

Latent Infection of Potato Seed Tubers by the Late Blight Pathogen, *Phytophthora infestans*

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Persistence of *Phytophthora infestans*, the cause of late blight, from year to year is a critical component of late blight epidemics. Understanding the means of pathogen survival is a major goal in developing management strategies for the disease. In the Pacific Northwest and intermountain region of North America, oospores are not currently known to be a factor in overwintering and infected tubers are considered to be the main means of overwintering for the pathogen and the source of initial inoculum. Infected tubers serving as overwintering and primary inoculum sources may be potato seed-tubers, potato tubers left in the field after harvest that produce volunteer plants, and cull potato tubers. The relative importance of the three types of infected tubers in temperate climates is unknown and may depend in part on microclimates, local conditions and the extent of infection the previous fall.

A continuum of viable host tissue is essential for survival and overwintering of *P. infestans* in potato growing regions where oospores are not an overwintering factor. Contemporary isolates, particularly the US-8 strain, are highly aggressive and rapidly rot tubers, limiting the availability of viable host tissue. However, rotting by the US-8 strain of *P. infestans* did not occur over seven weeks in inoculated tuber tissue at a storage temperature of 37°F. Recommended holding temperatures for tubers vary depending on end use. Seed potatoes are stored between 38 to 40°F, fresh market potatoes are stored between 38 to 50°F, while French fry and chip processing potatoes are stored between 44 to 50°F and 50 to 55°F, respectively. The optimal temperature for hyphal growth of *P. infestans* in potato tubers is about 50°F. However, the length of time infected tubers can remain intact in storage at temperatures used to store seed tubers is not known.

In the Columbia Basin of Washington and Oregon approximately 8.7×10^8 seed tubers (assuming mean seed piece weight of 60 g, mean seed tuber size of 170 g, and 5% waste) were cut and planted in 2007. *Phytophthora infestans* produces sporangia on infected tubers and the potential for multiple infections by *P. infestans* has been demonstrated when infected seed tubers are cut and handled (3). Because of the extremely large amount of seed tubers planted in a potato production region and the explosive polycyclic capabilities of *P. infestans*, a greater understanding is needed on the survival of *P. infestans* in potato seed tubers. Since infected seed tubers that survive in storage are a potential source of inoculum, the possibility of latent infection in stored seed tubers needs to be investigated. The purpose of this research was to test the hypothesis that potato tubers can be latently infected with *P. infestans* and to characterize the survival of *P. infestans* in infected potato seed tubers of susceptible and moderately resistant cultivars at temperatures (near 39°F) and time periods (6 to 7 months) used in commercial seed tuber production in the Pacific Northwest.

Methods and Materials

Four potato cultivars, Russet Burbank, Ranger Russet, Umatilla Russet, and Defender were selected for this study. Russet Burbank, Ranger Russet, and Umatilla Russet are major potato cultivars grown in the Pacific Northwest of the United States. Defender is a recently released cultivar and is not commonly grown. Tubers of Russet Burbank and Ranger Russet are susceptible to *P. infestans*. Tubers of Umatilla Russet and Defender are considered moderately resistant and resistant, respectively, to *P. infestans* when compared to Ranger Russet (5).

Four US-8 isolates of the A2 mating type, Wa02, Web04, BF05, and Wa06 of *P. infestans* were used in these studies. Isolates Wa02, Web04 and Wa06 were obtained from potato foliage collected from central Washington in 2002, 2004, and 2006 respectively. Isolate BF05 was obtained from potato foliage collected in northern Idaho in 2005. The isolates were maintained in potato tubers of cultivar Russet Burbank during winter months of October through March at 39.5°F. Isolates were then maintained and increased on excised leaflets of cultivar Russet Burbank. Sporangia were washed from excised leaflets with distilled water. Concentration of sporangia was adjusted to 10,000 per ml of distilled water using a hemacytometer. Sporangia used for inoculation were chilled for 2 h at 4°C to induce zoospore formation. Inoculation was done by applying 0.05 ml of inoculum with a micropipette to a Whatman #2 filter paper cut into 10 x 10 mm squares and then placing the saturated filter paper square to a single eye on a tuber.

