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UNIVERSITY OF NEBRASKA COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION

Research Bulletin 160

Pink Rot of Potatoes Caused by *Phytophthora erythroseptica* Pethyb.

R. W. Goss
Department of Plant Pathology

LINCOLN, NEBRASKA
JUNE, 1949

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Pink Rot of Potatoes Caused by *Phytophthora erythroseptica* Pethyb.

R. W. Goss [1]

INTRODUCTION

DURING the summer of 1943 reports were received of rotted tubers occurring in fields of early potatoes in central Nebraska. A survey [2] revealed that while late blight and blackleg were present in the fields, the tubers on about 75 per cent of the wilted and dead plants were infected with a tuber rot not attributable to either of these diseases. An estimated 10 per cent of the tubers were found rotted in some fields on August 5. In November and December of the same year the late-producing area of western Nebraska reported the occurrence, at harvest and in storage, of tuber rots differing from those previously recorded for that area. Specimens appeared similar to those observed during the summer in central Nebraska. Instances of serious storage rots causing 15 to 20 per cent loss were found in the irrigated area of the North Platte valley, whereas only a slight amount of rot occurred in the nonirrigated areas. Some growers reported that the rotted tubers were associated with wilted plants. In practically all instances of partially rotted tubers it was observed that the rot started at the stem end.

The fact that the tuber rot was present at harvest time and was associated with the early death of the plants rather than occurring as a postharvest disease indicated the presence of a disease factor previously unreported in Nebraska. Isolations were made and pathogenicity tests were conducted both on tubers and growing plants to study the influence of various factors on infection and on the development of the disease. These tests were reported in a preliminary note (*17*). The organism was subsequently identified as *Phytophthora erythroseptica*.[3]

Because of the paucity of information on this disease in the United States, its confusion with other tuber rots such as leak, and the lack of information concerning the effect of environmental factors on its distribution, it was considered desirable to publish the results of the experimental tests along with a review of previously published work.

[1] The author is indebted to J. H. Jensen who participated in this study during the first year's work and to M. W. Felton who assisted in later surveys and experimental work.

[2] Made by J. E. Livingston.

[3] Identified tentatively by Charles Drechsler and subsequently identified by C. M. Tucker.

HISTORY, HOSTS AND DISTRIBUTION

Pethybridge in 1913 (*23*) reported the occurrence of this disease in Ireland and proposed the name "pink rot." He attributed it to a new species of fungus which he named *Phytophthora erythroseptica*. He stated that the disease had been first observed in 1909.

Phytophthora erythroseptica was also reported by Buddin (*6*) as one of the fungi causing root rot, shoot rot and shanking of tulips in Great Britain. Isolations of the organism from potato were capable of infecting tulips. More recently Tompkins and Tucker (*27*) reported *P. erythroseptica* as the cause of a leaf blight of pink calla. They found, however, that this strain on calla failed to infect potato tubers of the White Rose variety. A strain of *P. erythroseptica* attacking *Atropa belladonna* L. was given the variety name *atropae* in 1926.[4]

Following the original description of the disease in Ireland, the subsequent chronological record of its appearance on potatoes is as follows: Holland, 1914 by Pethybridge (*25*), and in 1922 by Van Poeteren (*31*); Scotland, 1919 (*12*); England and Wales, 1921 (*12, 13, 14*); Java, 1923 (*20*); Sumatra, 1923 (*30*); Bulgaria, 1927 (*1*); The Isle of Jersey, 1935 (*26*); Canada, 1943 (*18*); and Tasmania, 1946 (*32*).

In the United States the disease was first reported by Bonde (*3*) as occurring in Maine to a limited extent each year. He stated that it was found on poorly drained land and was associated with high rainfall, such as occurred in 1938 when 20 per cent of the tubers in low portions of some fields were affected. The next year, 1939, Boyd (*4*) reported the disease from Massachusetts as occurring shortly before maturity and as being more prevalent in areas of several fields where decayed tubers had been dumped from storage the previous winter. In 1940, Person (*21*) observed the disease in Louisiana where it caused up to 5 per cent wilt in one field. It was not reported from any additional states until 1944 when Cassell (*10*) recorded its appearance in a low area of one field in Rhode Island. In 1945, Blodgett (*2*) reported the disease as having been observed in Idaho in 1943 and 1944 and believed it to have been present and the cause of serious losses in 1941.

In all the reports of pink rot since the first description of it in Ireland, the one consistent fact noted was its sporadic nature and the localized losses involved. Nowhere in the literature is there any evidence of its having caused widespread damage or of its occurrence in epidemic proportions. It is interesting to note its first appearance in such widely separated locations within a relatively few years and without any indication of its having spread from a common source. Since

[4] Tucker (*28*, p. 176) considers the evidence presented by Mrs. Alcock in naming this strain and concludes that "The reasons for separating the Atropa strain are not very convincing, and, pending further evidence, the writer prefers to include it in *P. erythroseptica*."

its first description in Ireland it has been considered a widespread but minor disease in the British Isles. The reports from the Continent and the one report from the Dutch East Indies indicate similar experiences. No explanation has as yet been offered for the almost simultaneous appearance of the disease on the North American continent in such widely separated places as New England, Louisiana, Nebraska, Idaho, and British Columbia.

Aside from Cotton's (*13*) statement that its first appearance in England was chiefly in seed from Scotland, and Paravicini's (*20*) report of its occurrence on potatoes in transit from Java to Holland, there is no evidence presented nor is it intimated that occurrence of the disease in any new locality could be traced to the seed source. This does not mean that the disease cannot be carried in the seed tubers but only that it is commonly thought to have been present for some time prior to the first reports.

It is possible that this is an endemic disease in each of the regions reporting its occurrence and that its identification has been delayed due to the similarity of the symptoms with those of other tuber-rot diseases. This similarity of symptoms with those caused by other parasitic and non-parasitic agents is mentioned in some detail by Pethybridge (*23*) and Cairns and Muskett (*7, 9*). It is also noted by Bonde (*3*) and Jones (*18*) and has been evident in the present study. The disease may be much more widespread than present reports indicate, although it should be remembered that in the extensive surveys for plant diseases conducted during the war years, 1943-1945, when an extra effort was being made to detect any new diseases, only the few reports mentioned above were recorded even though some of the pathologists were familiar with the disease and were looking for it.

Assuming that the organism has been present in the soil for some time, there is still no explanation for its occurrence under environmental conditions which at first glance appear quite dissimilar. It should be remembered however, that while there is much less rainfall in Idaho and Nebraska than in the other areas reporting this disease, the occurrence of the disease in Nebraska was generally more common and severe in the irrigated sections. In Idaho (*19*), where it is locally known as "water rot," its occurrence has been correlated with late irrigation. It was thus evident that studies of the relation of environmental factors to the occurrence of this disease would be desirable.

