mosaic
		%	%		%
1	1-leaf	6.6*	17.2†	1-leaf	25.0†
3	1-leaf	9.1
6	1-leaf	37.5	30.0	1-leaf	36.8
13	3-leaf	100.0	85.0	3-leaf	100.0
20	3-leaf	85.7	100.0	3-leaf	100.0
27	4 to 5-leaf	100.0	100.0	4-leaf	100.0
33	tiller	100.0	100.0	tiller	100.0
48	tiller	83.3	94.7	tiller	71.4
62	shoot	40.0	100.0	tiller	25.0
76	boot	10.5	61.1	tiller	61.1
90	head	00.0	00.0	shoot	50.0
103	head	00.0	00.0	shoot	78.6

*14 to 21 plants inoculated.

†17 to 29 plants inoculated.

stages of development, but it was not known whether susceptibility differed at different stages of growth. An experiment was conducted on the relation of age to the susceptibility of varieties of wheat representing the durum, hard red spring and hard red winter wheat types. Seeds of each variety were planted in pots at about two-week intervals. The intervals were reduced to two to three days in the case of the last plantings. When the plants in the first two plantings had headed, and the last planting had started to emerge, two pots of plants of each variety, planted at the various dates, were inoculated with yellow streak mosaic. One pot of each was held as a check. Disease records were taken four weeks after inoculation. The data are presented in Table 3.

Infection was inconsistent with very young seedlings and with plants nearing the heading stage, but virtually all plants of all varieties became infected when inocu-

lated from the three-leaf to the jointing stage. None of the Mindum or Marquis plants developed mosaic symptoms when inoculated after they had headed. Minter, being a winter wheat, did not reach the heading stage before the experiment was concluded.

Observations made in the field indicated that plants that were infected in the seedling stage usually suffered more severe damage from streak mosaic than plants that had been infected at a later stage of development. In other instances the reverse appeared to be true. An experiment was therefore conducted on the relation of age at time of inoculation to the effect of the virus on spring wheat plants grown in the greenhouse. Rushmore and Mindum were each sown in thirty-six 6-inch pots of soil. An isolate of streak mosaic virus was maintained on Minter wheat. This was used to inoculate the plants in four pots of each variety on each of eight dates varying from 6 to 55 days after emergence.

During this time the plants advanced from the one-leaf to the boot stage. After symptoms of mosaic appeared on plants in all inoculated series, the plants failing to develop symptoms were pulled out and the numbers uniformly reduced from the original 10 to 8 plants per pot. The plants were then grown to maturity.

The average heights at maturity of the Rushmore and Mindum plants inoculated on various dates as compared with non-inoculated checks is shown in Fig. 6. Plants inoculated in the one- and two-leaf stages (six and nine days after emergence) were more severely stunted than those inoculated at successively later stages. It therefore appears from this greenhouse experiment that the degree of stunting in the spring wheats tested may be related

to the age of the plants at the time of infection.

Attempts were made to study the relation of age at time of infection to the severity of disease loss in field plots. However, considerable natural spread of the disease occurred in the plots and there was no reliable means to separate plants infected at definite times nor to segregate checks, hence the desired yield comparisons could not be made.

Varietal Reaction

The susceptibility of different varieties of wheat, oats, barley and rye to this disease was tested in the greenhouse. Each variety was grown in eight 6-inch pots of soil at the rate of 10 plants per pot. When the plants reached the late three-leaf stage, three weeks after sowing, they were inoculated with an iso-

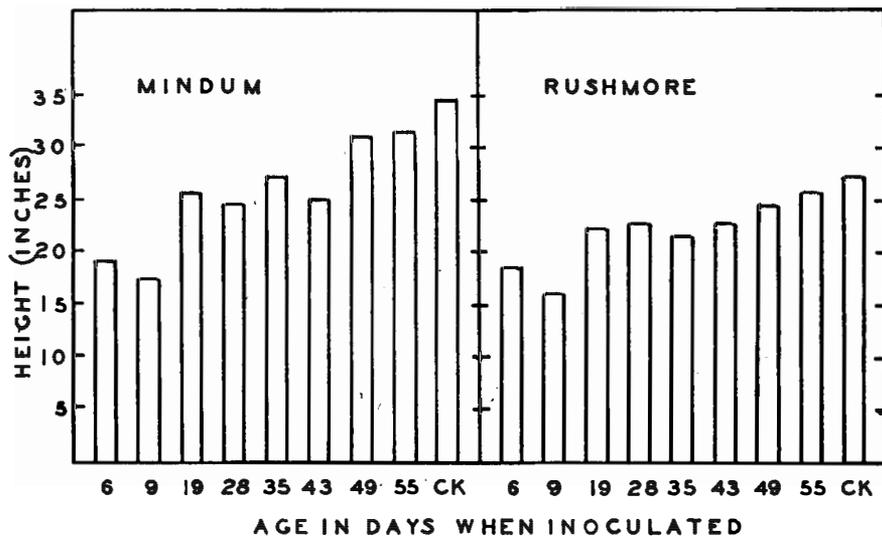


Fig. 6. The relation of time of inoculation with streak mosaic to plant height at maturity