Inoculated and non-inoculated tubers were placed in a humidity chamber and then allowed to dry. Tubers were then placed in one of three cold storages facilities from 30 to 209 days. Storage facility 1 was programmed at 47°F and was selected to represent storage temperature for French fry and chip processing potatoes. Storage facilities 2 and 3 were programmed at 39.5°F and 39°F, respectively, and were selected to represent temperatures used to store seed tubers.

Development of late blight in stored tubers of Russet Burbank and Umatilla –

Tubers of Russet Burbank and Umatilla Russet were inoculated in September 2006 with isolate BF05, placed in a mist chamber for 20 h at 63-73°F, and allowed to dry for 6 h at 68-73°F. Inoculated and non-inoculated tubers of each cultivar were then placed in storage at three storage facilities and arranged as a completely randomized design. Five inoculated and five non-inoculated tubers of each cultivar were used for each sample time and each storage facility.

In facility 1, tubers of each cultivar were destructively assessed at 34, 48, 71, 91, and 101 days. In facilities 2 and 3, tubers of each cultivar were destructively assessed at 101, 125, 146, 167, and 181 days. At each destructive sampling period, severity of late blight was visually assessed after cutting each tuber in cross section at four places of approximately equal intervals. The surface areas formed from the cuts were rated individually for the percent area of internal rot. Tubers in facilities 2 and 3 that were symptomless for late blight based on external observation on the last assessment date at 209 days were not destructively sampled, but instead were incubated at 72° to 73°F. Tubers were inspected every two to three days for late blight symptoms over a three week period. Tubers were

considered asymptomatic if no symptoms or signs were found following a thorough examination of the periderm for discoloration and eyes for necrosis. Small peels with a knife were made to observe internal tissue under the periderm and cuts were made into the eye where the inoculation was made to observe for discoloration and necrosis.

The experiment was repeated in September 2007 using the methods as described above except as noted. The number of inoculated and non-inoculated tubers for each cultivar and time period was four. Tubers stored in facility 1 (mean 47 °F) were destructively assessed at 30, 60 and 91 days. Tubers stored in facilities 2 and 3 (mean 39.5 ° and 39 °F, respectively) were destructively assessed for late blight at 30, 60, 91, 122, 150 and 182 days of storage.

Tuber slices from 18 asymptomatic tubers collected from the six sampling periods were incubated in humidity chambers at 59 °F and observed with a stereo scope at 10 to 62 X magnifications for sporulation of *P. infestans* four times per week over three weeks. Each humidity chamber consisted of tuber slices 2 cm thick placed on a nylon screen over moistened filter paper in glass Petri dishes 9.5 cm dia. by 2.5 cm in height. Petri dishes were then placed in a 24 x 35 x 5 cm glass tray which was then sealed in a plastic bag. Cross sections from four symptomatic tubers with severities of 20 to 70% of each Russet Burbank and Umatilla Russet from facilities 2 and 3 at the 150 day sampling period (n = 8) were also placed in humidity chambers and incubated at 59°F for 48 h to promote sporangia formation. The experiment was repeated (n = 8) at the 181 day sampling period. The cut surface and eyes of the tuber disks were then observed for sporangia of *P. infestans* at 21, 24, and 48 h of incubation. Time for sporangia to first be observed was recorded. Incubation period was the period in hours from initial incubation in the humidity chamber until sporangia were first observed.