DESCRIPTION OF THE DISEASE

In the vines. With the exception of Pethybridge's paper in 1914 (*24*), the published descriptions of the vine symptoms are rather meager, due to the emphasis placed on the tuber-rot phase of the disease. The descriptions given, however, are in general agreement with the symptoms observed on plants in the field in Nebraska and

with the symptoms produced by inoculation in the greenhouse. The disease in Nebraska is essentially a late-season wilt occurring a few weeks before normal maturity. The lower leaves of affected plants are the first to turn yellow, wilt, dry up and eventually fall off. The wilt gradually involves the entire plant and such wilted plants are difficult to distinguish from those affected by other wilt diseases. Occasionally only one stalk in a hill is infected. Stem lesions are sometimes observed below the ground line, where they are somewhat similar in appearance to Rhizoctonia lesions (Jones, *18*). Lesions of various lengths may also occur above the ground line and appear soft and watersoaked, particularly at the junction with healthy tissue (Person, *22*).

All infected plants observed by the author evidenced stem infection progressing from a slight basal rot of the stem with a watersoaking of the pith and a light brown discoloration of the vascular tissues to an extensive dark soft rot, chiefly of the underground stem (Figure 1, B) but sometimes extending up the stem beyond the lower leaves. Many inoculated plants, or those growing in inoculated soil, have produced aerial tubers in the leaf axils (Figure 1), as originally described by Pethybridge (*24*) and described and illustrated by Jones (*18*). Other workers mention the infection of stems and roots but place very little emphasis on this phase of the disease, which nevertheless has been of considerable diagnostic value in many plants observed by the author both in the field and in greenhouse experiments. The stem rot is usually softer and wetter than those caused by species of Fusarium, but when it is extensive and turns dark it is difficult to distinguish from the symptoms appearing on plants infected with blackleg. In such cases it is sometimes necessary to examine the tubers as an aid in identification.

In the tubers. Infected tubers usually show the first symptoms at the point of attachment to the stolon and the rot progresses rapidly throughout the tuber. In a very few instances infected tubers have been found in the field and in inoculated soil without showing symptoms at the stem end, indicating that infection may occur from the soil directly through either eyes (*9*), lenticels, or wounds under conditions extremely favorable for the disease. The surface of the infected portion of the tuber becomes dark brown although in red varieties there is first a fading of the red color (Figure 1, C). Often a black band is evident at the margin between healthy and infected tissue. Lenticels and eyes are often purplish or black. The skin of the rotted portion may be easily sloughed off by rubbing, exposing the slightly darkened tissue with small, black spots beneath the lenticels. There is little shrinking and even when the tuber is completely rotted it will often retain its shape but will be somewhat spongy or rubbery to the touch.

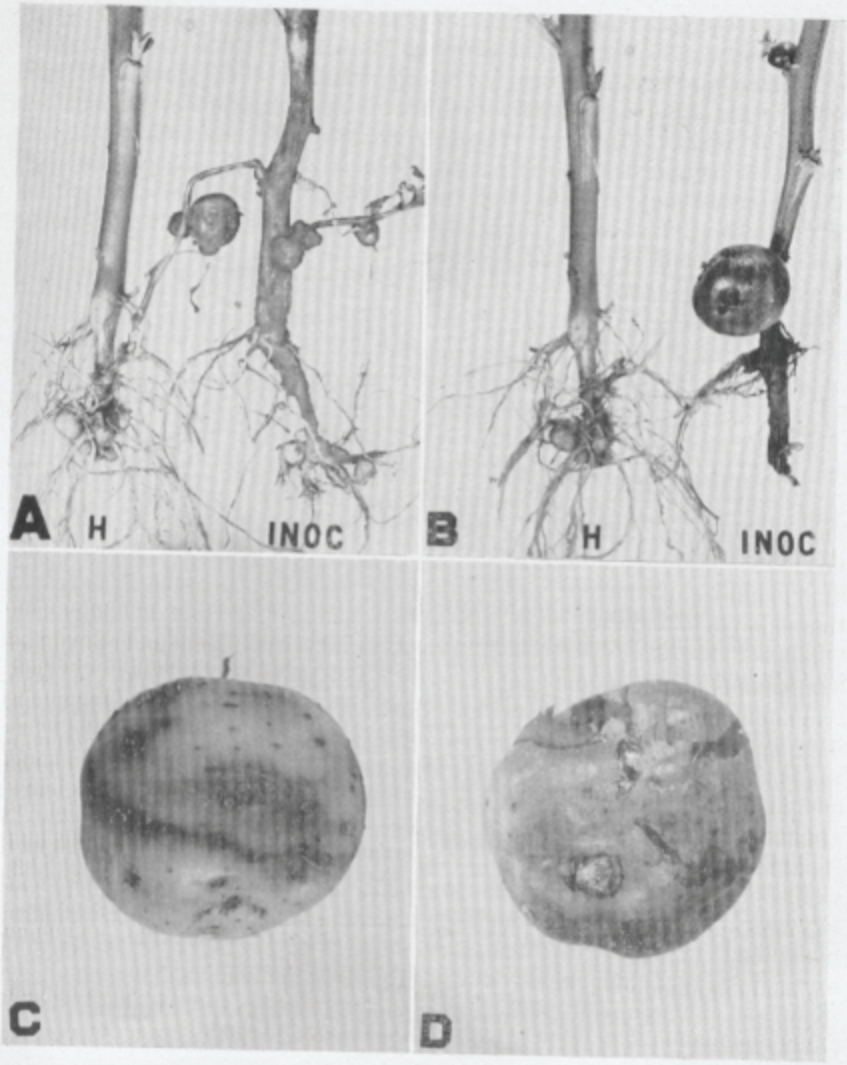

FIGURE 1.—(A and B) Stems from plants grown in soil inoculated with *Phytophthora erythroseptica* (labeled INOC) showing blackening and rotting of the underground stem, destruction of roots and production of aerial tubers as contrasted with healthy stems (labeled H).

(C and D) Bliss Triumph tubers showing pink-rot symptoms. C.—with faded infected area of stem-end half of tuber with darkened lenticels and darkened line at margin of rot. D.—showing exudation of liquid from eyes of infected tuber.

When such a tuber is squeezed droplets of liquid exude from the eyes and lenticels. Exudation of droplets from eyes and lenticels (Figure 1, D), may also occur naturally under conditions of high moisture and sometimes gases are given off which form small bubbles in the droplets. Tubers subject to pressure by squeezing do not regain their shape and this is noticeable when such tubers are in storage piles where they often become flattened. Rotted tubers do not produce the strong odor of potatoes affected with bacterial soft rot but give off a pungent odor somewhat like that of formaldehyde.

