THE RATE OF SPREAD OF POTATO VIRUS DISEASES IN WESTERN NEBRASKA[1]

By R. W. Goss[2]

Associate Plant Pathologist, Nebraska Agricultural Experiment Station

INTRODUCTION

The rate and distance of the spread of potato virus diseases has been the subject of considerable speculation and some experimentation because of its great importance in the production of disease-free seed potatoes. Various investigations have shown that both rate and distance of spread will vary in different localities and in successive seasons in the same locality. It is therefore impossible to forecast the amount of spread in one locality from the results of investigations conducted under different environmental conditions. The only experiments dealing with the subject which have been conducted under western dry-land or irrigated culture are those reported by Werner[3] in a study of the spindle-tuber disease.

Spindle tuber has for some time been recognized as the most prevalent virus disease in western Nebraska; the various mosaics are not so common; and leaf roll seldom occurs. This order of relative importance is the reverse of that observed in the eastern part of the United States.[4] It was therefore thought probable that the factors involved in the spread of these diseases in this western area were probably very different from those occurring in the East.

The present investigation was outlined to determine if possible the reasons for the above facts and to gain information which might be of value in the control of these diseases. Repeated observations have shown that these diseases often spread more rapidly under irrigated than under dry-land conditions, and therefore the experiment was designed to include both types of culture. Unfortunately the dry-land plot had to be discontinued after the second year, but the results obtained from studying the relative spread of four potato virus diseases—leaf roll, mild mosaic, rugose mosaic, and spindle tuber—under irrigation are presented for the four years 1924 to 1927, inclusive.

METHODS OF INVESTIGATION

Two different methods of experimentation have been employed in previous investigations of this type: (1) The sampling of commercial fields at different distances from the source of infection, as used by Folsom[5] et al., and (2) the replanting hill by hill, in the same relative position, for several successive generations, of plants which have

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[2] The author is indebted to R. W. Samson for the survey and identification of insects in 1925 and 1926, and to Karl Koch for similar assistance in 1927. Published with the approval of the director as paper No. 72, Journal Series, Nebraska Agricultural Experiment Station.

[3] WERNER, H. O. THE SPINDLE-TUBER DISEASE AS A FACTOR IN SEED POTATO PRODUCTION. Nebr. Agr. Expt. Sta. Research Bul. 32, 128 p., illus. 1926.

[4] FOLSOM, D., SCHULTZ, E. S., and BONDE, R. POTATO DEGENERATION DISEASES: NATURAL SPREAD AND EFFECT UPON YIELD. Me. Agr. Expt. Sta. Bul. 331, 112 p. 1926.

[5] FOLSOM, D., SCHULTZ, E. S., and BONDE, R. Op. cit.

been exposed to infection, as employed by Murphy [6] in the study of leaf roll. The chief advantage of the first method lies in the fact that the diseases are being studied under practical field conditions. This advantage is sacrificed in the second method for the greater accuracy made possible by the more detailed study under conditions having fewer variable and uncontrolled factors. The latter method was used in this investigation.

The investigation was carried out at the Scotts Bluff substation, Mitchell, Nebr. The irrigated plot was isolated in a cornfield each year and was at least 100 to 300 feet distant from the nearest potato field. It was impossible to arrange the plot so that the direction of spread could be studied for successive years. The dry-land plot was located on the same farm but was on a lighter soil to which no irrigation water was applied. It was bordered by fields of corn, wheat, and alfalfa.

The plots used were small in size and consisted of 12 rows spaced 3 feet apart, with 27 hills to the row spaced 18 inches apart. Healthy Bliss Triumph tubers which had been indexed in the greenhouse were used as the source of seed. The term "greenhouse indexing" as used in this paper refers to the removal of one seed piece from a potato. This seed piece was planted in the greenhouse during the winter under conditions favorable for the development of the symptoms of the disease being studied. The remainder of the tuber was planted in the field the following spring. Seed pieces from each tuber were planted in both the dry land and irrigated plots.

