COMPARATIVE STUDIES ON THE REACTION OF SOME WINTER WHEATS TO WHEAT STREAK MOSAIC VIRUS

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SOME WINTER WHEATS TO WHEAT

STREAK MOSAIC VIRUS

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CHAPTER I

INTRODUCTION

Wheat streak mosaic virus (WSMV) disease was first described by McKinney (29) in 1937, but an epiphytotic in Kansas in 1949, causing the loss of 30 million dollars in wheat, Triticum aestivum L. production (19), gave real impetus to research on the disease. So far, although certain other control measures such as destroying self-seeded or volunteer plants during the summer have been developed, the most promising and economical control measure is through the use of resistant cultivars.

Some winter wheat cultivars have exhibited field tolerance to WSMV. However, this tolerance varies greatly with environment, time of inoculation, and other factors. Also selection within domestic wheat cultivars for tolerance to the disease did not give satisfactory results (4). In recent years, it has been discovered that several selections from a wheat x Agropyron cross showed unusual resistance to the disease (44) and also to the mite vector, Aceria tulipae Keifer (27). The most promising selections of this cross were developed by cytological techniques by Sebesta and Bellingham (44). One of these selections is a translocation and the other a chromosome substitution involving resistance to both the virus and its vector (27). However, disease resistance testing was conducted by manual inoculation methods and no knowledge is available concerning

whether the resistance will prevail under field conditions when inoculation is accomplished by the vector. Observation on the reaction of the supposedly tolerant cultivars and these promising selections from the wheat x Agropyron cross to the vector, the virus and the effect of these organisms combined are needed to aid breeding for resistance against this disease and also in consideration of new cultivars for release for cultivation in areas where the occurrence of WSMV and its vector is common.

There were two purposes to this study. First, to determine the differences in growth, symptoms, yield and concentration of WSMV developed in infected plants of some supposedly tolerant winter wheats and two selections from the cross, wheat x Agropyron. Second, to observe the reaction of these selections to viruliferous mites under field conditions.

CHAPTER II

REVIEW OF LITERATURE

The occurrence of WSMV and estimates of losses in yield of infected fields have been reported from hard red winter and spring wheat areas of the United States, Canada, and many other countries (2, 14, 35, 38, 48). A sequence of weather conditions which favor the growth of volunteer wheat often leads to increases in the population of viruliferous mites which, then, may create an epiphytotic (28). In 1952 losses in wheat production ranging from a trace to 25% were reported in Wyoming and a few fields had 100% infection with total loss (34). More recently, in 1974, wheat production in Kansas was reduced by an estimated 30 million bushels (27). In addition, plants weakened by virus infection are more susceptible to leaf rust, Puccinia recondita f. sp. tritici (39). The milling properties of the grain from virus infected plants was also adversely affected (17). It has also been shown that chlorophyll content in leaves of infected plants was lower than in leaves of healthy plants (56).

The ability of the eriophyid mite, Aceria tulipae, to transmit WSMV was shown by Slykhuis in 1953 (48). Since then he and other research workers have studied many facets of the life pattern of the mite and its relation to virus transmission.

All stages of the eriophyid mites can survive the winter on

winter wheat (50). Both mites and eggs found on winter wheat and collected at various times through the winter and spring were found to be viable (49).

WSMV and its vector have a number of other hosts among the cereal crops (10, 12, 36, 47) and mites are a vector on some of them (21, 57).

Control of leaf curl mites by 6 systemic chemicals was reported but they did not effect the development of WSMV (24). Staples and Allington (53) recommended the elimination of volunteer wheat for control and stated that insecticide application to the winter wheat crop in autumn was not effective.

Screening for resistance to WSMV in both winter and spring wheat cultivars has not proved satisfactory (15, 30, 58). Bremer (11) tested 7000 plants collected from a native wheat population in Turkey and found that only four showed resistance. Some degree of tolerance has been reported for some cultivars of common wheat (4, 33, 41, 46). A few Scout derivatives such as Eagle and Sage exhibited moderate tolerance to WSMV in some years but were severely damaged in others (27).

Seeking higher levels of resistance, McKinney and Sando (31) reported that a high degree of resistance or immunity existed in a number of intergeneric hybrids involving wheat and Agropyron. This was confirmed by Fellows and Schmidt (16). Andrews and Slykhuis (1) inoculated 41 wheat x Agropyron hybrids with WSMV by mites and found that 16 were resistant while five appeared to be symptomless carriers. Mites failed to survive and reproduce normally on most of the resistant lines.

The association of resistance with grass-like characters was

observed by Schmidt, et al. (42). A genetic study using hybrids of wheat x Agropyron elongatum crossed with Pawnee wheat suggested that the gene or genes conferring resistance were probably located on a univalent chromosome derived from the Agropyron parent. The local lesion reaction was obtained only when both chromosomes carrying the resistant gene or genes was present (55). Resistance was believed to be partially dominant (45). Another study reported a high degree of resistance in a wheat x Agropyron derivative labelled P_3-19 which was governed by a single extra pair of chromosomes (44). Later two irradiated lines derived from P_3-19 (C.I. 15321 and C.I. 15322) were shown to be resistant to both WSMV and eriophyid mites. A few mites developed on each of these lines but failed to transmit the virus. It was believed that the gene(s) controlling WSMV resistance is (are) either linked to the gene(s) controlling mite resistance or both characters are governed by the same gene(s) coming from A. elongatum (27). Using some wheat x Agropyron substitution lines Larson and Atkinson (25) concluded that resistance to WSMV is not confined to any one A. elongatum chromosome. Substitution for chromosome 6D bestows considerable resistance while substitution 5D delays the development of the disease. Almost complete resistance to the mite vector is carried by an Agropyron chromosome substituting for 6D.

The presence of the virus and its multiplication in plants can be determined by various means. Infectivity assay has been used to measure the infectious particles but this method reflects only a relative concentration of virus. When no appropriate local lesion host is available for bio-assay, such as in the case of WSMV (32), suitable plants which produce clear systemic symptoms must be used.

Assay with such plants is less accurate, but in many cases has given reasonably accurate quantitative data (22).

Virus yield is very dependent on the conditions under which the inoculated plants are grown. Bawden and Roberts (3) stated that reduced light intensity increased yield of several viruses. However, using the infectivity assay, Haunold (20) found no effect of light intensity on WSMV concentration. He also showed that the time required for the virus to reach a maximum concentration decreased with an increase in temperature. In the case of WSMV the maximum concentration developed in 10 days at 24 C or above.

Most of other techniques of virus assay; for example, density gradient centrifugation (DGC) require removal of as much plant material as possible from the sample. A compromise must usually be reached between the amount of virus retained and the amount of plant materials discarded. There are a number of clarification methods used to obtain a more purified form of the virus. Centrifugation at speeds and periods of time insufficient to sediment the virus may be one of the simplest ways to separate the larger particles of contaminant materials (22). Heating at certain temperatures will coagulate plant protein so that it can be removed, however, in some cases with purified virus preparations in buffers above pH 6, heating at 45 C will inactivate the virus by releasing RNA from the virus protein shell (26). Brakke (6) estimated a loss of two-thirds of the virus during heating for one hour at 40 C. Freezing of plant tissue will also coagulate some proteins and inactivate some virus. Although this process gave the best yield of WSMV, the process alone was not effective in removing normal plant constituents that sedimented with

the virus in gradient columns (9).

After clarification by some methods or combination of methods the virus in the preparation may be sedimented into a compact pellet by ultracentrifugation and thus isolated and concentrated. The pellet is usually resuspended in a suitable buffer and allowed to disaggregate after centrifugation (22).

Density gradient centrifugation has been used to purify and separate virus (5, 6). Modification of the method, followed by photometric scanning, provided a much more accurate assay than infectivity. The concentration of virus particles was measured, whether they are infectious or not (7, 9). Being a nucleoprotein, the virus has an absorption spectrum which is highest at 260 nm. and, therefore, can be used for an estimation of nucleic acid content of virus (37). Using this method, it was found that the average concentration of virus in the two youngest leaves at five days after the first symptom appeared was highest in plants grown at 21 C. The concentration of virus in different cultivars of wheat determined by this method was: Bison, 0.016 A_{254} units of virus per gram of leaf; Blue Jacket, 0.030; Concho, 0.027; Scout, 0.014; Triumph, 0.008; and Pawnee, 0.030 (9).

CHAPTER III

MATERIALS AND METHODS

Two different experiments were made. A field experiment was used for testing the reaction of eight winter wheat cultivars and selections to WSMV and its eriophyid mite vector. Another experiment, under controlled conditions, was used for the estimation of virus concentration which developed within the same cultivars and selections used in the field. The results of all investigations were analyzed statistically.

Eight cultivars and selections which had previously been observed to be tolerant or resistant by other research workers were used in each experiment. They were: Eagle C.I.[1/] 15068; Osage C.I. 17292; Scout selections, OK66V2621, OK66V2629 and CO64A1002-2; selections derived from P_3-19, C.I. 15321 (Substitution line with amber seed) and C.I. 15322 (Translocation line with red seed) (43); and a selection from the cross Concho//Timstein/2*Pawnee, OK61V5262.

An experiment was made in the field at Panhandle State University Agricultural Experiment Station, Goodwell, Oklahoma, beginning in August 1974 and harvested July 1, 1975. The borders of the experimental plot were planted with Danne C.I. 13876 wheat one month before

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[1/] C.I. numbers are assigned by the Germplasm Resources Laboratory, ARS, U.S. Dept. of Agriculture, Beltsville, Md.

planting the cultivars and selections to be tested. The north and south border plants were infested with viruliferous mites when they were one and a half months old. Plants infected with WSMV and infested with mites were removed from a field near Sidney, NE., placed in 10 cm pots and used to brush the border wheat plants, thus spreading the viruliferous mites. In addition, 10 of these pots were transplanted at intervals in the south and two in the north border respectively. Survival of mites was checked a week later to ensure that infestation of the border wheat was accomplished.

Each of the eight entries in the study was planted in plots of 5 rows 20 cm apart and 3.1 m long with 8 replications in a latin square design.

A measure of the degree of infestation of the cultivars and selections in the test was made by counting the number of mites found on samples of five young leaves randomly taken from the center of each plot. Mite counts were made with the aid of a binocular microscope and a disecting needle used to unroll the leaves. Samplings were made twice in the fall, once in the winter and twice in the spring. The relative degree of symptoms of WSMV were recorded at the time leaves were collected for mite samples. Grain yield was harvested from three center rows of each plot at the end of the season.