When infected tubers are cut open the tissue is found to be of a somewhat granular consistency and dull white in color with no demarcation between diseased and healthy tissue except for the difference in texture. Areas of blackened tissue are often found about ¼ inch beneath the surface and sometimes the central pith is blackened, with much the same appearance as in black heart. After cutting and being exposed to the air for 15 to 20 minutes, the affected tissue changes to pink and then gradually to brown or even black. As stated above, severely infected tubers may show this blackening when dug and immediately cut. In other instances it develops within a day or two after digging, particularly at high temperatures. In partially infected tubers this blackening may not appear until after the tuber is cut, when the gradual change from white to pink and then to brown and black can be noted.

In the published reports of this disease from Great Britain emphasis is placed upon the absence of any internal cavities, thus distinguishing the rot from blackleg. In tubers obtained from the fields in Nebraska and in those grown in inoculated soil in the greenhouse small cavities about ⅛ inch in size were sometimes observed, usually located within ½ inch of the point of attachment to the stolon. Cavities were occasionally found in inoculated tubers in the laboratory. In no case, however, were the cavities as large as often occur in blackleg or black heart and in no instance was there a weft of fungus hyphae such as occurs in the cavities with rots caused by species of Fusarium.

If conditions are extremely wet, as in fields heavily irrigated late in the season or in very moist storage cellars, the rot becomes characteristically a wet rot. If such infections occur early enough or if the tubers are left in the ground after maturity, the infected tubers may be completely destroyed. In storage it is common to find a pocket of rotted tubers in the pile, clearly indicating that the fungus may spread from one rotted tuber to adjacent healthy ones. In this respect, as in many of the tuber symptoms, the disease is difficult to distinguish from leak. With the exception of Person's (*22*) report, leak caused by *Pythium debaryanum* has not been considered as a parasite of the growing plant but strictly as a postharvest disease, whereas pink rot

characteristically occurs in the field and is present as a tuber rot at time of harvest. *Phytophthora drechsleri* causes a similar postseason tuber rot but its occurrence had not been recorded in Nebraska at the time this investigation was started. During a survey of storage cellars in 1945 specimens, supposedly of pink rot, were obtained but some of the tubers yielded a fungus subsequently identified as *P. drechsleri*.[5]

EXPERIMENTAL DATA

Isolation of the Fungus

The first specimens received in 1943 were badly rotted and contained many secondary invaders, especially bacteria. Microscopic examination revealed an abundance of non-septate mycelium usually following the cell walls. The practice was followed of inoculating healthy tubers with such rotted tissue and subsequently isolating the fungus in pure culture from the advanced portions of the infected tissue. When tubers were only partially rotted and especially when they were procured directly from an infected plant, the organism could be isolated directly on corn-meal agar. The fungus usually produced typical amphigynous antheridia on the corn-meal agar plates within three to five days. It grew well on potato-dextrose agar and this was used for stock cultures and for the preparation of all inoculum.

Preliminary Pathogenicity Tests on Tubers

Preliminary tests of pathogenicity were made early in 1944 by inoculating healthy tubers with pure cultures of 15 isolates from 12 different tubers. Bliss Triumph tubers were used in all inoculation tests and these were disinfected with acidulated bichloride of mercury and washed with sterile water. Inoculations were made either by placing a disk of a Petri-dish culture on the freshly cut surface of a tuber or by removing a wedge-shaped piece of tissue about 1 inch long, inserting a section of an agar culture in the slit and replacing the wedge of potato tissue. Both methods of inoculation were successful but the latter method resulted in more uniform results and was used exclusively in all the following tuber inoculations. The inoculated tubers were placed in moist chambers and held at a temperature of 77° F. At least three tubers were used for testing each isolate in all tuber inoculation experiments.

After five days the tubers were removed and examined. All inoculations were successful and the most noticeable fact was the remarkable uniformity of the rot in the different tubers. In every instance the rot extended for about 1 inch from the point of inoculation. The freshly cut tissue of the rotted area appeared dull white and was of a granular consistency. The rotted area and the tissue for about ¼ inch beyond the rot turned pink in 20 to 30 minutes after being cut, and later

[5] Identified by C. M. Tucker.

turned black. Microscopic examination revealed the mycelium along the cell walls throughout most of the tuber. One tuber from each of four sets of inoculations was kept in the moist chamber for an additional four days. The tubers, which were about 2 inches in diameter, had completely rotted during this nine-day period. The pinkish color involved about three-fourths of the rotted tubers, and small cavities had formed in the pith. There was also a darkening of the eyes and lenticels and the exudation of liquid in droplets.

In most instances the organism could be recovered from tissue about 1/4 to 1/2 inch beyond the softened area as well as from the margin or the interior of the rot.

Comparative Tests of *Phytophthora erythroseptica* with *P. drechsleri* and *Pythium debaryanum*

Because of the similarity of symptoms of tubers infected with these three organisms, two series of tuber inoculations were made with various isolates. Inoculations with *Pythium debaryanum* were included in duplicate in each experiment. Results were so uniform that for purposes of brevity the data from the two tests will be summarized together.

Nine isolates of *Phytophthora erythroseptica* obtained from rotted tubers from western Nebraska were compared with 10 isolates of *P. drechsleri* from tubers showing very similar symptoms obtained from the same area, and sometimes from the same bins of potatoes. A culture of *Pythium debaryanum* obtained from Louisiana and another isolate of the same organism from Nebraska were included in the test.

All isolates were pathogenic. The tubers were examined eight to ten days after inoculation. *Pythium debaryanum* had caused the least rot, usually extending less than 3/4 inch and sometimes not more than 1/4 inch from the point of inoculation, whereas the rots caused by *Phytophthora erythroseptica* and *P. drechsleri* averaged about 1 inch in depth, varying from 3/4 to 1 1/2 inches. It was impossible to distinguish between the rots caused by the latter two organisms. The rotted tissue was dull white, soft and granular and rapidly turned pink after cutting. Some isolates of each of the species of Phytophthora produced small cavities in the pith and sparse aerial mycelium on the surface of the tubers at the point of inoculation. The tubers remained intact but were soft and spongy to the touch. Contrasting with this, the Pythium cultures not only caused less rot but the rotted tissue when cut was slightly darker, almost brown, and did not turn pink upon exposure to the air. The tissue remained firm, no cavities were formed, and abundant, coarse, aerial mycelium to the height of 1/8 to 1/4 inch had spread rapidly over the surface of the tubers within three days after inoculation.

