The Effect of Wounding, Temperature, and Inoculum on the Development of Pink Rot of Potatoes Caused by *Phytophthora erythroseptica*

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ABSTRACT

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The effect of wounding, temperature, and inoculum on the development of pink rot caused by *Phytophthora erythroseptica*, was studied for its potential impact on postharvest infection. Tissue plugs cut from pink rot infected tubers and plugs of similar size from laboratory cultures of the pathogen were highly effective inoculum sources on wounded tubers. Severe wounding, temperatures of 15 to 25ºC, and high inoculum density affected the infection risk. Regardless of source or amount of inoculum, any degree of wounding greatly increased incidence of infection of tubers by *P. erythroseptica*. Infections in unwounded tubers started at 15ºC, whereas in wounded tubers infection started at 10ºC. Incidence of pink rot was high when two or three of the factors (severe wounding, high temperature, high inoculum level) were favorable. Incidence of pink rot was intermediate when only one factor was favorable. Incidence of pink rot was low or absent without a favorable factor (no wounding, low temperature, and low inoculum), Since infected tuber tissue may serve as potential inoculum source for postharvest infection of tubers by *P. erythroseptica*, the removal of pink rot infected tubers at harvest is desirable. Avoidance of wounding and rapid cooling of storage bins to 10ºC may also help control pink rot.

Pink rot, caused by *Phytophthora erythroseptica* Pethybr., is an important disease of potato (*Solanum tuberosum* L.) (20). The name of the disease describes a characteristic and diagnostic pink color that appears after infected tissue has been cut and exposed to air for 20 to 30 min (8,12,17). Other symptoms of pink rot include dark discoloration of the skin and lenticels of infected parts, purplish discoloration of the eyes, and firm leathery texture of the rotted tissue (8,12,17).

Pink rot was first described on potatoes in Ireland by Pethybridge (17) in 1913, and first reported in the United States in Maine in 1938 (2). Pink rot is widely distributed in North America (22) and other parts of the world (25). Potato farmers often refer to pink rot as "water rot" (1) without distinguishing the pathogen(s) involved. In 1991 we examined tubers with "water rot" from 45 potato storage sites in seven states and one Canadian province (22). *P. erythroseptica* predominated in tubers from 32 (71%) of the sites, while *Pythium* spp. predominated in four locations. In locations where it was present, *P. erythroseptica* was recovered from 57% of rotted tubers. *P. erythroseptica* was recovered from samples from all regions included in the survey. A representative sample of isolates of *P. erythroseptica* was tested for pathogenicity. All caused typical pink rot symptoms when inoculated into potato tubers. Similar studies were done on a more limited regional basis in 1992, 1993, and 1994 with similar results (16).

Although the firm leather texture and the pink color of the infected tissue are diagnostic symptoms of pink rot, confirmation that the disease is caused by *P. erythroseptica* must be accomplished by culturing symptomatic tuber pieces on semiselective media (28) or on water agar (pH = 5.5). Since *P. erythroseptica* is homothallic, it forms its characteristic oogonia with amphigynous antheridia abundantly after 7 to 10 days of culture at 15 to 24ºC (4,9,25). Zoospores, sporangia, and oospores are the natural inoculum sources of *P. erythroseptica* (15,17,18,21). Inoculum sources for laboratory and greenhouse studies have included: Replacement of excised tuber tissue with colonized agar plugs (8,12), dipping of wounded tubers in a suspension of mycelium and oospores (14), pouring mycelia and/or zoospore suspensions onto injured roots (29) or uninjured roots, stems, stolons, tubers, and leaves (15), or the use of infected tissue pieces from artificially inoculated tubers (8,12,13).

Published information about factors influencing pink rot development relate to occurrence of the disease in the field or at harvest. Soil moisture is an important factor in the development of pink rot (1,5). The disease is frequently found in low-lying areas, wet fields, or in fields under