Development of late blight in stored tubers inoculated with four isolates – Tubers of Russet Burbank were inoculated at a single eye in October 2006 using the filter paper technique with one of the four *P. infestans* isolates. Inoculated tubers were placed in a mist chamber for 24 h at 64° to 69°F and air dried for 6 h at 69°F. Twenty-one tubers were inoculated with WA02, 24 with Web04, 17 with BF05 and 22 with WA06. Tubers were arranged as a completely randomized design and stored in facility 2 (mean 39.5°F). Twenty tubers were not inoculated and used as controls. Tubers were destructively assessed once after 209 days of storage. Asymptomatic tubers were not cut, but were held at 72° to 73°F for three weeks. Asymptomatic tubers in which late blight symptoms later developed were then placed in a humidity chamber and incubated at 59°F for 48 h to promote sporangia formation.

The experiment was repeated with Umatilla Russet tubers in September 2007. Methods and experimental design were the same as in the first trial except the number of tubers inoculated with each of the four isolates was 15. The number of non-inoculated tubers used as the control was 15. All tubers were destructively sampled after 182 days as described previously. Tuber slices from asymptomatic tubers were incubated in humidity chambers at 59°F and observed for sporulation of *P. infestans* four times per week over three weeks.

Effect of incubation time before cold storage on development of late blight in tubers

– Tubers of Russet Burbank, Ranger Russet, Umatilla Russet, and Defender were inoculated in mid September 2007 with isolate BF05. The number of tubers inoculated per cultivar was 60. Twenty tubers of each cultivar were then dried for 1, 6 or 24 h. Ten tubers for each drying time and cultivar were arranged in a completely randomized design and stored in facilities 2 and 3. The number of non-inoculated tubers used as controls for each drying time and temperature was 10. The drying time was considered the incubation period. Tubers were kept in storage for 182 days and symptomatic tubers were destructively sampled as previously described. Tubers that were asymptomatic for late blight based on external observation as previous described were not destructively sampled, but instead were incubated at 72° to 73°F. Tubers were then monitored at a two to three day interval for late blight symptoms over a three week period. Incubation until sporulation was determined for five tubers with severities between 1 and 10% as previously described. The experiment was repeated in October 2007.

Results

Development of late blight in stored tubers of Russet Burbank and Umatilla -

Severity of late blight increased during storage at 47°F in storage facility 1 (Fig. 1). Severity of late blight was significantly ($P < 0.05$) less for Umatilla Russet than for Russet Burbank at 47°F during the first (Fig. 1) and the second storage seasons (data not shown). Late blight severity did not significantly ($P > 0.05$) vary between the two cultivars and between 39.5°F and 39°F in storage facilities 2 and 3 the first (Table 1) and second (Fig. 2, data for temperatures and cultivars combined) storage seasons. For the second storage season at 39.5° and 39°F, 0 to 25% of the inoculated tubers sampled monthly up to 181 days of storage had severities less than 1% (Fig. 2). Incidence of tubers with late blight symptoms did not differ significantly ($P > 0.05$) between Umatilla Russet and Russet Burbank in each of the three storage facilities both seasons. Late blight did not develop in the non-inoculated control tubers.

For the first storage season at 39.5° and 39°F, 20% and 40% of the inoculated Umatilla Russet and Russet Burbank tubers, respectively, were asymptomatic after 209 days of storage, but later developed late blight symptoms when subsequently incubated at 73°F for three weeks. Thus, indicating a latent infection (Table 1). Some eyes on tubers produced sprouts 1.5 to 6 cm in length before blighting. Sporangia of *P. infestans* were produced on tuber eyes and slices when incubated in humidity chambers at 59°F. For the second storage season at 4.2° and 4.1°C, 6 to 44% of the inoculated tubers sampled monthly up to 181 days of storage were asymptomatic, but tuber slices later supported production of *P. infestans* sporangia when incubated in a humidity chamber at 59°F. Thus, indicating a latent infection of tubers (Fig. 2). Late blight symptoms did not develop in the non-inoculated control tubers.