Spread from Infected to Healthy Tubers

In preliminary tests it had been found that when sections of agar cultures of *Phytophthora erythroseptica* were inverted on the surface of healthy tubers the fungus failed to penetrate. The tubers used in those tests were mature tubers taken from storage in midwinter and were undoubtedly more resistant to infection than young immature tubers in the soil. Observations in potato bins, however, showed that pink rot often occurred in pockets, indicating that infection had spread from infected to healthy tubers. The following experiments were therefore conducted in an effort to more nearly duplicate the conditions which would exist in potato storage bins.

Healthy Bliss Triumph tubers were disinfected, washed in sterile water and placed in two jars 6 by 8 inches in size. Moist filter paper was placed at the bottom of each jar and a piece of moistened cheesecloth was placed under the lid. One tuber at the top of each jar was inoculated and the jars were held at 77° F. from February 9 until March 12, at which time all tubers were removed and examined.

In each jar the inoculated tuber at the top was completely rotted and exuding liquid. The three uppermost tubers in each jar which were not in contact with the inoculated tuber remained healthy. Twenty of the other 24 tubers became infected and were all from one-half to completely rotted. All of the rotted tubers were in contact with each other or with the inoculated tuber. Due to the soft, wet breakdown of the tubers, about ½ inch of liquid accumulated in the bottom of each jar.

Pethybridge (*24*) reported that the disease did not spread from diseased to healthy tubers but Cairns and Muskett (*7*) proved that with sufficiently moist conditions the disease could spread rapidly in an affected crop during storage, and that a great deal of the loss in storage occurs in this way. They suggested however, that the spread of the disease in storage might be due to infected soil adhering to the tubers rather than to actual transmission from infected to healthy tubers. It should be noted that their experiments were conducted in "clamps" covered with soil, or with herbage and soil, and were therefore not similar to storage conditions usually employed in the United States. The recorded observations of the disease in storage in Nebraska confirms their statement regarding storage losses but it is clear from the above experiment that spread in storage is not dependent upon infected soil adhering to the tubers.

It was evident that the fungus was capable of causing infection by contact and direct penetration under conditions of high moisture at a temperature of 77° F. Partially rotted tubers always had the rotted portion in contact with infected tissue of other tubers and those tubers not in direct contact with rotted tissue remained healthy. At lower

temperatures, such as would prevail under good storage conditions, it is probable that the disease would develop slowly until spring when with rising temperatures the rotting would become serious. Most reports of serious losses due to pink rot are received in the spring.

Effect of Temperature on Tuber Rot

Jones (*18*) determined the optimum for pink rot in the tubers to be approximately 25° C. (77° F.) but obtained no symptoms of decay in tubers incubated at 4° C. (39.2° F.) and 8° C. (46.4° F.). In pure culture studies the same author reports no growth on malt agar at 4° C. and 34° C. (93.2° F.) and he considered the optimum temperature for growth to be approximately 24° C. (75.2° F.) with the minimum between 4° C. and 8° C. and the maximum below 34° C. Tucker (*28*) found that "*P. erythroseptica* grew only slightly on corn-meal agar at 15° C., profusely at 27.5°, and did not develop at 30° C." He also reports that cultures failed to grow at room temperature after 96 hours incubation at 30° C.; *P. drechsleri*, on the other hand, grew most luxuriantly at or slightly above 30° C. Cairns and Muskett (*9*) considered as a result of their experiments that tuber infection would rarely take place below 50° F. or above 86° F. and that the optimum temperature for the development of the tuber rot would be in the neighborhood of 68° to 77° F.

In the present experiment healthy Bliss Triumph tubers were disinfected, washed in sterile water, and placed in moist chambers. Three moist chambers containing a total of 10 inoculated tubers were held at each temperature. The mean daily temperatures of the incubators in which the chambers were placed were 43°, 52°, 57°, 67°, 76°, 86°, and 94° F., as shown in Table 1. Inoculations were made by the wedge method and one or two tubers were wounded in the same manner, without the introduction of inoculum, and used as controls at each

TABLE 1.—Influence of temperature on development of rot in potato tubers inoculated with *Phytophthora erythroseptica*.

Temperature	Number of tubers	Number of infected tubers	Average extent of rot	Notes
Degrees F.	*No.*	*No.*	*mm.*	
43	10	10	7	Very little or no pink color.
52	10	10	8	Pink 5 mm. beyond rot.
57	10	10	11	Pink 15-20 mm. beyond rot.
67	10	10	25	Pink only in rotted tissue.
76	10	10	27	Pink only in rotted tissue.
86	10	10	22	Pink only in rotted tissue, liquid exuding from eyes.
94	10	8[1]	10	Pink only in rotted tissue, some black heart, and liquid exuding from eyes.

[1] Probably influenced by lower temperature of tuber tissue at time of inoculation. Compare with Table 2.

temperature. At the end of seven days all tubers were removed and examined for infection and the extent of rot.

The amount of rotted tissue was remarkably uniform in all tubers at the same temperature and progressed uniformly into the tuber from the point of inoculation without respect to the type of tissue involved. The rotted area was clearly marked by the dull white color and the softened tissue which was more granular at low than at high temperatures. Upon cutting and exposure to air the pink color appeared in the rotted tissue of tubers held at all temperatures except the lowest. At 52° and 57° F., however, this pink color extended beyond the rotted portion. As shown in Table 1, the rot was most rapid at a temperature of 76° F. It was greatly retarded at the lowest temperatures but some rotting occurred as low as 43° F. At the highest temperatures the rotted tissue was soft and there was an exudation of liquid from the eyes. The results obtained at 86° F. and 90° F. were surprising as this organism had been reported as unable to tolerate these temperatures. Infection in this experiment may have been influenced by the fact that the tubers had been held in cold storage prior to inoculation and that infection occurred before the tuber tissue reached the desired temperature. Another experiment was therefore started in which the tubers were held at approximately 76°, 85°, and 93° F. for about one week before inoculation and then held at the same temperatures for ten days before examination. It was also decided to compare *Phytophthora erythroseptica* with *P. drechsleri*, which had been reported to grow at 34° C. (93.2° F.). The results of this second test presented in Table 2 are in contrast to Table 1 and confirm published reports on the relation of temperature to the growth of the two organisms.

TABLE 2.—Comparison of *Phytophthora erythroseptica* and *P. drechsleri* at high temperatures when the tubers were held at each temperature for one week before inoculation.

Temperature for one week before and 10 days after inoculation	Extent of rot	
	Phytophthora erythroseptica	*P. drechsleri*
Degrees F.	*mm.*	*mm.*
76	33	18
85	9	25
93	0	16

The optimum temperature range (67°-76° F.) for *Phytophthora erythroseptica* closely approximates the daily mean air temperature for July and August in the potato growing area of central Nebraska. It is considerably above the temperature for the early harvested fields of western Nebraska and for good storage conditions but within the range to be expected in late spring storage cellars. The rapidity of the rot at optimum temperatures indicates the necessity of precooling and refrigeration of tubers in transit from the early harvest areas.