Table 4. Results of Manual Inoculation Tests with Wheat Streak-Mosaic Virus on Varieties of Wheat

Class	Variety	Reduction of Diseased Plants as Compared with Checks		
		Plants Infected*	Height†	Grain Yield
Durum	Kubanka	78.8	35.1	52.9
	Mindum	90.5	36.8	64.2
	Stewart	97.2	41.9	74.7
	Vernum	89.2	34.4	77.5
Hard red spring	Marquis	97.4	50.0	66.2
	Mida	94.7	43.7	52.8
	Pilot	81.6	33.7	34.0
	Rival	75.0	29.9	39.1
Hard red winter	Rushmore	85.3	32.7	53.2
	Iowin	45.9	17.9	24.3
	Minter	91.4	32.0	55.8
	Ncbred	56.7	28.0	69.1
	Minturki	69.2	26.9	67.1

*40 plants of each variety were inoculated.

†The heights of the checks averaged from 38 to 45 inches, depending on the variety.

late of yellow streak mosaic. The greenhouse temperature ranged from 15 to 20° C. for several weeks, but later, as spring approached, higher temperatures prevailed. Records were made of the percentage of inoculated plants that became infected. The wheat varieties were grown to maturity, and measurements were made of the heights and seed yields of infected and non-infected plants (Tables 4 and 5).

A high percentage of the plants of all varieties of wheat became infected after inoculation, indicating a

high degree of susceptibility (Table 4). Some variation in percentage of infection occurred between varieties, indicating possible variations in susceptibility to infection by the method used. Visible differences in the severity of the chlorosis in leaves was evident between the durum, hard red spring and winter wheat classes, but not between varieties within classes. The durum varieties developed the most severe chlorosis, with the hard red spring varieties next, and the hard red winter varieties the least. As shown in

Table 5. Results from Manual Inoculation Tests with Streak Mosaic on Varieties of Oats, Barley and Rye

Oat Varieties	Percentage Infected*	Barley Varieties	Percentage Infected	Rye Varieties	Percentage Infected
Brunker	25.6	Feebar	0.0	Emerald	0.0
Canadian	79.5	Mars	10.0	New Dakold	0.0
Cherokee	15.4	Moore	10.0	Pierre	0.0
Clinton	34.1	Odessa	16.2	White Soviet	0.0
James	7.9	Plains	23.8		
Mindo	42.5				
Nemaha	20.0				
Trojan	17.5				

*40 plants of each variety were inoculated.

ible symptoms or in the positive results of tests to re-isolate the virus on wheat. However, McKinney and Fellows (12) showed that 11 perennial grasses which they tested were infected with mosaic, and although some of them did not produce visible symptoms, others produced local lesions or mild mosaic symptoms. None of the susceptible grasses which they used have been tested in South Dakota, but some of them are known to occur in certain areas of the state and are therefore potential perennial hosts of the virus.

Spread of Streak Mosaic under Field Conditions

In order to determine if mosaic could spread during the summer, a number of wheat fields, in areas of the state where mosaic occurred, were selected for observation in 1950. In each field four drill rows were selected, and a length of each row containing 25 plants was marked off with stakes. The percentages of plants that showed symptoms of mosaic were recorded. This was done on two different dates in three winter wheat fields, and on three dates in four spring wheat fields. The observations were made

at about two-week intervals between June 6 and July 21 in the various fields. They showed that the percentage of wheat plants developing symptoms of mosaic increased between the successive dates of observation in both June and July (Table 8), indicating that the virus was spreading in those fields during these months.

Further evidence of rapid summer spread of streak mosaic in 1950 was obtained in a date of seeding experiment, conducted in Gregory county. The varieties Mindum, Rushmore and Minter were sown in a randomized rod row plot designed with four replications. The dates of seeding were spaced at approximately two-week intervals from May 12 to August 17. Each time the plots were visited, at intervals of about two weeks, counts were made to determine the percentage of plants showing symptoms of mosaic. However, during August leaf rust developed so rapidly and abundantly on the wheat that it was not possible to make an accurate diagnosis of mosaic symptoms after the second observation. The percentage of diseased plants is shown in Table 9 for the May 12 to August 17 plant-

Table 8. Percentage of Wheat Plants Showing Mosaic Symptoms Under Field Conditions at Different Dates in 1950

Wheat Class	County	Percentage of Plants Infected on			
		June 6-7	June 21-23	July 6	July 19-21
Hard red winter	Tripp	30	44		
	Tripp	52	70		
	Bennett ...	12	19		
Hard red spring	Tripp		38	88	100
	Tripp		28	59	90
	Tripp		4	16	38
Durum	Tripp		5	20	86

Table 9. Natural Spread of Streak Mosaic on Wheat Planted in Gregory County at Different Dates in 1950

Date of Planting	Percentage Mosaic at Different Dates										
	May 22	June 6	June 21	July 6	July 20	Aug. 3	Aug. 17	Sept. 1	Sept. 17	Oct. 13	May 21, 1951
May 12*	0.0	?	tr	20.8	86.6						
May 22		0.0	tr	28.1	89.0						
June 6			0.0	21.4	86.4						
June 21				5.8	82.3						
July 5					12.9	73.1					
July 19						tr	55.0				
Aug. 3							tr	49.5			
Aug. 17								0.0	8.0		
Sept. 1									0.0	3.0	20.0
Sept. 8											9.0
Sept. 15											tr
Sept. 25											0
Oct. 13											0

*May 12 to August 17 included Rushmore, Mindum and Minter, but the planting of September 1 and later included Minter only.

ings and represents the averages for the three varieties of wheat which appeared to be equally susceptible. The plantings on September 1 to October 13 consisted of Minter wheat only, and for these plantings observations were made during the fall and again in the spring.