Incubation period until sporulation ranged from 6 to 20 days and had a mean of 9.6 days when tuber slices from asymptomatic tubers were incubated in a humidity chamber at 59°F (Table 2). Sporangia were observed on the cut surface and eyes of 14 tuber slices from symptomatic tubers at 24h and on two tuber disks at 21h. The difference in length

of incubation period until sporulation between asymptomatic and symptomatic tubers disks was significant at $P < 0.0001$. Sporulation was light at 21h with less than 20 sporangiophores with sporangia on an eye or cut surface. The amount of sporulation increased with time of incubation.

Soft rot and dry rot symptoms occurred in some late blight symptomatic tubers sampled during the latter assessment times both storage seasons. During the first storage season at 181 and 209 days, mean incidence and severity of bacterial soft rot symptoms were each 10%. Fusarium dry rot was not evident. During the second storage season at 150 and 182 days, mean incidence and severity of Fusarium dry rot symptoms were 13% and 15%, respectively. Bacterial soft rot did not exceed 1% severity.

Development of late blight in stored tubers inoculated with four isolates– Incidence of tubers with late blight symptoms ranged from 32 to 100 % for Russet Burbank tubers inoculated with one of four isolates of *P. infestans* and stored at 39.5°F for 209 days during the first storage season. Mean severity of late blight symptoms for tubers with symptoms ranged from 68 to 89%. Severity of late blight was significantly ($P < 0.05$) greater in tubers inoculated with isolate Web04 than with isolates BF05 and Wa06 (Table 3).

Late blight symptoms developed in inoculated tubers that were asymptomatic after 209 days of storage when they were subsequently incubated at 73°F for three weeks, indicating a latent infection of tubers. Percent latent tuber infection ranged from 0 to 33% of the inoculated tubers for the four isolates (Table 2). Sprouts from tuber eyes grew 1.5 to 4 cm in length before developing late blight symptoms when latently infected tubers were incubated at 73°F. Sporangia of *P. infestans* were produced on tubers slices, tubers, and sprouting eye upon incubated in humidity chambers at 59°F. Late blight symptoms did not develop in the non-inoculated control tubers. Some symptomatic tubers for late blight also had soft rot and dry rot symptoms. Mean incidence and severity of bacterial soft rot symptoms was 33% and 10%, respectively. Mean incidence and severity of Fusarium dry rot symptoms was 18% and 5%, respectively.

During the second storage season, incidence of tubers with late blight symptoms ranged from 60 to 100 % for Umatilla Russet tubers inoculated with one of four isolates of *P. infestans* and stored at 39.5°F for 182 days. Mean severity of late blight symptoms for tubers with symptoms ranged from 47 to 77 %. Severity of late blight symptoms was significantly greater in tubers inoculated with isolates Web04 and BF05 than with isolate Wa02 (Table 3).

Twenty percent of the inoculated tubers inoculated with isolate WA02 did not exhibit late blight symptoms after 182 days of storage at 39.5°F. However, sporangia of *P. infestans* developed on tuber slices from these tubers when incubated in humidity chambers at 59°F, indicating a latent infection of tubers (Table 3). Incubation period until sporulation ranged from 7 to 15 days with a mean of 10 ($n = 3$) when tuber slices from asymptomatic tubers were incubated in humidity chamber at 59°F (Table 4). Late blight symptoms did not develop in the non-inoculated control tubers. Bacterial soft rot was not evident in

tubers. Some tubers with late blight symptoms also had Fusarium dry rot symptoms. Mean incidence and severity of Fusarium dry symptoms were both 5%.

Effect of incubation time before cold storage on development of late blight in tubers-

Incidence and severity of infected tubers were each significantly ($P < 0.05$) greater for Ranger Russet than for the other three cultivars except for Russet Burbank in the first trial (Table 4). Data for the 39° and 39.5°F temperatures were combined because they were similar ($P > 0.05$). Late blight incidence and severity were similar ($P > 0.05$) among the 1, 6 and 24 h incubation periods between the end of the mist period and placement of tubers in cold storage, and thus data were combined (Table 4).