Pathogenicity Tests on Plants

In all of the following experiments, unless otherwise noted, the seed pieces were sprouted in peat moss and were transplanted to unsterilized soil when the sprouts were 1 to 2 inches long. A higher percentage of infection would probably have been obtained with soil inoculations if the soil had been sterilized but in studying the effect of environmental factors it was believed that unsterilized soil would more nearly approximate field conditions.

Either stem or soil inoculations were used. Stem inoculations were made by inserting mycelium from cultures on potato-dextrose agar into slits made with a sterile scalpel in the stem just below the ground line. Soil inoculations were made by pouring a suspension of the organism over the soil at the rate of 1 to 1½ Petri-dish cultures per plant. The inoculum was prepared by growing cultures in Petri dishes on potato-dextrose agar. The entire cultures were placed in a Waring Blendor with a little water for about 1 minute, and then strained through muslin. Additional water was added so that each 100 c.c. of inoculum represented one Petri-dish culture.

Preliminary tests by means of soil inoculations were made in the greenhouse and infection resulting in both wilt and tuber rot was obtained in Bliss Triumph plants. The organism was recovered from stems, roots, stolons, and tubers of infected plants. Soil inoculations made when the plants were young sometimes resulted in the infected plants dying before tuber formation. In other cases, tubers were completely rotted and only a few remnants of the tubers could be found in a soil cavity the size of the tuber. In a number of instances tubers cut and examined at harvesting were recorded as healthy only to find that typical tuber rot developed after 24 to 48 hours when they were held at room temperature. In all the following experiments plants were listed as infected when they wilted and died before the formation of tubers or when tuber infection had occurred even though symptoms were not recorded on the vines prior to harvest. All tubers listed as healthy at the time of digging were held for two to five days at room temperature and any such tubers developing symptoms were included in the data for infected plants.

Stem inoculations. In order to test the relative virulence of different isolates, a series of inoculation tests was conducted in the greenhouse with 8 isolates, tentatively identified as *Phytophthora erythroseptica*, and 10 other isolates classified as *P. drechsleri* which had been obtained from tubers in the bin showing symptoms similar to those of tubers infected with *P. erythroseptica*. In view of Person's (22) report of a strain of *Pythium debaryanum* capable of causing both a wilt and tuber rot, it was considered desirable to compare the pathogenicity of his culture with the isolates of Phytophthora and a Nebraska isolate of

Pythium. The Louisiana culture obtained was not the one on which Person based his publication but was thought by him to be similar to it.

Bliss Triumph plants growing in 7-inch clay pots were cut back to one or two stems per pot and were inoculated on December 31, six weeks after transplanting, when the plants averaged 10 to 12 inches in height. Three to six plants were inoculated with each isolate tested. The soil was kept near the saturation point by frequent watering. The plants were dug on March 2 and the stems and tubers examined for infection.

The results of the test (Table 3) corroborated preliminary experiments in which no infection resulted from the inoculation of plants with *Pythium debaryanum*. None of the 9 isolates of *Phytophthora drechsleri* caused wilt although one plant from each of two cultures produced a few rotted tubers which may have become accidently infected with *P. erythroseptica*. All 9 isolates of *P. erythroseptica* produced the typical symptoms of the disease. Some plants were killed prior to tuber formation and in one instance all tubers were completely rotted at time of digging. Of the 22 tubers listed as infected, 11 did not show symptoms at time of digging but the disease developed during the next five days. Typically, the infection progressed from the point of inoculation both up and down the stem, producing a soft, black rot that would have been difficult to distinguish from blackleg. In some plants aerial tubers were produced abundantly. The number of tubers on the plants inoculated with *P. erythroseptica* was greatly reduced in comparison with those plants inoculated with the other organisms.

TABLE 3.—Comparative pathogenicity of different isolates of *Phytophthora erythroseptica*, *P. drechsleri*, and *Pythium debaryanum* as determined by stem inoculations of Bliss Triumph potato plants.

	Number of isolates tested	Number of plants	Number of plants infected	Number of tubers	Number of tubers infected
Phytophthora erythroseptica	9	30	15	77	22[1]
Phytophthora drechsleri	9	27	2[2]	101	8
Pythium debaryanum	2	9	0	30	0
Control	–	9	0	37	0

[1] In addition, all the tubers of one wilted plant were completely rotted before harvest.
[2] On the basis of further tests and isolations, these two plants were considered as accidentally contaminated with *P. erythroseptica*.

Soil inoculations. In these tests which were more comparable to conditions existing in the field, all of the isolates used in the stem inoculations were again tested for pathogenicity by soil inoculation. Small, whole seed tubers of the Warba variety were planted in unsterilized composted soil in 7-inch clay pots. The soil was inoculated on January 28 when the plants were 8 to 10 inches high, using 10 plants

for each isolate to be tested. Some of the plants were dug on March 23 and the remainder on April 3.

The first symptom resulting from inoculation with *Phytophthora erythroseptica* appeared in about three weeks as a soft, black rot of the stem from the base to about 8 inches above the ground line. This was rapidly followed by wilting. Because of the high soil moisture many infected plants were able to survive and produced aerial tubers. The actual number of tubers infected was undoubtedly higher than is indicated in Table 4 due to the complete rotting of some tubers.

TABLE 4.—Comparative pathogenicity of different isolates of *Phytophthora erythroseptica, P. drechsleri,* and *Pythium debaryanum* as determined by soil inoculation, using the Warba variety of potatoes.

	Number of isolates tested	Number of plants	Number of plants infected	Number of tubers	Number of tubers infected
Phytophthora erythroseptica	9	90	67	437	258
Phytophthora drechsleri	9	90	0	444	0
Pythium debaryanum	2	20	1	107	6
Control	–	20	2	109	9

No infection was obtained by inoculation with *Phytophthora drechsleri.* One plant inoculated with *Pythium debaryanum* wilted and the tubers were completely rotted so that identification of the causal organism was impossible. In view of the lack of infection with stem inoculations and the fact that two of the control plants wilted and produced infected tubers, it is probable that this one plant was accidentally infected with *P. erythroseptica.* The percentage of infection with cultures of *P. erythroseptica* was uniformly high with the exception of one culture that produced only one infected plant. Seven of the 9 isolates tested produced 7 to 10 infected plants out of each 10 inoculated.