Two methods were used to determine the relative amount of WSMV development in the eight cultivars and selections under controlled conditions. They were: (1) Infectivity assay; (2) Density gradient centrifugation (rate zonal centrifugation) and spectophotometric assay.

The 'Salina' strain of WSMV was used to inoculate the plants to be tested. This source of the virus was obtained from Dr. E. E. Sebesta, ARS, U.S. Dept. of Agriculture, Dept. of Agronomy, Oklahoma State University. This virus was maintained on Blue Jacket C.I. 11502 wheat. This cultivar was also used as an assay plant in the infectivity test.

All the seeds used in the tests were treated with Arasan (50% Thiram) before planting in 11 cm, one liter, plastic pots. Each pot was firmly packed with a uniformly-mixed soil composed of clay loan and peat moss to within two cm of the top of the pot. Thirty five seeds were spread on the soil surface and then covered with about one cm of soil. Two pots per cultivar or selection were used for each kind of assay. The pots for each assay were thoroughly watered and placed in a growth chamber (Percival Model PGC 78C). The pots for the infectivity assay were placed in a completely randomized design and the pots planted for the density gradient centrifugation test were arranged in a randomized block design. The growth chamber was set for a temperature of 21 ± 1 C and to provide 10550 lx. light intensity at the top of the pots with a 12 hour photo-period. After planting, each pot was watered alternately with water or a solution containing 0.5% of Ortho-gro liquid fertilizer (12-6-6, N-P-K, formulation) sufficient to maintain optimum soil moisture. Blue Jacket wheat was planted 10 days later in 32 pots in a similar manner for use as assay plants. Each pot was thinned to 20 plants one day before being used for assay.

When the plants of the cultivars and selections in the test were two weeks old and had reached the three leaf stage, they were

thinned to 15 plants per pot. The height of 10 randomly selected plants was measured before inoculation. Inoculum of WSMV was prepared from 10 grams of Blue Jacket wheat leaves showing pronounced symptoms. The leaves were cut into one cm lengths and ground in a Waring microcup on a blender (Waring Model 700B) for two minutes with 150 ml of distilled water chilled to 5 C. Plant fiber was removed by passing the preparation through two layers of cheese cloth (grade 40). Since WSMV is not absorbed by celite (40), five grams of this abrasive were added to the inoculum. Finger-thumb rubbing method of inoculation was used. Each plant was rubbed three times from the base to the tip of the leaf. Three plants were inoculated together at a time. After inoculation, pots were returned to their respective positions in the growth chamber. Three days after the inoculation, the temperature in the growth chamber was raised to 24 $\pm$ 1 C and maintained at that level until the experiment was completed. Observation of the severity of symptom expression and counts of the numbers of systemically infected plants in the infectivity test were made 12 days after inoculation, whereas those in the density gradient centrifugation test were made 14 days after inoculation. Following the observations, the plants in each pot were harvested at soil level and weighed before being processed in any assay test.

Diseased plants from each of the two pots of each cultivar and selection were cut into pieces about one cm long. One gram of such plant tissue from each pot was used to prepare the extract in a 1:100 dilution. Ten ml of the 1:100 dilution was then used to prepare a 1:1000 dilution of plant extract. A 50 ml sample of each

dilution was mixed with 2.5 grams of celite and used to inoculate 20 Blue Jacket wheat plants. After inoculation, the pots of assay plants were placed in the growth chamber in a completely randomized design and maintained at 24 $\pm$ 1 C. The number of diseased plants in each pot of assay plants was counted two weeks later.

For the most part, the procedures followed were those described by Brakke (9) and Young (59) except for utilization of a fractionator (Isco Model E).

After being harvested and weighed, plants from the two pots of each entry were combined. Ten grams of diseased plants of each entry were frozen overnight. On the following day, the plants were thawed, cut into small pieces about one cm long and ground with 30 ml of chilled .01 M phosphate pH 7.0 buffer for two minutes. The extract was passed through two layers of cheese cloth and centrifuged in a refrigerated automatic centrifuge (Servall Model RC-2) at a speed of 10,000 rpm for 10 minutes. Each supernatent was saved and divided into three aliquats, and transferred to three centrifuge tubes fitting the fixed angle rotor of an ultracentrifuge (Beckman Model L). These aliquats were centrifuged at 5 C at 40,000 rpm for one hour and 25 minutes. The pellets were saved and dispersed with a small smooth-ended glass rod. The three pellets belonging to the same entry were recombined together with 2.5 ml of .01 M phosphate pH 7.0 buffer. These suspensions were allowed to stand overnight at 5 C.

Sucrose solutions used for setting gradient columns were prepared as follows:

Sucrose (gm)	Phosphate buffer (ml)	Final concentration (% sucrose)
10	94	10
36	158.4	20
54	147.6	30
72	136.8	40

The gradient columns were set by laying 8, 8, 8, and 4 ml of 40%, 30%, 20%, and 10% solution respectively in each of the 1 x 3" plastic centrifuge tubes for the swinging head rotor (SW 25.1). The gradient tubes were allowed to stand overnight.

On the next day, the pellet suspensions were centifuged at 10,000 rpm for 10 minutes and the supernatants were saved. Two ml of each supernatant were floated on top of a gradient column and centrifuged for two hours at 25,000 rpm. The remainder of each supernatant from the last low speed centrifugation was used to inoculate 5 plants of Blue Jacket wheat dusted with celite to detect the infectivity of the partly purified preparation. After the rate zonal centrifugation, fractions of 0.5 ml each were drawn starting from the meniscus of the gradient column by using a 20 gauge needle and a small syringe. Each fraction was diluted with 2.5 ml of .01 M phosphate buffer and the absorbance unit at 254 mμ was recorded using a spectophotometer (Beckman Model 24). A graph was drawn using the absorbance units multiplied by the dilution factor. The virus concentration was determined by the area under the peak measured by a planimeter.

This experiment was repeated in its entirety.

CHAPTER IV

RESULTS

Field Experiment

After the introduction of viruliferous mites into the border of the field test, the population gradually increased. Streak mosaic symptoms, however, occurred only on four entries in the fall. Even these symptoms were later suppressed during the cold weather of winter but reappeared in the spring on most of the entries. The 1974-1975 winter season was drier than normal and one scheduled application of supplemental irrigation could not be applied at the proper time due to pump malfunction. Consequently, moisture stress may also have been a factor in response. From whatever cause, stunting and yellowing was severe in most entries (Figure 1). Only the two wheat x Agropyron derivatives, C.I. 15321 and C.I. 15322, had a resistant response to WSMV in this test. Osage had a moderately resistant response and all of the other entries had a susceptible response (Table I).

The cultivar Osage which showed moderate stunting and yellowing symptoms still had a good growth (Figure 2) which was comparable to that developed by the wheat x Agropyron selections (Figure 3). The growth of cultivars and selections in the test was poor by comparison (Figure 4).

Figure 1. Stunting and Yellowing of Many of the Wheat Cultivars and Selections Tested in the Field in 1974-1975 After Wheat Streak Mosaic Viruliferous Mite Infestation.

TABLE I

REACTION OF 8 WINTER WHEAT CULTIVARS AND SELECTIONS TO WSMV 180 DAYS FOLLOWING INOCULATION BY VIRULIFEROUS MITE INFESTATION

Cultivar or Selection	Reaction to WSMV[1]
Eagle	6
C.I. 15321	2
OK66V2621	7
C.I. 15322	2
Osage	4
OK66V2629	7
OK66V5262	8
CO64A1002-2	7

[1]Estimates of disease severity where 0 = immune and 9 = killed by the disease.

Figure 2. Response of the Cultivar Osage 60 Days After Inoculation With WSMV Viruliferous Mites

Figure 3. Response of the Wheat x Agropyron Selections C.I. 15321 (Above), and C.I. 15322 (Below) to WSMV 60 Days Following Inoculation With Viruliferous Mites.

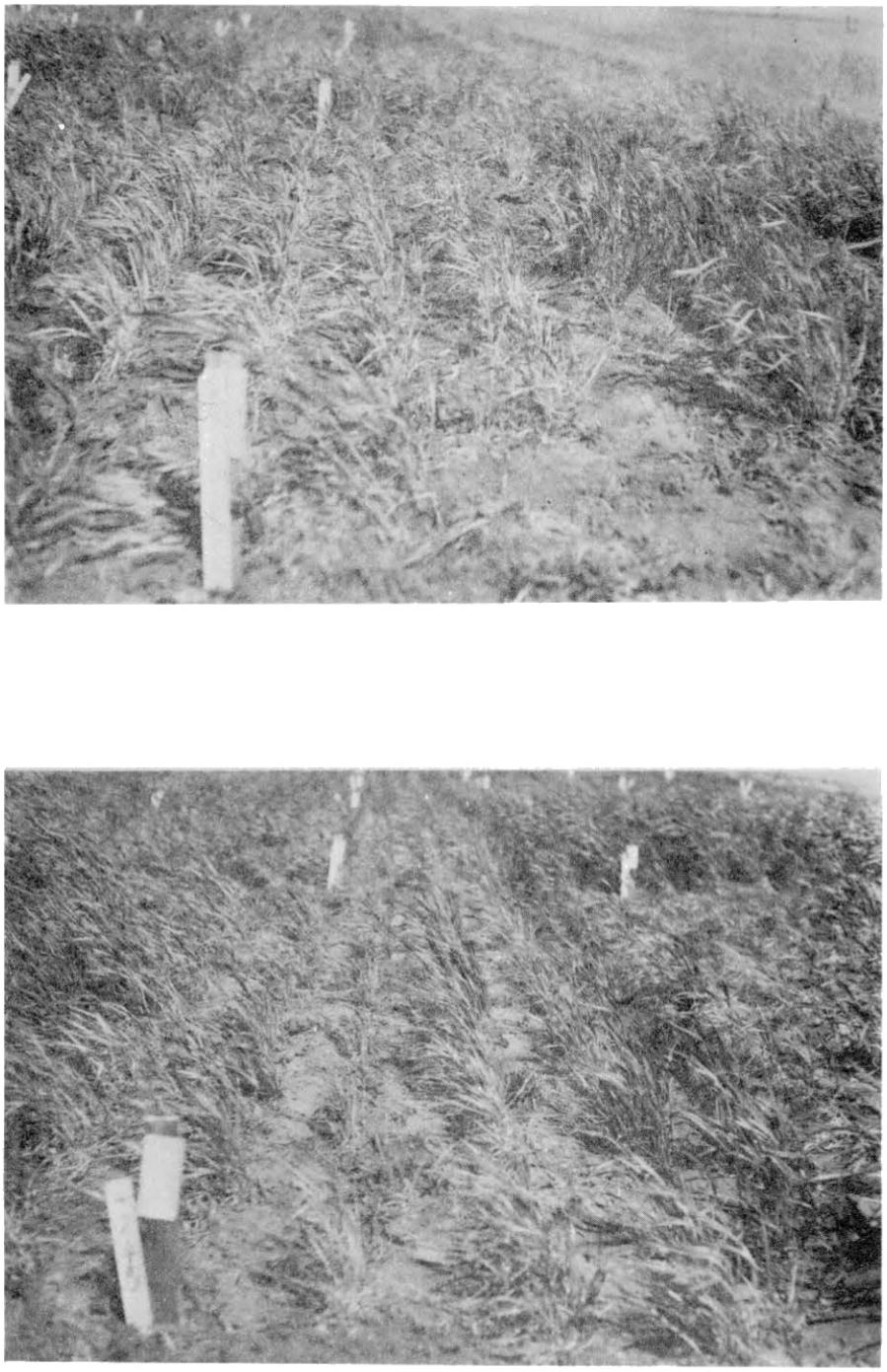

Figure 4. Response of Two Selections of the Cultivar Scout, OK66V2621 (Above), and OK66V2629 (Below) to WSMV 60 Days After Inoculation by Viruliferous Mites

