Epiphytology of Winter Wheat Mosaic

Johnson, Folke
EPIPHYTOLOGY OF WINTER WHEAT MOSAIC

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In the spring of 1919 there appeared in Madison County, Illinois, a disease in winter wheat previously unknown in the United States. Subsequent observations revealed the same disease existing in Indiana. The disease has been referred to by such names as "take-all," "so-called-take-all," "wheat rosette," and finally "wheat mosaic," after the causal agent was proved to be a virus. Previous to the discovery of the virus nature of the malady by McKinney (17), speculation arose that the trouble was caused by the feeding of certain insects, such as the Hessian fly, Phytophaga destructor Say, wheat straw worm Hormolita grandis Riley, or wheat stem maggot Miromyza americana Pitch, or that unfavorable soil relations were responsible (22). Wheat mosaic virus Marmor tritici H. ² is of unusual interest because under natural conditions the causal agent is transmitted through the soil (16, 17, 30). When seed of a susceptible variety of winter wheat is planted in virus-infested soil in the autumn, disease symptoms do not usually appear in the plants until the following spring after winter dormancy is broken (16, 32). Furthermore, soil which previously has produced a diseased crop of wheat will retain the virus in an active state for at least six years even though no susceptible plants are present during this interval.

Because of these interesting facts the writer undertook a study of the disease to determine, if possible, how the plants became inoculated under natural field conditions. It is the purpose of the present paper to discuss some experiments on this and related problems.

GEOGRAPHIC DISTRIBUTION

In the United States wheat mosaic has now been reported from Illinois, Indiana, Kansas, Maryland, Nebraska, North Carolina and Virginia (20). Wheat mosaic has been found also in Egypt (14), Japan (29) and Russia, where it is present in almost all provinces where winter wheat is grown (33).

1This study reports investigations conducted while the writer held the Elizabeth Clay Howald Scholarship, and the Muellhaupt Scholarship, Department of Botany, Ohio State University. The writer's present address is: Washington Agricultural Experiment Stations, P. O. Western Washington Experiment Station, Puyallup, Washington. Grateful acknowledgment is made to Dr. R. M. Caldwell of Purdue University, and to Dr. Benjamin Koehler of the University of Illinois, for their kind assistance in getting this study started, and to Dr. E. N. Transeau, Dr. W. G. Stover and Dr. C. C. Allison, Ohio State University, for their aid in the preparation of the manuscript. Paper from the Department of Botany, The Ohio State University, No. 471.

²The Latin name of the virus follows the system of nomenclature in the Handbook of Phytopathogenic Viruses (4).
Symptomatology

It is not possible in this paper to give the characteristics of each virus known to cause mosaic in wheat, but only a brief description of the disease will be given as the symptoms appear on susceptible varieties infected under field conditions in the area east of the Mississippi river. Very detailed and comprehensive descriptions of disease symptoms have been made by other investigators (6, 16, 20, 22, 23).

Field Symptoms

Wheat mosaic is best recognized in the spring. The field is spotted with areas containing diseased plants scattered at random regardless of the soil type or condition. The plants in these areas are severely dwarfed and in some instances may be dead and lying on the surface of the ground with a few healthy appearing plants present among the diseased, thus giving an uneven appearance. The affected areas are irregular in shape, varying in size from a few feet in circumference to patches which may comprise almost the entire field. The margins of these patches are more sharply defined than those circumscribing diseased areas caused by unfavorable soil relations.

Host Symptoms

There are two types of symptoms of wheat mosaic, depending upon the variety of wheat observed. In the variety Harvest Queen, a rosetted condition develops which is characterized by excessive tillering, giving the plants an unusually dwarfed, compact appearance. Such plants are darker green than healthy ones.

In very susceptible varieties such as Purdue No. 1, Purkof and Illinois No. 2, wheat mosaic virus produces stunting without excessive tillering in addition to a mottled condition consisting of light yellow areas intermingled with the normal green (Fig. 1). These light yellow patches may be nearly circular to oblong in shape, or may take the form of large chlorotic streaks which are parallel to the leaf veins. Similar characteristics are seen on the glumes, leaves, leaf-sheaths and stems. This type of mottling is generally referred to as yellow mosaic in contrast with green mosaic which exhibits a mottle consisting of small patches or streaks of a darker green color than normally present in healthy plants. Diseased plants may survive the acute phase of the disease and produce imperfectly filled spikes which are shorter than the spikes of healthy plants.