The observations on the occurrence of symptoms in the various plantings are summarized in Table 9. On June 6, symptoms were observed that appeared to be the early symptoms of streak mosaic, but there remained some doubt as to whether the symptoms were those of streak mosaic. However, by June 21, a few of the plants definitely had symptoms of mosaic. Assuming an incubation period of eight days from the time of infection until the appearance of symptoms, some of the plants must have become infected on or before June 13. All later plantings during the summer developed symptoms of the disease. The percentage of plants showing symp-

toms four weeks after planting indicated a high rate of spread from mid-June to mid-August but a much lower rate during late August and September. Although only 3 percent of the plants in the planting of September 1 showed symptoms as late as October 13, 20 percent showed symptoms when examined on the following May 21, 1951. Plantings made on later dates showed diminishing amounts of infection until those on September 25 and October 13 showed no symptoms the following summer.

According to the above results, the highest rate of spread occurred during the crop-growing season in 1950 and diminished rapidly after harvest. It should be recognized that the above data on rates of virus spread were obtained in an area where mosaic was abundant in nearby wheat fields. The period when the virus spread most rapidly was during mid-summer when both the winter and spring wheat crops were

ible symptoms or in the positive results of tests to re-isolate the virus on wheat. However, McKinney and Fellows (12) showed that 11 perennial grasses which they tested were infected with mosaic, and although some of them did not produce visible symptoms, others produced local lesions or mild mosaic symptoms. None of the susceptible grasses which they used have been tested in South Dakota, but some of them are known to occur in certain areas of the state and are therefore potential perennial hosts of the virus.

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May 22		0.0		28.1	89.0						
June 6			0.0		86.4						
June 21				5.8	82.3						
July 5					12.9	73.1					
July 19						tr	55.0				
Aug. 3							tr	49.5			
Aug. 17								0.0	8.0		
Sept. 1									0.0	3.0	20.0
Sept. 8											9.0
Sept. 15											tr
Sept. 25											0
Oct. 13											0

*May 12 to August 17 included Rushmore, Mindum and Minter, but the planting of September 1 and later included Minter only.

ings and represents the averages for the three varieties of wheat which appeared to be equally susceptible. The plantings on September 1 to October 13 consisted of Minter wheat only, and for these plantings observations were made during the fall and again in the spring.

The observations on the occurrence of symptoms in the various plantings are summarized in Table 9. On June 6, symptoms were observed that appeared to be the early symptoms of streak mosaic, but there remained some doubt as to whether the symptoms were those of streak mosaic. However, by June 21, a few of the plants definitely had symptoms of mosaic. Assuming an incubation period of eight days from the time of infection until the appearance of symptoms, some of the plants must have become infected on or before June 13. All later plantings during the summer developed symptoms of the disease. The percentage of plants showing symp-

toms four weeks after planting indicated a high rate of spread from mid-June to mid-August but a much lower rate during late August and September. Although only 3 percent of the plants in the planting of September 1 showed symptoms as late as October 13, 20 percent showed symptoms when examined on the following May 21, 1951. Plantings made on later dates showed diminishing amounts of infection until those on September 25 and October 13 showed no symptoms the following summer.

According to the above results, the highest rate of spread occurred during the crop-growing season in 1950 and diminished rapidly after harvest. It should be recognized that the above data on rates of virus spread were obtained in an area where mosaic was abundant in nearby wheat fields. The period when the virus spread most rapidly was during mid-summer when both the winter and spring wheat crops were

too advanced to be seriously affected by the disease.

During the 1951 season similar observations were made, but in contrast to 1950, there was no evidence of spread during the summer in either winter or spring wheat fields. In the dates of seeding experiment there was no evidence of mosaic until late July. However, by the end of August about 35 percent of the plants in plots sown on August 8 were showing symptoms of mosaic, and some of the plants in plots sown as late as September 2 showed symptoms of mosaic on October 2.

Transmission of Streak Mosaic

The experiments and observations described above show that mosaic may spread during long periods ranging from early June, as in 1950, until after mid-September. However the method of transmission under field conditions still remains in doubt. Tests for transmission by soil and seed have given negative results. Transmission tests have been conducted on leafhoppers, fulgoroidea, thrips, aphids (2) and other insects occurring commonly in fields where the disease was present. Although infection sometimes occurred during transmission tests with certain species of leafhoppers, there is no satisfactory evidence that any of the insects tested in South Dakota are vectors of streak mosaic.