Seed tubers obtained from plants affected with the virus diseases to be studied were planted in each plot as follows: Four leaf-roll plants were grown in row 4 as hills 4, 5, 6, and 7 and four mild-mosaic plants as hills 21, 22, 23, and 24. In the same way four rugose-mosaic plants were grown in row 9 as hills 4, 5, 6, and 7 and four spindle-tuber plants as hills 21, 22, 23, and 24. Thus the sources of infection for these four virus diseases, which will hereafter be referred to as the original disease units, were located, one in each corner of the plot. These original disease units are represented in Figures 1 and 2 by the dotted circles.

At the time this experiment was started the distinguishing symptoms of spindle-tuber and the very similar disease unmottled curly dwarf had not been clearly defined in the Bliss Triumph variety. As a result the original spindle-tuber units may have included some unmottled curly dwarf which had simply been diagnosed as severe spindle tuber. In this paper the term "spindle tuber" is therefore used to include both diseases.

One of the usual difficulties in an experiment of this type is the partial or incomplete infection of a hill. To eliminate this trouble as far as possible, each hill was cut back to a single stalk every year. Notes on the symptoms appearing in the field were made at one to two week intervals. Each hill was harvested separately, and a record was made of all symptoms of spindle tuber appearing in the tubers. One tuber from each hill was then selected for indexing in the greenhouse. In some instances a hill had to be classified as questionable spindle tuber, in which case the tuber exhibiting in the

[6] MURPHY, P. A. INVESTIGATION OF POTATO DISEASES. Canada Expt. Farms, Div. Bot. Bul. (2) 44 86 p., illus., 1921.