Histopathology

Microscopic examinations of stained sections of diseased plants from areas where the virus is carried in the soil reveal intracellular vacuolated bodies in the host cells (21). Similar bodies are not found in healthy plants and this fact has been used to determine whether plants are infected if no other macroscopic symptoms are visible. This criterion is not reliable in all cases, since no intracellular bodies are produced in wheat infected with the virus (18) occurring west of the Mississippi river. These vacuolated bodies may occur singly or in groups of two or three, and may be found in any position within the cytoplasm. Similar bodies have also been described from mosaic diseased wheat in Japan (28, 29) and Russia (35).

Experiments on Virus Transmission

Mechanical Methods

Wheat mosaic virus is transmitted with difficulty by mechanical means from diseased to healthy susceptible wheat. It has been shown that cool temperatures are favorable for infection (20, 30), but since these conditions do not always exist in most greenhouses in the spring and summer, considerable difficulty is encountered in keeping a viable culture of the virus throughout the year. This is
especially true when one considers that the greatest source of the virus is lost after field-infected plants are matured.

In an attempt to determine the best method of inoculation, the rubbing method described by Jones (8) was compared with the needle-prick method. Carborundum powder was dusted over the plants before inoculation with infectious plant juice which was prepared by grinding parts of diseased plants in a mortar with a pestle. The mortar and pestle were previously sterilized, and a few drops of tap water were added to the inoculum to facilitate inoculation. Only young plants in a stage of rapid growth were inoculated. For the needle-prick method of inoculation a small piece of cotton was wrapped around the point of a dissecting needle allowing the point to protrude slightly through the cotton. The needle-point was kept moist by dipping the cotton in the inoculum at frequent intervals, after which the plants were pricked in several places. Inoculations were made mostly on the leaves and stems but in one experiment plants were inoculated on the roots. In this case the plants were first grown in sand then removed and the debris washed from the roots in running tap water, after which they were inoculated and transplanted in non-infested soil in clay pots. Infectious plant juice was extracted from either the roots or tops of plants and used separately as inoculum in comparative tests.

Table I summarizes the results obtained with four susceptible wheat varieties. It will be noticed from the table that there was no advantage in inoculating the roots, and no infection was obtained with

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**Fig. 1.** Symptoms of mosaic in Purdue No. 1 wheat. The two leaves on the left show different types of mottle and are from plants which became infected with virus through the soil. The leaf on the right is healthy.
inoculum extracted from the roots of diseased plants. Neither method of inoculation was very efficient in transmitting the disease; however, these experiments were performed in late spring when the temperature was relatively high and often reached 80° F., or higher. For best results a cool uniform temperature of about 60° F. is desirable (20).

**TABLE I**

**Comparison of the Rubbing Method of Inoculation with the Needle-prick Method, Using Infectious Plant Juice as Inoculum Extracted from Roots or Tops of Diseased Wheat Plants and Inoculations Made in Either Roots or Tops of Healthy Plants**

<table>
<thead>
<tr>
<th>Suspects</th>
<th>Plants Inoculated in Roots</th>
<th>Plants Inoculated in Leaves and Stems</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Needle-prick Method</td>
<td>Rubbing Method</td>
</tr>
<tr>
<td></td>
<td>Inoculum from Roots</td>
<td>Inoculum from Tops</td>
</tr>
<tr>
<td></td>
<td>Inoculum from Roots</td>
<td>Inoculum from Tops</td>
</tr>
<tr>
<td>Harvest</td>
<td>0/75</td>
<td>0/75</td>
</tr>
<tr>
<td>Purd. No. 1</td>
<td>0/75</td>
<td>0/75</td>
</tr>
<tr>
<td>Purkof.</td>
<td>0/75</td>
<td>0/75</td>
</tr>
<tr>
<td>Illinois No. 2</td>
<td>0/75</td>
<td>0/75</td>
</tr>
</tbody>
</table>

*The numerator indicates the number of plants diseased and the denominator the number of plants inoculated.