Up to 5% of the inoculated tubers had late blight severities less than 1% after 182 days of storage (Table 4). Fifteen tubers (6.3%) had severities of 5 to 10% in the two trials (data not shown). Five percent of the Ranger Russet and 1.7% of both the Umatilla Russet and Defender tubers in the first trial were asymptomatic after 182 days of storage but later developed late blight symptoms when incubated at 72° to 73°F for 13 days.

Incubation period until sporulation on tubers with late blight severities of 1 to 10% ranged from 3 to 8 days (mean = 4.6 days) when tubers that eventually developed late blight symptoms were incubated in a humid chamber at 59°F. Late blight symptoms did not develop in the non-inoculated control tubers. For both trials, incidence and severity of bacterial soft rot symptoms were 2% and 30%, respectively. Incidence and severity of Fusarium dry rot symptoms were 8 and 50%, respectively.

Discussion

Phytophthora infestans is known to persist in potato tubers during storage (1), but survivability in seed tubers under extended cold storage conditions and at typical seed storage temperatures has not been known until this study. Isolates of the US 8 and other new clonal lineages of *P. infestans* are aggressive in potato tubers and quickly rot infected tubers at temperatures above 50°F. Mycelium of *P. infestans* is no longer able to survive in tubers once the host tissue is completely rotten. Tubers of Russet Burbank and Umatilla Russet infected with US 8 isolates in this study rotted within 3 months at 47°F. However, all tubers at 39.5° and 39°F did not completely rot and isolates of the US8 clonal lineage persisted in potato seed tubers during an extended storage season of 6 to 7 months at temperatures used to store seed tubers.

Variation in the severity of late blight symptoms in infected tubers stored in long term cold storage was high in this study. Tubers with late blight severities of less than 1% were not uncommon. All tubers with low severities of symptoms are not likely to be detected and disposed during inspection, handling, cutting and planting. Such tubers are capable of supporting sporangia and perpetuating the pathogen as they continue through the process of handling to planting.

A latent infection of tubers was demonstrated in that some tubers were asymptomatic and did not exhibit late blight symptoms of discoloration or necrosis on the external or in the internal tissues at the end of a storage period. However, symptoms and sporangia of *P.*

infestans developed on asymptomatic tubers when they were placed at temperatures of 59°F and above. Eyes of tubers with low late blight severities and of tubers with latent infections were viable and sprouted after storage. Sporangia developed on sprouts from asymptomatic tubers after storage when later incubated at high humidity and 59°F. A relatively high number of tubers may be latently infected when taken out of environments typical of commercial seed tuber storage, which likely depends on the level and extent of infection the preceding fall. Various factors influence infection of tubers near harvest (4, 6). Latently infected seed tubers could be another important inoculum source of *P. infestans*.

A potential for secondary cycles of infection by *P. infestans* during seed-tuber cutting and handling has been documented (3). Sporulation of *P. infestans* occurred within 21 h at high humidity after seed tubers with late blight symptoms were removed from cold storage to a warmer environment in this study. Sporangia can be readily transmitted by direct contact from tubers or seed pieces to non-infected seed pieces (2). Sporangia can potentially become air borne and carried by air currents to cut tuber surfaces or tuber eyes within a storage and cutting facility or to plants and soil in the field, resulting in additional infections. Potato handling and cutting facilities are generally enclosed, blocking incoming solar radiation which would also increase longevity of sporangia.

The extended incubation period until sporulation of 6 to 20 days for latently infected tubers, 3 to 8 days for tubers with 1 to 10% severity, and 1 to 2 days for tubers with 20 to 70% severities indicated different levels of establishment in tuber tissue by *P. infestans*. Sporulation of *P. infestans* over an extended time period on tubers taken from storage could be expected because of varying degrees of infection. This would provide a longer time period for sporangia to be present during handling and cutting of seed tubers and increase the probability for infected tubers to become exposed to environmental conditions favoring sporulation, dissemination and infection.