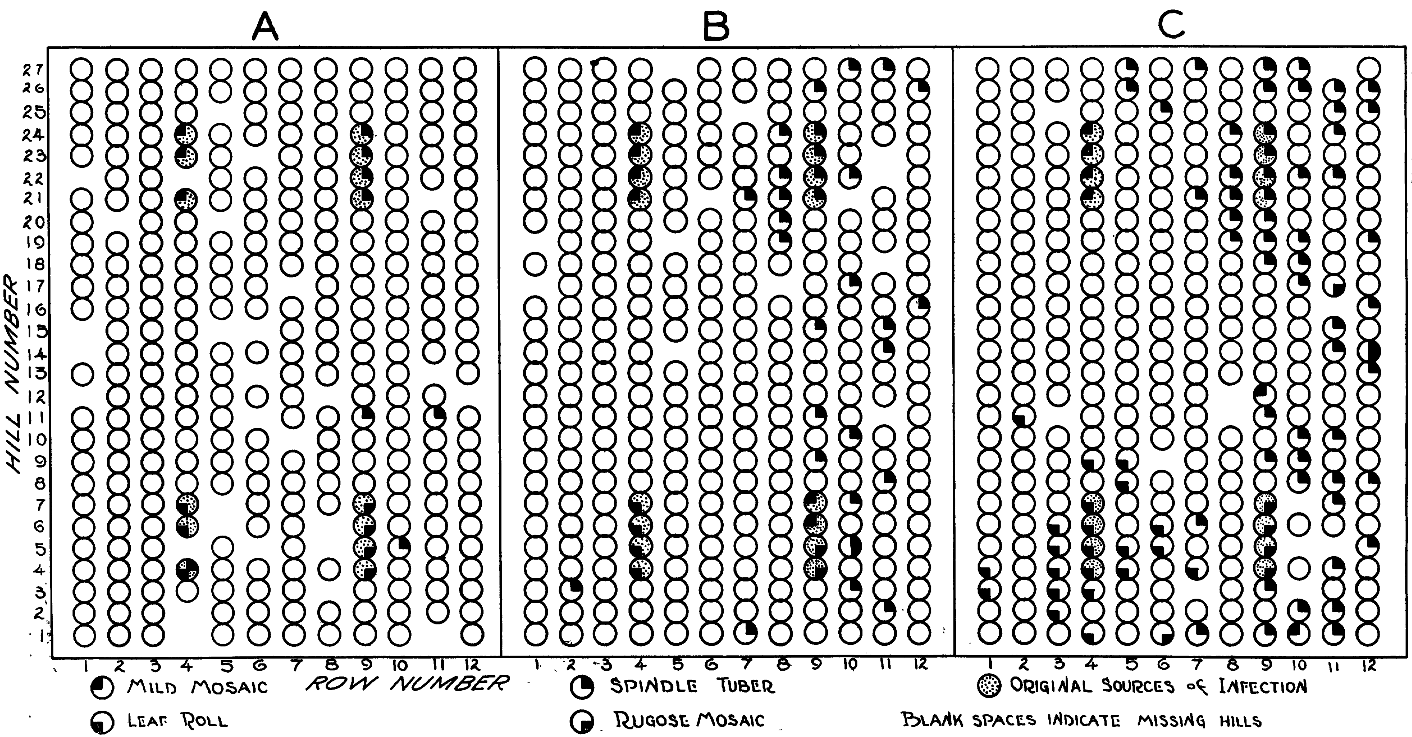

FIGURE 1.—Diagrammatic representation of the irrigated transmission plot for the years 1924 (A), 1925 (B), and 1926 (C). Each circle represents a hill planted in 1924 with healthy seed, except as noted by symbols. Each hill was cut back to a single stalk and one seed piece from each was planted in the same position the following year. The spread of the diseases studied can be followed by attention to the symbols. The plants marked as infected are those having symptoms in the field, but this does not include late-season infection as revealed by indexing (cf. Table 1). Such plants are listed in this figure for the following year when the disease appeared in the field