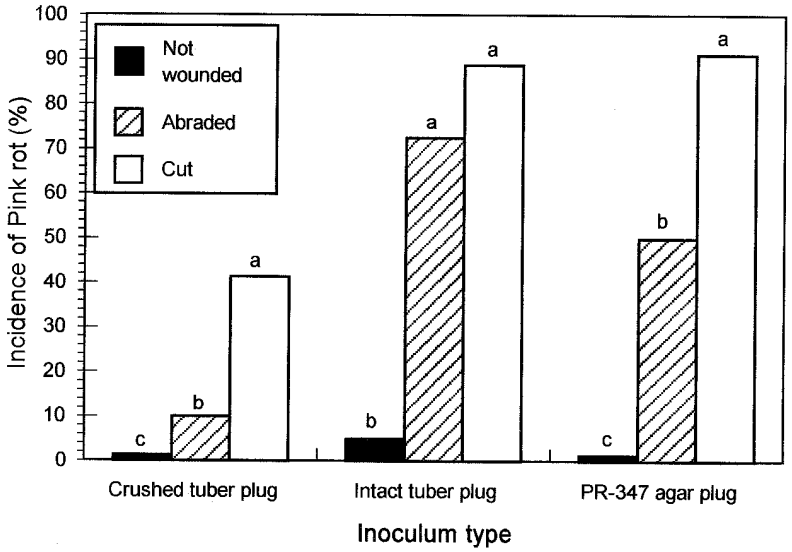

Fig. 1. Effect of source of *Phytophtora erythroseptica* inoculum × wounding interactions on incidence of pink rot, 10 days postinoculation at 20°C. Cut = periderm disc (5 × 1 mm) removed with scalpel. Abraded = periderm tissue rubbed once with Scotch brite. Not wounded = sound periderm. PR-347 agar plug = culture of *P. erythroseptica*. Crushed tuber plug = Intact plug crashed. For each inoculum type, columns with the same letter are not significantly different according to LSD at $P = 0.05$.

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irrigation (1,2). Pink rot, however, can also be found in sandy soils without obvious excessive moisture (1). In infested soil and under field capacity of moisture, infection can occur through the stem end via an infected stolon (4,8). Under high soil moisture in the field, or high humidity in storage, infection may occur directly through eyes; low moisture inhibits infection (4,5). Under high soil moisture conditions, pink rot can develop at soil temperatures from 10 to 30ºC, and the optimum temperature for infection is 25ºC (29). High humidity in storage facilities with poor ventilation can cause heavy losses of affected crops (4). The optimum temperature for the development of tuber rot is 25ºC (8,12). Management of pink rot includes crop rotation (4,13), avoiding excessive moisture in fields late in the season or in storage (8,13), application of metalaxyl (mefenoxam) (27), elimination of diseased tubers, careful grading of tubers before storage (8,12), avoiding or separate harvest of tubers from infected areas (8).

Potatoes are subject to a variety of injuries during harvest and bin-filling operations. These injuries may reach from 15 to 87%, depending on cultivar, degree of skin-set, and soil conditions (10,19). During harvest, pink rot infected tubers are smashed into pieces, and many of these pieces came in contact with healthy tubers, suggesting that dispersal of the pink rot pathogen and infection may occur at harvest. This differs from the concept that all *P. erythroseptica* infection occurs prior to harvest via an infected stolon (1,4,8). Thus, the objective of this study was to determine if wounds on tubers, similar to those that occur during harvest, provide suitable infection courts for *P. erythroseptica* and to determine how such infection is influenced by temperature, and inoculum type or level.

Table 1. Combined analysis of variance of data for the effect of inoculum type, wounding, and cultivar on the incidence of pink rot caused by *Phytophthora erythroseptica*

Sources of variation	df	Sum of squares	Mean square	*F* value[a]	*PR* > *F*
Experiment	1	1,168.0556	1,168.056		
Rep (Exp)	2	313.8888	156.9444		
Inoculum type (IT)[b]	2	19,202.7778	9,601.3889	363.84**	0.0027
Wounding (W)[c]	2	61,502.7778	30,751.3889	111.26**	0.0089
Cultivar (C)[d]	1	34.7222	34.7222	1.00	0.5000
IT × W[e]	4	9,605.5556	2,401.3889	13.94**	0.0128
IT × C[f]	2	86.1111	43.0556	0.18	0.8450
W × C[g]	2	452.7778	226.3889	1.23	0.4493
IT × W × C[h]	4	1,238.8889	309.7222	1.25	0.4162
Experiment × IT	2	52.7778	26.3889		
Experiment × W	2	552.7778	276.3889		
Experiment × C	1	34.7222	34.7222		
Experiment × IT × W	4	688.8889	172.2222		
Experiment × IT × C	2	469.4444	234.7222		
Experiment × W × C	2	369.4444	184.7222		
Experiment × IT × W × C	4	988.8889	247.2222		
Error	34	4936.1111	145.1797		
Total	71	101,698.6111			

[a] Values followed by (**) are statistically significant at $P = \leq 0.01$.
[b] Significance tested using experiment × inoculum type as an error term.
[c] Significance tested using experiment × wounding as an error term.
[d] Significance tested using experiment × cultivar as an error term.
[e] Significance tested using experiment × inoculum type × wounding as an error term.
[f] Significance tested using experiment × inoculum type × cultivar as an error term.
[g] Significance tested using experiment × temperature × inoculum level as an error term.
[h] Significance tested using experiment × wounding × temperature × inoculum level as an error term.