It is evident from both the stem and soil inoculations (Tables 3 and 4) that of the organisms tested only *Phytophthora erythroseptica* is capable of causing a wilt of the plant and a rot of the developing tubers similar to the disease as observed in the field. The strains of *Pythium debaryanum* tested failed to produce infection of the growing plant and *P. drechsleri* which causes a similar tuber rot in storage did not infect growing plants and cause a tuber rot before harvest.

Preliminary experiments on effects of soil temperature and moisture. Many of the reports in the literature on this disease emphasize the importance of high moisture, particularly in relation to tuber rots (Cairns and Muskett, 9), but there are no reports of the effect of moisture on infection of the plant under controlled conditions. Reported studies on the relation of temperature to the disease have been limited

to the tuber-rot phase or to pure culture studies of the organism. In Nebraska the disease occurs in the early potato growing sections where the temperature is high during the period of tuber formation and it is more prevalent in the irrigated than in the dry-land areas. The following experiments were therefore planned with the object of obtaining a clearer conception of the influence of environment on the occurrence of this disease.

The first preliminary experiment in the spring of 1944 was conducted with Bliss Triumph potato plants which had been grown in 7-inch clay pots at a temperature of approximately 72° F. At the time of inoculation one lot consisted of 39 large plants approaching maturity (79 days old) with well developed tubers. The other lot contained 33 small plants (26 days after planting) and had not started tuber formation. The soil was inoculated and one-half of each lot of plants was placed in a greenhouse at a temperature of 85°-90° F. and again divided, one-half of the plants being watered heavily to keep the soil near the saturation point and the others watered just enough to keep them above the wilting point. A comparable series of plants was kept at 72° F. The older plants were dug and examined 21 days after inoculation while the younger plants were not dug until 46 days after inoculation.

It is evident from the data in Table 5 that the disease is greatly favored by high soil moisture. Only slight infection of tubers occurred at the low soil moisture, usually appearing as a small, rotted area at the point of attachment to the stolon. The only exceptions were those two plants noted in the table as having been mistakenly watered after the death of the tops with resulting high soil moisture and extensive tuber rots.

A temperature of 72° F. appeared to be more favorable for the disease than the higher temperature of 87° F. The temperatures listed

TABLE 5.—Effect of temperature and soil moisture on infection of Bliss Triumph plants with *Phytophthora erythroseptica*.

Age of plants at time of inoculation	Temperature	Soil moisture	Number of plants	Number of plants with	
				Wilt	Infected tubers
Days	*Degrees F.*		*No.*	*No.*	*No.*
79	72	low	10	4	3[1]
79	72	high	9	6	3
79	87	low	10	1	1
79	87	high	10	–	3
26	72	low	8	0	0
26	72	high	9	9	9
26	87	low	8	0	0
26	87	high	8	3	0

[1] Two of these plants died prematurely and were mistakenly watered, thus bringing the soil moisture near the level of that for the high moisture plants.

are greenhouse air temperatures and it should be remembered that the actual soil temperatures in the clay pots, particularly in the high moisture sets, were probably 3° to 5° below the air temperature. The change to a high temperature greatly hastened the death of the older plants, even when not infected, and made it difficult to determine infection. Eight of the older plants in the high moisture set at 87° F. died prematurely and accurate diagnosis was impossible. The results were more definite with the younger plants. Most infection occurred with young plants at high moistures and at the lower temperatures. It was evident, however, that plants approaching maturity and with well developed tubers at the time of inoculation could become infected, die prematurely and produce infected tubers.

Soil moisture. The results of the preliminary experiment prompted a larger experiment in which Bliss Triumph plants were grown in unsterilized soil in greenhouse benches instead of in clay pots. The soil moisture in one bed was kept just above the wilting point, another bed was kept at about optimum level for plant growth, while the soil in a third was kept near the saturation point. Soil moisture samples taken during the experiment averaged 11.5, 17.6, and 28.3 per cent moisture, respectively, on a dry-weight basis. Fifty plants were grown in inoculated soil and 30 control plants in uninoculated soil at each soil moisture content. Five weeks after transplanting, when the plants were 12 to 18 inches tall, the soil was inoculated. The greenhouse was held at a temperature of about 72° F. Soil temperature records were taken three times daily and the mean soil temperature in the high moisture set was 66.5° F., while in the optimum and low moisture soils the temperature was approximately that of the greenhouse, 72° F.

The plants were dug 15 weeks after inoculation at which time they were all 90 to 100 per cent mature. No definite symptoms of wilt occurred and the rot of the underground stems recorded in other experiments could not be correlated with the occurrence of infected plants. The data presented in Table 6 are therefore based on the number of plants producing tubers with typical symptoms of the

TABLE 6.—Effect of soil moisture on infection of tubers with *Phytophthora erythroseptica*.

Soil moisture	Soil treatment	Number of plants	Plants with infected tubers	Number of tubers	Infected tubers
		No.	*Per cent*	*No.*	*Per cent*
Low	Inoculated	50	0	93	0
Low	Control	30	0	77	0
Optimum	Inoculated	50	18	219	5
Optimum	Control	30	0	120	0
High	Inoculated	50	56	266	23
High	Control	30	10	209	1

disease. The organism was isolated from many of the infected tubers. The effect of soil moisture on the percentage of infection was more pronounced than in the preliminary experiment. It was clear that this disease would not be serious in the field except under conditions of high soil moisture. The practice in central Nebraska of applying a late irrigation to prepare the soil for easier digging is obviously a dangerous one and care should be taken to avoid overwatering.

Soil temperature. In the preliminary experiment the disease was favored by low rather than high temperatures. This was also true of the tuber-rot experiments and has been demonstrated in published data on the growth of the fungus in pure culture. The results, however, did not explain why the disease was just as serious in central Nebraska, where the crop is harvested in the hot weather of late July and early August, as in western Nebraska where the crop matures under relatively cool conditions in late September and early October. Experiments were therefore started to obtain more evidence on the effect of soil temperature.

Bliss Triumph potatoes were grown in unsterilized soil in greenhouse benches equipped with electric heating cables which were placed on top of a layer of soil and then covered with another layer of soil which was watered thoroughly. Ten inches of soil was then placed on top and sprouted seed tubers were transplanted. Four soil temperature beds were used, each containing 48 plants in inoculated soil and 24 uninoculated controls. All of these were held at air temperatures of 50° to 55° F. at night and 60° to 65° F. in the day for 43 days after transplanting in order to produce uniformly normal plants before changing the temperatures to the desired points and inoculating the soil. Five days before inoculation the heating coils in the beds were turned on and the temperatures gradually raised to the desired levels. The soil thermostats in two of the beds were set at 61° and 68° F. and the air temperatures held as before. The other two beds were set at 79° and 86° F. In order to maintain these high temperatures it was found necessary to change the air temperature to 73° at night and 85° F. during the day. Soil temperatures at a depth of 4 inches were recorded twice daily and maximum and minimum thermometers were set each morning and evening to record the air temperatures. The mean temperatures recorded for the experiment were as follows:

Mean soil temperatures	Air temperatures: Mean minimum (night)	Air temperatures: Mean maximum (day)
Degrees F.	*Degrees F.*	*Degrees F.*
61	58	68
68	58	68
80	73	85
87	73	85

The soil was inoculated 49 days after transplanting and 5 days after the temperatures were adjusted, at which time the plants were uniformly large and vigorous and the tubers had started to develop. The inoculum was applied at the rate of 1½ Petri-dish cultures per plant.

