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Colonization and Sporulation of *Phytophthora infestans* on Volunteer Potatoes Under Western Washington Conditions

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Abstract Growth, sporulation, and survival of *Phytophthora infestans* on volunteer potato tubers, was investigated under temperatures representative of winter (4°C, 7°C, and 10°C) and spring (13°C, 16°C, 19°C) soil conditions in western Washington. Inoculated tubers stored at 10°C for 8 days had a significantly ($P<0.05$) higher percentage of disease symptoms on tuber surfaces and a higher number of lenticels and eyes with *P. infestans* sporulation compared to those stored at 4°C or 7°C. Sporulation of *P. infestans* on cut tuber surfaces was observed following 3-week storage at the three winter soil temperatures. After 12-week storage, tubers inoculated with a US-8 isolate had a significantly higher percentage of late blight on cut surfaces than those inoculated with a US-11 isolate (70% versus 50%, respectively). For spring soil temperature studies, tubers inoculated with the US-8 isolate and held at 19°C had a significantly higher number of lenticels per tuber with *P. infestans* sporulation than tubers held at 13°C or 16°C. Sporulation of *P. infestans* on tuber surfaces was detected on infected tubers buried 5-cm deep in potting medium at all tested winter and spring temperatures for 3- or 6-day periods, respectively. The site or depth of tuber inoculation with *P. infestans* did not influence tuber-to-sprout infection events and whether apical end or stem sprouts become infected. Tubers with late blight that survive the winter in western Washington and support sporulation of *P. infestans* via lenticels and eyes may enable the transmission of *P. infestans* from infected tissues to sprouts of volunteer plants. However, the impact of these events on primary inoculum production by *P. infestans* in the region is probably limited by the mild, winter conditions favoring tuber breakdown in soil.

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Resumen El crecimiento, esporulación y supervivencia de *Phytophthora infestans,* en tubérculos de papa que quedaron remanentes en campos de cultivo después de la cosecha, fueron investigados bajo diferentes temperaturas las cuales representaban las condiciones del suelo en invierno (4°C, 7°C y 10°C) y en primavera (13°C, 16°C, 19°C) para la región oeste del estado de Washington. Los tubérculos inoculados almacenados a 10°C por 8 días mostraron un porcentaje significativamente mayor ($P<0.05$) de síntomas de la enfermedad en la superficie del tubérculo, así como un número más alto de lenticelas y yemas con esporulación de *P. infestans* comparado con aquellos tubérculos que fueron almacenados a 4°C o 7°C. La esporulación de *P. infestans* en la superficie de tubérculos cortados fue observada después de 3 semanas de almacenamiento a las tres temperaturas de suelo establecidas para invierno. Después de 12 semanas de almacenamiento, los tubérculos inoculados con el tipo US-8 tuvieron un porcentaje significativamente mayor de infección de tizón tardío en las superficies cortadas que aquellos inoculados con el tipo US-11 (70% vs. 50%, respectivamente). En los estudios de temperatura de suelo en primavera, los tubérculos inoculados con el tipo US-8 y mantenidos a 19°C tuvieron un número más alto de lenticelas por tubérculo con esporulación de *P. infestans* que los tubérculos mantenidos a 13°C o 16°C. Esporulación de *P. infestans* en la superficie de tubérculo fue detectada en tubérculos infectados y enterrados a 5-cm de profundidad del suelo de cultivo, esto ocurrió en todas las temperaturas evaluadas tanto de invierno y primavera después de periodos de 3 o 6 días, respectivamente. El sitio o la profundidad de la inoculación de *P. infestans* en los tubérculos no influyó en

las chances de transferencia de infección de tubérculo a brotes, ni tampoco si los brotes apicales o de tallo fueron preferentemente infectados. Los tubérculos con tizón tardío que sobrevivieron el invierno en el oeste de Washington y permitieron esporulación a través de lenticelas y yemas, pueden permitir también la transmisión de *P. infestans* de tejidos infectados hacia los brotes de tubérculos remanentes en campos de cultivo. Sin embargo, el impacto de estos eventos en la producción de inóculos primarios de *P. infestans* en esta región esta probablemente limitado por las condiciones de invierno moderado que favorecerían mas bien la desintegración de los tubérculos en el suelo.

Keywords Late blight · Survival · Volunteer potato tubers · Lenticels · Eyes

Introduction

Fresh market potato production is an increasingly valuable sector of agriculture throughout the coastal region of western Washington where the mild, marine climate offers excellent potato growing conditions (Dorrance et al. 1999). Potato acreage in Skagit County alone increased from 1,600 to 4,900 ha between 1998 and 2001 and reached more than 5,700 ha in some years (McMoran 2006). Extensive land sharing and shorter rotation intervals between potato crops have increased the potential for volunteer potato plant and tuber tissues in many fields.

In this region, as is true for the rest of North America outside of Mexico, asexual spores produced on plants and tubers by *Phytophthora infestans* (Mont.) de Bary are considered to be the primary source of inoculum for the development of late blight (Erwin and Ribeiro 1996). Naturally-occurring sexually-produced propagules (oospores) of the pathogen have yet to be detected in North America (Goodwin et al. 1998). However, populations of two clonal lineages of *P. infestans* representing both A1 and A2 mating types (US-8 and US-11, respectively) have been identified in western Washington. In addition, this population of *P. infestans* has persistently maintained complex pathotypes (Derie and Inglis 2001; Dorrance et al. 1999).

Seed potato tubers, volunteer potatoes left in the field after harvest, cull potato tubers and tare dirt containing potato tissue from storage units are suspected as primary potato inoculum sources in the late blight disease cycle (Murphy 1922; Peterson 1947; Van der Zaag 1956). Although the impact of infected seed potato tubers on the potential for survival and transmission of *P. infestans* has been documented (Platt et al. 1999; Lambert et al. 1998, Inglis et al. 1999; Powelson et al. 2002), the significance of these other sources of inoculum for initiating late blight epidemics has not been clearly identified.

Western Washington's mild, winter temperatures are rarely severe enough to render buried potato tubers non-viable (Boydston and Seymour 1994; Newberry 2002) and the vigorous growth and reproductive ability of *P. infestans* make volunteer potatoes a perpetual weed and disease management issue. Survival of *P. infestans* on potato tubers and transmission to sprouts and plants that develop from the tubers is largely dependent on the viability of the tuber tissue throughout the winter and the pathogen's physiological capability of surviving or avoiding low temperatures or freezing conditions. De Bruyn (1926) observed that mycelium of *P. infestans* could withstand temperatures as low as −17°C provided the mycelium was associated with various organic substrates; this observation has not been confirmed in more recent studies. Thermal properties within cull piles, especially those exceeding 1,000 kg in size, can aid in the survival of meristematic tissue by protecting tubers from low ambient temperatures in winter months (Kirk 2003b). When *P. infestans* is present in seed tubers, obvious late blight symptoms, including decay, usually do not develop on tubers in storage environments maintained at commercial temperatures (3°C), but the rate of late blight symptom development often increases at 7°C to 10°C, temperatures frequently used for storing fresh market and processing potatoes (Kirk et al. 2001).

Colonization and sporulation of *P. infestans* on potato tubers, as influenced by soil temperatures and relative aggressiveness of genotypes of the pathogen, may affect the amount of tuber breakdown and the potential for survival and transmission (Partipilo 1999). Even though the infection, incubation and sporulation stages of the *P. infestans* life cycle in soil likely govern survival and transmission, these stages are not fully understood even after 150 years of research on this infamous pathogen (Andrivon 1995). The objectives of this study were to assess (i) the influence of western Washington winter and spring soil temperatures on the colonization and sporulation of the current genotypes of *P. infestans* in the region and (ii) the potential of volunteer and cull potatoes to serve as sources of *P. infestans* inoculum in an area where long-term freezing temperatures fail to occur on an annual basis.

Materials and Methods

Inoculum Production

Isolates of *P. infestans* from the WSU-Mount Vernon Northwestern Washington Research and Extension Center's Vegetable Pathology Laboratory were used in all experiments. Isolate 'MV04-28', representing the US-8 genotype, was collected from potato (cv Red La Soda) field trials near Mount Vernon, WA in 2004. Isolate 'MV110 B', representing

the US-11 genotype, was collected from hairy nightshade (*Solanum sarrachoides* L.) in Skagit Co. in 1994. The US-11 isolate has been successfully used in multiple late blight investigations (Dorrance and Inglis 1998; Inglis et al. 1999; Powelson et al. 2002). Allozyme analysis, as described by Goodwin et al. (1998), was used to verify the genotype of both of these isolates.