Although the response of the cultivar Osage was only moderately resistant, it was able to produce about the same grain yield as were the two resistant entries (Table II). The remainder of the entries in the test were actually almost killed before heading time. The number of productive spikes was so small that no attempt to harvest for grain yield was made.

The mite counts showed considerable variation in population among leaves of the same entry. The coefficient of variation was high and variance increased as means increased. Therefore, the data were transformed into log (base 10) of one more than the count in order to stabilize the variance. Analysing these transformed data significant difference was obtained at the fourth sampling date (April 23, 1975). The mean number of mites found on each entry at four sampling dates is presented in Table III. Although a significant difference was encountered among entries at the fourth sampling this difference was small and inconsistent. The mean of all four samplings indicated no significant difference among the cultivars and selections tested. Significant differences were found in the mite population at different times during the growing season. The mite population increased rapidly and peaked by the end of the fall season (November 1) and then decreased throughout the winter. Living mites were found in January although the daily minimum temperatures during December and January 1975 were mostly below freezing. No mites were encountered on any cultivars or selections as plants approached maturity in the late spring.

TABLE II

GRAIN YIELD OF TWO WHEAT X AGROPYRON SELECTIONS AND THE CULTIVAR OSAGE WHEAT INOCULATED WITH WSMV BY VIRULIFEROUS MITE INFESTATION

Cultivar or Selection	Grain Weight in gms/plot[1]
C.I. 15321	90.9
C.I. 15322	99.9
Osage	83.0
Overall Mean	91.2

LSD 0.05 53.8

[1]Each figure is the mean of 8 replications of 3 3.1 m rows 20 cm apart.

TABLE III

NUMBER OF MITES (ACERIA TULIPAE) FOUND ON 8 CULTIVARS OR SELECTIONS OF WINTER WHEAT AT 4 DATES FOLLOWING ARTIFICIAL INFESTATION OF BORDER ROWS

Cultivar or Selection	Mean No. of Mites[1] Sampling Date Oct. 10	Nov. 1	Jan. 24	Apr. 23	$\bar{X}$
C.I. 15321	98.0	160.3	48.4	3.3	77.5
OK66V2629	114.6	170.0	18.1	1.9	76.2
Osage	28.5	220.3	43.5	7.4	74.9
Eagle	90.5	142.5	15.3	2.3	62.7
C.I. 15322	59.1	155.6	29.8	1.6	60.8
OK61V5262	63.4	123.3	43.1	0.8	57.7
C064A1002-2	72.4	105.3	45.4	3.6	56.7
OK66V2621	34.5	127.5	24.5	4.6	47.8
Mean	70.1	150.6	33.5	3.2	64.3
LSD 0.05	93.8	113.2	28.0	4.1	

[1]Mean of 8 replications of 5 leaves per sample.

Growth Chamber Experiments

Plant Height

Measurements of plant height before inoculation indicated no significant difference in most of the entries tested (Table IV). The only test where there was a significant difference in height between entries was that grown for the first density gradient centrifugation test. That difference also lead to a significant difference among entries when information from both growth chamber experiments were combined. However, there was no statistical difference in height between the resistant group (wheat x Agropyron selections) and the reportedly tolerant group (remainder of the entries). The average height of one of the resistant selections, C.I. 15322, was shorter than some of the other entries. The overall average height of plants grown in the first growth chamber experiment was slightly higher than that of the second experiment.

Plant Weight

There was a significant difference in plant weight between entries at the 5% level only with plants prepared for infectivity assay test in the second growth chamber experiment (Table V). Unlike plant height, there was a significant difference in weight observed between the resistant group and the tolerant group of entries. The resistant line C.I. 15321 yielded the highest fresh weight whereas C.I. 15322 did not weigh more than any of the tolerant cultivars and selections. This was probably correlated with its smaller plant height. The Scout selections and Osage weighed less than the other

TABLE IV

HEIGHT IN CM OF SEEDLINGS OF 8 WHEAT CULTIVARS AND SELECTIONS

Cultivar or Selection	Height of Plants Used for:[1] Infectivity Test Exp. 1	Infectivity Test Exp. 2	Infectivity Test Mean	Rate Zonal Centrifugation Test Exp. 1	Rate Zonal Centrifugation Test Exp. 2	Rate Zonal Centrifugation Test Mean
Eagle	27.9	25.2	26.5	25.5	24.3	24.9
C.I. 15321	26.8	23.0	24.9	25.3	24.6	25.0
OK66V2621	23.0	24.0	23.5	24.5	21.9	23.2
C.I. 15322	23.6	23.2	23.4	21.5	22.1	21.8
Osage	25.7	23.1	24.4	24.5	22.9	23.7
OK66V2629	27.7	23.8	25.8	23.1	23.5	23.3
OK61V5262	24.2	20.9	22.6	25.7	22.1	23.9
C064A1002-2	27.1	24.8	26.0	26.9	25.1	26.0
Experiment Mean	25.8	23.5	24.6	24.6	23.3	24.0
LSD 0.05	3.9	4.8	2.8	2.5	3.8	2.0

[1]Mean from 2 pots of 10 plants each.

TABLE V

FRESH WEIGHT IN GRAMS OF SEEDLINGS OF 8 WHEAT CULTIVARS AND SELECTIONS

Cultivar or Selection	Weight of Plants Used for:[1] Infectivity Test Exp. 1	Infectivity Test Exp. 2	Infectivity Test Mean	Rate Zonal Centrifugation Test Exp. 1	Rate Zonal Centrifugation Test Exp. 2	Rate Zonal Centrifugation Test Mean
Eagle	7.8	6.2	7.0	9.6	6.4	8.0
C.I. 15321	9.1	9.3	9.2	9.1	9.2	9.2
OK66V2621	6.5	5.8	6.2	7.7	6.2	6.9
C.I. 15322	7.7	7.9	7.8	7.3	8.5	7.9
Osage	6.8	6.0	6.4	7.4	5.7	6.5
OK66V2629	7.1	5.8	6.5	8.9	6.5	7.7
OK61V5262	7.3	5.4	6.3	7.7	7.0	7.3
C064A1002-2	8.1	6.0	7.1	7.7	6.3	7.0
Experiment Mean	7.6	6.6	7.1	8.2	7.0	7.6
LSD 0.05	1.8	2.1	1.3	2.6	2.6	1.7

[1]Mean weight of 15 plants.

tolerant entries but this difference was not significant. Similarly to height, the fresh weight of plants of the first growth chamber experiment exceeded that of the second experiment. However, none of these differences in height and weight of plants were believed to be significant enough to influence the results obtained with the infectivity or density gradient assays.

Varietal Reaction to WSMV

When the entries were inoculated their reaction to the virus varied as measured by symptom expression and the number of diseased plants. Means of the number of systemically diseased plants are presented in Table VI. The wheat x Agropyron selections, as in the field, were resistant to WSMV. In spite of the fairly large local lesions on inoculated leaves, no typical systemic symptoms were observed on 12-14 day old leaves developed at the temperature and incubation period used (Figure 5). Systemic symptoms were observed on all the rest of the entries, however, some variation in symptoms existed. A few faint chlorotic streaks were observed on leaves of the cultivar Eagle whereas prominent chlorotic streaks developed on leaves of certain other entries and the older leaves of the Scout selections turned completely yellow. Osage had pronounced systemic symptoms, but growth was comparable to the resistant wheat x Agropyron selections (Figure 6). It is also interesting that this cultivar exhibited considerable resistance in the field. Scout selection C064A1002-2 was the most susceptible entry in the test having strong symptoms and weak plants (Figure 7). In contrast to the field experiment, no obvious stunting was observed in any entry.