Table 2. Combined analysis of variance of experiments for the effect of wounding, temperature, and inoculum level on the incidence of pink rot caused by *Phytophthora erythroseptica*: Two temperatures (10 and 20ºC)

Sources of variation	df	Sum of squares	Mean square	*F* value[a]	*PR* > *F*
Experiment	1	868.055556	868.05556		
Rep (experiment)	2	19.290123	9.64506		
Temperature (T)[b]	1	4,459.876543	4,459.87654	1,156.00*	0.0187
Wounding (W)[c]	2	39,249.614198	19,624.80709	74.53**	0.0132
Inoculum level (ID)[d]	1	43,734.567901	21,867.28395	17.33*	0.0545
W × T[e]	2	2,119.984568	1,059.99228	1.73	0.3669
W × ID[f]	4	22,804.783951	5,701.19598	24.63**	0.0044
T × ID[g]	2	3,063.271605	1,531.63580	56.71*	0.0173
W × T × ID[h]	4	2,075.617284	518.90432	1.08	0.4718
Experiment × W	2	526.620370	263.310185		
Experiment × T	1	3.858025	3.858025		
Experiment × ID	2	2,523.148148	1,261.574074		
Experiment × W × T	2	1,228.780864	614.390432		
Experiment × W × ID	4	925.925926	231.481481		
Experiment × T × ID	2	54.012346	27.006173		
Experiment × W × T × ID	4	1,925.154321	481.288580		
Error	34	2,827.93210	83.17447		
Total	71	128,410.49383			

[a] Values followed by (*) (**) are statistically significant at $P = 0.05$ and $P = < 0.01$, respectively.
[b] Significance tested using experiment × temperature as an error term.
[c] Significance tested using experiment × wounding as an error term.
[d] Significance tested using experiment × inoculum level as an error term.
[e] Significance tested using experiment × wounding × temperature as an error term.
[f] Significance tested using experiment × wounding × inoculum level as an error term.
[g] Significance tested using experiment × temperature × inoculum level as an error term.
[h] Significance tested using experiment × wounding × temperature × inoculum level as an error term.

MATERIALS AND METHODS

Tubers. Potato 'Norchip' was used throughout this study. Potato 'Snowden' was used only in the initial test of inoculum type. Tubers were obtained from commercial potato producers in North Dakota and stored on arrival at 5ºC until inoculation. Only sound tubers of similar size (140 to 190 g) were selected for inoculations. Tubers were soaked in tap water for 30 min, hand washed, and dried at room temperature (20 to 24ºC) without surface sterilization 24 to 48 h before inoculations.

Isolate. Isolate PR-347 of *P. erythroseptica* was obtained from an infected tuber from Rice, MN, received in 1991, and was used throughout this study. Isolation was made on a selective medium similar to that of Tsao and Ocana (28) (P10VP) (17 g of Difco corn meal agar, 0.4 ml of pimaricin, 200 ppm vancomycin, and 160 mg of pentachlorinitrobenzene per liter). A hyphal-tip culture of the isolate was grown on modified V8 juice agar (150 ml of V8 juice, 1.5 g $CaCO_3$, 850 ml distilled water, and 20 g of agar), and tested for aggressiveness on potato tubers as follows: tubers were cut wounded and inoculated with PR-347 on V8 juice agar. Inoculated tubers were placed in a plastic moist chamber (40 cm long × 27 cm wide × 17 cm high) lined top and bottom with two layers of wet paper towels and incubated in darkness at 20ºC for 10 days. Isolate PR-347 was among the most aggressive in a survey of *P. erythroseptica* iso-

lates (22), and has been used as the pathogenic control in numerous experiments in our laboratory (21,23,24). Pathogenicity has been maintained through periodic inoculations to potato tubers and re-isolation on V8 juice agar since 1991.

Inoculum and inoculations. Three *P. erythroseptica* inoculum types were investigated, including infected intact tuber plug, infected crushed tuber plug, and agar culture plug. Infected tuber plugs were obtained by excising (with a no. 2 cork borer) cylinders of infected tissue from the edge of pink rotted lesions caused by PR-347 on Norchip potatoes, and cutting in pieces of 5 × 3 mm. Each infected intact tuber plug was crushed in a porcelain mortar to obtain infected crushed tuber plugs. Agar culture plugs (5 × 3 mm) were cut from the colony margin of 10-day-old plate cultures of *P. erythroseptica* grown on modified V8 juice agar. These inoculum plugs were equivalent to the high inoculum level of experiment 2. All inoculations were made near the middle of one side with either tuber or agar inoculum plugs or control plugs onto the wounded or marked inoculation sites.

Wounding. Three types of wound severity (cut, abraded, and unwounded) were included in this study. These wounds were produced before inoculations in an area near the middle of one side of each tuber. Only one type of wound was applied per tuber. Cutting was the removal with a scalpel of the periderm tissue of a previously cut periderm tissue (5 × 1 mm disk) with a cork borer no 2. Abrading (grazing) consisted of a superficially rubbing the periderm (0.5 × 1 cm) once with a plastic scouring pad (Scotch-Brite, 3M, Minneapolis, MN). Unwounded tubers were selected on the basis of an intact periderm.

Experiment 1: Infected tuber tissue as source of inoculum. This experiment was conducted to test the hypothesis that infected tuber pieces (8,12) could be a source of inoculum for the spread of pink rot. It also compared the inoculum potential of plugs cut from infected tubers to similarly sized agar culture plugs used in experiment 2. Treatments included in this study were three inoculum types (infected intact tuber plug, infected crushed tuber plug, and *P. erythroseptica* agar plug), three wound types (cut, abraded, and unwounded), and two cultivars (Norchip and Snowden). The full factorial combination (3 × 3 × 2) of treatments was arranged in a completely random design with two replications. Each experimental unit was a set of 10 tubers. The experiment was performed twice.