Despite the negative results obtained with specific insects, there is considerable circumstantial evidence that insects may be the major agents of spread. There have been a number of instances noted where the

pattern of infection in wheat fields has appeared similar to the distribution that might be expected in the mass migration of certain types of insects from one crop to another. Several instances have been noted where mosaic became severe in winter wheat planted adjacent to a field that had grown a crop of wheat severely infected with mosaic the previous season. But little or no disease occurred in remote sections of the same field adjacent to some other crop or to summer fallow. Similarly, late-sown spring wheat has become severely infected when adjacent to an infected winter wheat crop, but was only slightly infected in other areas of the same field.

Factors in the Survival and Severity of Streak Mosaic

Although there remains a possibility that certain perennial grasses may function as important reservoirs of the virus, the information obtained from field experiments and observations indicates that winter wheat is probably the most important means of overwintering streak mosaic in South Dakota. In localities where mosaic is destructive, there have been numerous cases of positive correlation between early seeding of winter wheat and high rates of infection. Although early-sown winter wheat crops may show symptoms of mosaic during the fall, the symptoms may not show on many of the infected plants until the following spring. The infected plants that have overwintered not only represent losses from the disease, they also represent

reservoirs from which the virus may spread to other plants and to spring wheat crops.

Evidently the time and rate of spread during the summer may vary considerably from year to year as evidenced by the 1950 and 1951 observations. If the spread does not start until July as in 1951, spring wheat may escape all serious infection, but if the disease begins to spread in early June as in 1950, a late spring wheat crop may become severely damaged if it is situated near a source of infection such as severely diseased winter wheat. Susceptible annual weeds, which may be present in the wheat fields during the summer, constantly afford susceptible hosts for mosaic infection, and also aid the virus to survive during and after harvest until volunteer and fall-sown wheat emerges.

Control

All commercial varieties of wheat tested are susceptible to streak mosaic. Similar results were reported by McKinney and Sando (14) for a wide range of varieties that they have tested. Although they have found high resistance in certain *Agropyron* x *Triticum* crosses, much work will be required before desirable commercial wheat varieties resistant to mosaic will be available to farmers.

Evidence obtained indicates that certain cultural practices may prove valuable in controlling this virus disease. One of the most important of these appears to be a carefully

chosen date of seeding. It was shown above that the virus spreads more readily to winter wheat sown in August and very early in September than to wheat sown later. In agreement with this observation, the most severely infected winter wheat fields observed in South Dakota were those that were sown unusually early for the area, whereas later sown fields were seldom seriously infected. Therefore, in order to escape as much fall infection as possible in areas where mosaic is a menace, winter wheat should be planted as late as sound agronomic practices permit.

Certain sanitary measures may also be of considerable importance in controlling this disease. The susceptible annual weeds appear to supply an important reservoir for the virus from the time the wheat crops have been harvested until severe frosts occur in September. The control of such weeds before winter wheat is planted in the fields should aid considerably in reducing primary infection of the new winter wheat.

With regard to spring wheat, high rates of infection have occurred only in fields planted near heavily infected winter wheat, and severe losses have been observed only in fields planted unusually late. Hence, according to the behavior and spread of the disease as observed in 1950 and 1951, little damage should result to spring wheat that is sown at the early dates usually recommended in South Dakota.

Wheat Striate Mosaic

During the late summer of 1950 the presence of another mosaic disease was detected on wheat in Gregory County, South Dakota. In 1951 the same disease was found in six counties in the southern part of the state. In most instances it occurred in fields where streak mosaic was also present.

This virus disease, which in several respects resembles a Russian wheat mosaic (20), has been named "striate mosaic" because of the fine, parallel chlorotic streaks and dashes which developed on the leaves of all varieties of wheat on which it has

been studied (Fig. 8). These chlorotic markings are closely associated with the veins of the leaf and are at first visible only on the lower surfaces of the leaves. As the chlorosis becomes pronounced, the streaks become vaguely visible on the upper leaf surfaces. However, the definition of the streaking remains clearer on the lower sides of the leaves. In later stages the chlorosis becomes more or less general throughout the leaf. White to brown necrotic flecks, dashes and stripes may become evident. In some varieties necrosis may cause severe de-