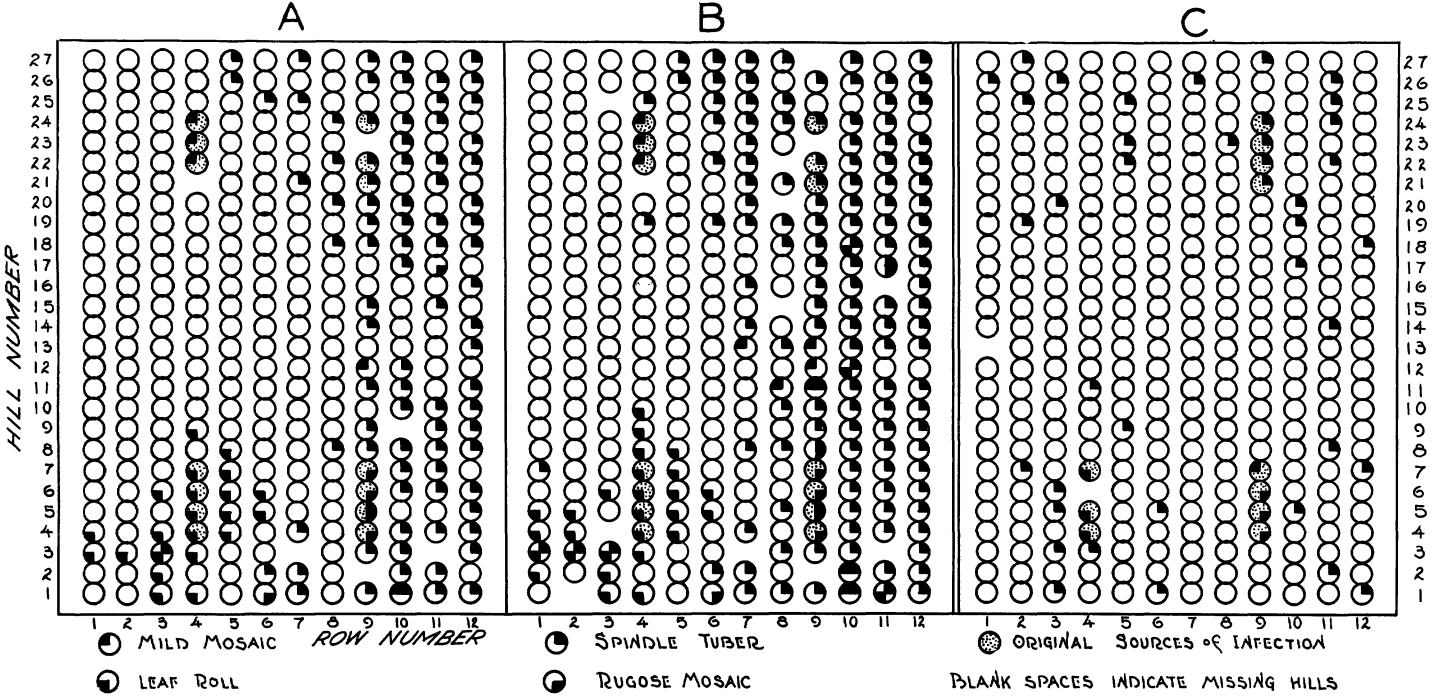

FIGURE 2.—Diagrammatic representation of the irrigated plot for the year 1927 (A); results of indexing the tubers in the greenhouse (B); the dry-land plot for 1925 (C) in which the tubers as original sources of infection in 1924 were planted in a manner similar to that used for the irrigated transmission plot. See Figure 1 for further explanation

greatest degree symptoms resembling those of spindle tuber was selected for indexing. Readings were made in the greenhouse for mosaic, leaf roll, and spindle tuber, and the plants were kept until the tubers had developed sufficiently for the detection of spindle-tuber symptoms. This usually required from two to two and a half months. This greenhouse indexing, which was carried out each year except 1926, was found to be a very great aid in the detection of leaf roll and mosaic, particularly the latter, which, because of the masking of symptoms under high-temperature conditions, is often very difficult to detect in the field in western Nebraska. The indexing in the greenhouse also served to determine the amount of transmission that occurred late in the season of the previous year but did not produce current-season symptoms.

The same tuber indexed in the greenhouse was used for planting in the field the following year. Each seed piece was planted in the plot in the same relative position. In case of missing hills due either to disease or to other causes the hill was planted with healthy seed the following year.

In 1925 and 1927 weekly notes were made of the prevalence of all insect species appearing in the plot. In 1924 and 1926 general observations were made of the insect population at various times throughout the season. No application of either spray or dust was made at any time during the four years.

RESULTS

The progressive spread of the diseases in the plots is shown graphically in Figures 1 and 2. The plants listed as infected are those which exhibited symptoms of the specified disease, either in the greenhouse the previous winter or in the field, and with only one exception the progeny of these hills showed similar symptoms. These plants may therefore have been the result of late infection the previous season or early current-season infection.

In the data presented in Table 1 and in the following discussion, the attempt has been made to determine the time of infection on the basis of the results secured by indexing in the greenhouse. Because of the above facts the figures presented in Table 1 and in the discussion do not check exactly with the data presented in Figures 1 and 2. The inclusion in the diagrams of data on the time of infection would have resulted in a complicated set of symbols and has therefore been omitted.

During 1924 and 1925 no precautions were taken against the spread of these diseases by the cutting knife. In 1924, however, the healthy seed was cut before the infected seed so that no disease could have been transmitted to healthy seed in this way. In 1925 there was no evidence of knife transmission having occurred as all seeds were cut in the same sequence as planted and no infection occurred in the hills immediately following the infected hills of the previous year. This lack of transmission by the cutting knife was probably due to the fact that the seed was cut a considerable time in advance of planting.

By examining Figures 1 and 2 it will be found that many plants listed as infected one year are marked as healthy the following year. In every instance but one this is due to missing hills or to the replant-

ing of infected hills with healthy seed because of an absence of seed tubers. These missing hills are noted in Table 1.