**INFECTION OF VERNALIZED WHEAT FOLLOWING GERMINATION IN VIRUS-INFESTED SOIL**

Mosaic symptoms develop in wheat in the spring following winter dormancy, but not in winter wheat planted in spring except in rare instances when unusually low temperatures prevail for a prolonged period (20). Spring wheat is also susceptible to infection when planted in the fall, but not when spring sown (18, 20). It seemed interesting to determine if wheat could be infected under artificial winter conditions produced in the laboratory and greenhouse.

The experiment was divided into two parts. In one test the seeds were sown in virus-infested soil and allowed to grow at room temperature for 18 days, after which time the plants were vernalized by subjecting them to a temperature between 2° and 3° C. for 60 days. Water was added to the soil in the low temperature chambers to keep the soil moist. After the cold treatment the plants were transplanted in either infested or non-infested soil in the greenhouse. The roots were washed in tap water to remove as much of the infested soil as possible before transplanting the plants in non-infested soil. In the second part of the experiment the seeds were germinated in sand known to be free from virus, and the wheat vernalized as previously described. Following the cold treatment the plants were transplanted in virus-infested soil.

It will be seen by referring to Table II that it is possible to produce mosaic in winter wheat by duplicating in the laboratory some of the natural conditions to which winter wheat is normally exposed. First, by allowing the plants to grow for a brief period in virus-infested soil and second, by subjecting them to a cold treatment, followed by normal growth development. Webb (30) has shown...
that the wheat seedlings become infected in the fall before winter dormancy; this condition also seems to hold true under artificial laboratory conditions, although in this case the percentage of plants showing disease is much lower than under natural field conditions. This result was possibly caused by the small quantity of infested soil used in germinating the wheat, prior to the cold treatment. It has not been possible to produce mosaic in vernalized wheat germinated in sand free from virus, followed by transplanting in virus-infested soil. One thousand seedlings of the variety Purdue No. 1 were treated in this manner and not one plant showed mosaic.

### TABLE II

<table>
<thead>
<tr>
<th>Seed Germinated in Infested Soil and Plants Transplanted in:</th>
<th>Seed Germinated in Non-infested Sand and Plants Transplanted in:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-infested Soil</td>
<td>Non-infested soil</td>
</tr>
<tr>
<td>Infested Soil</td>
<td>Infested Soil</td>
</tr>
<tr>
<td>Purdue No. 1...</td>
<td>17/100*</td>
</tr>
<tr>
<td>15/100</td>
<td>0/100</td>
</tr>
<tr>
<td>0/1000</td>
<td>0/1000</td>
</tr>
</tbody>
</table>

*Numerator indicates number of plants diseased, denominator the number of plants transplanted.

**INSECTS**

It is reported that the wheat virus occurring west of the Mississippi river is transmitted by an unidentified aphid (3), but such evidence is lacking for the virus present east of the Mississippi (18). In Russia it has been demonstrated (33) that the leaf hopper *Laevicocephalus (DeltocephaHus) straitus* (L.) DeLong, is a vector of the wheat virus occurring in that country, but it is not definitely known if the Russian virus is related to any of the wheat viruses in the United States. In an attempt to gain some information on the natural spread of the disease, it seemed important to study several species of local insects as vectors of the wheat mosaic virus.

Diseased plants used as a source of the virus were naturally infected by planting the seed in the fall in infested soil. The healthy test-plants, to which the insects were transferred after their viruliferous feed, were grown in clay pots and were about four inches tall. Insect cages made of celluloid were placed over the wheat and pushed into the soil to the depth of one inch. Wheat of the variety Purdue No. 1 was used exclusively in these tests.

One hundred twenty-five mature leaf hoppers, *Laevicocephalus straitus*, were collected from a pasture and placed under a cage with diseased wheat. There was a high mortality among the insects. Only 23 adults remained alive after a feeding period of seven days when they were transferred to five healthy wheat plants. Seven days later the insects were removed and the plants observed for mosaic symptoms, but no disease developed up to the time when the plants were in bloom.

In another experiment the leaf hopper, *Agalia sanguinolenta* Prov., was tested. Twenty adult insects were fed on diseased plants for six days, then transferred to five healthy wheat plants where they fed for an additional 17 days. No mosaic had developed on the wheat after an observation period of 60 days.