All *P. infestans* isolates were grown on rye agar at 16°C with a 16 h light cycle. To increase inoculum, and maintain and confirm pathogenicity, agar plugs (5-mm in diameter) were placed on the abaxial side of leaflets of the potato cv White Rose (3 plugs per leaflet). Inoculated leaflets were kept in glass Petri dishes lined with moist filter paper, and sterile water (50 μl) was added to each plug to facilitate pathogen establishment and infection. Petri dishes with inoculated leaflets were incubated in clear plastic boxes with lids and held at 16°C for 5 to 7 days. Following late blight lesion development, the leaflets were rinsed with distilled water and sporangial suspensions were quantified using a hemacytometer (Spotlite Hemacytometer; American Scientific Products, McGaw Park, IL). Isolates were regularly transferred (every 1 to 3 months) from rye agar in storage to either potato leaflets or tuber tissue, then re-isolated from actively sporulating lesions.

Seed Tubers

All potato tubers used in these studies were purchased from a commercial seed grower as Blue Tag Certified Potato Seed from lots that were harvested during the 2004 growing season. Only healthy seed tubers were used and any tubers with evidence of disease or rot were discarded. Prior to inoculation, potato tubers were kept in cold storage at 3.8°C.

Winter Soil Temperature Experiments

Three experiments were completed to simulate *P. infestans* survival in potato tubers under a range of winter soil temperatures (4°C, 7°C and 10°C) typical of western Washington winter months (October–February) based on a 49-year average soil temperature at 10-cm depth. These temperature experiments were designed to help characterize: (i) growth in infected potato tubers and sprouts (Experiment A), (ii) sporulation on buried potato tubers (Experiment B), and (iii) survival and sporulation on potato tubers (Experiment C).

Growth in infected tubers and sprouts (Experiment A) Winter soil temperatures (4°C, 7°C and 10°C) and incubation period (3, 8 and 15 days) treatments were evaluated in two experiments (Test 1 and Test 2). Each treatment was replicated five times with six tubers per replication. One replication of a tuber was treated with sterile water instead of *P. infestans* as a reference control treatment.

Seed tubers (4 oz) of cv Russet Burbank were wounded (3 mm wide×3 mm long×5 mm deep) at one eye located near the center of the tuber. One rye agar plug (5-mm in diameter) colonized by the US-8 genotype (MV04–28) was placed in each wound and the inoculated tubers were stored in plastic bags (six tubers per bag) with moist toweling for 6 days at 16°C. Infected tubers were then incubated in the dark in growth chambers set at 4°C, 7°C, or 10°C. At each sampling time (3, 8 or 15 days) three tubers per replication were peeled, cut transversely, and the amount of late blight symptom development on the peeled tuber surface, assessed. Estimated values were averaged for the two halves of the tuber.

Three tubers per replication were used to assess both sporulation and transmission of *P. infestans*. To assay sporulation, infected tubers were cut transversely, and placed cut surface-down on moist paper within a plastic box. Each box was individually sealed in a plastic bag with additional moist paper toweling to sustain high humidity. The tubers were incubated for approximately 72 h at 16°C. Tuber pieces were then observed with a dissecting microscope (×40 magnification) to determine whether or not sporulation of *P. infestans* had occurred. The number of lenticels with active *P. infestans* sporulation was counted and the tubers were weighed. The amount of sporulation was then based on tuber weight (g). The number of tuber eyes that supported *P. infestans* sporulation was also counted and the percentage with sporulation of the pathogen was based on the total number of eyes on each tuber.

A *P. infestans* transmission assay for these tubers was set-up in a greenhouse under shade cloth (60% shade, Steuber's, Co. Snohomish, WA) in order to assess potential of *P. infestans* to grow from infected tubers to developing sprouts. Each tuber piece was planted 5-cm deep into a 10-cm diameter plastic pot filled with potting medium (Sunshine Mix #1, Steuber's, Co. Snohomish, WA) and watered to approximately field capacity (Spence 2002). Pots were arranged in the greenhouse in a randomized complete block design. Growing conditions in the greenhouse ranged from 16 to 25°C and 60% to 90% relative humidity. Plants were watered in order to maintain optimum moisture level for potato growth. To confirm that symptoms were caused by *P. infestans* each symptomatic sprout was removed from the pot and placed in a moist chamber (glass Petri dishes with moistened filter paper) at 16°C, and monitored for *P. infestans* sporulation every 24 h for 1 week. Pots were maintained in the greenhouse until emergence of potato sprouts which occurred approximately 3 to 4 week after planting.

Sporulation on buried potato tubers (Experiment B) Healthy whole seed tubers (4 oz) of cv Russet Burbank were inoculated with the US-8 isolate as described above, but

were stored in plastic bags (five replications, six tubers per bag) with moist toweling for 6 days at 7.2°C in order to promote late blight development without accompanying bacterial soft rot (Spence 2002). Tubers then received either 4°C, 7°C or 10°C incubation temperature treatments for 8 days. Following, infected tubers were each planted 5-cm deep with potting medium in 10-cm diameter plastic pots and stored in growth chambers (Percival E-36 L; Percival Scientific, Inc.; Boone, IA) at 13°C with a 16 h light cycle. After 3 days, three pots per replication were removed from growth chambers. The tuber in each pot was exposed by gently removing the top layer of potting medium. It was then examined for the number of lenticels and the number of eyes with *P. infestans* sporulation. Each tuber was weighed (g) and peeled in order to assess the percentage of the whole tuber surface with late blight symptoms typical of *P. infestans*. One replication of sterile water inoculated control tubers was also set up for reference for each experiment. The entire experiment was repeated.

To evaluate the potential of belowground sporulation to affect tuber-to-sprout infection, the remaining three pots in growth chamber were examined daily for emergence and symptomatic sprouts. For this part of the experiment, the growth chambers were kept at a constant 13°C with a 16 h light cycle for 20 days and then at 19°C with a 16 h light cycle for 10 to15 days to promote transmission of the pathogen, as described by Spence (2002). Additionally, after symptomatic sprouts were removed and incubated as described above, the incidence of either late blight or bacterial soft rot on tuber pieces was recorded as a percentage out of the total number of tubers per sample. Severity of either tuber late blight or bacterial soft rot was also recorded as a percentage of each tuber seed piece with characteristic symptoms of each particular disease.

Survival and sporulation on potato tubers (Experiment C) Winter soil temperatures (4°C, 7°C and 10°C) and incubation period (3, 6 and 12 week) treatments were replicated four times with six tubers per replication. One replication of tubers was treated with sterile water instead of *P. infestans* inoculum as a control treatment. Healthy seed tubers (4 oz) of cv Russet Burbank were inoculated with either of the two isolates of *P. infestans* described above, US-8 (MV04–28) or US-11 (MV110-B) genotype. For the inoculation, a small disc of periderm (5-mm in diameter) was partially removed from the apical end of each tuber. A 10 µl aliquot of a suspension of 5×10^3 sporangia ml^{-1} of the appropriate isolate was placed on the exposed tuber surface and the periderm disc was replaced over the tuber wound. Inoculated tubers were placed in plastic bags (six tubers per bag) with moist toweling for 5 days at 18°C, and then at 13°C for 2 days. The experiment was repeated (Test 1 and Test 2)

Infected tubers were then stored at 4°C, 7°C or 10°C for 3, 6, or 12 week. Following each storage period, three whole inoculated tubers were each planted 5-cm deep in a 10-cm diameter plastic pot, and stored in a cool, dry location to assay transmission potential of *P. infestans* at a later date. The remaining three tubers per replication of each treatment tubers were cut transversely. One half was assessed for the percentage of the cut tuber surface with disease symptoms (a single assessment for late blight or soft rot symptoms combined), before placing each tuber cut surface-down in a plastic box. Sporulation of *P. infestans* on the tubers was observed following 4 to 6 days of incubation at 16°C on one half of each tuber. The remaining half of each tuber was placed in a small paper bag and returned to the appropriate growth chamber at either 4°C, 7°C or 10°C. Sporulation on each tuber half was assessed after 24, 48, and 72 h for the 3, 6 and 12 week storage periods.

Spring Emergence Temperature Experiment

The effect of potential spring emergence temperatures (13°C, 16°C, and 19°C) and pathogen genotype (US-8 (MV04–28) or US-11 (MV110)) on the growth of *P. infestans* on potato tubers was investigated. Temperatures were determined based on a monthly range (March–June) of soil temperatures from the 49-year average measured at 10-cm depth. For temperature and genotype treatments, four replications of three tubers per replication were used. The experiment was repeated (Test 1 and Test 2) and one replication of reference control tubers treated with sterile water was included in each test.

Healthy tubers (4 oz) of cv Russet Burbank were used in this experiment. The inoculation procedure was the same as Experiment C, except that a 20 µl aliquot of a suspension with 1×10^3 sporangia ml^{-1} of the appropriate genotype of *P. infestans* was placed on the exposed tuber surface before the periderm disc was replaced to the tuber. Inoculated tubers were placed in plastic bags with moist toweling for 5 days at 18°C, and then at 4.4°C for approximately 2 week. After this initial storage period, noticeable late blight symptoms had developed on inoculated tubers.