The results of this experiment were somewhat disappointing as only a small percentage of infection was obtained, with most disease occurring at 61° F. where 19 per cent of the plants produced infected tubers. Tuber infection was usually preceded by wilt. All of the plants were dug at the same time and as a result some of the plants which had died early or on which all the tubers were completely rotted had to be listed as questionable, particularly in view of the fact that some of the control plants at the high soil temperatures were likewise affected. It is evident from the data in Table 7 that this is not a high temperature disease nor one that requires a weakened host for infection. The greatest amount of disease developed under conditions that were ideal for growth and where the uninoculated control plants were all healthy with luxuriant foliage and a normal set of tubers. The effect of the soil temperatures might have been more clear-cut if a higher percentage of infection had been obtained by the use of a more susceptible variety, soil sterilization prior to inoculation or a heavier application of inoculum.

TABLE 7.—Influence of soil temperatures on infection caused by *Phytophthora erythroseptica.*

Soil temperature	Treatment	Number of plants	Number of plants infected [1]	Number of plants questionable [2]	Number of tubers	Number of tubers infected
Degrees F.		*No.*	*No.*	*No.*	*No.*	*No.*
61	Inoculated	48	9	5	189	16
61	Control	24	0	0	98	0
68	Inoculated	48	2	3	185	3
68	Control	24	0	1	89	0
80	Inoculated	48	1	2	169	2
80	Control	24	0	1	152	0
87	Inoculated	48	3	18	103	4
87	Control	24	0	6	141	0

[1] Plants producing infected tubers or with severe wilt.
[2] Plants killed before tuber formation or plants with completely rotted tubers.

Varietal Susceptibility

While pink rot had been found in the Warba and Triumph varieties in Nebraska the field observations had not been sufficiently extensive to provide information on varietal susceptibility. A review of the literature failed to reveal any reports of varietal resistance or to provide any encouragement for the possible use of resistant varieties as a control measure. Cairns and Muskett (7) reported that 35 varieties were tested in field experiments during a three-year period and 30

varieties were tested by tuber inoculations without disclosing any variety that could be considered highly resistant. None of the varieties tested by Cairns and Muskett is commonly grown in America and the only report on American varieties is that of Jones (*18*) who confined his tests to the tuber-rot phase of the disease. He found by tuber inoculations that Warba, Epicure, Irish Cobbler, White Rose, Netted Gem, Burbank, Green Mountain, Columbia Russett, and Sequoia were all susceptible to pink rot. In spite of these discouraging reports and because no data had been reported on the susceptibility of American varieties to wilt in the field, it was decided to conduct a preliminary test in the greenhouse with 7 varieties and 2 numbered selections.

Unsterilized soil was inoculated when the plants, growing in the greenhouse bench, were about 12 inches tall. Two rows of 10 plants each were grown of each variety, the rows being spaced 10 inches apart and the plants 7 inches apart in the rows. The soil was kept very moist and the temperature of the greenhouse was held at about 72° F. The plants were dug 72 days after inoculation.

All varieties were susceptible, but the Irish Cobbler and Kasota varieties had much less infection in both vines and tubers than the other varieties in the test, as shown in Table 8. The Warba variety was the most susceptible and it is of interest to note that this is one of the chief varieties in the early potato growing section of central Nebraska where pink rot has been a problem. The evidence is sufficient to justify further tests on a larger scale with new varieties being developed in the breeding programs.

TABLE 8.—Varietal susceptibility to pink rot.

Variety	Number of plants	Infected plants	Number of tubers	Infected tubers
	No.	*Per cent*	*No.*	*Per cent*
Triumph	20	60	109	26
Pawnee	20	55	71	42
Mesaba	20	60	33	18
SND 48-2	20	55	84	19
Warba	20	60	83	46
Kasota	20	30	59	10
SCI A-27	19	42	54	19
Cobbler	20	15	77	6
White Rose	20	45	95	32

DISCUSSION

The discovery of pink rot of potato in Nebraska in 1943 was not accompanied by any evidence of its recent introduction into the state as a new parasite. Its occurrence in widely separate parts of the state, on different soil types, with different cropping sequences and without relation to seed source is evidence that it has probably been present in the soils of the state for some time and has not been recognized because

of its sporadic nature and its similarity at various stages of its development to other diseases of the potato. This conclusion is similar to those reported from other sections of the world where this disease has been observed.

Losses due to pink rot may be of considerable significance locally in some years, depending on soil and weather conditions. Pethybridge (*24*) in 1914 reported up to 12 per cent loss on land planted five years continuously to potatoes and 4 per cent loss on land in potatoes for two years. Bonde (*3*) reports that in Maine losses of 20 per cent occurred in low lying fields in wet years and he found as much as 10 per cent of the tubers from such fields affected with pink rot in storage. Blodgett (*2*) reports that in some infected fields in Idaho as much as 50 per cent of the tubers may show symptoms of pink rot as they are dug. In central Nebraska losses were usually confined to fields which had been subjected to heavy rains or late irrigation, and the wilted plants had as much as 75 per cent of the tubers showing symptoms at harvest. In western Nebraska up to 10 to 15 per cent infection was found in some storage bins.

Infected plants may produce tubers which show no symptoms of the disease when dug but which are infected and may become completely rotted within a few days. This results in tubers from the early-marketing area breaking down in transit or in the market after having been graded as "healthy" directly from the field. Similarly, in the late-producing areas, such tubers escape observation at harvest and break down in storage, usually contaminating the surrounding tubers and resulting in pockets of rotted tubers.

No attempt was made in this investigation to study the means of overwintering and dissemination, or the details of infection phenomena. It has been shown by several workers that the sexual spores of the organism are present in roots, stolons, tubers, and stems. De Bruyn (*5*) reported that the organism could live for one and one-half years in sterilized soil in test tubes and that it produced oogonia and aerial mycelium, but conidia only when drops of water were present. She also found that the organism could survive five months during the winter in unsterilized soil and that the oospores could live over winter. The organism can therefore be considered capable of persisting in the soil in the form of resting spores, or of existing as a saprophyte in the soil in the absence of the host plant. Crop rotation obviously will not serve to eliminate the disease but successive crops of potatoes would increase the prevalence of the organism in the soil and this practice should be avoided.