The third experiment consisted of testing the leaf hopper, *Agalia constricta* (Van Duzee) and both macropterous and brachypterous forms of the fulgorid *Delphacodes campestris* (Van Duzee) as vectors of the virus. There were 19
insects of *A. constricta* and 60 of *D. campestris*. All insects were placed in one cage and fed on diseased wheat. After a feeding period of six days the insects were removed and separated according to species. Each group was then transferred to four healthy wheat seedlings in separate cages. Daily transfers were made to a new set of plants from April 30 to May 21, but in no case did any plants become diseased with mosaic.

One of the common aphids feeding on wheat is *Toxicoptera gramineum* Rond. Specimens of this insect were fed on diseased wheat for three days, then transferred and fed an additional six days on healthy wheat. No mosaic developed in the test plants. In a second trial the same species of insects were fed on diseased plants for six days, then transferred to 50 healthy vernalized wheat seedlings with five mature aphids placed on each plant. After six days the insects were destroyed by fumigation and the plants observed for mosaic symptoms, but there was no evidence of virus transmission.

It must be concluded that the insects tested are not vectors of the virus under the conditions of these experiments.

**NEMATODES**

As will be seen from the following discussion, there is a certain amount of information which suggests that a soil vector of some kind is responsible for transmission of the wheat virus. It is known that the virus is not carried in the water drained from infested soil (31), and if insects hatched from eggs deposited in infested soil were responsible for transmission it could be expected that healthy, susceptible wheat grown in non-infested soil in alternate rows with plants in infested soil would also become inoculated as the insects emerged from the soil. This does not happen, as only the plants in the virus-infested soil show disease. Furthermore, insects emerging from the infested soil could be trapped by inserting an insect-proof cage over the soil. This the writer has attempted to do, but no insects were found in the cages. It has also been reported by McKinney (20) and confirmed by the writer that the disease develops in wheat grown in infested soil in cages which excludes all outside insects. This circumstantial evidence may suggest that the vector is not necessarily an insect, but some other organism present in the soil. Such an organism must be able to resist periods of alternate moisture and drought for a considerable length of time, as infested soil which has been air dried for at least three years produces just as severely infected plants when replanted to wheat as similar soils cultivated regularly (20).

One kind of soil-borne organism which fulfills these requirements is the nematode. It is known that species of nematodes are able to remain dormant from five to ten years (2, 27) and resume parasitism upon the advent of favorable moisture conditions. The feeding technique of plant parasitic nematodes has been studied in considerable detail by Linford (11, 12, 13). From this work it is concluded that the nematodes puncture the host cells with their stylets and injest the cell contents into their bodies by the pulsation of their esophageal bulbs. There is also evidence that saliva is injected through the stylet of the parasite into the host (11). This method of feeding is similar to that of certain insects which are important vectors of many plant viruses. From these considerations it seemed worth while to study the nematodes normally present in virus-infested soil with regard to their capacity to act as vectors of the wheat virus.

The nematodes were separated from the virus-infested soil by employing the well-known Baermann technique as described by Cort et al., (1). The apparatus used in this study is shown in Fig. 2. The nematodes were collected in watch glasses by opening the pinch cock on the funnel from six to twelve hours after the soil was flooded with water. The nemas were then drawn up in a pipette made from glass tubing, one end of which was drawn out to a fine point and either transferred directly to non-infested soil planted to a susceptible variety of wheat or
transferred to Petri plates containing cultures of the fungus Fusarium. The nemas multiplied rapidly on the fungus isolates and after two weeks time, from the date the nema cultures were started, the substratum was covered with nematodes in all stages of development from eggs to mature individuals. The nemas were separated from the agar by inverting the Petri plates in water. After four hours the nemas were drained off in great abundance and transferred to non-infested soil planted to wheat. In some cases vernalized wheat was used to test for virus transmission. These trials have been repeated six times and many hundreds of plants were involved, but in no case was there evidence that the nematodes transmitted the virus.
In subsequent tests wheat seeds were surface sterilized and germinated in a
water-agar medium in Petri plates to which nematodes previously separated from
virus-infested soil were added. The nemas multiplied rapidly and were seen in
great abundance on the roots of the wheat; however, it could not definitely be
ascertained if the nemas actually fed on the roots. The plants were later trans-
planted in non-infested soil and observed for mosaic, but no disease developed.
From this work it seems apparent that the nematodes collected from the
infested soil were not vectors of the wheat mosaic virus, but it should be pointed
out that these experiments were conducted at a time when laboratory and green-
house temperatures were high and often reached 90° F., a condition which is not
conducive for the development of mosaic.