TABLE VI

NUMBER OF SYSTEMICALLY INFECTED PLANTS OF 8 CULTIVARS AND SELECTIONS OF WHEAT 12-14 DAYS AFTER INOCULATION WITH WSMV

Cultivar or Selection	Number of Infected Plants Among Those Used for: Infectivity Test[1] Exp. 1	Exp. 2	Mean	Rate Zonal Centrifugation Test Exp. 1	Exp. 2	Mean
Eagle	13.5	15.0	14.3	14.0	14.5	14.3
C.I. 15321	0.0	0.0	0.0	0.0	0.0	0.0
OK66V2621	15.0	14.5	14.8	15.0	15.0	15.0
C.I. 15322	0.0	0.0	0.0	0.0	0.0	0.0
Osage	14.5	14.0	14.3	14.5	15.0	14.8
OK66V2629	14.0	11.5	12.8	14.0	15.0	14.5
OK61V5262	14.0	12.5	13.3	14.0	14.5	14.3
C064A1002-2	13.5	15.0	14.3	14.5	14.5	14.5
Experiment Mean	10.6	10.3	10.4	10.8	11.1	10.9
LSD 0.05	1.0	1.5	1.0	1.6	1.1	0.9

[1]Means from 2 pots of 15 plants each

[2]Means from replications of 15 plants per replication

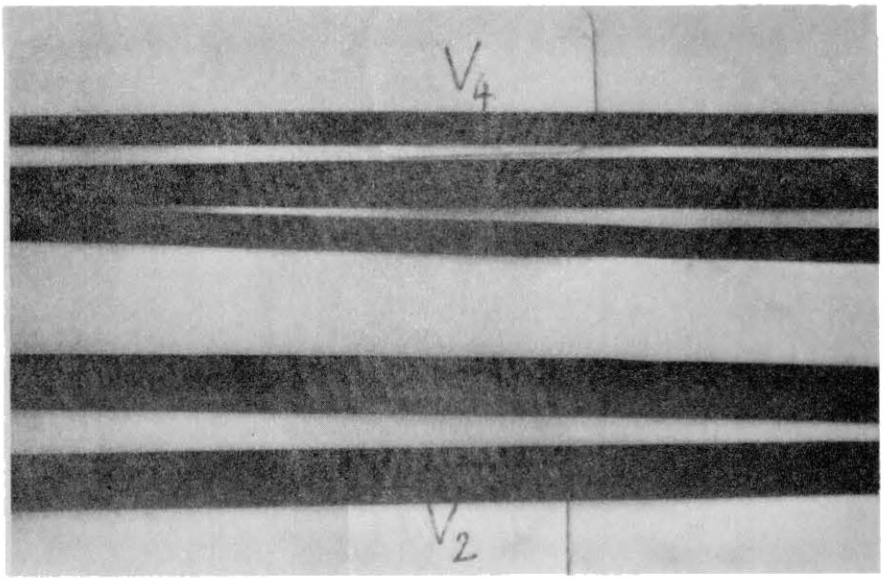

Figure 5. Leaves of the Wheat x Agropyron Selections C.I. 15322 (Above) and C.I. 15321 (Below) 12 Days After Inoculation With WSMV. No Symptom Expression Occurred.

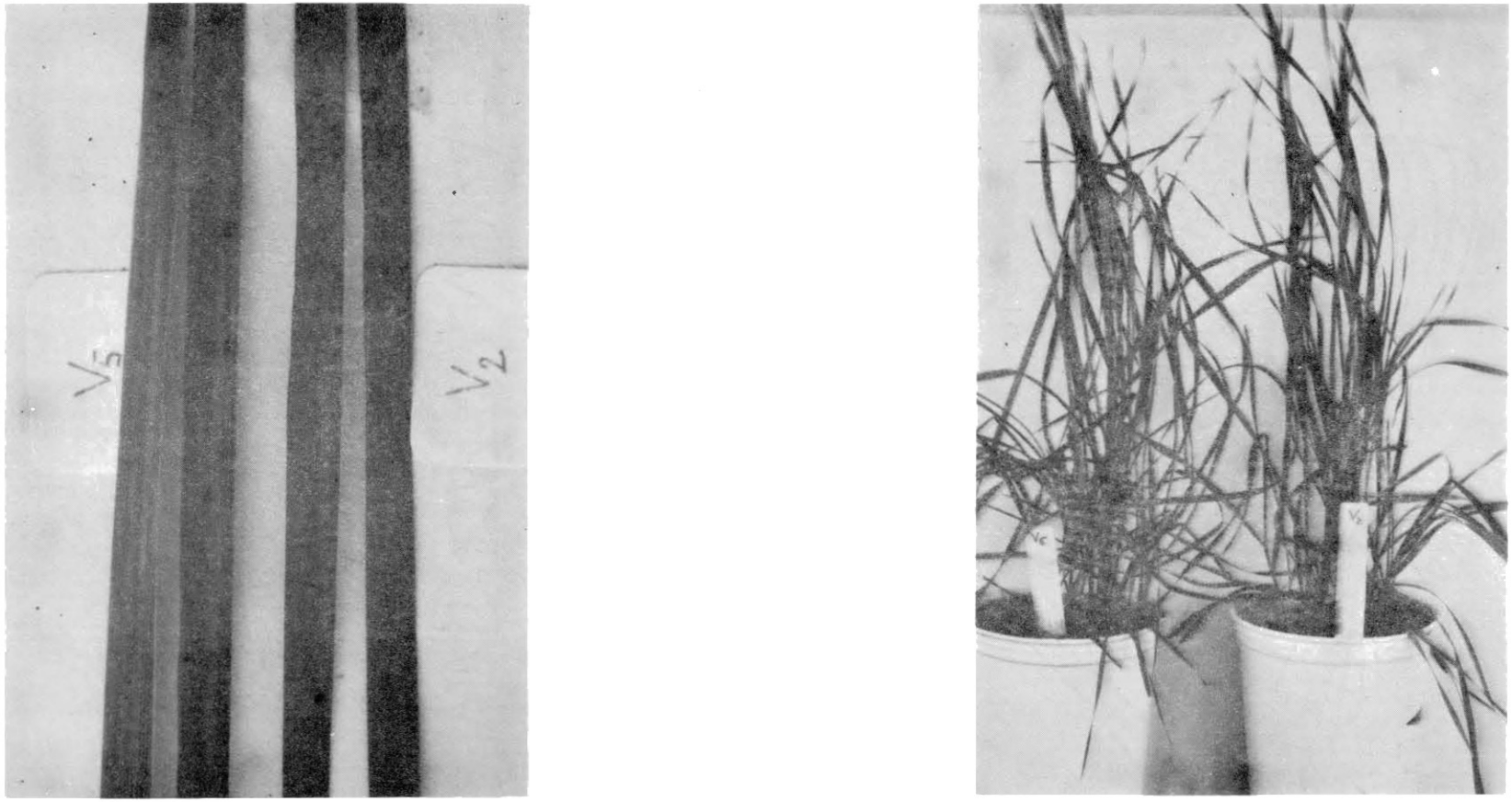

Figure 6. A Comparison of the Symptoms (Left) and Growth (Right) of Osage (Left in Each Case) and the Wheat x Agropyron Selection, C.I. 15321 (Right in Each Case) 12-14 Days After Innoculation With WSMV.

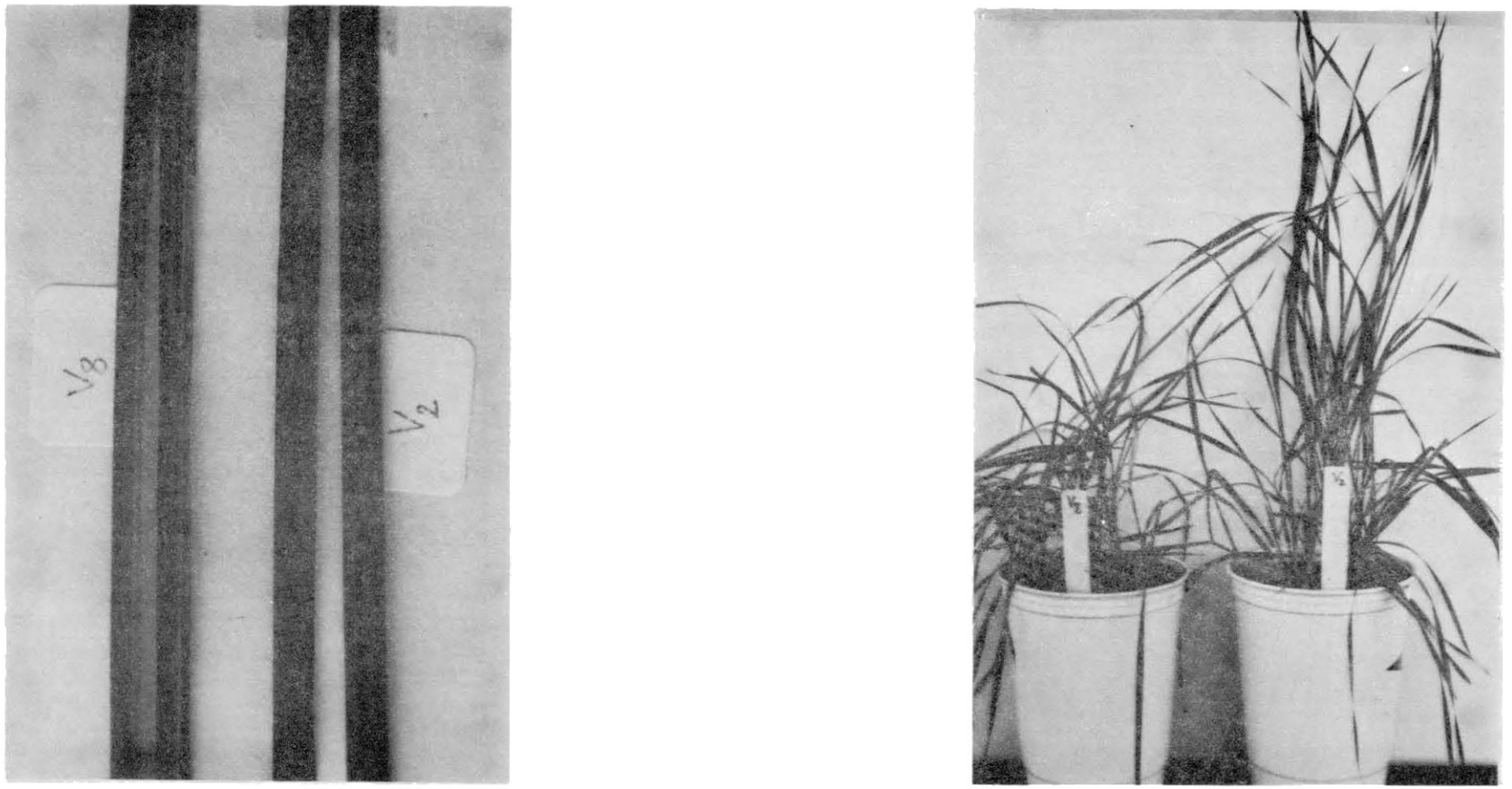

Figure 7. Comparison of the Symptoms (Left) and Growth (Right) of Scout Selection C064A1002-2 (Left in Each Case) With the Wheat x Agropyron Selection, C.I. 15321 (Right in Each Case), 12-14 Days After Inoculation With WSMV.

Infectivity Assay

A higher number of infected assay plants should reveal a higher number of infectious virus particles in the plant extract. The number of assay plants showing symptoms differed greatly between those inoculated with extract from plants of previously inoculated wheat x Agropyron selections and from plants of the other entries (Table VII). Although only a small number of assay plants became infected using extract from the infected wheat x Agropyron selections the results indicated that virus development in these selections was sufficient to cause some local lesions and induce some systemic symptoms on a few assay plants.