TABLE 1.—*Comparative yearly increase of leaf roll, mild mosaics, rugose mosaic, and spindle tuber in a plot of healthy potatoes grown under irrigation and originally planted with one 4-hill unit of each disease in 1924*

Year	Number of hills [a]	Total of infected hills [b]		New infections		Healthy replants or missing hills of infected seed
		Number	Per cent	Number	Per cent of healthy hills	
LEAF ROLL						
1924	295	3	1.0	0	0.0	1
1925	311	14	4.5	10	3.3	0
1926 [c]	312	26	8.3	12	4.3	0
1927	318	31	9.7	9	3.0	4
MILD MOSAIC						
1924	295	3	1.0	0	.0	1
1925	311	[c] 8	2.6	2	.7	0
1926	312	6	1.9	0	.0	0
1927	318	10	3.2	5	1.6	1
RUGOSE MOSAIC						
1924	295	4	1.3	0	.0	0
1925	311	[c] 6	1.9	4	1.3	0
1926	312	7	2.2	0	.0	1
1927	313	7	2.2	1	.3	0
SPINDLE TUBER						
1924	295	13	4.4	9	3.1	0
1925	311	35	11.2	24	8.0	2
1926 [d]	312	55	14.4	23	9.1	6
1927	318	136	42.4	87	37.6	6

[a] Three hundred and twenty-four seed pieces were planted each year.
[b] The total number of infected hills includes those showing symptoms when indexed.
[c] Two additional mild-mosaic plants were accidentally introduced in place of two rugose-mosaic plants.
[d] No indexing was done in 1926. Therefore part of those listed as 1927 infections may have occurred in 1926. This error does not affect the mild and rugose mosaic readings, as these infections occurred late in 1927.

The following discussion of the spread of these diseases refers entirely to the irrigated plot unless otherwise stated.

LEAF ROLL

The seed in one hill of the original leaf-roll unit planted in 1924 failed to sprout, while a second became infected with spindle tuber, possibly by the cutting knife. These were replaced in 1925 by other seed infected with leaf roll. No spread of leaf roll occurred in 1924. In 1925 no additional leaf-roll plants appeared in the field, but evidently some spread occurred, as 10 new leaf-roll plants were found when the progeny were indexed in the greenhouse. The infection probably occurred late in the summer of 1925. In 1926, 22 leaf-roll plants were found. Of these, 4 were in the original leaf-roll unit while 10 were due to previous season infection as noted above. The remaining 8 plants all showed slight symptoms of leaf roll early in July and were easily identified as leaf-roll plants by the 10th of August.

The disease was evidently caused by early season transmission. In 1927 only 4 new leaf-roll plants were found and these appeared as distinctly diseased early in July. The symptoms were as severe and appeared about as early as in the original leaf-roll unit, thus indicating that infection had probably occurred late in the season of 1926, and they are therefore listed in Table 1 as 1926 infections. The greenhouse index of 1927, however, revealed the fact that 9 new infections had occurred during the summer.

It may therefore be concluded that the greatest spread of leaf roll occurred late in the season of 1925. With three times as many sources of infection present in 1926, only 12 new infections occurred. Eight of these were evidently transmitted early and 4 late in the season. Only a slight amount of transmission occurred in 1927, as evidenced by 9 new infections when there were 22 plants to serve as sources of infection.

It is clearly evident from Figures 1 and 2 that the disease did not spread any great distance. Even after four years all the leaf-roll plants were restricted to that corner of the plot containing the original leaf-roll unit and no new infections appeared at any time more than three or four plants removed from leaf-roll plants. There was no apparent difference in spread from row to row and hill to hill within the row.

MILD MOSAIC

Only three of the four seed pieces in the original mild-mosaic unit sprouted in 1924. No transmission from these plants occurred in 1924 and there were no additional mild-mosaic plants found in the field in 1925. Two of the hills planted in 1925 in the original rugose-mosaic unit in row 9 were found to have been mild rather than rugose mosaic so that in 1925 there were six mild-mosaic plants in the plot. Two transmissions occurred, apparently from these two additional sources of infection, the symptoms appearing in the greenhouse and in the field in 1926. (Fig. 1, C, row 9, hill 12, and row 10, hill 1.) No spread of mild mosaic occurred in 1926 and no additional mild mosaic was observed in the field in 1927. Some transmission, however, probably occurred late in the season of 1927 as the indexed plants in the greenhouse revealed the presence of five new infections. Judging from the location of these hills in the plot (fig. 2, B, rows 7, 8, 9, and 10) none of these infections were transmitted from the original mild-mosaic unit but rather from the two new mild-mosaic plants of 1926, which in turn could be traced to the two mild-mosaic plants accidentally introduced in the original rugose-mosaic unit in 1925.