Three tubers were cut transversely and set-up in plastic boxes as described above. Boxes were held at either 13°C, 16°C or 19°C for 6 days and the number of lenticels and eyes with *P. infestans* sporulation per tuber was recorded, in addition to the percentage of the cut tuber surface with disease symptoms. The remaining half of each tuber was planted 5-cm deep in 10-cm diameter plastic pots in potting medium and held at the corresponding spring soil temperature. Each buried half-tuber was unearthed after 6 days and observed for *P. infestans* sporulation using a dissecting microscope (×40 magnification). All instruments

were sterilized using 70% ethanol between individual tubers to prevent cross-contamination. After viewing all samples, tuber pieces were carefully re-buried in their respective pots, incubated again at the same spring soil temperatures, and assayed for transmission as described above.

Tuber Inoculation Site Assay

Inoculation location (apical- or stem-end), depth (1 or 5 mm) and pathogen genotype (US-8 (MV04–28) or US-11 (MV 110B) treatment effects were explored in an experiment repeated twice that consisted of four replications of three tubers per treatment combination. One replication of tubers treated with water was also set-up as a reference control treatment for each experiment. Healthy whole tubers (4 oz) of the cv Russet Burbank were inoculated with 10 µl aliquot of a 1×10^3 sporangia ml^{-1} suspension of *P. infestans*. Shallow wounds were made by marking the tuber surface with a 5-mm diameter cork borer. Using a sterile scalpel, the periderm within the area of the core was cut away and the spore suspension was pipetted onto the wounded tuber surface. Deep wounds were made by inserting the cork borer 5 mm into the tuber and removing the entire core before pipetting the sporangial suspension onto the wound. Tubers were propped upright in egg cartons to ensure that the liquid suspension stayed within the wound. The tissue removed to make the shallow or deep core was replaced immediately after the tuber was inoculated. Tubers were stored within the cartons in plastic bags with moist toweling for 6 days at 16°C. Following incubation, whole tubers were planted 5-cm deep in 10-cm diameter plastic pots in potting medium. Pots were arranged in the greenhouse in a randomized complete block design. Transmission of *P. infestans* was confirmed as described previously. However, when transmission of the pathogen was detected tubers were dug up so that the location of the infected sprout on the tuber could be recorded.

Statistical Analyses

Variables that were measured and analyzed included: the percentage of the cut or whole tuber surface with symptoms typical of *P. infestans* (Experiment A or Experiment B from winter soil temperature experiments, respectively), percentage of cut tuber surface with disease symptoms (late blight and soft rot combined) (Experiment C from winter soil temperature experiment and spring temperature experiment), and percentage of cut tuber surface with *P. infestans* sporulation (Experiment C). Variables measured and analyzed from sporulation and tuber-to-sprout infection assays included: percent transmission, the number of lenticels per tuber with *P. infestans* sporulation, the percentage of eyes per tuber with *P. infestans* sporulation (Experiment A, B, and C as well as spring temperature experiment); and, the incidence and severity of tubers with late blight and soft rot at harvest (Experiment B). All parameters were analyzed using the analysis of variance (ANOVA) procedure in SAS (SAS Institute, Cary, NC). Means were separated by the least significant difference (LSD) if *P*-values were significant at $P<0.05$ (Fisher's protected LSD). Pearson correlation coefficients were calculated to examine the relationship between the percent diseased area on cut tuber surface and the number of lenticels with *P. infestans* sporulation (spring temperature experiment). The tuber inoculation site assay observations were examined graphically since sprout emergence was unpredictable and yielded unequal sample sizes.

Results

Winter Soil Temperature Experiments

Growth in infected tubers and sprouts (Experiment A) Winter soil temperature (4°C, 7°C and 10°C) and incubation period (3, 8 and 15 days) treatments were evaluated. There was a significant interaction between Test 1 and Test 2 for colonization and sporulation variables measured, presumably because of differences in inoculation effectiveness which affected initial disease development on tubers prior to incubating at different temperatures. The mean percentage of the tuber surface with symptoms typical of *P. infestans* (Fig. 1a) increased with longer incubation periods at all three winter temperatures evaluated. For each incubation period the percentage of late blight on tuber surfaces was higher at 10°C compared to tubers stored at 4.4°C. This response occurred in both Test 1 and Test 2. The number of lenticels per tuber with *P. infestans* sporulation (Fig. 1b) was significantly higher at 10°C than at 4°C when tubers were incubated for 3 or 8 days. After 15 days of incubation the number of lenticels per tuber with *P. infestans* sporulation at 10°C dropped to an average of 15% from an average of 55% at the 8 day incubation period in the first test. A slight decrease from 70% to 60% was also seen in the second test. For tubers held at 10°C the mean percentage of eyes per tuber with *P. infestans* sporulation declined between 8 and 15 days of incubation in Test 1 (Fig. 1c). In Test 2 the percentage of eyes per tuber with *P. infestans* sporulation (Fig. 1c) was generally high (50 to 90%) on tubers stored at 10°C, but low (10 to 25%) on tubers stored at 4.4°C over the 15-day interval of storage. No emergence of sprouts was detected in the transmission assay for either test because of a 100% incidence of tuber soft rot at all winter storage temperatures evaluated. In this and subsequent experiments, reference control tubers were asymptomatic for both soft rot and late blight.

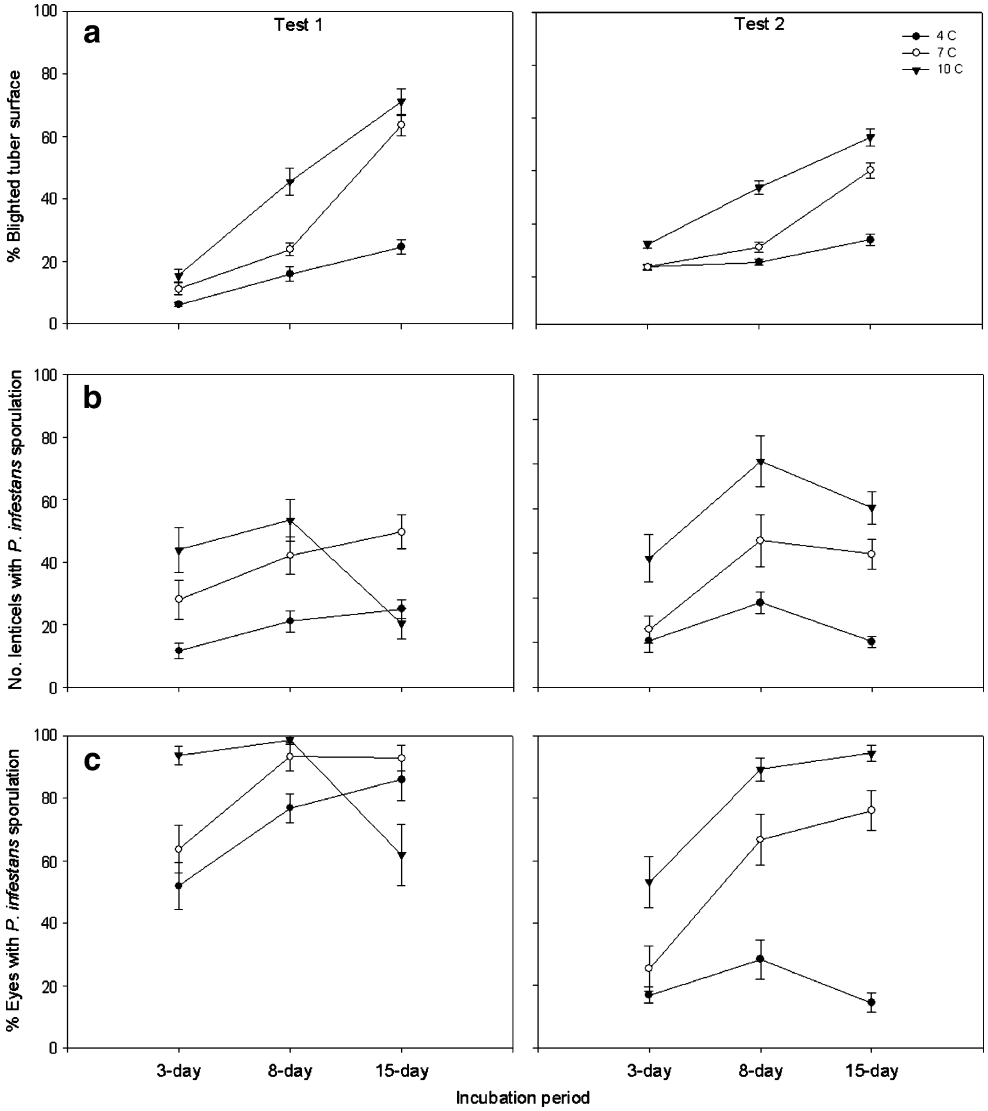

Fig. 1 Experiment A: Growth of *Phytophthora infestans* in infected tubers stored at soil temperatures (4°C, 7°C and 10°C) representative of winter conditions in western Washington. **a** percentage of blighted tuber surface, **b** number of lenticels per tuber with *P. infestans* sporulation, and **c** percentage of eyes per tuber with *P. infestans* sporulation for Test 1 and Test 2. Data analyzed by incubation period. Error bars indicate the standard deviation from the mean and each mean is an average of 15 data points

Sporulation on buried potato tubers (Experiment B) When whole, infected potato tubers were exposed first to 4°C, 7°C or 10°C for 8 days and then buried for 3 days at 13°C in potting medium, they exhibited obvious *P. infestans* sporulation. The number of lenticels on these tubers with *P. infestans* sporulation (Fig. 2a) was significantly ($P<0.05$) higher for tubers held initially at 10°C than for those held initially at 4°C. Also, the percentage of tuber surfaces with late blight was significantly ($P<0.05$) higher for tubers incubated at 7°C and 10°C as opposed to those incubated at 4°C (Fig. 2b). There were no significant interactions between Test 1 and Test 2 and data were combined.