Infectivity of the plant extracts decreased with dilution, as would be expected. Good comparisons between entries were made with the 1:100 dilution, whereas the 1:1000 dilution appeared to be near the maximum dilution for the purpose of comparison.

In any analyses in which the response variable is a number related to a uniform total number, as the number of infected plants per pot in these experiments the question of the validity of standard analysis of variance arises. Steel and Torrie (54) recommend that the arcsine of the response variable be used in such cases. For this reason, all analyses of this kind in the present study were repeated using the arcsine transformation; that is, the response variable used was arcsine (P) where P is the proportion of infected plants per pot. However, since the analyses of variance for the transformed data gave essentially the same result as the original data, all of the analyses reported here are given for the original data.

TABLE VII

NUMBER OF ASSAY PLANTS INFECTED WITH WSMV WITH 2 DILUTIONS OF EXTRACT PREPARED FROM PREVIOUSLY INOCULATED PLANTS OF EACH OF 8 CULTIVARS AND SELECTIONS OF WHEATS

Cultivar or Selection	Number of Plants Infected			
	Exp. 1 Dilution		Exp. 2 Dilution	
	1:100	1:1000	1:100	1:1000
Eagle	12.0	2.0	15.5	7.5
C.I. 15321	2.5	0.5	1.0	0.5
OK66V2621	10.5	1.0	19.0	8.5
C.I. 15322	0.0	0.0	6.0	1.5
Osage	16.0	4.0	11.5	2.5
OK66V2629	11.0	2.0	14.0	3.5
OK61V5262	8.5	4.0	8.5	3.5
C064A1002-2	9.5	1.5	16.5	8.0
Mean	8.8	1.9	11.5	4.4
LSD 0.05	6.8	1.8	10.6	4.6

[1]Each figure is the mean of 2 pots of 20 plants each.

Density Gradient Centrifugation and Spectophotometric Assay

Although the experiment was originally arranged in a randomized complete block model having one pot of each entry represented in each replication, the material from a single pot was insufficient for the testing procedure which made it necessary to combine the plants harvested from 2 pots of the same entry. Therefore, the analysis of variance was conducted in randomized complete block design using experiments as blocks.

The highest absorbance unit related to the virus was obtained from the fractions drawn at 10 to 10.5 ml below the meniscus. Means of the absorbance units of the fractions at this depth, diluted 6 times with phosphate buffer, are presented in Table VIII. The results, after multiplying with the dilution factor and the unit area under the peak, are also given.

Significant differences between the absorbance units at 254 mμ and between the area under the peaks revealed variation of the relative amount of virus developed within different entries after inoculation. There was no significant difference in absorbance units for the two resistant lines, C.I. 15321 and C.I. 15322. No peak was obtained at the expected depth for C.I. 15321 while C.I. 15322 showed a small peak. A scanning pattern of rate gradient columns for each entry are presented in Figures 8 through 15, respectively.

When the remainder of partly purified extract of each entry was used to inoculate 5 assay plants, extract from the wheat x Agropyron selections induced one diseased plant each, whereas that from each of other cultivars and selections produced four diseased plants each.

These results indicate that infectious particles remained in the extract after the purification procedures.

TABLE VIII

ABSORBANCE UNITS OF THE FRACTIONS AT 10-10.5 ML BELOW THE MENISCUS CONTAINING PURIFIED VIRUS FROM 8 CULTIVARS AND SELECTIONS OF WHEAT AND UNIT AREA UNDER THESE PEAKS

Cultivar or Selection	Absorbance at 254 mμ[1] Diluted	X6	Unit Area Under Peak
Eagle	0.0565	0.339	0.425
C.I. 15321	0.0315	0.189	0.000
OK66V2621	0.0440	0.264	0.450
C.I. 15322	0.0335	0.201	0.135
Osage	0.0505	0.303	0.435
OK66V2629	0.0465	0.279	0.440
OK66V5262	0.0450	0.270	0.280
C064A1002-2	0.0410	0.246	0.685
Mean	0.0435	0.261	0.356
LSD 0.05	0.01	0.06	0.08

[1]Mean of 2 replications (experiments)

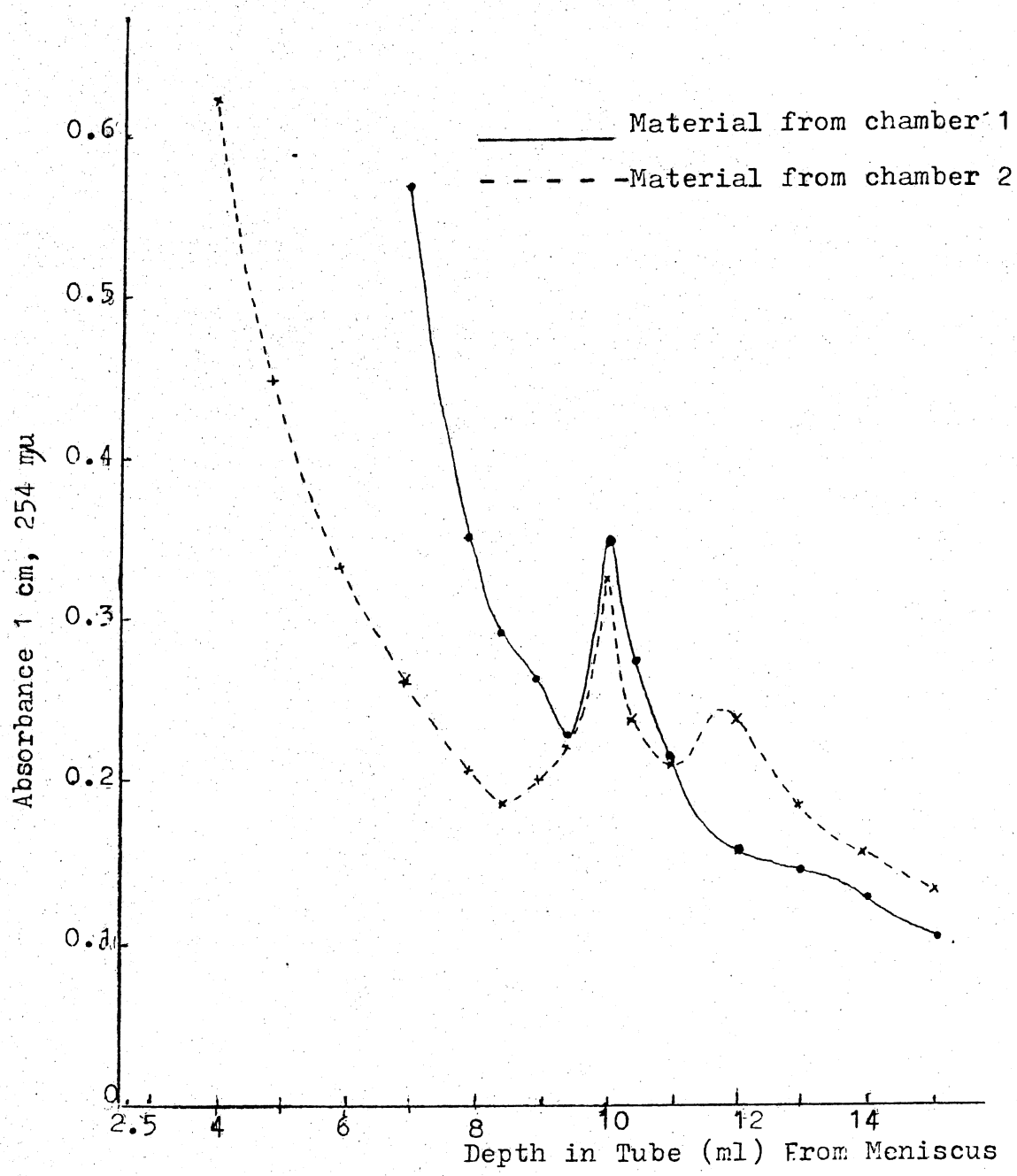

Figure 8. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From the Cultivar Eagle

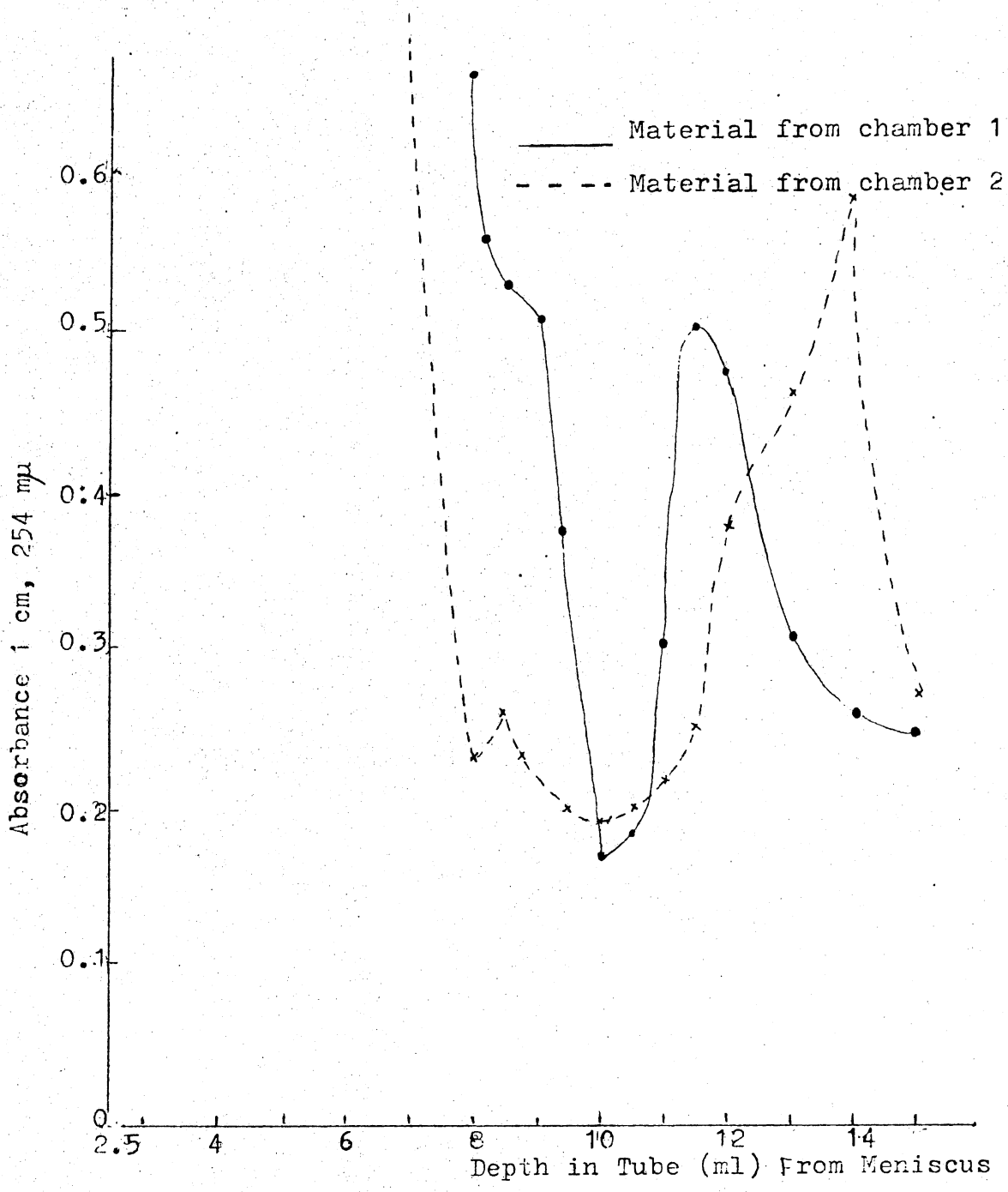

Figure 9. Absorbance Pattern of Fractions Drawn from Gradient Tube Containing WSMV from Wheat x Agropyron Selection C.I. 15321.