Severity of late blight was significantly less for Umatilla Russet than for Russet Burbank at 47°F up to 100 days of storage, but not at 39.5° and 39°F for 182 to 209 days of storage. Results of the longer storage periods near 39°F differed from a previous study where Umatilla Russet was more resistant than Russet Burbank based on tuber severity. Inoculated tubers were stored for 36 days at 48°F in the previous study (5). Long storage periods at temperatures near 39°F appear to have negated the effects of the moderate resistance in Umatilla Russet in this study. Incidence of late blight also did not differ between Umatilla Russet and Russet Burbank in this study, indicating that resistance to infection does not differ between the two cultivars. Tubers of Defender and Umatilla Russet were more resistant than those of Ranger Russet for 182 days in storage at 39 to 39.5°F based on incidence and severity of infection in this study and based on severity of infection in a previous study (5).

Pectolytic bacteria often infect potato tubers after initial infection with *P. infestans*. Latently infected tubers that were detected were not affected by bacterial soft rot or Fusarium dry rot in this study. *Phytophthora infestans* is a poor competitor against soft rotting bacteria and dry rot *Fusaria*. Secondary infection by these organisms would

eliminate long term survival of the late blight organism in stored tubers. Wounding of tubers facilitates infection by pectolytic bacteria, and soft rot was not a major issue in this study likely because tubers were not wounded before inoculating with *P. infestans*. Also tubers surfaces were dry before placing in cold storage, eliminating possible anaerobic conditions created by a water film on tuber surfaces that favor pectolytic bacteria. Wounding tubers to inoculate with *P. infestans* may alter resistance reaction to *P. infestans*. Storage temperatures below 40°F also inhibit development of bacterial soft rot in potato tubers.

In summary, *P. infestans* is capable of surviving asymptotically and at various levels of symptom development in potato seed tubers for extended time periods at temperatures around 39°F. Latent infection of seed tubers was demonstrated and poses a challenge for management of late blight. Visual inspection of tubers will not reveal latently infected tubers and molecular techniques and sampling procedures need to be developed to accurately detect infection levels in potato seed lots.

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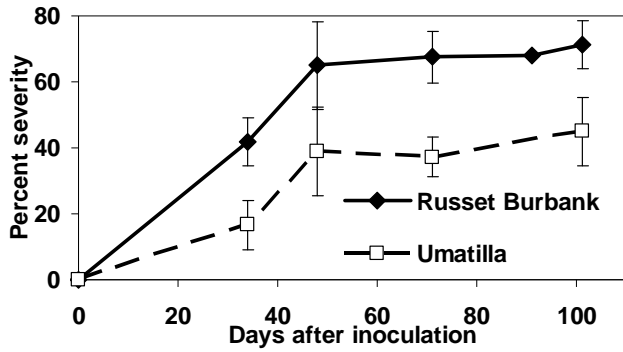


Figure 1. Severity of late blight symptoms in tubers of Russet Burbank and Umatilla Russet stored at 47°F for 100 days.

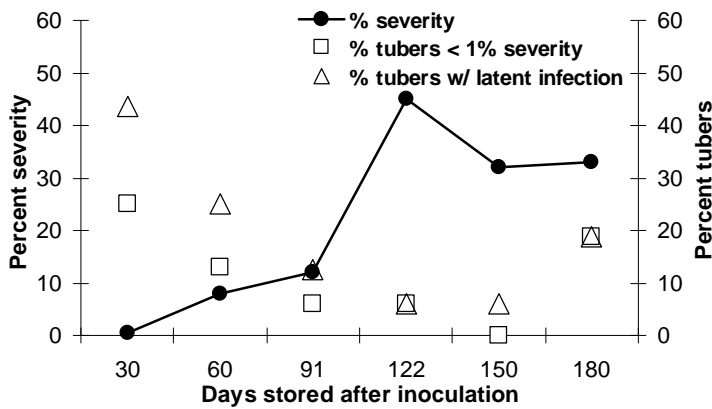


Figure 2. Severity of late blight symptoms in Russet Burbank and Umatilla Russet tubers, percentage of tubers with late blight symptom severity less than one percent severity, and percentage latent infection of tubers inoculated with *Phytophthora infestans* and stored at 39.5 and 39°F for 30 to 182 days during the 2007-2008 storage season.