Suscept Range

Winter wheat is not a suitable experimental plant for greenhouse and lab-
oratory work since plants must be subjected to a low temperature for a considerable
period of time before they will develop normally. For this reason it was desirable
to test other species of plants which might more easily become infected, and which
could be used to study the virus in greater detail. All tests were conducted in a
greenhouse and the plants inoculated by the rubbing method. Carborundum was
dusted over the leaves before inoculation and all the test plants were young and
in a stage of rapid growth. Following inoculation the plants were washed with
water from a sprinkling can. Attempts were made to recover the virus from
inoculated test plants which deviated in appearance from the normal by inoculating
wheat with plant juice extracted from the test plants. It will be seen from Table III
that only wheat in the Gramineae family was susceptible to infection. This fact
is in agreement with McKinney's earlier work (16, 18) in which he found that
all cereal species in the tribe Hordae were susceptible to the disease by natural
infection.

Control

Although wheat mosaic does not develop in wheat grown in infested soil treated
with formaldehyde (16) or in soil heated at 60° C. for ten minutes (7), the only
practical method of control is by planting resistant varieties. It is beyond the
scope of this paper to list all the varieties reported resistant since this information
is available elsewhere (16, 23, 32). Recent work by Koehler, Bonnett, and
McKinney (9) has shown that several varieties produce good yields when planted
in virus-infested soil. These varieties, listed according to their order of yield
over a four-year period in three different fields are as follows: Fulhard, Prairie,
Nabob, Wabash, Fulcaster, Duffy, Thorne, Cooperatorka, Fulhio, Michigan
Amber, Inivira, Harvest Queen 34–1, Red Wave, Shepherd, and Trumbull. Records
on lodging resistance were also taken and in this regard their order of importance
is: Thorne, Prairie, Fulhard, Nabob, Duffy, Fulcaster, and Wabash.

Discussion

Several viruses are reported as inducing mosaic in winter wheat in the United
States. The viruses causing mosaic west of the Mississippi river differ from
those east of the Mississippi in not being transmitted through the soil, and are
reported transmitted by an aphid, while no insect-vector is known to transmit the
eastern viruses which are carried with the soil. The two viruses may also be
differentiated upon the fact that vacuolated bodies are found in the cells of plants
infected with the eastern virus, while no such inclusions are produced by the
western virus (18).

Two types of mosaic are described from the west (19), namely, green mosaic
and yellow mosaic. The latter appears to cause the most pronounced damage,
and more recently McKinney (20) isolated seven different viruses from diseased
plants grown east and west of the Mississippi river. The distinctive characteristics were based on the symptoms produced in Harvest Queen wheat grown under a definite photoperiod, host range, and whether the viruses were transmitted through the soil. Each wheat virus was designated by a numeral from one through seven. It appears to the writer that a better method would be to consider only two distinct viruses as causing wheat mosaic in the United States. Wheat mosaic