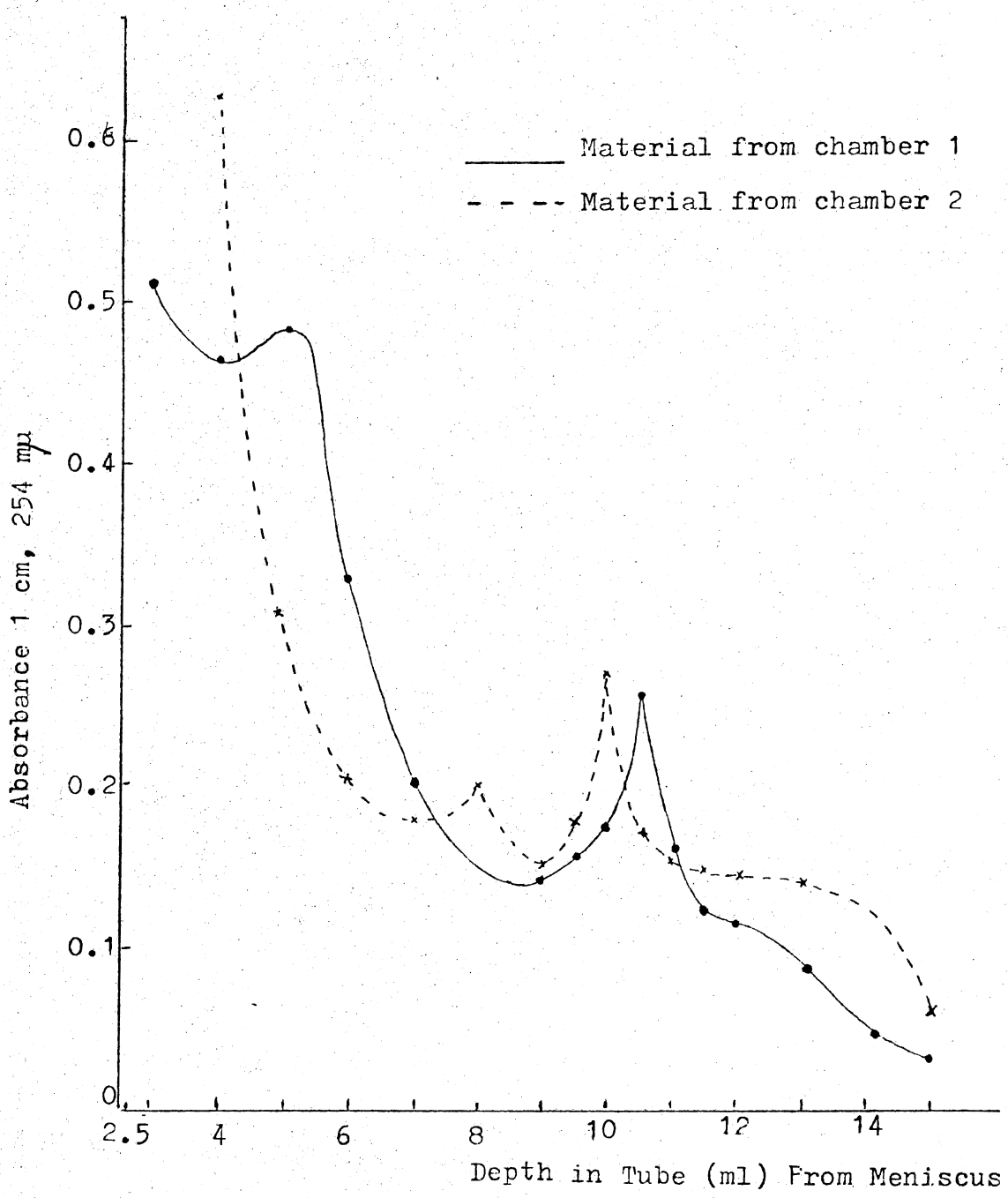

Figure 10. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From Scout Selection OK66V2621.

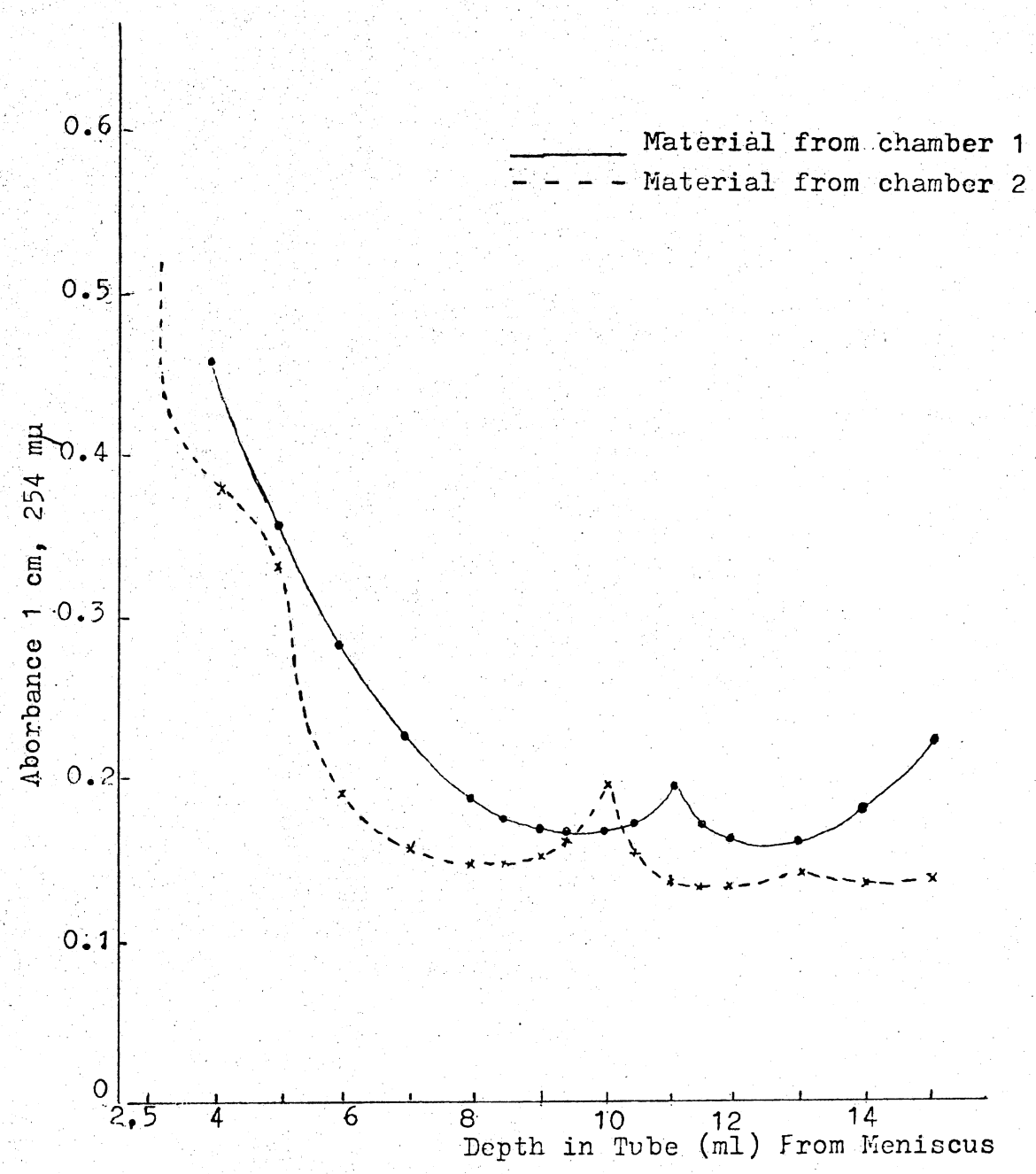

Figure 11. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From Wheat x Agropyron Selection C.I. 15322.