Table 1. Incidence of Russet Burbank and Umatilla Russet tubers with symptoms of late blight, severity of late blight symptoms, and percentage of tubers with latent infection of tubers inoculated with *Phytophthora infestans* and stored at 39 and 39.5 F for 209 days during 2006 – 2007.

Treatment ^a Cultivar	Late blight		
	Incidence of tubers with symptoms ^b (%)	Severity of late blight symptoms (%) ^b	Percent latent tuber infection
R. Burbank	50	90	20
Umatilla R.	70	70	10

^aNumber (n) each value a mean of 10 tubers.

^bIncidence and severity of late blight did not differ significantly between Russet Burbank and Umatilla Russet ($P > 0.05$).

Table 2. Incidence and severity of late blight symptoms and percentage latent infection of tubers of Russet Burbank inoculated with one of four isolates of *Phytophthora infestans* and stored at 39.5°F for 209 days during 2006-2007^a.

Isolate	Total tubers (n)	Late blight		
		Incidence of tubers with symptoms (%)	Severity of tubers with symptoms (%)	Percent latent tuber infection
Wa02	21	62	81 ab	33
Web04	24	75	89 a	4
BF05	17	100	68 b	0
Wa06	22	32	69 b	9

^a Values within a column with the same upper case letter are not significantly different at $P = 0.05$, according to Fisher's Protected LSD.

Table 3. Incidence and severity of late blight symptoms, percentage of tubers with late blight symptom severity less than one percent, and percentage latent infection of tubers of Umatilla Russet tubers inoculated with one of four isolates of *Phytophthora infestans* and stored at 39.5°F for 182 days during 2007-2008^a.

Isolate	Late blight			
	Incidence of tubers with symptoms (%)	Severity of tubers with symptoms (%)	Percent of tubers with symptom severity < 1%	Percent latent tuber infection
Wa02	60	47 b	20	20
Web04	100	72 a	7	0
BF05	93	77 a	7	0
Wa06	87	65 ab	13	0

^a Total inoculated tubers per isolate (n) was 15. Values within a column with the same upper case letter are not significantly different at $P = 0.05$, according to Fisher's Protected LSD.

Table 4. Incidence and severity of late blight symptoms, percentage of tubers with late blight symptoms less than one percent severity, and percentage latent infection of tubers of four potato cultivars inoculated with isolates BF05 of *Phytophthora infestans* and stored at 39° and 39.5°F for 182 days in two trials during 2007-2008^a.

Temperature Cultivar ^a	Late blight			
	Incidence of tubers with symptoms (%)	Severity of tubers with symptoms (%) Mean ± se	Percent of tubers with symptom severity < 1%	Percent latent tuber infection
First trial				
Ranger R	60 a	85 a	5.0	5.0
R Burbank	33 ab	50 ab	0	1.7
Umatilla R	3 b	21 b	1.7	0
Defender	2 b	20 b	0	1.7
Second trial				
Ranger R	71 a	85 a	3.3	0
R Burbank	49 b	41 b	0	0
Umatilla R	0 c	-	0	0
Defender	7 c	11 c	0	0

^a Total number of tubers per cultivar (n) at each temperature was 30. Values within a column with the same upper case letter are not significantly different at $P = 0.05$, according to Fisher's Protected LSD. Data combined for temperatures and pre-storage incubation periods.