In the *P. infestans* tuber transmission assay, the incidence of tuber late blight (Fig. 2c) was lowest for tubers held at 10°C. Tubers initially incubated at 7°C and 10°C had an average of 80% to 90% soft rot per tuber (Fig. 2d) as compared to tubers incubated at 4°C which had an average of approximately 40% soft rot. Severity of tuber late blight was significantly ($P<0.05$) higher (10%) for tubers initially incubated at 4°C as compared to tubers incubated at 7 and 10°C (<10%), with no significant difference in severity of tuber blight between the latter two temperatures. No tuber-to-sprout infection on remaining tubers was detected when tubers infected with *P. infestans* were initially incubated at 4°C, 7°C and 10°C for 8 days and then grown at 13°C and 19°C (20- and 10-day intervals, respectively) in growth chambers (*data not shown*).

Survival and sporulation on potato tubers (Experiment C) Winter soil temperature (4°C, 7°C and 10°C) and incubation period (3, 6 and 12 week) treatments were evaluated. There were no significant interactions between Test 1 and Test 2 so data were combined. After 3 week of storage of inoculated potato tubers, there was no significant difference between the US-8 and US-11 isolates in percentage of cut tuber surface with disease symptoms (Fig. 3a) at any of

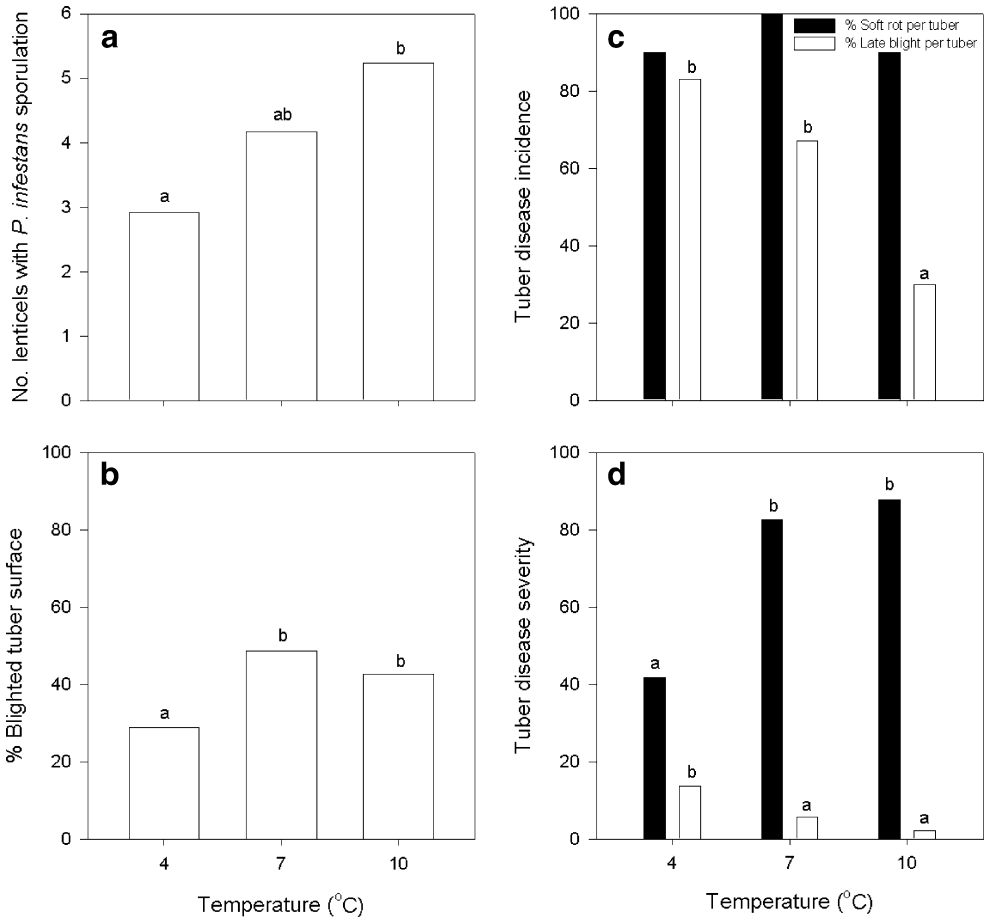

Fig. 2 Experiment B: Sporulation of *Phytophthora infestans* on buried potato tubers as affected by winter soil temperatures (4°C, 7°C and 10°C) representative of winter conditions in western Washington. **a** number of lenticels per tuber with *P. infestans* sporulation on buried tubers, **b** percent of blighted surface on whole tuber, and **c** incidence and **d** severity of soft rot and late blight on potato tubers at harvest. Data were analyzed by temperature. Data for Test 1 and Test 2 combined. Columns identified by the same letter are not significantly ($P<0.05$) different according to least significant difference test

the initial incubation temperatures evaluated. Results were similar after 6 week (Fig. 3b), except that the percentage of cut tuber surface with disease symptoms was significantly higher (21%) for tubers inoculated with the US-11 genotype than those inoculated with the US-8 genotype (11.7%) at 10°C (but not at 4°C or 7°C). After the 12 week storage period, the US-8 genotype produced a significantly higher percentage of symptomatic tissue (Fig. 3c) on cut surfaces of tubers held at either 4°C and 10°C (50% and 65%, respectively) than on tubers inoculated with the US-11 isolate and held at the same temperatures (20% and 45%, respectively). Also after 12 week storage, for tubers held at 7°C, the percentage of cut tuber surfaces with disease symptoms was significantly higher when inoculated with the US-11 isolate (60%) than with the US-8 isolate (40%).

After 3 week exposure to all three winter soil temperatures, tubers inoculated with the US-8 isolate had a significantly ($P<0.05$) higher number of lenticels per tuber with *P. infestans* sporulation (Fig. 4a) than tubers inoculated with the US-11 isolate. After the 6 week storage period (Fig. 4b) the number of lenticels per tuber with *P. infestans* sporulation was extremely low, and sporulation was no longer detected on tuber lenticels after 12 week of storage. Overall, only tubers held at 4°C and inoculated with the US-11 isolate produced viable sprouts in the moist chamber boxes.

Sporulation on tuber halves incubated at 4°C, 7°C or 10°C for periods of 24, 48 and 72 h after cutting occurred only after 3 week of storage, but not after the 6 and 12 week storage periods (Table 1). For the 24 h observation time, no sporulation was detected on tubers inoculated with the US-8 isolate. However by 72 h, tuber halves inoculated with the US-8 isolate supported sporulation (4.2%, 20.8%, and 87.5%, respectively) at 4°C, 7°C and 10°C. Significantly more sporulation occurred at 10°C than at 4°C or 7°C for both the 48 and 72 h intervals. Tubers inoculated with the US-11 isolate first sporulated at 7°C after 24 h. Sporulation on tubers inoculated with US-11 was significantly greater at 10°C for both the 48 and 72 h intervals compared to 4°C. Overall, the percentage of sporulating tubers was lower for those inoculated with the US-11 isolate than those inoculated with the US-8 isolate.