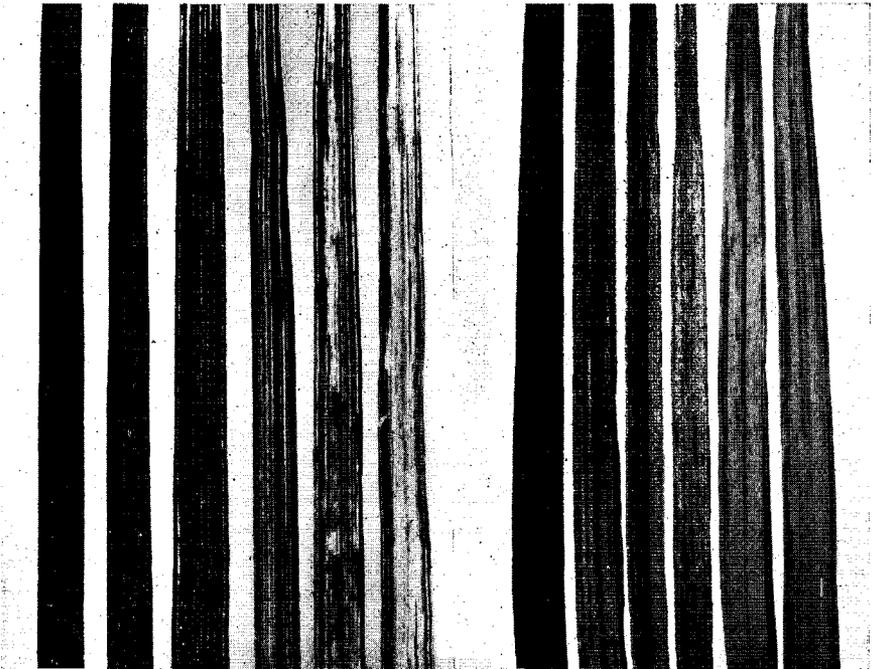


Fig. 8. Leaves of Minter wheat (left) and Mindum wheat (right), illustrating the foliage symptoms of striate mosaic. For each variety, the leaves on the left are healthy, the others show symptoms varying from the early mild dashes and streaks to severe chlorosis

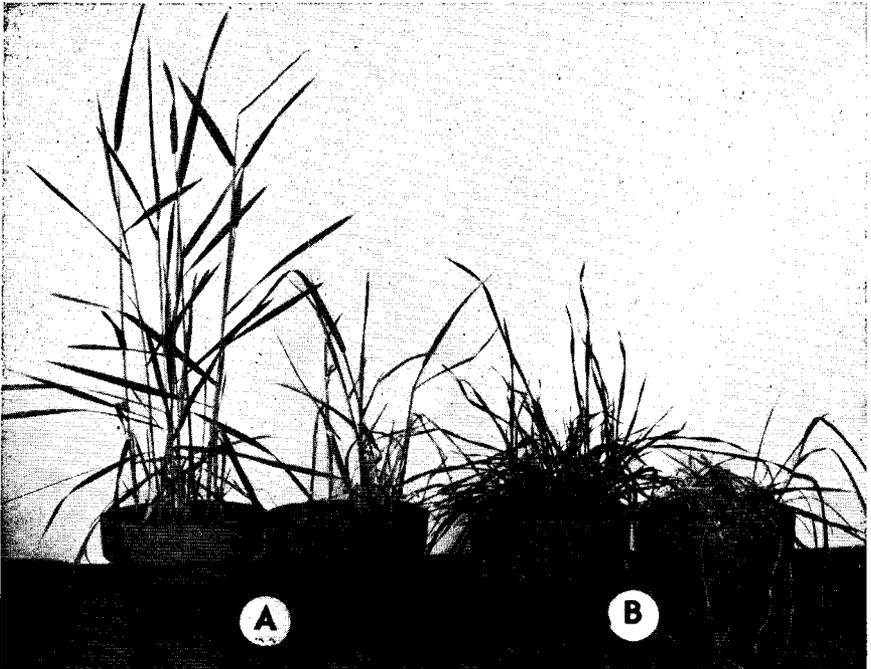


Fig. 9. The stunting effect of wheat striate mosaic on Rushmore (A) and Minter (B). The plants on the left are healthy, on the right diseased. Note the dead plants in the pot with diseased Minter

struction of leaves. The infected plants usually become stunted in varying degrees, while in some cases death may occur (Fig. 9). If diseased plants head, the heads may be partly sterile, or the quality of grain may be seriously lowered.

When striate mosaic was first discovered by the author in 1950, there was evidence that it was caused by a virus transmitted by a common, widely distributed leafhopper, *Endria inimica* Say (18). Experiments have confirmed this and have shown that the leafhopper *E. inimica* can become viruliferous during both the nymphal and adult stages. The leafhoppers may remain viruliferous for

varying periods, sometimes exceeding a month, after feeding on diseased plants.

The major host of striate mosaic appears to be wheat. Data from field plots showed considerable variation in the percentage of plants infected by natural spread, and, in addition, there was considerable variability in the severity of symptoms expressed. Therefore, it appears reasonable that a thorough testing program may uncover certain varieties or lines which possess practical degrees of resistance.

Thus far little is known of the host range of striate mosaic, but several plant genera other than wheat ap-

pear to be susceptible. In one test striate type symptoms developed on Clinton oats on which viruliferous leafhoppers had been allowed to feed. There was also an indication of mild susceptibility in barley. In addition striate mosaic has been isolated, by means of leafhoppers, from two annual grass weeds, *Eragrostis cilianensis* (All.) Lutati and *Panicum capillare* L. that were found naturally infected in wheat fields.

The annual cycle of striate mosaic is very similar to that of streak mosaic, although the vector of the latter is not known. The striate-mosaic virus can survive the winter on winter wheat plants that become infected in the fall. During the following summer, susceptible leafhoppers may become viruliferous by feeding on the overwintered wheat, then spread the virus to wheat and other susceptible plants. The disease can bridge the post-harvest period with the aid of susceptible annual weeds and leafhoppers. Some leafhoppers can remain viruliferous for more than a month after feeding on diseased plants. By these means the

virus can be carried to volunteer and early fall-sown wheat. As is the case with streak mosaic, the spread of striate mosaic appears to diminish rapidly during September; consequently, the later sown crops have less infection than earlier ones.