It is evident that in 1924 and 1926 no transmission of mild mosaic occurred and only a slight amount of spread took place in 1925 and 1927.

RUGOSE MOSAIC

Except in 1925, when two mild-mosaic plants were accidently inserted in place of rugose-mosaic ones, all plants in the original rugose-mosaic unit exhibited the typical symptoms every year. No transmission occurred in 1924 and only one additional rugose-mosaic plant was found in 1925, the symptoms appearing early in September. Three other infections, however, must have occurred late in 1925. as the symptoms appeared on the indexed plants in the greenhouse and in the field in 1926. No new infections were noted in 1926 and

only one in 1927, which probably occurred late in the season as the disease appeared for the first time in the indexed plant. The only instance of partial or incomplete infection of a tuber occurred with hill 14 in row 12 (fig. 1, C), which showed typical symptoms of rugose mosaic in the field in 1926 but failed to show any symptoms of the disease in 1927.

It is clearly evident that only a very slight amount of transmission, five infections, occurred in two of the four years. Two of these were to hills adjoining the original rugose-mosaic unit and the other three were somewhat scattered but none was more than a distance of 12 hills from a rugose-mosaic plant.

SPINDLE TUBER

Although the amount of transmission obtained with the mosaic diseases was slight, spindle tuber spread much more extensively. (Figs. 1 and 2.) The first evidence of spindle-tuber transmission was found when the tubers produced in 1924 were examined. Four plants produced tubers with distinct spindle-tuber symptoms and in addition 5 new infections were found when the tubers were indexed. In 1925 there were 19 new spindle-tuber plants as evidenced by either foliage or tuber symptoms, and 5 additional infections were discovered by indexing. In 1926 there were 26 infections, resulting in the appearance of current-season symptoms on either foliage or tubers. As no index was made in 1926, it is impossible to determine how many of the 38 new spindle-tuber plants that appeared in the field in 1927 were due to transmission late in the season of 1926. The index of the 1927 crop disclosed the fact that in addition to these 38 new spindle-tuber plants there were 49 late-season infections that did not cause symptoms in the tubers but did produce the typical disease when these tubers were indexed.

Even with the large amounts of spindle tuber present after the first year only 42.4 per cent of the plants were infected after four years. Furthermore, the disease did not spread for any great distance after the first year. In 1924, in addition to the original spindle-tuber unit, there were nine scattered infections, four of which are indicated in Figure 1, A. The five additional infections, which were found by indexing and which are listed in Figure 1, B, occurred in hills 1 and 21 in row 7, hill 22 in row 8, hill 9 in row 9, and hill 27 in row 11. Most of the spread in the following years was centered around these plants and the original spindle-tuber unit, with the exception of hill 3 in row 2, which became infected in 1925, and hills 26 and 27 in row 5, infected in 1926. An examination of Figure 2, A and B, might lead one to assume that the spread of this disease occurred chiefly in one direction. As previously noted, however, the plot was not laid out in the same direction each year. It is more probable that the large amount of spread in rows 9 to 12 was due to the distribution of the infections which occurred in 1924 and 1925. (Fig. 1, A, B.) The remarkable thing is that after four years there were only six spindle-tuber plants more than three rows removed from the row containing the original spindle-tuber unit, a fact which showed that the disease did not spread for any great distance. It was also notable that in these four heavily infected rows there still remained a half dozen healthy plants at the end of the four years. These are being tested to determine whether they possess any inherent resistance to the disease.

COMBINATIONS OF DISEASES

It would be expected that in a plot of the type used in these experiments there would be a considerable number of plants infected with more than one disease. It was fairly easy to distinguish disease combinations, with the possible exception of mild mosaic combined with rugose mosaic, and as these two diseases did not spread very extensively it is doubtful that this combination occurred. There were 18 plants infected with spindle tuber in addition to 1 of the other virus diseases, 4 of these were combinations with mild mosaic, 6 were rugose mosaic, and 8 were leaf roll.