Experiment 2: Effect of wounding, temperature, and inoculum level. In this two-part experiment only the *P. erythroseptica* agar culture inoculum plug was used. The first part included two temperatures (10 and 20ºC), the second part included six temperatures (5, 10, 15, 20, 25, and 30ºC). The three wound types (cut, abraded, and unwounded) were included at both low and high inoculum levels based on size and uninoculated controls. Inocula were obtained from the colony margin of 10-day-old plate cultures of *P. erythroseptica* grown on modified V8 juice agar. The low-level inoculum was a small agar culture plug (1.5 × 1.5 mm) obtained with a biscuit cutter, and contained mycelia plus approximately $3.2 \times 10^2 \pm 27.2$ oospores. The high level inoculum was a larger (5 × 3 mm) agar culture plug cut with a cork borer no. 2 and contained $1.5 \times 10^4 \pm 914.7$ oospores. The number of oospores was determined by counts made on 1.5 × 3 mm of agar culture plug inoculum. Oospore numbers are only given as reference; it is unlikely that 10-day old oospores were the primary source of inoculum in this study. All full factorial sets of wounding and inoculum treatments, including controls, were present at each temperature for a full

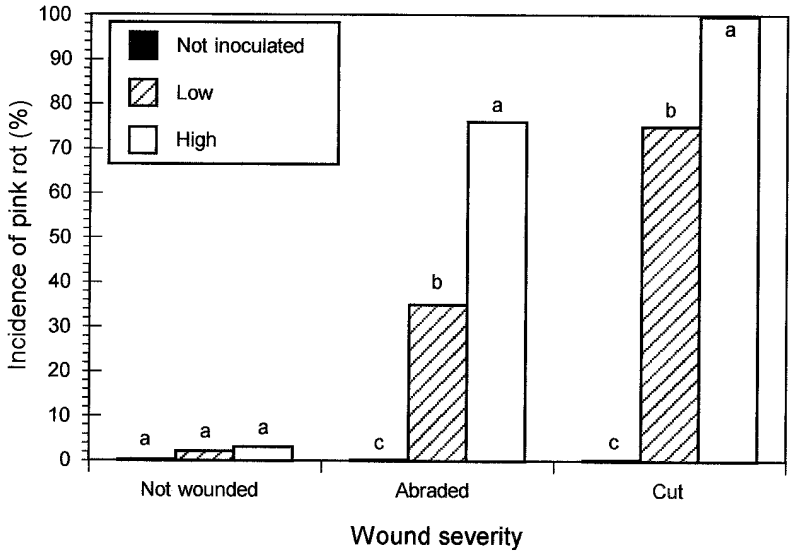

Fig. 2. Effect of wounding × inoculum level interactions on the incidence of pink rot caused by *Phytophtora erythroseptica*. Values averaged over 10 and 20°C. Cut = periderm disk (5 × 1 mm) removed with scalpel. Abraded = periderm tissue rubbed once with Scotch brite. Not-wounded = sound periderm. Not inoculated = control tubers. High inoculum = 5 × 3 mm agar plug of *P. erythroseptica*. Low inoculum = 1.5 × 1.5 mm agar plug of *P. erythroseptica*. For each wound severity, columns with the same letter are not significantly different according to LSD at $P = 0.05$.

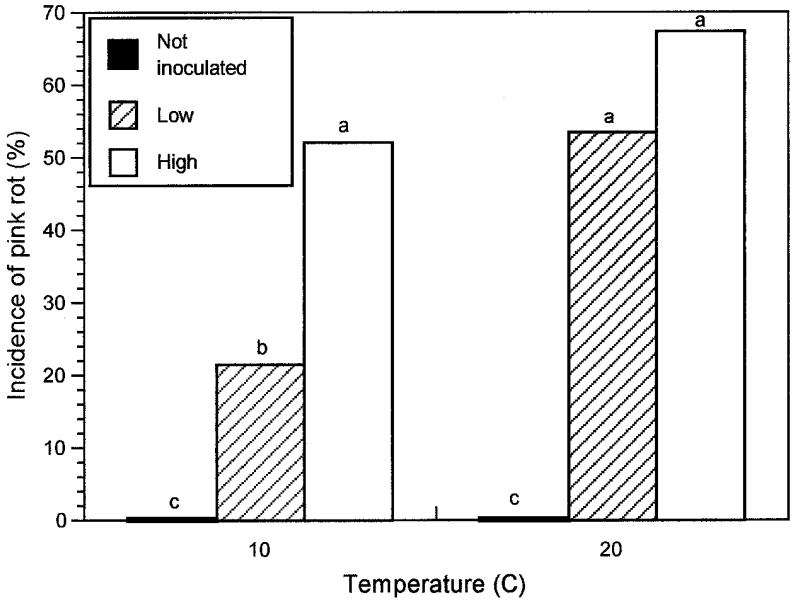

Fig. 3. Effect of temperature × inoculum level interaction on the incidence of pink rot caused by *Phytophtora erythroseptica*, 10 days after inoculation. Values averaged over wound severity. Not inoculated = control tubers. High inoculum = 5 × 3 mm agar plug of *P. erythroseptica*. Low inoculum = 1.5 × 1.5 mm agar plug of *P. erythroseptica*. For each temperature, columns with the same letter are not significantly different according to LSD at $P = 0.05$. Temperature in °C.