Although there has been no evidence of serious economic losses from striate mosaic, the disease has shown considerable virulence on certain varieties. If conditions should favor this disease, it might become very destructive; hence, an early consideration of control measures may be highly desirable.

Since there appears to be considerable variation in the symptoms expressed on different varieties of wheat, there is a possibility that suitable resistant varieties may be selected. In the meantime, cultural practices like those suggested above for the control of streak mosaic may have considerable merit. Destruction of annual grass weeds following harvest, avoidance of unnecessarily early sowing of winter wheat, and of late sowing of spring wheat are some such practices.

Barley False Stripe

In 1950, McKinney (11) showed that false stripe of barley, a disease hitherto considered to be of a non-infectious nature, was in reality caused by a virus. He reported that the virus was seed-borne. It could also be transmitted readily by the carborundum-rub method.

Traces of false stripe were observed in barley nurseries at Brookings and Highmore as well as in oth-

er localities during 1951. Little damage was attributed to this disease which has been recognized mainly because of the characteristic stripe symptoms on the leaves. However, since the potentialities of the disease have not been fully investigated a number of inoculation experiments were conducted, and a number of wild and cultivated grasses were inoculated with false stripe.



Fig. 10. Plants of Batna barley grown from seed from infected plants. The three plants on the left show symptoms of false stripe and the young plants are noticeably stunted

Leaves infected with false stripe were collected from Batna barley plants growing in a nursery at Brookings⁴ and from Kindred barley at Highmore.⁵ The virus was isolated on Plains, Odessa and Chevron barleys by macerating the diseased leaves, diluting the juice about 1:10 and inoculating the plants by the carborundum-rub method. Other cultures of false stripe were obtained by sowing seed from Batna barley plants that had shown symptoms.

The early symptoms of false stripe on seedlings growing from infected seed consist of a mild chloro-

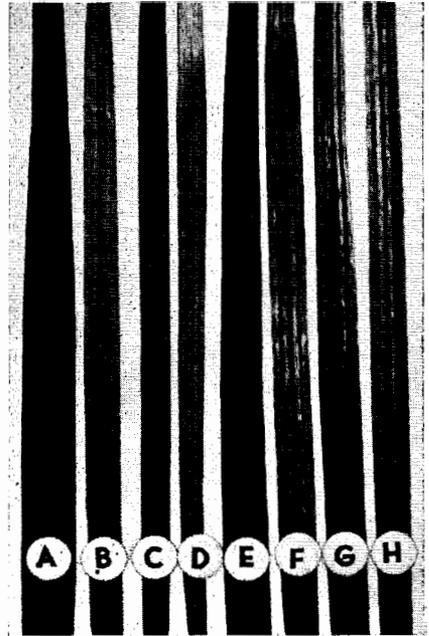


Fig. 11. Symptoms of false stripe on barley, rye and wheat leaves. (A) (B) healthy and infected Chevron; (C) (D) healthy and infected New Dakold; (E) healthy; (F) (G) (H) infected Rushmore

sis and general mottling of the seedling leaves (Fig. 10), or a granular-appearing mottle with more severe chlorosis at the tips or in stripes often at the margin of the leaves (Fig. 11). In some instances the young plants may be quite noticeably stunted (Fig. 10), but in other cases the plants may appear to suffer little from the disease. Manually inoculated plants develop a granular-appearing mottle which is first apparent on new leaves emerging after

⁴Courtesy of Dr. G. W. Bruchl, United States Department of Agriculture.

⁵An additional sample of infected leaves was obtained from Dr. W. A. F. Hagborg, Dominion Laboratory of Plant Pathology, Winnipeg, Manitoba.

Table 10. Reaction of Different Crop Varieties to Three Virus Diseases

Species	Variety	Barley False Stripe	Agropyron Streak Mosaic	Wheat Streak Mosaic
<i>Avena sativa</i> L.	Brunker	—	—	+
	Clinton	—	—	+
	Landhafer	—	—	+
<i>Hordeum vulgare</i> L.	Chevron	+	—	+
	Odessa	+	—	+
	Plains	+	—	+
<i>Panicum miliaceum</i>	Proso C.I. 217	+	—	—
<i>Setaria italica</i> (L.) Beauv.	Kursk No. 78	+*	—	—
	Siberian No. 7	+*	—	—
<i>Secale cereale</i> L.	New Dakold	+	+	—
	Pierre	+	+	—
<i>Sorghum vulgare</i> Pers.	Norghum	—	—	—
	Modoc x Sooner (white seeded)	—	—	—
	Modoc x Sooner (brown seeded)	—	—	—
<i>Triticum durum</i> Desf.	Mindum	+	+	+
<i>T. vulgare</i> Vill.	Minter	+	+	+
	Rushmore	+	+	+
<i>Zea mays</i> L.	Dakota White	L†	—	—
	Northwest Dent	+	—	—
	Falconer	+	—	+
	Minhybrid 250	L	—	—
	Golden Cross Bantam	+	—	L

*Severe stunting and necrosis.

†Local lesions that appeared to be caused by the virus.