Spring Emergence Temperature Experiments

Spring emergence temperature (13°C, 16°C and 19°C) and pathogen genotype US-8 (MV04–28) or US-11 (MV 110B) treatments were evaluated. There was a significant interaction

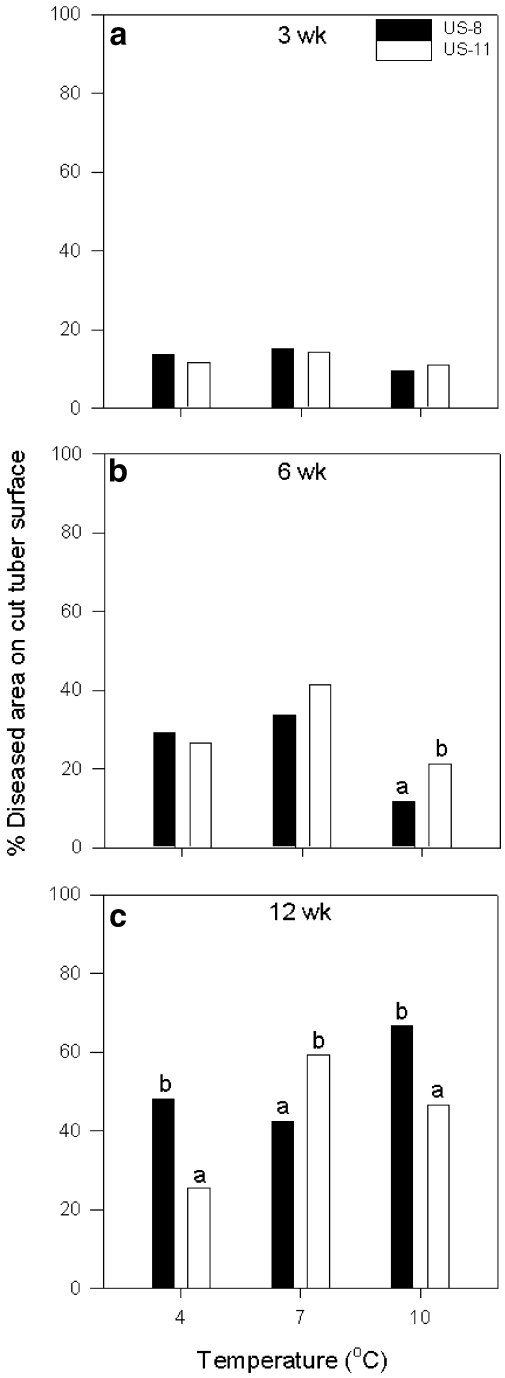

Fig. 3 Experiment C. Survival and sporulation of *Phytophthora infestans* as influenced by soil temperatures (4°C, 7°C and 10°C) representative of winter conditions in western Washington. Percentage of diseased cut tuber surfaces after **a** 3 week, **b** 6 week, and **c** 12 week. Data were analyzed by pathogen genotype. Data for Test 1 and Test 2 combined. Columns identified by the same letter are not significantly ($P<0.05$) different according to least significant difference test

between Test 1 and Test 2 for percentage of cut tuber surfaces with disease symptoms and sporulation variables and the corresponding transmission assay. For the US-8 isolate, the percentage of cut tuber surfaces with disease symptoms (Fig 5a) was higher for tubers held at 19°C (60.4%, 21.7%) versus those held at 13°C (30.8%, 6.7%) or 16°C (33.3%, 2.2%) in Test 1 and Test 2, respectively. This difference was significant in Test 1 only. For the US-11 isolate, the percentage of cut tuber surfaces with disease symptoms was significantly higher at 19°C (60.4%) versus 16°C (33.3%) in Test 1, and significantly higher at 19°C (34.8%) versus 13°C (21.7%) in Test 2. In the sporulation assay, tubers inoculated with the US-8 isolate and held at 19°C consistently had a significantly higher number of lenticels per tuber with *P. infestans* sporulation (Fig 5b) than tubers held at 13°C or 16°C. There were no significant differences between 13°C or 16°C treatments. This was true for both tests. Tubers inoculated with US-8 and held at 19°C also had the highest percentage of eyes with *P. infestans*

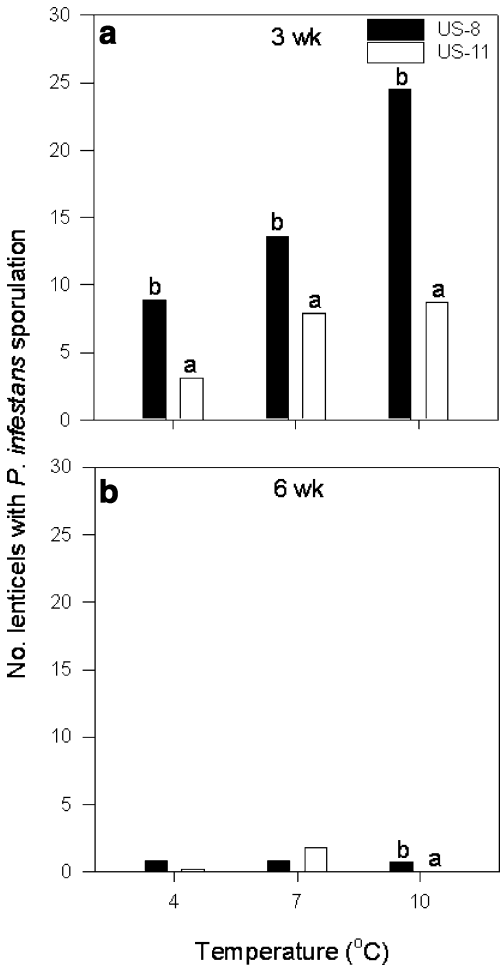

Fig. 4 Experiment C. Survival and sporulation of *Phytophthora infestans* as influenced by soil temperatures (4°C, 7°C and 10°C) representative of winter conditions in western Washington on the number of lenticels per tuber with *P. infestans* sporulation after **a** 3 week and **b** 6 week. Data were analyzed by pathogen genotype. Data for Test 1 and Test 2 combined. Columns identified by the same letter are not significantly ($P<0.05$) different according to least significant difference test

Table 1 Percentage of tubers with *Phytophthora infestans* sporulation on cut tuber surfaces after exposure to winter soil temperatures (4°C, 7°C and 10°C) for 3 week

	Genotype of *P. infestans*					
	US-8[b]			US-11[f]		
Temperature (°C)	24 h[c]	48 h	72 h	24 h	48 h	72 h
4	0.0[d]	0.0 a	4.2 a	0.0	0.0 a	0.0 a
7	0.0	0.0 a	20.8 a	4.2	8.3 ab	25.0 ab
10	0.0	66.7 b	87.5 b	0.0	29.2 b	62.5 b
LSD (P=0.05)[a]	NSD[e]	24.21	24.95	NSD	22.65	45.29

[a] Means followed by the same letter within a column are not significantly different ($P= 0.05$) by least significant difference test
[b] Isolate MV 04–28 of *P. infestans* from potato (cv Red La Soda)
[c] Time interval for monitoring sporulation on the cut tuber surface
[d] Data rank-transformed for analysis and back-transformed for presentation
[e] Not significantly different
[f] Isolate MV-110B of *P. infestans* from hairy nightshade (*Solanum sarrachoides*)

sporulation (Fig. 5c). This result was not significantly different among tests. Tubers inoculated with the US-11 isolate had a significantly ($P<0.05$) higher percentage of eyes with *P. infestans* sporulation when stored at 19°C compared to tubers stored at 16°C in Test 1 or 13°C in Test 2 (Fig. 5c). For tubers inoculated with the US-8 isolate, a high number of sporulation sites per tuber in the moist chamber assay was significantly ($P<0.05$) and positively correlated with the percentage of diseased cut tuber surfaces in both tests (Table 2). However, the correlation coefficient was not significant for the US-11 isolate in either test (Table 2).

P. infestans sporulated on the cut surfaces of tubers buried 5-cm deep in potting medium incubated at 13°C, 16°C and 19°C for 6 days. In Test 1, the percentage of tubers inoculated with the US-8 isolate that sporulated at 13°C, 16°C and 19°C was 75.0%, 75.0% and 83.3%, respectively. The percentage of tubers inoculated with the US-11 isolate that sporulated at 13°C, 16°C and 19°C was 25.0%, 41.7% and 8.3%, respectively. In Test 2, the percentage of tubers inoculated with US-8 that sporulated at 13°C, 16°C and 19°C was 50.0%, 66.7% and 50.0%, respectively. The percentage of tubers inoculated with the US-11 isolate that sporulated at 13°C, 16°C and 19°C was 8.3%, 41.7% and 16.7%, respectively.

In Test 1, the highest percentage of *P. infestans* transmission (16.7%±0.33) from tubers to sprouts occurred at 19°C with tubers that had been inoculated with the US-8 isolate. In Test 2, the highest percentage of *P. infestans* transmission (25.0%±0.33) occurred at 13°C with tubers that also had been inoculated with the US-8 isolate.