factorial design, with 3 × 2 × 3 = 18 and 3 × 6 × 3 = 54 treatment combinations, for the first part and second part, respectively. The first part was conducted in a completely random design with two replicates. There were 12 tubers for each wound-temperature-inoculum treatment. The second part was conducted in a split plot design with two replicates, with temperature as main plots and wounding and inoculum as split plot factors. The experimental unit was a set of three tubers for each wound-temperature-inoculum treatment. The first part of this experiment was performed twice and the second part was performed three times.

Disease assessment. Pink rot was assessed 10 to 12 days after inoculation. Tubers were cut longitudinally through the inoculation point and covered with moist paper towels for 30 to 60 min to enhance the development of the typical pink discoloration symptom. Number of tubers showing symptoms of pink rot in each experimental unit was recorded after 30 min. Incidence of pink rot was calculated as follows: (number of tubers showing symptoms of pink rot/number of inoculated tubers) × 100.

All data were subjected to analysis of variance (PROC GLM, SAS Institute, Cary, NC). Data from repeated experiments were pooled after testing the error mean squares for homogeneity (26). Least significant difference (LSD) values for the effect of interactions in combined experiments were calculated as outlined by Carmer et al. (6).

Table 3. Combined ANOVA of experiments for the effect of wounding, temperature, and inoculum level on the incidence of pink rot caused by *Phytophthora erythroseptica:* Six temperatures (5, 10, 15, 20, 25, and 30ºC)

Sources of variation	df	Sum of squares	Mean square	*F* value[a]	*PR* > *F*
Experiment	2	2,479.42387	1239.71193		
Rep (experiment)	3	77.16049	25.72016		
Temperature (T)[b]	5	125,210.90535	25042.18107	66.69**	0.0001
T × rep (exp)	15	2,978.39506	198.55967		
Wounding (W)[c]	2	170,442.38683	85221.19342	106.54**	0.0003
Inoculum level (ID)[d]	1	11,363.16872	11363.16872	3.75	0.1924
W × T[e]	10	39,866.25514	3986.62551	7.17**	0.0001
W × ID[f]	2	936.21399	468.10700	0.74	0.5317
T × ID[g]	5	7,433.12757	1486.62551	3.31*	0.0508
W × T × ID[h]	10	7,026.74897	702.67490	2.34*	0.0504
Experiment × W	4	3,199.58848	799.89712		
Experiment × T	10	3,755.14403	375.51440		
Experiment × ID	2	6,059.67078	3029.83539		
Experiment × W × T	20	11,121.39918	556.06996		
Experiment × W × ID	4	2,520.57613	630.14403		
Experiment × T × ID	10	4,495.88477	449.58848		
Experiment × W × T × ID	20	5,997.94239	299.89712		
Error	90	16,388.88889	182.09877		
Total	215	421,352.88066			

[a] Values followed by (*) (**) are statistically significant at $P = 0.05$ and $P = < 0.01$, respectively.
[b] Significance tested using experiment × temperature as an error term.
[c] Significance tested using experiment × wounding as an error term.
[d] Significance tested using experiment × inoculum level as an error term.
[e] Significance tested using experiment × wounding × temperature as an error term.
[f] Significance tested using experiment × wounding × inoculum level as an error term.
[g] Significance tested using experiment × temperature × inoculum level as an error term.
[h] Significance tested using experiment × wounding × temperature × inoculum level as an error term.