Table 11. Reaction of Several Perennial Grasses to Three Manually-Transmissible Viruses

Grass species*	Common Name	Barley False Stripe	Agropyron Streak Mosaic	Wheat Streak Mosaic
<i>Agropyron ciliare</i> (Trin.) Franch.		—	—	—
<i>A. cristatum</i> (L.) Gaertn.	Crested Wheatgrass	—	—	—
<i>A. dasystachyum</i> (Hook.) Scribn.	Thickspike Wheatgrass	—	—	—
<i>A. desertorum</i> (Fisch.) Schult.	Desert Wheatgrass	—	—	—
<i>A. elongatum</i> (Host) Beauv.	Tall Wheatgrass	—	+†	—
<i>A. inermis</i> (Scribn. and Smith) Rydb.	Beardless Wheatgrass	—	+	—
<i>A. intermedium</i> (Host.) Beauv.	Intermediate Wheatgrass	—	+	—
<i>A. junceum</i> (L.) Beauv.		—	+	—
<i>A. pertense</i> (Meyer) Nevski		—	+	—
<i>A. repens</i> (L.) Beauv.	Quackgrass	—	+	—
<i>A. rigidum</i>		—	+	—
<i>A. trachycaulum</i> (Link) Malte.	Slender Wheatgrass	—	—	—
<i>A. trichophorum</i> (Link) Richt.	Stiffhair Wheatgrass	—	—	—
<i>Bromus inermis</i> Leyss.	Smooth Brome	—	—	—
<i>Festuca rubra</i> L.	Red Fescue	—	+	—
<i>Phalaris arundinacea</i> L.	Reed Canary Grass	—	—	—
<i>Phleum pratense</i> L.	Timothy	—	—	—
<i>Poa pratensis</i> L.	Kentucky Bluegrass	—	—	—

*Seed was supplied by Dr. J. G. Ross, Department of Agronomy, Agricultural Experiment Station, Brookings, S. D.

†Severe stunting and necrosis.

Table 12. Reaction of Annual Grasses to Three Manually-Transmissible Viruses

Species	Common Name	Barley False Stripe	Agropyron Streak Mosaic	Wheat Streak Mosaic
<i>Avena fatua</i> L.	Wild Oats	—	—	—
<i>Bromus japonicus</i> Thunb.	Japanese Chess	L*	—	+
<i>B. secalinus</i> L.	Cheat	++	—	+
<i>B. tectorum</i> L.	Downy Bromegrass	+	—	+
<i>Digitaria sanguinalis</i> (L.) Scop.	Crabgrass	+	—	+
<i>Echinochloa crusgalli</i> (L.) Beauv.	Barnyard Grass	+	—	+
<i>Eragrostis ciliaris</i> (All.) Lutati	Stink Grass	+	—	+
<i>Hordeum jubatum</i> L.	Wild Barley	L	—	—
<i>Panicum capillare</i> L.	Witch Grass	+	—	+
<i>Setaria lutescens</i> (Weigel) Hubb.	Yellow Foxtail	—	—	—
<i>S. verticillata</i> (L.) Beauv.	Bristly Foxtail	++	—	++
<i>S. viridis</i> (L.) Beauv.	Green Foxtail	++	—	++

*Local lesions.
 †Severe chlorosis and stunting.

inoculation. Although the oldest leaves on inoculated plants may not acquire the mottle, the symptoms usually appear on the subsequent new leaves. Later, the leaves may partially recover from the chlorosis becoming a normal green color. The usual mottle becomes more clearly delineated often into broad, irregular stripes in the leaf blade or along its edges.

A number of cultivated and wild grasses were tested for their reaction to false stripe (Tables 10, 11 and 12). The various grasses germinated unevenly; hence the ages varied considerably, but in general they were in the two- to four-leaf stages when inoculated. Since the weeds grew slowly in the early stages, they were inoculated on two different occasions at 10-day intervals. The species of plants showing systemic symptoms of false stripe included all varieties of barley, wheat, rye and millet tested, and in addition three varieties of corn and seven annual grasses. The Italian

types of millet were extremely susceptible to this disease (Figs. 12 and 13).



Fig. 12. Leaves of Siberian Millet illustrating foliage symptoms of barley false stripe



Fig. 13. Barley false stripe on Siberian millet. Left: healthy plants; right: diseased plants

Agropyron Streak Mosaic

A virus disease was found on *Agropyron repens* growing in roadside ditches near Brookings in 1950. The disease appears to be similar to a mosaic disease reported by McKinney (8) from Virginia.

The symptoms of Agropyron streak mosaic consist of mild green to a yellow streak-mosaic pattern on the leaves (Fig. 14). The green mosaic symptom is readily seen in young, succulent leaves, but as the leaves become older the mosaic may become masked. Under certain conditions an intense yellow mosaic may develop on older leaves. The virus has little apparent effect on the vigor of *A. repens* plants.