Many observations have been reported of the occurrence of this disease under wet soil conditions and the results of the present study show that the disease is favored by high soil moisture. The only

observations to the contrary are those of Person (*21*), Blodgett (*2*), and Cassell (*11*). Person reported the disease in a very dry field but stated that the earlier part of the growing season was extremely wet. Blodgett reported the disease as occurring in Idaho in loose, sandy soils with adequate drainage and no evidence of excessive moisture. Cassell reported 2 to 3 per cent loss in one high, well drained field. Observations in Nebraska have shown the disease to be more prevalent in the irrigated than in the nonirrigated areas and more abundant in fields which had been subjected to heavy rains or irrigation late in the season. The practice sometimes employed, particularly in the early-crop areas, of irrigating just before harvest in order to put the soil in better condition for digging operations should be avoided if possible in soils where this disease is known to occur.

No information was obtained in this study relative to the effects of soil fertility. Blodgett (*2*) observed that in Idaho the disease was found in fields never before planted to potatoes but heavily fertilized with manure. He also reported the disease as more severe on soils where a heavy stand of alfalfa had been plowed under but this may have been due to changes in soil texture and indirectly to moisture content rather than to fertility. No controlled experiments on the effect of soil fertility have been reported as far as the author is aware.

The tests here reported on varietal susceptibility were not extensive or conclusive enough to warrant definite recommendations. While no variety was found to be highly resistant, there was evidence of different degrees of susceptibility as contrasted with the negative results of other investigators. In view of the extensive breeding programs under way in the United States and the release of many new varieties, it would appear desirable to conduct further tests of varietal resistance.

The data herein presented are limited almost entirely to pink rot caused by *Phytophthora erythroseptica* but it should be remembered that other organisms cause pink-rot symptoms. *P. drechsleri* causes a similar tuber rot, but not a wilt, and is capable of growing at higher temperatures than *P. erythroseptica*. *P. megasperma* has been reported as the cause of a similar potato rot in Northern Ireland (*8*), and is known (*16*) to be present in Virginia and the District of Columbia where it causes a crown rot of hollyhocks resulting in a wilt of the plant. *P. parasitica* has been reported on rotted tubers from Kentucky and Oklahoma (*29*), and Dastur in 1913 (*15*) produced infection on leaves and stems of potatoes with symptoms resembling those of late blight. He found tuber infection to occur only through wounds.

The related late-blight organism *Phytophthora infestans* also produces a tuber rot but the mode of infection and the general appearance of infected tubers are quite different from pink rot; in fact the infected tubers do not turn pink upon cutting, thus distinguishing the late-

blight rot from all the other tuber rots caused by other species of Phytophthora.

Tuber rots closely resembling pink rot may also be caused by a number of species of Pythium, the most common of which are *P. debaryanum* and *P. ultimum*. With the exception of the one report by Person (22) for *P. debaryanum*, these species are not known to produce wilts and are essentially wound parasites.

No experiments were conducted in the present study on methods of control but certain conclusions can be drawn from the experimental data, observations and the literature. It is evident that high soil moisture is favorable for the disease and late season irrigations should be avoided or used with caution. If the disease is present to a small extent only, it would be advisable to rogue out the diseased plants and destroy all tubers under such plants whether or not they appear healthy. If only a portion of a field is infected, the potatoes should be dug separately and not marketed with the potatoes from the uninfected portions of the field. Care should be used in grading to remove all suspicious tubers. It should be remembered that infected plants often have some infected tubers in which the disease has not developed sufficiently to cause visible rot and that these tubers may develop rot in a few days in transit or storage. Tubers with only slight symptoms are difficult to detect unless washed. When infected tubers are stored under moist conditions the infection spreads to the potatoes in contact with the infected ones and pockets of rotten tubers will occur in the bin.

Inasmuch as the organism lives over in roots, stems, and stolons as well as in tubers, fields showing infection should not be replanted to potatoes without an interval of three or four years. For the same reasons, infected tubers should be carefully eliminated at planting time to prevent contamination of the soil. Rotation and healthy seed may not eliminate the disease but will prevent the increase of the organism which would occur by successive plantings of the susceptible host. The danger of losses in years with favorable weather conditions for the disease would be greatly lessened by these measures.

SUMMARY

A disease previously unreported in Nebraska was observed in 1943 and subsequently identified as pink rot caused by *Phytophthora erythroseptica*. The disease was first reported in the United States from Maine in 1938 and has since been observed in Massachusetts, Rhode Island, Louisiana, and Idaho.

Inoculation experiments were conducted in the greenhouse and the disease was produced with symptoms similar to those observed in the field. The disease is typically a late-season wilt and the stems may become rotted from the basal portion to 6 or 8 inches above the ground line. Aerial tubers are sometimes produced in the leaf axils.

Infected tubers retain their shape and are soft and rubbery. The surface of the tuber shows dark bands between healthy and infected tissue and the eyes and lenticels darken, often exuding droplets of liquid. The freshly cut surface of infected tubers turns pink in 15 to 20 minutes and eventually becomes black.

Inoculation experiments proved that tuber infection could occur through the stolons, through wounds or by contact of healthy and infected tubers in storage.

The effect of temperature on the development of tuber rot was studied in the laboratory and it was found that the disease occurred over a range of temperature from 43° to 86° F., with the most rapid and extensive rot occurring at 76° F. Contrasted with this, another similar tuber rot caused by *Phytophthora drechsleri* produced a rot at 93° F. and caused more rotting at 85° than at 76° F. This tuber rot (*P. drechsleri*) was identified for the first time in Nebraska in 1945.

Phytophthora erythroseptica caused a wilt and tuber rot by stem and soil inoculation in the greenhouse but no infection was obtained by similar inoculation with *P. drechsleri* and *Pythium debaryanum*.

More infection was obtained in the greenhouse at low than at high temperatures and with high rather than low soil moisture. More infection was obtained by inoculating the soil when the plants were young, 26 days after planting, than when old, 79 days after planting, but some infection occurred even in those plants approaching maturity at the time the soil was inoculated.

Soil inoculation tests for varietal susceptibility failed to reveal any variety that could be classed as resistant. The Warba and Pawnee varieties were the most susceptible, whereas the least infection occurred on Irish Cobbler.

Suggestions offered for the control of this disease include crop rotation, roguing, separate harvesting of infected portions of fields, careful grading before shipping or storing, and avoidance of excessively high moisture in storage or in the field late in the season.

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