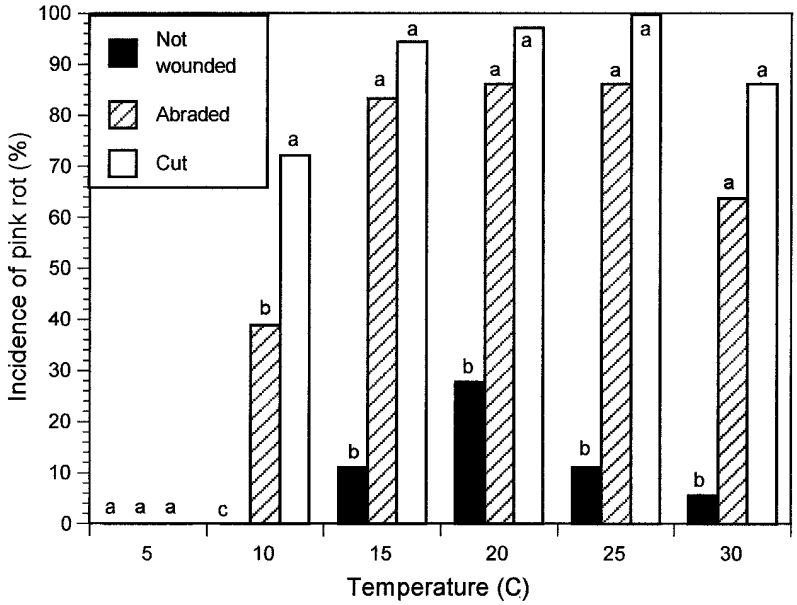

Fig. 4. Effect of wounding × temperature interaction on the incidence of pink rot caused by *Phytophtora erythroseptica*. Values averaged over inoculum levels. Cut = periderm disk (5 × 1 mm) removed with scalpel. Abraded = periderm tissue rubbed once with Scotch brite. Not wounded = sound periderm. For each temperature, columns with the same letter are not significantly different according to LSD at $P = 0.05$. Temperature in °C. At 5°C none of the inoculated tubers showed infection by *P. erythroseptica* at 12 days after inoculation.

RESULTS

Experiment 1: Infected tuber tissue as source of inoculum. The analysis of variance (ANOVA) for the effect of inoculum type, wounding, and potato cultivar showed that inoculum type, wounding, and their interaction had a highly significant effect ($P \leq 0.01$) on the incidence of pink rot on potato tubers caused by *P. erythroseptica* (Table 1). Intact plugs or crushed plugs obtained from *P. erythroseptica* infected tubers were capable of causing pink rot on wounded potato tubers (Fig. 1). Infected intact plugs and agar culture plugs were more effective than infected crushed plugs. Unwounded tubers showed only a low incidence of infection regardless of inoculum type (Fig. 1). On tubers wounded by cutting, infected intact plugs and agar culture plugs caused an overall similar mean infection incidence of pink rot, 88.8 and 91.3%, respectively. Incidence of infection caused by infected intact plugs on cut (88.8%) and abraded (72.5%) tubers were also similar; however, incidence of infection on abraded tubers was greater for intact tuber plugs (72.5%) than for agar plugs (50%) ($P = 0.05$).

Experiment 2: Effect of wounding, temperature and inoculum level. Table 2 shows the ANOVA for the effect of wounding, temperature, and inoculum level conducted at 10 and 20ºC on the incidence of pink rot. Wounding, temperature, inoculum level ($P \leq 0.05$), the interaction of wound × inoculum level ($P = 0.004$), and the interaction of temperature × inoculum level ($P = 0.017$) had a significant effect on the incidence of pink rot caused by *P. erythroseptica*. The significant interaction of wounding × inoculum level was mainly due to a nonsignificant effect of inoculum level on unwounded tubers (Fig. 2). Incidence of pink rot in unwounded tubers was very low regardless of inoculum level.

Incidence of pink rot on cut or abraded tubers was higher with the high inoculum level than with the low inoculum level (P = 0.05). The significant interaction of temperature × inoculum level was primarily due to a significant effect of inoculum level at 10ºC (Fig. 3). Incidence of pink rot at 10ºC was higher with a high inoculum level than with a low inoculum level, 52.1 to 21.5%, respectively. In contrast, incidence of pink rot at 20ºC at high (67.4%) or low inoculum (53.5%) level was similar (Fig. 3).

The ANOVA of data including six temperatures shows that as in the experiment with two temperatures, wounding, temperature ($P \leq 0.02$), and the interaction of temperature × inoculum level (P = 0.017) had a significant effect on the incidence of pink rot caused by *P. erythroseptica* (Table 3). In addition, the effect of the interaction wound × temperature and wound × temperature × inoculum level (P = 0.05) was also significant. The significant interaction of wounding × temperature was due to the effect of 5, 10, and 15ºC temperatures (Fig. 4). At 10ºC incidence of pink rot was significantly (P = 0.05) influenced by wounding, with infections being highest on tubers wounded by cutting (72%), intermediate on abraded tubers (38.9%), and least in not-wounded tubers (0%). At 15ºC or higher, wounds were no longer required for infections to occur (Fig. 4). Incidences of pink rot at 10 to 30ºC on cut or abraded tubers were significantly higher (P = 0.05) than on unwounded tubers. Incidences of pink rot on cut or abraded tubers at 15ºC to 30ºC were similar, but greater than in unwounded tubers. The significant interaction of temperature × inoculum levels was due mainly to results obtained at 5 and 10ºC (Fig. 5). Incidences of pink rot at 15 to 30ºC were similar regardless of the inoculum level. Incidence of pink rot at 10ºC, however, was higher with high inoculum level than with low inoculum level. None of the tubers inoculated at 5ºC developed symptoms of infection by *P. erythroseptica* whether wounding or inoculum was imposed (Fig. 4 and 5). However, 32.1% of these tubers developed symptoms of pink rot after transferring to 20ºC.