Tuber Inoculation Site Assay

Inoculation location (apical- or stem-end), depth (1 or 5 mm deep), and pathogen genotype (US-8 (MV04–28) or US-11 (MV 110B) were evaluated (Fig. 6). Transmission events were variable, and not associated with treatments. For US-8, tubers inoculated at the apical end resulted in tuber-to-sprout infection events ranging from 8.3% (Test 2) to 24.8% (Test 1) for sprouts emerging at the apical end, and 16.6% (Test 2) and 33.2% (Test 1) for sprouts emerging at the stem end. For US-11, tubers inoculated at the apical end resulted in tuber-to-sprout infection events ranging from 4.1% (Test 2) to 16.5% (Test 1) for sprouts emerging at the apical end, and 0% (Test 2) to 12.4% (Test 1) for sprouts emerging at the stem end. For US-8 and US-11, tubers inoculated at the stem end resulted in tuber-to-sprout infection events ranging from 0% (Test 2) to 4.1% (Test 1) for sprouts emerging at the apical end. Further, tuber inoculations at the stem end resulted in 4.1% (Test 1) to 16.5% (Test 2) for US-8, and 12.4% (Test 1) to 12.5% (Test 2) for US-11, sprout transmissions at the stem end.

The percentage of tubers with *P. infestans* transmission was highest when tubers were inoculated at the apical end with a shallow versus a deep wound in Test 1 (Fig. 6b). However, the opposite was true for Test 2. Inoculations at the stem end via a shallow wound (1-mm deep) resulted in to 0% (Test 2) to 4.1% (Test 1) transmission to apical end sprouts, and 8.3% (Test 1 and Test 2) transmission to stem-end sprouts. Inoculations at the apical end via a deep wound (5-mm deep) resulted in 4.1% (Test 2) to 12.4% (Test 1) transmission to apical end sprouts, and 0% (Test 2) and 16.6% (Test 1) to stem end sprouts.

Discussion

Sporulation of *P. infestans* on whole tubers and cut potato seed pieces, as a result of both natural and artificial

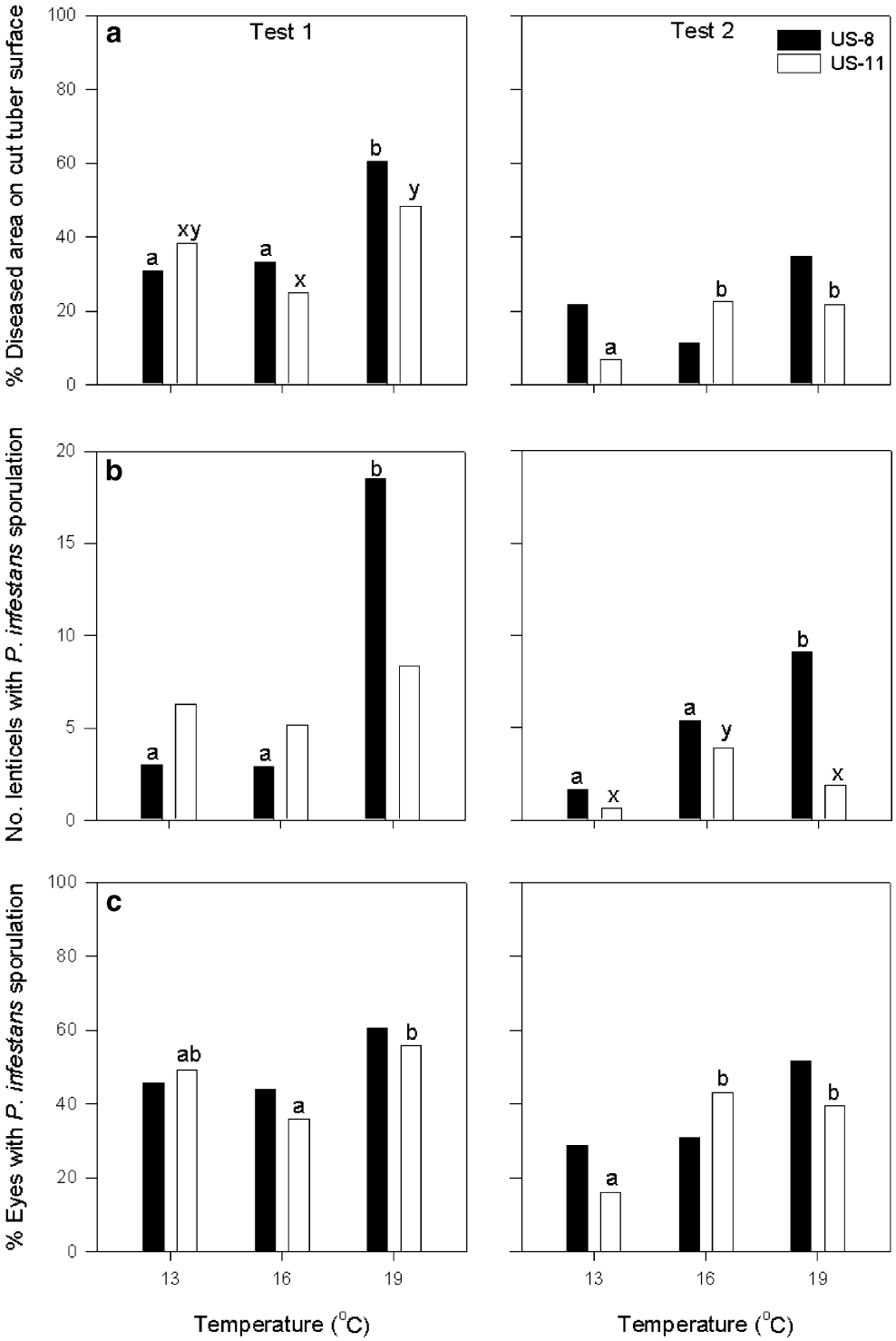

Fig. 5 Influence of soil temperatures (13°C, 16°C, and 19°C) representative of spring conditions in western Washington in each of two trials assessing the **a** percentage of diseased cut tuber surface, **b** number of lenticels per tuber with *Phytophthora infestans* sporulation, and **c** the percentage of eyes per tuber with *P. infestans* sporulation. Data were analyzed by temperature. Columns identified by the same letter are not significantly ($P<0.05$) different according to least significant difference test

inoculations, has been previously reported from commercial storage locations (Dowley and O'Sullivan 1991; Lambert et al. 1998; Platt et al. 1999). However, the growth of *P. infestans* mycelium and sporulation from lenticels and eyes has not been extensively monitored in relation to overwintering of the pathogen. This study documents the influence of soil temperatures, representative of winter and spring conditions in western Washington, on tuber sporulation of *P. infestans*. Throughout these experiments, sporulation of *P. infestans* was found at lenticels and on eyes of potato tubers after exposure to incubation temperatures ranging from 4°C to 19°C. For the winter temperature experiments (4°C, 7°C and 10°C), the most sporulation was found on eyes and lenticels on tubers incubated at 10°C, but after 15 days of

Table 2 Correlation analysis between the percent of cut tuber surfaces with symptoms of tuber blight, and the number of lenticels per tuber with *Phytophthora infestans* sporulation on tubers incubated in moist chambers at 16°C after inoculation with the pathogen

Percent diseased area[a]	No. lenticels with *P. infestans* sporulation[d]	
	Corr. coef[e]	*P*-value
US-8, T1[b]	0.63079	0.00001*
US-11, T1	0.06676	0.69890
US-8, T2[c]	0.47729	0.00320*
US-11, T2	0.39628	0.01670*

*$P<0.05$ (significant)
[a] Percent diseased area on cut tuber surface (visual assessment)
[b] Test 1
[c] Test 2
[d] Number of lenticels with *P. infestans* sporulation quantified using dissecting microscope (×40 magnification). To account for variation in tuber size, the number of lenticels with *P. infestans* sporulation was divided by tuber weight (g) and multiplied by 100
[e] Pearson's correlation coefficient

incubation the amount of *P. infestans* sporulation was reduced, likely because of competition with other fungi and soft rot bacteria (Lacey 1965). In the spring temperature experiments (13°C, 16°C and 19°C), the most sporulation occurred at 19°C on tubers that had been inoculated with the US-8 isolate.

This is the first investigation of conditions mediating *P. infestans* sporulation on buried whole potato tubers. Sato (1980) hypothesized that this event occurred on whole, infected tubers in field soil and Spence (2002) observed a single sporulation event on a cut seed piece incubated at 13°C in potting medium. In this study, when whole, infected potato tubers were exposed first to 4°C, 7°C or 10°C for 8 days and then buried in potting medium, they exhibited obvious *P. infestans* sporulation after 3 days at 13°C. After exposure to the higher spring temperatures, *P. infestans* was found sporulating on tubers that had been buried for 6 days. The ability of this pathogen to sporulate for very limited times in soil over a range of temperatures may facilitate tuber-to-sprout infection events. Kromann et al. (2008) reported potato sprout infections can occur prior to emergence from soil in Ecuador. In northwestern Washington, potato tissues in tare dirt and cull potato piles discarded from potato storage units after the winter have been observed by the authors to support infected sprouts during the spring. Tuber sporulation may be one source of the inoculum for these foliage infections.