RELATION OF INSECTS TO SPREAD

IRRIGATED PLOT

The greatest amount of infection with all four diseases occurred in 1925 and the next largest amount in 1927. Only leaf roll and spindle tuber were transmitted in 1926 and only spindle tuber in 1924.

By checking over the insect survey made on five different dates between July 2 and August 26 in this plot in 1925, it was found that a small number of aphids were present on July 2 and a much larger number on August 26. On the latter date 183 plants were carefully examined and from 1 to 7 aphids were found on each of 38 per cent of the plants. While this could hardly be called a heavy infestation of aphids, it was the largest number found at any time during the four years and probably accounts for the greater amount of transmission that occurred in that year. The other insects noted in 1925 were Colorado potato beetles, gray blister beetles, leaf hoppers, tarnished plant bugs, and grasshoppers. The tarnished plant bugs were the most abundant

In 1927 the only aphids observed were found very late in the season just before digging. This may explain the fact that the only transmission of mosaic and leaf roll occurred late in the season and was not evident until the tubers were indexed in the greenhouse. A considerable number of flea beetles were present early in July and August, but no other insects were noted except Colorado potato beetles, a few leaf hoppers, and some grasshoppers.

In 1924 and 1926 the records of insect infestations were not made as accurately as in the other years, but a careful lookout was kept for aphids both in this plot and in the other experimenal plots on the farm. None, however, were noted.

From these observations it would appear that the few instances of leaf-roll transmision in 1926 and the extensive spindle-tuber transmission in all four years must be explained on some other basis than that of aphid transmission. Grasshoppers,[7] which have been shown to be capable of transmitting spindle tuber, were possibly the chief agents in the spread of this disease, although the other insects present can not be eliminated until further tests of their ability to transmit the virus have been made.

DRY-LAND PLOT

The type of spread of spindle tuber occurring in the dry-land plot was in sharp contrast to that presented above for the irrigated plot.

[7] GOSS, R. W. TRANSMISSION OF POTATO SPIDNLE TUBER BY GRASSHOPPERS (LOCUSTIDAE). Phytopathology 18: 445-448. 1928.

The dry-land plot was only used for two years and the detailed data are only presented for one year, 1925. (Fig. 2, C.) This plot was planted in the same manner as the irrigated plot, both the infected and healthy seed being from the other halves of the seed tubers used for the irrigated plot. Because of unfavorable conditions, the stand was very poor in 1924. Only 207 hills were produced from 324 seed pieces planted. Only two plants in addition to the original spindle-tuber unit exhibited the symptoms of this disease and there was no evidence of spread of the other three diseases.

This plot suffered a severe infestation of grasshoppers during 1924 from an adjoining alfalfa plot, the first three rows being almost entirely defoliated. Grasshoppers were also present in 1925. Figure 2, C, shows the amount of transmission which occurred in 1924 as evidenced by symptoms appearing in 1925 in addition to the current-season symptoms that appeared from transmission early in the season of 1925. There were 40 spindle-tuber plants in 1925. Six of these were present in 1924, and 20 of them occurred in plants grown from healthy seed used to replace the missing hills of 1924, so that not more than 14 of these infections could have occurred late in the season of 1924. This total of 16 possible infections in 1924 is much greater than the number that occurred in the irrigated plot, and the distance of spread is greater than in the irrigated plot even after four years. Undoubtedly the grasshoppers were the chief agents in the spread of spindle tuber. In addition to the 20 new infections that appeared in the field in 1925, there were 16 additional instances of transmission as revealed by indexing the tubers. Most of these infections centered around the plants infected in 1924 and were widely scattered over the entire plot.

In 1925 it was determined by greenhouse indexing that there were two instances of leaf-roll transmission and one of rugose mosaic. This transmission was probably due to late-season infection by aphids, which were present in August, though less abundantly than in the irrigated plot. Neither of these diseases was transmitted in 1924. Due to an error the original mild-mosaic unit was not planted in 1925 and one hill of the original rugose-mosaic unit was accidentally planted with mild-mosaic seed. No transmission of mild mosaic occurred in 1924 from the original unit, nor in 1925 from the single plant in row 9.