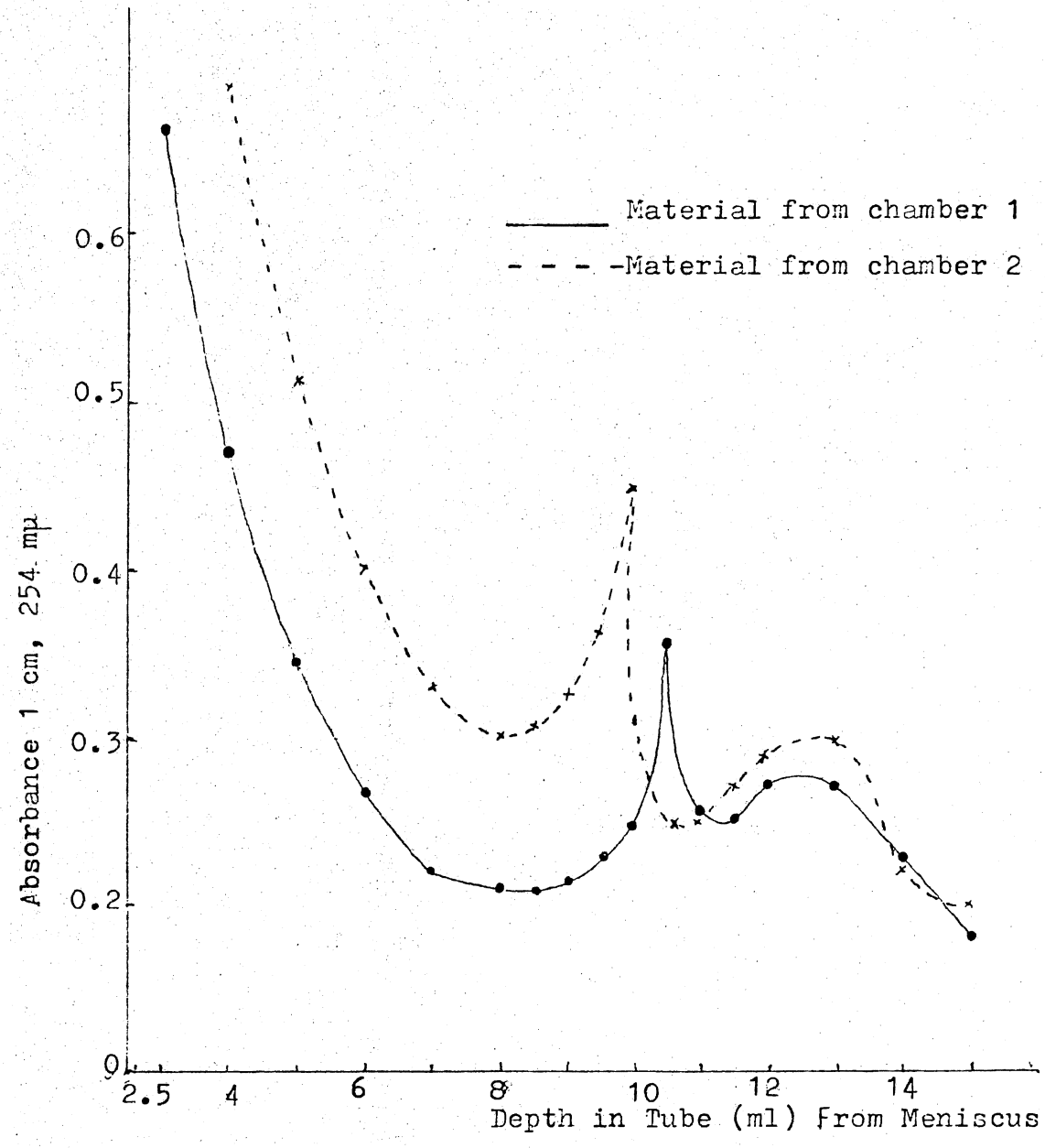

Figure 12. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From the Cultivar Osage.

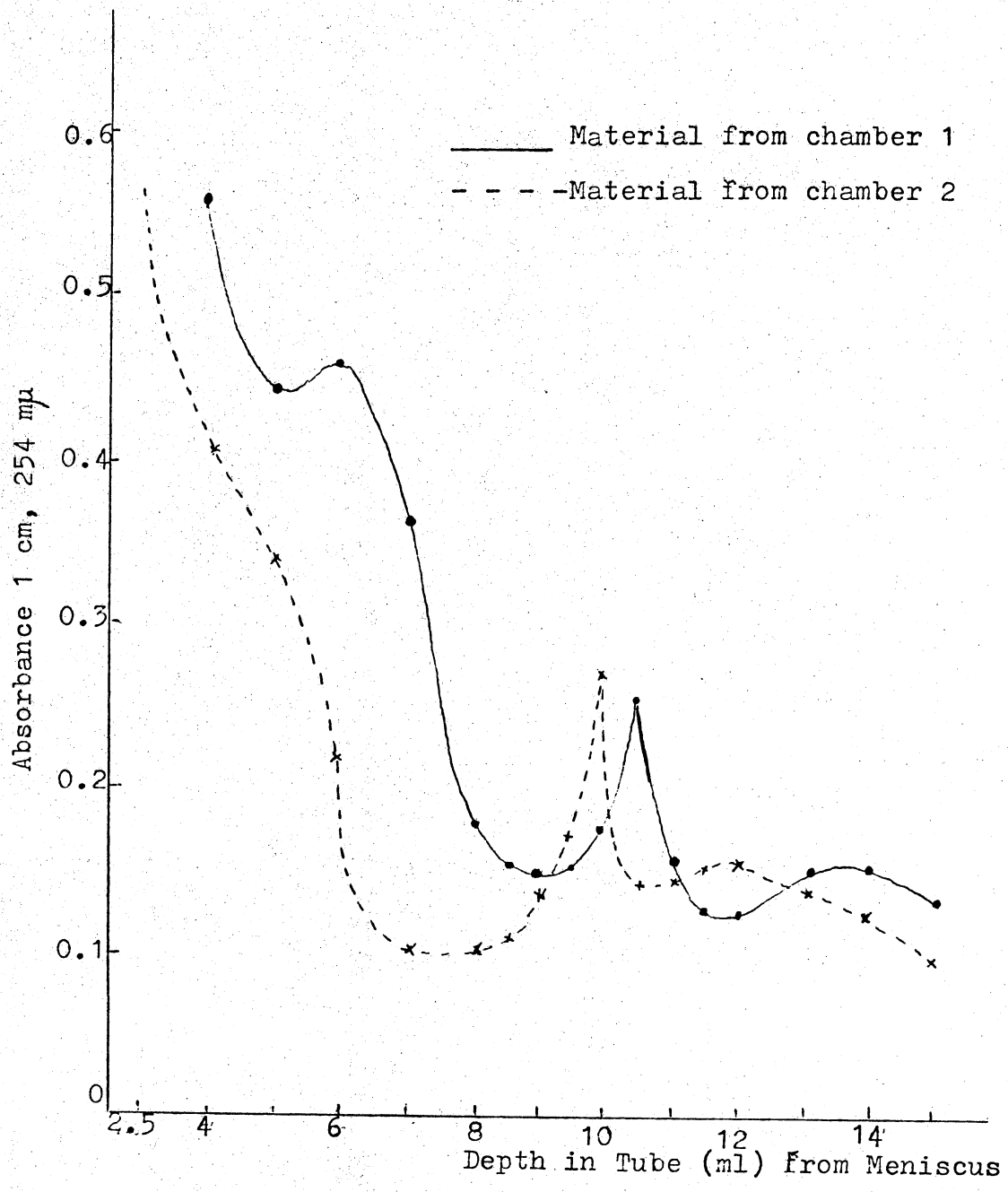

Figure 13. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From Scout Selection OK66V2629.

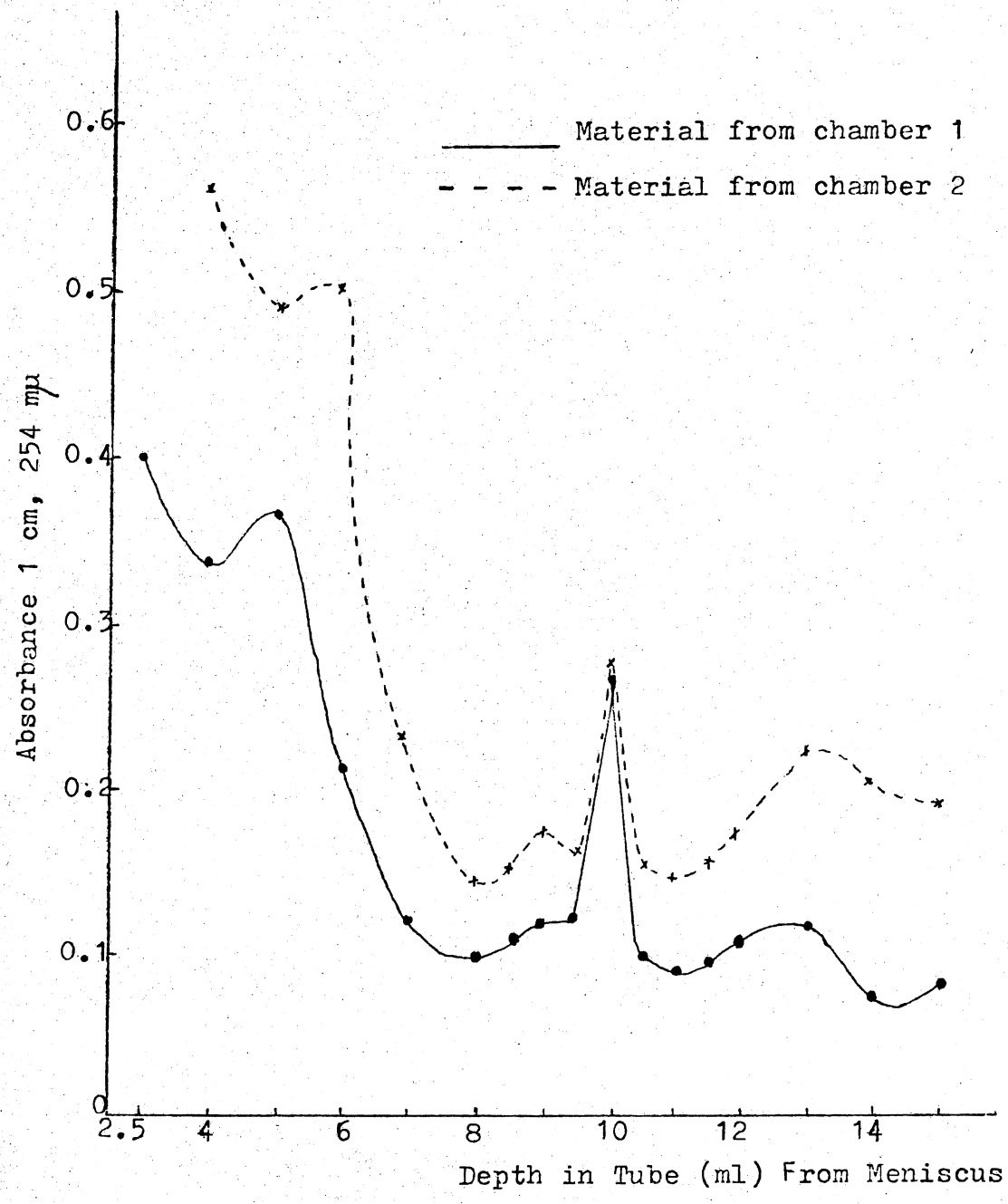

Figure 14. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From a Selection of the Cross Concho//Timstein/2*Pawnee.