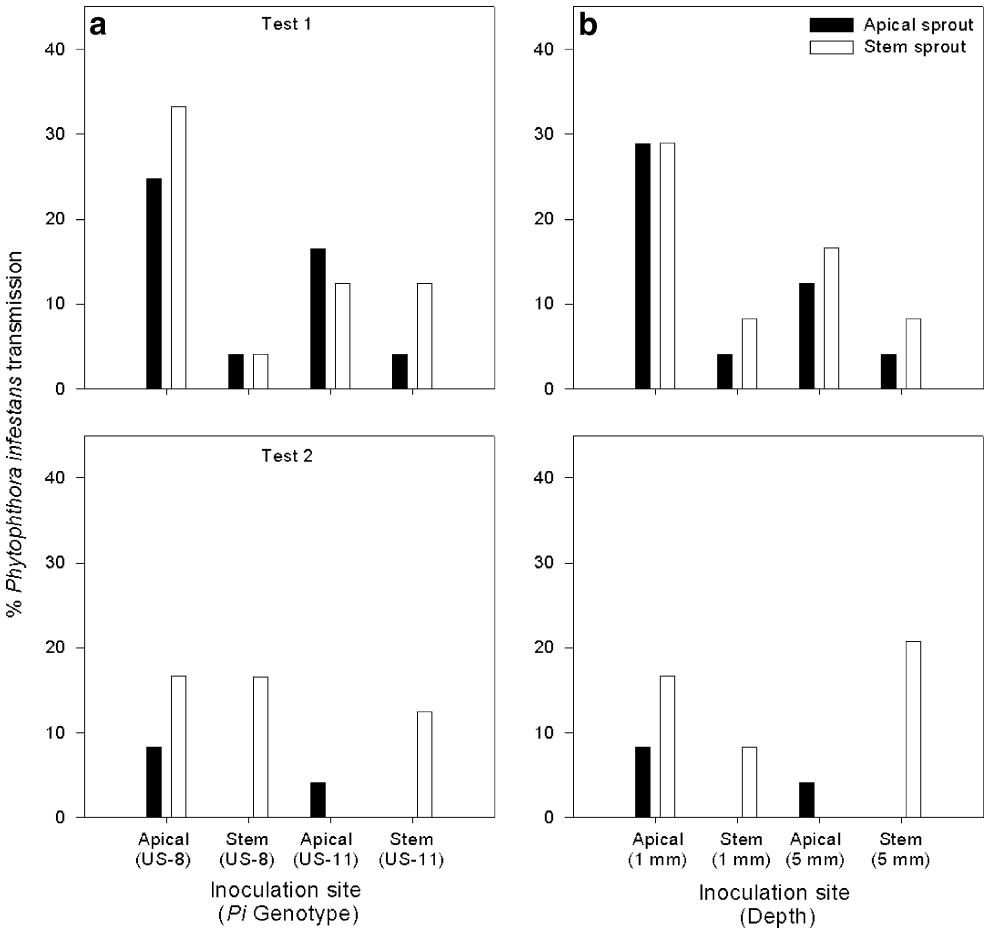

Fig. 6 Tuber inoculation site assay on the percentage of sprouts with *Phytophthora infestans* transmission as affected by **a** tuber inoculation site (apical- vs. stem-end) and genotype (US-8 vs. US-11), and **b** tuber inoculation site (apical- vs. stem-end) and depth (1 or 5 mm) for Test 1 and Test 2

Following a 12 week storage period, tubers inoculated with the US-8 isolate developed a high percentage of diseased cut tuber surfaces at both 4°C and 10°C (45% and 65%, respectively), suggesting that this western Washington US-8 isolate is more tolerant of cold temperatures compared to the western Washington US-11 isolate. In an *in vitro* study, Kirk (2003a) found significant differences between potato genotype, temperature, and exposure periods while examining tolerance to freezing by *P. infestans* mycelium of various genotypes (US-1, US-8, US-11, and US-14). In general, exposure of *P. infestans* mycelium to 0°C for 5 days was not lethal to any of the genotypes evaluated in that study; however, exposure of the mycelium to -5°C for 1 day was lethal to all genotypes. Overall, the US-8 isolate showed more resilience to cold temperatures in comparison to other genotypes in that study (Kirk 2003a). In the spring emergence temperatures experiment no clear relationship between temperature and transmission of *P. infestans* was found. However, pathogen genotype influenced tuber-to-sprout infection at all three spring temperatures. In general, more transmission events occurred on tubers inoculated with the US-8 isolate than the US-11 isolate, despite the high amount of tuber decay associated with the US-8 genotype. Observations were similar when US-8 was compared to other genotypes in experiments by Marshall and Stevenson (1996). Tubers in our experiments infected with the US-8 isolate and held at 13°C, had less soft rot than tubers held at either 16°C or 19°C (43% versus 60% and 99%, respectively). Also, in our study, infected tubers held at temperatures ranging from 13°C to 19°C showed sporulation by *P. infestans* at the tuber eyes and lenticels in moist chambers as well as in potting medium.

The site of tuber inoculation with *P. infestans* appears not to influence tuber-to-sprout infection events and whether apical end or stem sprouts become infected. As seen in the spring temperature experiments, tubers inoculated with the US-8 isolate generally had a higher amount of transmission of the pathogen compared to tubers inoculated with the US-11 isolate, regardless of inoculum location (stem-end or apical-end). Although growth of *P. infestans* may be directed toward the apical end of the tuber, since the majority of stem growth is initiated in this region (Cutter 1978), transmission may only occur if *P. infestans* colonization does not damage buds in this region of the tuber. Diseased buds may explain some of the variability noted in these assays.

All of the experiments in this study were done in greenhouse facilities, using a sterile potting medium. Several studies have indicated that *P. infestans* is a poor competitor in soil (Lacey 1965) and is influenced by microbial antagonism, soil pH and soil organic matter content (Andrivon 1994a & b; Oyarzun et al. 2005). Colonization and sporulation events on tuber tissue may be suppressed under field soil conditions, but recent research reports have documented the survival of sporangia of *P. infestans* in field soil for 2 months in potato growing regions in the Netherlands (Evenhuis et al. 2006) and for a maximum of 23 to 30 days in field soil under potato growing conditions in the Columbia Basin of eastern Washington (Porter and Johnson 2007). Further research examining sporulation on tubers in field soil is needed.

In western Washington, the recovery of the US-8 genotype from solanaceous plants increased while the recovery of US-11 decreased from 1996 to 1999 (Derie and Inglis 2001). Currently, the US-8 genotype is the most commonly collected *P. infestans* genotype collected from potato plants in this region, although isolates of US-11 still can occasionally be detected on tomato. The prevalence of US-8 isolates may be, in part, a result of the sporulation, colonization and tuber-to-sprout infection ability of this genotype on potato tubers. However, the aggressiveness of this isolate, characterized by the high amount of bacterial colonization and tuber decay (Powelson et al. 2002) may also limit survival of this genotype in volunteer tuber tissue in soil (Montarry and Andrivon 2007). Other forms of overwintering, particularly those which are suspected to occur in potato storages on non-symptomatic tubers, may be important in the durability of this genotype in the region.

While transmission rates of *P. infestans* on volunteer tubers of different cultivars under field conditions have not been determined, and were variable in one of our preliminary field studies, transmission rates probably approximated the low rates (0.1%) observed in potato seed piece transmission research (Powelson et al. 2002). A majority of volunteer tubers most likely succumb to soft rot and decay under western Washington winter and spring soil conditions. Field trial results in western Washington showed that when tubers inoculated with *P. infestans* were planted in the fall, emergence the following spring ranged from 14% to 70% depending on the cultivar (Gigot, Inglis, and Johnson, not published). Given the projected average of 16,000 potential volunteer plants ha^{-1} as estimated by Newberry (2002) and the development of cultivars with durable tuber resistance to late blight, a *P. infestans* transmission rate as low as 0.1% could lead to 16 infected sprouts ha^{-1} supporting *P. infestans* sporulation. This could be a significant source of primary inoculum for initiating late blight epidemics. However, for this inoculum to be effective, susceptible recipient host material, such as emerged potato plants or other solanaceous hosts (Inglis et al. 2000) must also be present in the vicinity at the same time infected volunteer sprouts emerge. Continued monitoring and management of field crops hosting volunteer potatoes is needed, particularly those fields not planted to potatoes but supporting volunteer plants and, therefore, not receiving late blight foliar fungicide treatments.