### TABLE III

PLANTS TESTED FOR SUSCEPTIBILITY TO THE WHEAT MOSAIC VIRUS

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Varieties</th>
<th>No. Plants Tested</th>
<th>No. Plants Tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chenopodiaceae</td>
<td><em>Beta vulgaris</em> L.</td>
<td><em>Beta vulgaris</em> L. (sugar beet)</td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Callistephas chinensis</em> Nees</td>
<td></td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Helianthus annuus</em> L.</td>
<td></td>
<td></td>
<td>0/25</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lactuca sativa</em> L.</td>
<td></td>
<td></td>
<td>0/7</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Papaytae erecta</em> L.</td>
<td></td>
<td></td>
<td>0/6</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Taraxacum officinale</em> Weber</td>
<td></td>
<td></td>
<td>0/20</td>
<td></td>
</tr>
<tr>
<td>Cucurbitaceae</td>
<td><em>Cucumis melo</em> L.</td>
<td></td>
<td></td>
<td>0/7</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>C. sativus</em> L.</td>
<td></td>
<td></td>
<td>0/32</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Evergreen Pickling</em></td>
<td></td>
<td></td>
<td>0/20</td>
<td></td>
</tr>
<tr>
<td>Cruciferae</td>
<td><em>Brassica rapa</em> L.</td>
<td></td>
<td></td>
<td>0/20</td>
<td></td>
</tr>
<tr>
<td>Gramineae</td>
<td><em>Oryza sativa</em> L.</td>
<td></td>
<td></td>
<td>0/26</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Acadia</em></td>
<td></td>
<td></td>
<td>0/24</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Blue Rose 41</em></td>
<td></td>
<td></td>
<td>0/29</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Early Prolific</em></td>
<td></td>
<td></td>
<td>0/29</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Improved Blue Rose</em></td>
<td></td>
<td></td>
<td>0/20</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Rexoro</em></td>
<td></td>
<td></td>
<td>0/20</td>
<td></td>
</tr>
<tr>
<td>Saccharum officinarum L.</td>
<td><em>Sorghum vulgare</em></td>
<td></td>
<td></td>
<td>0/20</td>
<td></td>
</tr>
<tr>
<td>Sorghum vulgare</td>
<td><em>var. caffrorum</em> (Thum.) Hubb. &amp; Rehder</td>
<td></td>
<td></td>
<td>0/30</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. saccharatum</em> (L.) Boerb.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Amber</em></td>
<td></td>
<td></td>
<td>0/38</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Atlas</em></td>
<td></td>
<td></td>
<td>0/48</td>
<td></td>
</tr>
<tr>
<td>Triticum aestivum L.</td>
<td><em>var. Harvest Queen</em></td>
<td></td>
<td></td>
<td>0/76</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Illinois No. 1</em></td>
<td></td>
<td></td>
<td>3/84</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Purdue No. 1</em></td>
<td></td>
<td></td>
<td>5/68</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Purkof</em></td>
<td></td>
<td></td>
<td>3/83</td>
<td></td>
</tr>
<tr>
<td>Zea mays L.</td>
<td><em>Hybrid Golden Cross Bantam</em></td>
<td></td>
<td></td>
<td>0/50</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>var. Indiana 616</em></td>
<td></td>
<td></td>
<td>0/50</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Hybrid Iowa 930</em></td>
<td></td>
<td></td>
<td>0/50</td>
<td></td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Medicago lupulina</em> L.</td>
<td></td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td>Liliaceae</td>
<td><em>Allium cepa</em> L.</td>
<td></td>
<td></td>
<td>0/5</td>
<td></td>
</tr>
<tr>
<td>Linaceae</td>
<td><em>Linum usitatissimum</em> L.</td>
<td></td>
<td></td>
<td>0/12</td>
<td></td>
</tr>
<tr>
<td>Solanaceae</td>
<td><em>Capsicum frutescens</em> L.</td>
<td></td>
<td></td>
<td>0/3</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lycopersicon esculentium</em> Mill.</td>
<td></td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Nicotiana glutinosa</em> L.</td>
<td></td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>N. rustica</em> L.</td>
<td></td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>N. tabacum</em> L.</td>
<td></td>
<td></td>
<td>0/10</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Solanum nigrum</em> L.</td>
<td></td>
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<td>0/7</td>
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</tbody>
</table>

*The numerator indicates the number of plants diseased; the denominator indicates the number of plants inoculated.

Plants checked with an asterisk indicates these plants showed unusual symptoms following inoculation and that attempts were made to recover virus from them by using wheat as a test plant; but no virus could be demonstrated.
virus occurring east of the Mississippi river and classified by Holmes (4) as *Marmor tritici* H., would retain the name wheat virus 1, according to the numerical classification. What McKinney refers to as wheat virus 2 and wheat virus 3 may be regarded as strains of wheat virus 1, and thus would be designated as wheat virus 1A and 1B, respectively. The viruses occurring west of the Mississippi may be designated as wheat virus 2, with the virus referred to by McKinney as wheat virus 4 considered the type strain. Following this system further, wheat viruses 5, 6 and 7 would be regarded as wheat viruses 2A, 2B, and 2C, respectively. Until more is known about the distinctive properties, a Latin binomial is not suggested for the western virus.