Several general responses can be derived from the significant (P = 0.05) effect of the interaction of wound × temperature × inoculum density presented on Table 4. With low inoculum level, pink rot infections on wounded tubers (11.1%) started at 10ºC, whereas, in unwounded tubers (16.7%) infections started at 20ºC. In contrast, with high inoculum level, pink rot infections in unwounded tubers started at 15ºC. The combined effect of wounding by cutting, high inoculum level, and temperatures of 15 to 25ºC favored higher incidences of pink rot. In contrast, unwounded potatoes and those subject to temperatures of 5 or 10ºC, or low inoculum had low or no incidences of pink rot (Table 4). An attempt to assign infection-risk values to the various levels of wounding, temperature, and inoculum is presented in Table 5. This table shows that a combination of at least two favorable factors caused high levels of pink rot infection. With one favorable factor, pink rot infections were intermediate. With no favorable factor, pink rot infections were low or wanting.

DISCUSSION

It is commonly recognized that all infections to tubers by *P. erythroseptica* occur before digging (1,20). These infections are mostly through diseased stolons (7,8,15,17,18). Infections through eyes, however, were also noted in wet soils and in storage (4,7,8). We have frequently observed a high incidence of pink rotted tubers in storage bins containing potatoes originating from a single field with low levels of pink rot. The high incidence of pink rotted tubers was associated with only a portion of the field. In observations of commercial potato digging operations, we have noted many intact and smashed pieces of pink rotted tubers on digger chains and bin pilers. Pieces of diseased tubers readily adhere to harvested tubers going into storage and could serve as inoculum if wounds occur during handling. The potential of infected tubers or pieces from a still spreading lesion to cause pink rot has been reported (3,30). Data presented here agree with these findings. Thus, postharvest infections by *P. erythroseptica* may occur via infected tuber pieces provided tubers are wounded during harvest operations.

Wounding, temperature, inoculum level, and their interactions appear to affect incidence of infection of pink rot on potato tubers. Tubers are wounded with cuts and

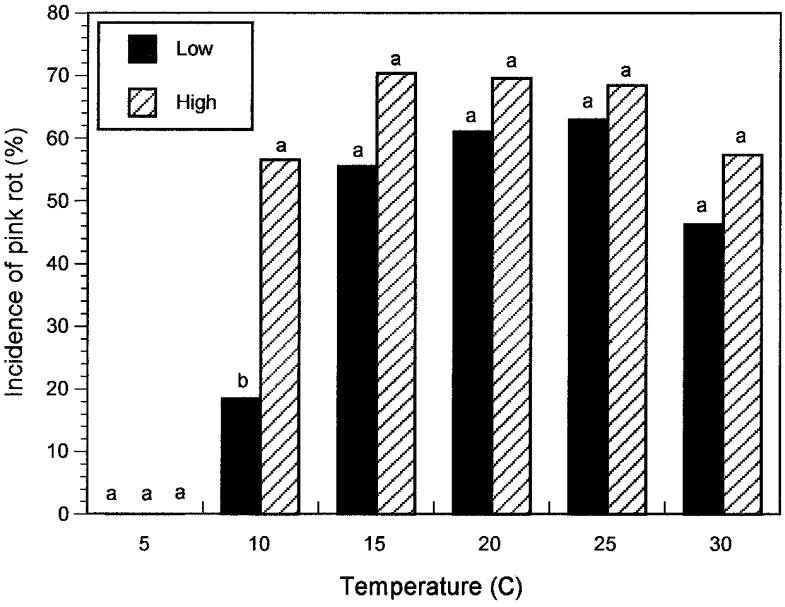

Fig. 5. Effect of temperature × inoculum level interaction on the incidence of pink rot caused by *Phytophtora erythroseptica*. Values averaged over wound severity. High inoculum = 5 × 3 mm agar plug of *P. erythroseptica*. Low inoculum = 1.5 × 1.5 mm agar plug of *P. erythroseptica*. For each temperature, columns with the same letter are not significantly different according to LSD at P = 0.05. Temperature in °C. At 5°C none of the inoculated tubers showed infection by *P. erythroseptica* at 12 days after inoculation.

Table 4. Means of the effect of interaction wounding × temperature × inoculum level on the incidence of pink rot caused by *Phytophthora erythroseptica*, 10 to 12 days postinoculation

	Tubers infected by *P. erythroseptica* (%)					
	Unwounded[a]		Abraded[b]		Cut[c]	
Temp. (ºC)	Low inoc.[d]	High inoc.[e]	Low inoc.	High inoc.	Low inoc.	High inoc.
5ºC	0	0	0	0	0	0
10ºC	0	0	11.1	66.7	44.4	100
15ºC	0	22.2	77.8	88.9	88.9	100
20ºC	16.7	38.9	72.2	100	94.4	100
25ºC	5.6	16.7	83.3	88.9	100	100
30ºC	5.6	5.6	55.6	72.2	77.8	94.4