Management options for volunteer potatoes include multiple herbicide applications, tillage, minimization of tuber debris left in the field after harvest and competitive crop rotation selection, but these strategies have proven only minimally successful throughout the Pacific Northwest (Lutman 1974; Askew 1991; Boydston and Seymour 1994; Newberry 2002). Given the aggressiveness of US-8 isolates of this pathogen (Miller and Johnson 2000), *P. infestans* survival on tuber tissue in soil may be of limited importance in areas like western Washington where winter soil temperatures are rarely sustained at or below 4.4°C. Sporulating *P. infestans* in potato cull piles or on potato tissues in tare dirt piles left near storage units in the spring, may present greater potential for primary inoculum production compared to overwintering volunteer tubers in field soils given the mild, marine conditions of western Washington. All of these inoculum sources should be monitored and managed prior to emergence of potato plants in commercial fields at the beginning of the growing season.

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References

Andrivon, D. 1994a. Dynamics of the survival and infectivity to potato tubers of sporangia of *Phytophthtora infestans* in three different soils. *Soil Biology & Biochemistry* 26: 945–952.

Andrivon, D. 1994b. Fate of *Phytophthora infestans* in a suppressive soil in relation to pH. *Soil Biology & Biochemistry* 26: 953–956.

Andrivon, D. 1995. Biology, ecology, and epidemiology of the potato late blight pathogen *Phytophthora infestans* in soil. *Phytopathology* 85: 1053–1056.

Askew, M.F. 1991. *The bio-dynamics of volunteer potatoes*. Proceedings of the Brighton Crop Protection Conference—Weeds, Brighton, UK. pp 219–223.

Boydston, R., and M. Seymour. 1994. Volunteer potato control in rotational crops. Proceedings of the 33rd Annual Washington State Potato Conference and Trade Fair, Washington State Potato Commission, Moses, Lake, WA. pp 27–28.

Cutter, E. 1978. Structure and development of the potato plant. In *The potato crop*, ed. P. Harris, 70–152. London: Chapman and Hall.

De Bruyn, H.L.G. 1926. The overwintering of *Phytophthora infestans* (Mont.) de Bary. *Phytopathology* 16: 121–140.

Derie, M.L., and D.A. Inglis. 2001. Persistence of complex virulences in populations of *Phytophthora infestans* in Western Washington. *Phytopathology* 91: 606–612.

Dorrance, A.E., and D.A. Inglis. 1998. Assessment of laboratory methods for resistance of potato tubers to late blight. *Plant Disease* 82: 442–446.

Dorrance, A.E., D.A. Inglis, M.L. Derie, C.R. Brown, S.B. Goodwin, W.E. Fry, and K.L. Deahl. 1999. Characterization of *Phytophtora infestans* populations in western Washington. *Plant Disease* 83: 423–428.

Dowley, L.J., and E. O'Sullivan. 1991. Sporulation of *Phytophthora infestans* (Mont.) de Bary on the surface of diseased tubers and tuber to tuber spread during handling. *Potato Research* 34: 295–296.

Erwin, D.C., and O.K. Ribeiro. 1996. *Phytophthora diseases worldwide*. 146–184. St. Paul: American Phytopathological Society.

Evenhuis, A., G.J.T. Kessel, and P.J. Van Bekkum. 2006. Epidemiology of *Phytophthora infestans* in relation to tuber blight. Survival of *P. infestans* in field soils. PPO-Special Report No 11. pp 223–227.

Goodwin, S.B., C.D. Smart, R.W. Sandrock, K.L. Deahl, Z.K. Punja, and W.E. Fry. 1998. Genetic change within populations of *Phytophthora infestans* in the United States and Canada 1994–1996: role of migration and recombination. *Phytopathology* 88: 939–949.

Inglis, D.A., M.L. Powelson, and A.E. Dorrance. 1999. Effect of registered potato seed piece fungicides on tuberborne *Phytophthora infestans*. *Plant Disease* 83: 229–234.

Inglis, D., M. Derie, B. Gundersen, E. Vestey, R. Ludy, and M. Powelson. 2000. Solanaceous hosts as sources of inoculum for late blight on potato in the Pacific Northwest. *Phytopathology* 91: S184.

Kirk, W.W. 2003a. Tolerance of mycelium of different genotypes of *Phytophthora infestans* to freezing temperatures for extended periods. *Phytopathology* 93: 1400–1406.

Kirk, W.W. 2003b. Thermal properties of overwintered piles of cull potatoes. *American Journal of Potato Research* 80: 145–149.

Kirk, W.W., B.A. Niemira, and J.M. Stein. 2001. Influence of storage temperature on rate of potato tuber tissue infection caused by *Phytophthora infestans* (Mont.) de Bary estimated by digital image analysis. *Potato Research* 44: 86–96.

Kromann, P., J.L. Andrade-Piedra, L. Munk, and G. Forbes. 2008. Preemergence infection of potato sprouts by *Phytophthora infestans* in the highland tropics of Ecuador. *Plant Disease* 92: 569–574.

Lacey, J. 1965. The infectivity of soils containing *Phytophthora infestans*. *Annals of Applied Biology* 59: 257–264.

Lambert, D.H., A.I. Currier, and M.O. Olanya. 1998. Transmission of *Phytophthora infestans* in cut potato seed. *American Journal of Potato Research* 75: 257–263.

Lutman, P.J.W. 1974. Factors affecting the overwintering of volunteer potato tubers and the emergence of sprouts in the spring. Proceedings of the 12th British Weed Control Conference, Brighton, UK. pp 285–292.

Marshall, K.D., and W.R. Stevenson. 1996. Transmission of *Phytophthora infestans* from infected seed potato tubers to developing sprouts. *American Potato Journal* 73: 370–371. (Abstr.).

McMoran, D. 2006. Skagit County Agricultural Statistics. www.skagit.wsu.edu.

Miller, J.S., and D. Johnson. 2000. Competitive fitness of *Phytophthora infestans* isolates under semi-arid conditions. *Phytopathology* 90: 220–224.

Montarry, R.C., and D. Andrivon. 2007. Is there a trade-off between aggressiveness and overwinter survival of *Phytophthora infestans*? *Functional Ecology* 21: 603–610.

Murphy, P. 1922. The bionomics of the conidia of *Phytophthora infestans* (Mont.) de Bary. *Scientific Proceedings of the Royal Dublin Society* 16: 442–466.

Newberry, G. 2002. Integrated methods for suppression of volunteer potatoes (*Solanum tuberosum*) in Washington State. Ph.D. dissertation. Washington State University, Pullman, WA. pp 128.

Oyarzun, P.J., C.D. Garzon, D. Leon, I. Andrade, and G.A. Forbes. 2005. Incidence of potato tuber blight in Ecuador. *American Journal of Potato Research* 82: 117–122.

Partipilo, H. 1999. Seedbourne *Phytophthora infestans*: Effect of pathogen clonal tissue and potato cultivar on seed transmission of late blight and plant growth responses. Master's thesis. Oregon State University. Corvallis, OR. pp 138.

Peterson, L.C. 1947. The overwintering of *Phytophthora infestans* (Mont.) de Bary under Long Island conditions. *American Potato Journal* 24: 88–197.

Platt, H.W., R.D. Peters, M. Medina, and W. Arsenault. 1999. Impact of seed potatoes infected with *Phytophthora infestans* (US-1 or US-8 genotypes) on crop growth and disease risk. *American Journal of Potato Research* 75: 67–73.

Porter, L.D., and D.A. Johnson. 2007. Survival of sporangia of new clonal lineages of *Phytophthora infestans* in soil under semiarid conditions. *Plant Disease* 91: 835–841.

Powelson, M.L., R. Ludy, H. Partipilo, D. Inglis, B. Gundersen, and M. Derie. 2002. Seed borne late blight of potato. *Plant Health Progress*. doi:10.1094/PHP-2002-0129-01-HM.

Sato, N. 1980. Sources of inoculum and sites of infection of potato tubers by *Phytophthora infestans* in soil. *Annals of the Phytopathological Society of Japan* 46: 231–240.

Spence, R. 2002. Effects of soil temperature and moisture on the transmission of *Phytophthora infestans* from potato seed tubers to sprouts. Master's thesis. Washington State University. Pullman, WA. pp 93.

Van der Zaag, D.E. 1956. Overwintering en epidemiologie van *Phytophthora infestans*, tevens enige nieve bestrijdingsmogelijkheden. *Tijdschrift Over Plantenziekien* 62: 89–156.

Author: Jessica Gigot

Caption: Sporulation of *Phytophthora infestans* in the eyes and lenticels of a Russet Burbank tuber.

Significance: The ability of this pathogen to sporulate on potato tubers for limited times over a range of temperatures may mediate certain transmission events. The Gigot et al. study showed that sporulating *P. infestans* in potato cull piles or on potato tissues in tare dirt piles left near storage units in the spring, may present greater potential for primary inoculum production compared to overwintering volunteer tubers in field soils given the mild, marine conditions of western Washington. These inoculum sources should be monitored and managed prior to emergence of potato plants in commercial fields at the beginning of the growing season.