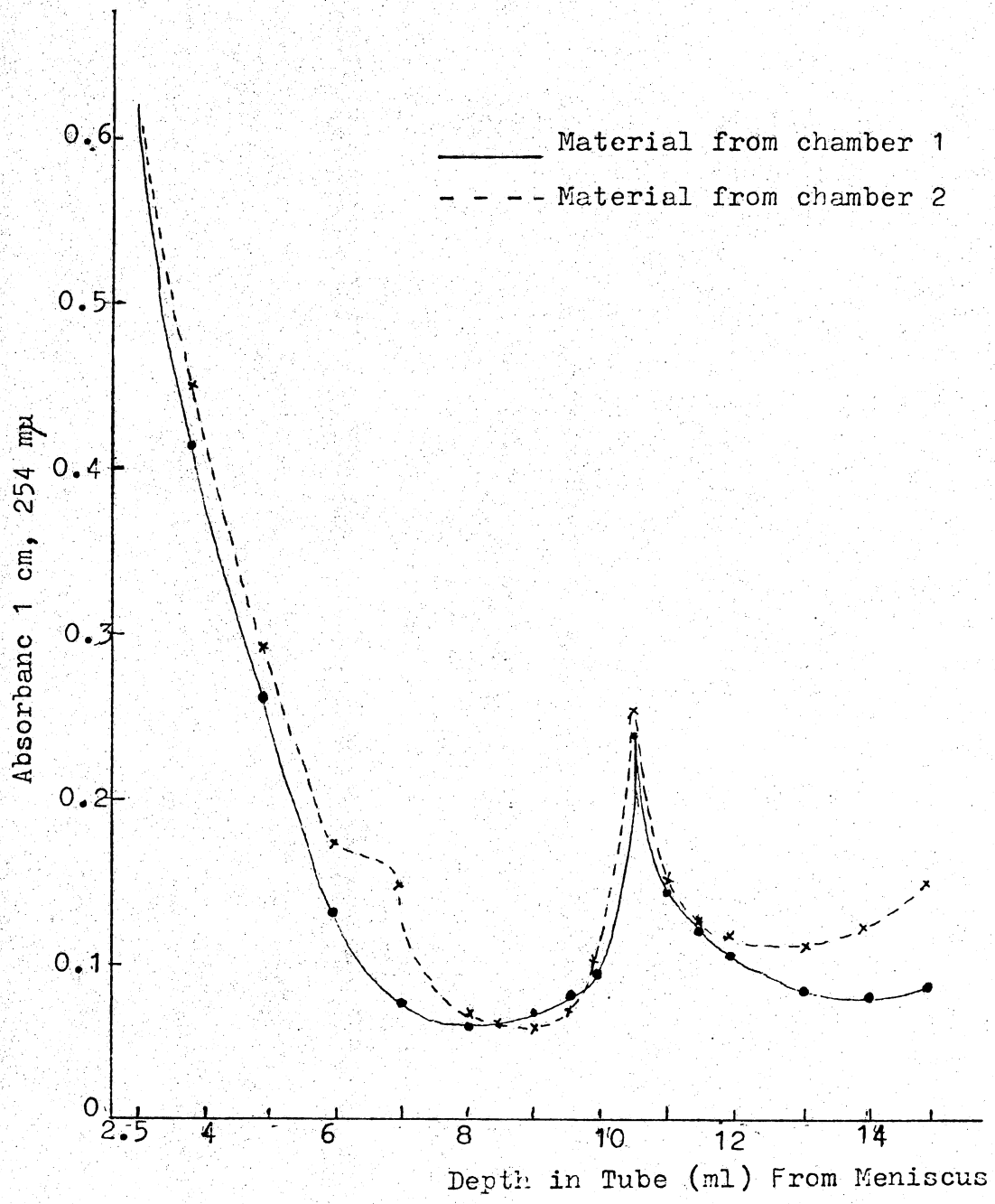

Figure 15. Absorbance Pattern of Fractions Drawn From Gradient Tube Containing WSMV From Scout Selection C064A1002-2

CHAPTER V

DISCUSSION

Although Somsen and Sill (52) noted the susceptibility of A. elongatum to the eriophyid mite Aceria tulipae, there are a number of reports of mite resistance in some wheat x Agropyron lines (1, 25, 27). In this study, the selections of winter wheat tested exhibited different levels of susceptibility to WSMV under the field conditions but no evidence of difference in susceptibility to the vector was detected among the entries before the boot stage of development. The two wheat x Agropyron selections were resistant to WSMV, but seemed to develop a mite infestation similar to other entries in the test. The results, therefore, did not agree with the work of Martin, et al. (27) who found a lack of reproduction of mites on these same selections. This may be partly due to the different time of the season and methods by which the two experiments were made. Environmental factors and age of plants seemed to have more effect on the mite population than did the difference in the wheats tested.

The yield capacity of the two wheat x Agropyron lines is lower than Osage in the absence of WSMV and mites (51). In this study, with both WSMV and mites present during the season the yield of the two selections and Osage was not significantly different. This suggested some level of resistance in Osage. Eagle showed the same response, but to a lesser degree. The rest of the entries

appeared to be quite susceptible to the combination of WSMV and mites in this study.

Because of the similarity in height of the tested entries in most of the experiments, it was likely that the surface area being inoculated manually would be about the same for every entry. However, at least one of the wheat x Agropyron selections C.I. 15322, may have possessed fewer susceptible sites as a result of slightly smaller leaves. Regardless of the initial quantity of virus entering the plants, the amount of virus developed in the two resistant wheat x Agropyron selections was lower than in the other six entries. This was established by each of the methods used; the number of infected plants of each entry, the number of infected assay plants, and the purification-photometric results.

The purpose of this study was only to compare the virus content in the resistant selections relative to the other entries and not to analyse the exact amount of virus multipled in each of them. Therefore, a number of procedures used were different from some previous assay studies on WSMV.

In these experiments, not only the young leaves which emerged after inoculation but the whole plants, except roots, were harvested for virus analysis because any amount of virus produced or retained in viable condition in the above ground plant parts following infection was of interest. Local lesions on the wheat x Agropyron selections revealed the development of virus to some extent with the incubation period used. They appeared to be neither symptomless carriers nor immune to the virus. Dhotre (13) reported that the resistance in P_3-19, from which the two resistant selections derived, broke down

at high temperature. Hence, virus particles normally confined to local lesions were also important.

Brakke (8) discussed the interpretation of infectivity assay and stated that the percentage of infected plants obtained approached the expected with the "Poisson Distribution". Since the number of inoculated plants of each entry in each test was the same, the results of the present infectivity assay was reported as the number of systemically diseased plants.

Brakke has also indicated that host heterogeneity has more effect on the results at high percentages of infection than at low (8). In this experiment, infectivity assay using 1:10 dilution was not included, but the percentage of infection at 1:100 dilution was sufficiently high except for the extract from the two resistant lines to produce significant differences. At 1:1000 dilution, even though the number of infected assay plants induced by the extract of the resistant wheat x Agropyron lines was less than those induced by extract of the other entries, the difference was not significant. Although significant comparisons could be made using the 1:100 dilution, the results were not always consistent with results obtained from the density gradient centrifugation test. Materials used in the infectivity test were harvested 2 days before those harvested for density gradient centrifugation. Amount of virus in infected plants has been noted to vary from day to day (9), and probably the rate of change is different from one variety to another. The selection of the cross Concho//Timstein/2*Pawnee OK61V5262 revealed a low concentration of virus in both types of the assays despite its susceptible reaction to WSMV in the field. A third entry in this study, Scout

selection OK66V2621 in contrast, had high virus content which corresponded directly with its susceptible reaction in the field test.

The absorbance units of the purified WSMV in this experiment were rather high even for the resistant wheat x Agropyron selections. This may be due to the procedures used and the time at which the plants were harvested for assay. Higher amounts of virus were expected from freezing the leaves, but this may not be effective in removing plant constituents that sediment with the virus in gradient column (9). Because of the low concentration of WSMV in the host plant, Gold, et al., (18) once stated that attempts to separate the virus from other tissue components were unsuccessful. Also, Razvyazkina, et al., (40) could not concentrate the virus by using Brakke's method. Although the concentration of virus was estimated by the area under the peak of the absorbance at 254 mμ, Brakke reported most of his results in terms of the absorbance unit. However, in this experiment, the absorbance unit did not always correspond with the area under its peak. Absorbancy for Scout selection C064A1002-2 was not significantly higher than that for the other entries but yielded a much larger area under the peak. The absorbance units for the two wheat x Agropyron selections did not differ significantly from each other, but C.I. 15322 had a small area under the peak at about 10.5 ml below the meniscus whereas C.I. 15321 did not. It had a peak at a deeper depth which was probably due to unseparable plant protein. Such peaks did not appear in any of the more susceptible entries, and it has been reported by Kanevcheva, et al., (23) that synthesis of plant protein in susceptible plants was inhibited.

The assay methods used in this study were able to differentiate the virus content in the resistant selections from that in the susceptible entries, but they were not effective in comparisons made between entries within either the resistant or susceptible class. In other words, the methods were able to indicate significant differences only when they were large. Whether or not virus confined to the local lesions of the resistant wheat can be transmitted by the vector to other susceptible hosts has yet to be studied.

CHAPTER VI

SUMMARY

1. Eight selections of winter wheat previously noted as tolerant or resistant to WSMV were tested to compare their reaction to the virus and its vector, the eriophyid mite (Aceria tulipae Keifer). Differences in virus content were determined by direct and indirect assays.
2. In the field, the varieties Eagle and Osage showed systemic symptoms but performed relatively well under viruliferous mite infestation. They were more tolerant to the virus than other direct selections from the cultivars Scout.
3. The wheat x Agropyron selections, C.I. 15321 and C.I. 15322 were more resistant to WSMV than other entries but did not differ from other entries in their susceptibility to the vector.
4. These two resistant selections did not produce significantly higher yield than did the cultivar Osage in this experiment.
5. After the inoculation of WSMV, the resistant selections produced local lesions and the amount of virus developed within them was sufficient to induce systemic symptom in a few assay plants by using extracts of 1:100 and 1:1000 dilutions.
6. After the inoculation, only C.I. 15321 yielded more fresh weight than did other entries.
7. The virus content in the wheat x Agropyron selections was lower

than in other entries. This was revealed both by an infectivity assay and by density gradient centrifugation and spectrophotometry.

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