[a] Unwounded = sound periderm.
[b] Abraded = periderm tissue rubbed once with Scotch-Brite.
[c] Cut = periderm disk (5 × 1 mm) removed with scalpel.
[d] Low inoculum = 1.5 × 1.5 mm plug of *P. erythroseptica* grown on V8 juice agar.
[e] High inoculum = 5 × 3 mm plug of *P. erythroseptica* grown on V8 juice agar.

bruises varying in size and severity during harvest and storage operations (10). Our data show that any degree of wounding greatly increases the risk of *P. erythroseptica* infection. In contrast, unwounded tubers are less likely to be infected by *P. erythroseptica*, unless temperatures reach 15ºC or higher. The optimum temperature range for tuber infection by *P. erythroseptica* is 20 to 25ºC, with infections being rare at 5ºC or above 30ºC temperature (5). Our data agree with these results. In practice, potatoes are harvested when tuber temperatures are between 15 and 20ºC, favorable to infection. These temperatures during harvest (September and October) cause a high tuber pulp temperature (>18ºC) and poor skin set favoring "skinning" (wounding) of the periderm. It takes several weeks before a storage bin of potatoes can be cooled to 10ºC where the infection process can be arrested to some degree. Hence, tubers that are held for any period of time at temperatures above 10ºC can be expected to be at much greater risk for infection by *P. erythroseptica*. Tubers held at 10ºC for processing can be infected to a lesser extent and may develop pink rot in storage in cases where they were free of infection at time of harvest, but wounded. Infected tubers that are quickly cooled to 5ºC are unlikely to develop pink rot, but might do so after they are warmed.

Our attempt to assign infection-risk values (Table 5) to the various levels of temperature, wounding, or inoculum indicated that at least a combination of two favorable factors (wounding, high temperature, and high inoculum level) was needed for high levels of infection by *P. erythroseptica*. When only one factor was favorable, incidences of infection were intermediate. If no factor was favorable (no wound, low temperature, low inoculum level), infections were low or none. The combined effect of all these factors may explain the incidence of pink rot during or after harvest.

The data presented here indicate the potential of tuber pieces infected by *P. erythroseptica* for causing postharvest infection. Likewise, high temperatures and any degree of wounding increases the infection risk. Therefore, a management strategy for pink rot must incorporate removal of infected tubers prior to storage, wound prevention by achieving maximum skin set, tarping of trucks to avoid rapid dehydration, and temperature and air checking in storage facilities. These strategies are already recommended (12,13,19) to manage potato storage diseases, including leak (*Pythium ultimum* Trow), a similar disease that is also favored by wounding and high temperatures (11).

Table 5. Effect of the interaction wounding × temperature × inoculum level on incidence of pink rot caused by *Phytophthora erythroseptica*, 10 to 12 days after inoculations

Line[a]	Wounding method	Temp. (ºC)	Inoculum level	Infected tubers (%)	Disease potential[b]
1	Cut	25	High	100.0	+ + +
2	Cut	20	High	100.0	+ + +
3	Cut	15	High	100.0	+ + +
4	Cut	10	High	100.0	+ – +
5	Cut	25	Low	100.0	+ + –
6	Abraded	20	High	100.0	0 + +
7	Cut	20	Low	94.4	+ + –
8	Cut	30	High	94.4	+ 0 +
9	Cut	15	Low	88.9	+ + –
10	Abraded	15	High	88.9	0 + +
11	Abraded	25	High	88.9	0 + +
12	Abraded	25	Low	83.3	0 + –
13	Abraded	15	Low	77.8	0 + –
14	Cut	30	Low	77.8	+ 0 –
15	Abraded	20	Low	72.2	0 + –
16	Abraded	30	High	72.2	0 0 +
17	Abraded	10	High	66.7	0 – +
18	Abraded	30	Low	55.6	0 0 –
19	Cut	10	Low	44.4	+ – –
20	Unwounded	20	High	38.9	– + +
21	Unwounded	15	High	22.2	– + +
22	Unwounded	20	Low	16.7	– + –
23	Unwounded	25	High	16.7	– + +
24	Abraded	10	Low	11.1	0 – –
25	Unwounded	25	Low	5.6	– + –
26	Unwounded	30	High	5.6	– 0 +
27	Unwounded	30	Low	5.6	– 0 –
28	Unwounded	10	High	0.0	– – +
29	Unwounded	15	Low	0.0	– + –
30	Cut	5	High	0.0	+ – +
31	Cut	5	Low	0.0	+ – –
32	Abraded	5	High	0.0	0 – +
33	Abraded	5	Low	0.0	0 – –
34	Unwounded	5	High	0.0	– – +
35	Unwounded	5	Low	0.0	– – –
36	Unwounded	10	Low	0.0	– – –

[a] Line numbers to facilitate interpretation of data.

[b] Disease potential due to the significant effect ($P = 0.05$) of the interaction wounding × temperature × inoculum level. + = favorable, – = not favorable, 0 = intermediate. Wounding: cut = +, abraded = 0, and unwounded = –; temperature: 15 to 25°C = +, 5 and 10°C = –; inoculum level: high = +, and low = –.

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