Under natural conditions the virus can spread with the rhizomes of infected *A. repens*, but there has been no evidence of spread to other plants. However, it can be transmit-

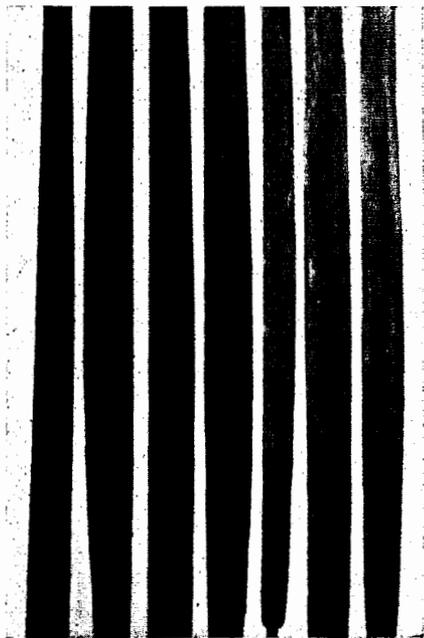


Fig. 14. Agropyron streak mosaic on *A. repens*. Left: healthy leaf; others show varying symptoms

ted by the carborundum-rub method.

Transmission tests were made on a number of wild and cultivated grasses. The results are presented in Tables 10, 11 and 12. They show that the susceptible hosts included all varieties of wheat and rye tested in addition to several species of Agro-

pyron. The symptoms on young wheat leaves resembled those of wheat streak mosaic, but were milder. They became even less apparent as the foliage became more mature. The most seriously affected grass tested was *A. elongatum* (Host) Beauv. which was severely stunted by the disease.

Virus Identification With Differential Hosts

The four viruses that are at present known to occur on grasses in South Dakota can infect a wide range of cultivated and wild grasses. Some of the hosts are susceptible to several or all of these viruses. Wheat, for example, is susceptible to all four. Experiments have demonstrated that wheat plants can be infected by more than one virus at a time, such as wheat streak and wheat striate mosaics, or with wheat streak and Agropyron streak mosaics. Under field conditions it is often

difficult to distinguish one virus from another on the basis of symptoms. The possibility of compound infection of plants makes the problem of virus identification on the basis of symptoms even more difficult and the practice unreliable.

Although these grass viruses have many hosts in common, their host ranges are not identical. They can therefore be differentiated by transmission tests to a selection of hosts as is illustrated in Table 13.

Table 13. Reaction of Differential Hosts of Four Viruses Affecting Grass

Virus	Method of Transmission	Host		
		Wheat (Rushmore)	Rye (New Dakold)	<i>A. repens</i> (Wild Type)
Agropyron streak mosaic	Manual	+	+	+
Barley false stripe	Manual	+	+	-
Wheat streak mosaic	Manual	+	-	-
Wheat striate mosaic	Manual	-	-	-
Wheat striate mosaic	<i>E. inimica</i>	+		

Summary and Conclusions

Four virus diseases affecting cereal crops have been found in South Dakota. They include wheat streak mosaic, wheat striate mosaic, barley false stripe and Agropyron streak mosaic.

Wheat streak mosaic has been found on wheat in 22 counties. Although it has been severe only in areas where winter wheat is grown extensively, it has caused losses in both spring and winter wheat. Oats,

barley and certain varieties of corn are mildly susceptible. In addition, nine common annual grass weeds that occur frequently in South Dakota grain fields are susceptible to streak mosaic. Although the virus can be transmitted readily by manual methods, the natural methods of transmission remain in doubt.

Young winter wheat plants infected in the fall can carry the streak-mosaic virus over winter. During the next summer the virus spreads to other winter and spring wheat plants, and to susceptible annual grasses. Infected annual weeds appear to help sustain the virus during and after harvest until volunteer and fall-sown wheat is growing.

Recommendations for control of streak mosaic include the destruction of susceptible weeds after harvest, and a judicious selection of seeding dates. Winter wheat should be sown late enough to escape the period in late August and early September when spread is rapid, and spring wheat should be sown early enough to make substantial growth before spread becomes rapid in June and July. No satisfactory resistant varieties of wheat are known.

Striate mosaic was discovered on wheat in Gregory county, South Dakota, in 1950. It has since been found in six counties of the state. Unlike streak mosaic, this disease has not been transmitted by manual methods. It is spread naturally by a common leafhopper, *Endria inimica*. Striate mosaic, like streak mosaic, overwinters in winter wheat.

Young leafhoppers begin spreading the virus from overwintered plants by early June. Leafhoppers continue spreading the virus throughout the summer, infecting other wheat and susceptible grasses including a number of annual weeds. During late August and early September the infection is carried into the early winter wheat plantings.

Traces of false stripe have been found on barley in various parts of the state. A factor involved in the spread of this disease is its ability to be seed-borne. It also can be transmitted manually. Barley, wheat, rye, millet and three varieties of corn became systemically infected after inoculation with false stripe. The *Setaria* types of millet tested were severely affected. Nine annual grass weeds also were found susceptible to false stripe.

A mild streak mosaic was found on *Agropyron repens* (quackgrass). The virus causing this disease was pathogenic to wheat as well as to several species of *Agropyron*. The most severely affected host was *A. elongatum* (tall wheatgrass). Although the virus spreads with the rhizomes of *A. repens*, natural methods of transmission to other hosts have not been discovered.

Some of the above mentioned viruses may be difficult to identify on the basis of field symptoms on a host such as wheat; however, they can be distinguished readily by inoculating a selection of differential hosts.

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