DISCUSSION

While the experimental plots used in these tests are not strictly comparable to large commercial fields, the results obtained are in harmony with the writer's observations of the spread of these diseases in western Nebraska. The relative amount of spread of these four diseases in any one year and of each disease for the four years portrays quite accurately the conditions existing in the commercial fields of the same area during the same period.

It is clearly evident that mild and rugose mosaic are not readily transmitted under these conditions. The amount of spread was negligible as contrasted with that observed in the eastern part of the United States by other investigators. Leaf roll, while transmitted more extensively, was still limited in extent and the amount of transmission was much less than that reported by investigators in other sections of the country. These three diseases may be chiefly de-

pendent upon aphid transmission, and therefore have not become as serious a menace under western conditions, where aphids are less frequent than in other parts of the country. Murphy,[8] however, reports transmission of leaf roll by capsid bugs (*Calocoris bipunctatus*), jassids (*Typhlocyba ulmi*), and flea beetles (*Psylliodes affinis*). It is therefore quite probable that insects other than aphids were responsible for some of the leaf-roll transmission, particularly in 1926, when aphids were not present.

Spindle tuber was found to be quite extensively transmitted, although not to as great distances as reported by other investigations nor in as large amounts as indicated by Werner.[9] Werner's experiments, conducted in 1923, in which he found a very extensive spread of spindle tuber, are not strictly comparable to the tests reported in this paper, for there may have been in that year a much more severe insect infestation than in any of the following four years. It is clearly evident, however, that this disease is a more serious problem in western Nebraska than the other three diseases studied. The increase from 14 to 42 per cent in 1927 gives some indication of the rapidity with which it may increase when conditions are favorable. It must be remembered, however, that part of this increase probably occurred late in the season of 1926, but was not determined because no indexing was done that year. Judging from the results of these four years' study, which included a considerable range of variation in weather conditions, the disease would hardly be expected to much more than double in amount in an average year. It is also evident that this disease is transmitted by other insects than aphids, and it is quite probable that in addition to grasshoppers it will be found that a number of other insects can act as transmitting agents.

It was found very difficult to detect the mosaic plants in the field because of the masking of symptoms. They were easily distinguished, however, by greenhouse indexing. Leaf roll was usually distinguishable both in the field and by indexing, but under certain field conditions it was very difficult to separate it from severe spindle tuber. The latter disease could usually be detected, however, by the tuber symptoms. Nevertheless, in the final readings for spindle tuber the previous history and the performance of the progeny had to be taken into consideration in order to avoid inaccuracies that would have occurred if the readings for any one year had been considered alone. This difficulty in accurately diagnosing spindle tuber was due, of course, to the number of environmental factors that could seriously affect the intensity of the symptoms.

SUMMARY

Mild and rugose mosaic were transmitted in small amounts in only two of the four years of the experiment, and their spread can be correlated with the occurrence of aphids.

Leaf roll was transmitted slightly more extensively, that is, there was 9.7 per cent infection after four years, but the disease spread only to a distance of about three hills from possible sources of infection. The spread could be correlated with aphid transmission except in 1926, when other insects were probably involved.

[8] MURPHY, P. A. INVESTIGATIONS ON THE LEAF-ROLL AND MOSAIC DISEASES OF THE POTATO. Ireland Dept. Agr. and Tech. Instr., Jour. 23: 20–34. illus., 1923.

[9] WERNER, H. O., Op. cit.

Spindle tuber was transmitted more extensively, that is, there was 42.4 per cent after four years. Transmission occurred in all four years, but was more abundant in 1925 and 1927, when aphids were present. The spread of this disease could also be correlated with the presence of grasshoppers, although other insects may have been involved. None of these diseases were spread more than a few rows distant from the sources of infection.

Of the four diseases studied, spindle tuber is undoubtedly the one most to be feared under western conditions, although there was evidence that leaf roll may become a serious problem if it once becomes established in the West.