The viruses inducing mosaic of wheat in Japan are probably closely related to the eastern virus in the United States (5, 28). Two types of mosaic have been described, namely, green mosaic and yellow mosaic. These are distinguished by the difference in vacuolated bodies present in the host cells of diseased plants and by differential wheat varieties susceptible to the viruses (29, 15).

In Russia there appears to be two distinct viruses capable of causing mosaic in cereals, the virus causing mosaic of oats known as "zakooklivanie" (pupation disease), and the virus of winter wheat mosaic. Both viruses are infectious for both oats and wheat as well as other plants, but certain characteristics differentiate them. The virus causing "zakooklivanie" produces vacuolated bodies and protein crystals in cells of infected plants, while the wheat virus does not induce the formation of protein crystals (24). In diseased spring crops the oat virus causes excessive tillering, while the wheat virus seems to have no such effect (34). Furthermore, different insect vectors are involved. The virus causing mosaic in oats, "zakooklivanie," is transmitted from diseased to healthy plants by *Delphax striatella* Fallen (26), while *Laevoccephalus (Deltocephalus) striatus* (L.) De Long, is reported a vector of the wheat mosaic virus (33). Neither virus is transmitted by mechanical methods and wheat does not become infected through the soil (34), although the reports on infection through the soil by the oat virus are in conflict (10, 25).

What the relationship is between the Russian viruses and those present in the United States is not clear. If we compare soil transmission then the wheat virus in Russia is much like our western virus, and if we consider the histopathology then the Russian virus compares favorably with our eastern virus since both induce the formation of intracellular inclusions.

There is not enough information on the wheat virus occurring in Egypt to make comparisons with any of the other known cereal viruses.

From what is known about the wheat mosaic virus occurring east of the Mississippi river in the United States, the writer is constrained to believe that a soil-borne organism is the vector. This might be an insect, or some other parasite living in the soil. Although nematodes did not transmit the virus in this study, the writer feels that more work should be done on this problem. It is possible that the technique employed was inadequate to demonstrate this point. For instance, the next logical step would be to subject the plants to winter conditions after the nematodes were allowed to come in contact with the wheat plants to be inoculated.

**SUMMARY**

Wheat mosaic is present in Illinois, Indiana, Kansas, Maryland, Nebraska, North Carolina and Virginia. From abroad the disease has been reported in Egypt, Japan and Russia.

The virus causing the disease east of the Mississippi river is transmitted to susceptible plants through the soil and produces two distinct types of symptoms. In the variety Harvest Queen a stunted, rosetted condition is produced, with or without mottling. In other varieties such as Purdue No. 1, Purkof, and Illinois
No. 2, stunting is pronounced without excessive tillering. In these varieties a mosaic mottling is the predominant early symptom of disease. Vacuolated intracellular bodies are present in cells of diseased plants, but not in healthy.

The virus is transmitted, with difficulty, from diseased to healthy wheat plants by mechanical means. Inoculum extracted from roots of diseased plants did not produce infection in healthy plants by the rubbing method of inoculation nor by the needle-prick method. It is possible to induce the disease in wheat by artificially subjecting the plants to the normal temperatures to which winter wheat is exposed after allowing the plants to grow in virus-infested soil for 18 days.

The insects, *Laevocephalus* (*Delocephalus*) *striatus*, *Agalia sanguinolenta*, *A. constricta*, *Delphacodes campestris*, and *Toxicoptera gramineum*, did not transmit the virus. Nematodes were also tested as vectors but the results obtained, with regards to transmission, were negative.

Several species of plants were tested for susceptibility to the disease by mechanical inoculation, but symptoms were produced only in wheat.

The only practical method of control in areas where the disease is prevalent is to grow resistant varieties. Several of these have been found to produce good yields on virus-infested land.

Two viruses may be considered as causing mosaic of winter wheat in the United States. The virus east of the Mississippi river is transmitted through the soil and induces the formation of vacuolated intracellular bodies in cells of diseased plants. The western virus is not transmitted through the soil and produces no intracellular bodies in cells of infected plants.

The virus causing mosaic in Japan is probably closely related to the eastern virus present in the United States, but the wheat virus in Russia has characteristics of both our eastern and western viruses.

**LITERATURE CITED**


