Pathogenicity and Aggressiveness of Three *Alternaria* spp. on Potato Foliage in the U.S. Northwest

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Abstract

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Alternaria spp. were collected from potato foliage showing symptoms of early blight and brown spot in the Columbia Basin, WA and Bonners Ferry and Rupert, ID between 2009 and 2011. The aggressiveness of three *Alternaria* spp. on potato was quantified on nonwounded and wounded detached leaves of 'Russet Norkotah' potato; wounded detached leaves of 'Alturas', 'Ranger Russet', 'Russet Burbank', and 'Umatilla Russet'; and whole plants of Russet Norkotah. Mean infection frequencies (MIF) and area under the lesion expansion curve (AULEC) were significantly greater for *Alternaria solani* ($P = 0.0072$ and 0.0002 , respectively) than for *A. arborescens* or *A. arbusti* on nonwounded leaves. Wounding of tissue significantly increased MIF and AULEC for *A. arbusti* ($P = 0.008$ and

0.0047 , respectively) and AULEC for *A. arborescens* ($P = 0.01$) relative to nonwounded tissue. AULEC did not differ significantly among the three *Alternaria* spp. when inoculated onto wounded foliage of whole plants ($P = 0.34$); the AULEC of whole plants was positively and significantly correlated with AULEC on detached leaves ($P = 0.03$). Umatilla Russet was the most susceptible and Russet Burbank was the least susceptible based on MIF and AULEC for all three pathogen species. Results indicate that *A. solani* was the more aggressive pathogen of potato in the Columbia Basin, because both *A. arborescens* and *A. arbusti* require wounds and *A. arbusti* lesions do not expand significantly in comparison with *A. solani* or *A. arborescens* following inoculation.

Alternaria solani Sorauer, which causes early blight of potato, was first described in 1882 by Ellis and Martin (1882). Infection results in tan-colored lesions that are often surrounded by a chlorotic halo due to the presence of fungal metabolites (Rotem 1994). *A. alternata* (Fr.) Keissl. causes brown spot of potato and lesions are smaller and darker compared with *A. solani* (Kirk and Wharton 2012). *A. alternata* was isolated from potato leaf lesions in 1984 and Koch's postulates were fulfilled on intact, detached potato leaves (Droby et al. 1984). Inoculum concentration and disease incidence were positively correlated.

Potato early blight and brown spot are diseases of senescing tissue (Douglas and Pavek 1972; Lawrence et al. 2013; MacKenzie 1981; Rotem 1994; Shtienberg et al. 1995). Older leaves of potato are more susceptible to infection by *A. solani* and *A. alternata* than younger leaves (Droby et al. 1984; Dita Rodriguez et al. 2006). However, young leaves are also susceptible, particularly as the growing season progresses (Kirk and Wharton 2012; Wharton and Kirk 2007). Susceptibility of hosts is also dependent on overall plant vigor. Plants under drought stress or less than optimal nutrition regimes are more susceptible to infection, most likely due to the premature senescence of foliage (Blachinski et al. 1996; Rotem 1994).

Traditional management strategies for *A. solani* and *A. alternata* include the use of moderately resistant cultivars and fungicides in an integrated management strategy (Fry 2007). Resistance is determined by the ability of the plant to inhibit lesion development and expansion and has been directly correlated with cultivar maturity. However, no cultivar is known to be completely resistant to infection (Douglas and Pavek 1972).

Although a number of *Alternaria* spp. have been identified as pathogens on potato internationally (Ardestani et al. 2010; Rodrigues et al. 2010; van der Waals et al. 2011), only *A. solani* and *A. alternata* have been described as pathogens in the United States.

In the U.S. Northwest, *A. solani* has been the dominant pathogen; however, *A. alternata* is increasingly affecting American potato production (Nolte 2008).

Species delimitation within the *Alternaria* spp. is challenging due to similarities in conidial morphology and morphological plasticity in response to environmental conditions, particularly within species with small conidia (Rotem 1994; Simmons 2007). This poses an issue with identification. Morphospecies classifications, based on morphological characteristics (Simmons 1992), often agree with clade structure based on molecular systematics (Hong et al. 2005; Peever et al. 2004; Pryor and Gilbertson 2000). However, some studies have shown that morphospecies classifications are not always congruent with molecular systematic analyses (Andrew et al. 2009; Lawrence et al. 2013; Peever et al. 2004).

A survey of *Alternaria* spp. that colonize potato in the U.S. Northwest was conducted between 2009 and 2011 (Tymon and Johnson 2011). Isolates of *Alternaria* spp. were collected from early blight and brown spot lesions on potato. Four morphologically and genetically distinct *Alternaria* spp. were isolated: *A. solani*, *A. alternata*, *A. tenuissima*, *A. arborescens*, and *A. arbusti*, which has not been described on potato (Tymon et al. 2015). Previous studies of *Alternaria* spp. on potato have identified *A. alternata* as the predominate small-spored *Alternaria* sp. and have characterized its pathogenicity (Droby et al. 1984). In this survey, *A. arborescens* was isolated more frequently than *A. alternata*. Because previous work has not been conducted on the aggressiveness of *A. arborescens* or *A. arbusti* on potato, these two fungi were the focus of this study. Additionally, a preliminary pathogenicity assay suggested that *A. arborescens* was more aggressive than *A. alternata* (data not shown). Therefore, the objectives of this study were to (i) quantify and compare the aggressiveness of *A. arborescens* and *A. arbusti* isolates sampled from the U.S. Northwest on potato to *A. solani*, which is the dominant pathogen on potato; and (ii) quantify and compare the aggressiveness of *A. arborescens* and *A. arbusti* to *A. solani* on different potato cultivars, including 'Alturas', 'Russet Burbank', 'Ranger Russet', 'Umatilla Russet', and 'Russet Norkotah'.

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Materials and Methods

Collection, preservation, and identification of isolates. Potato foliage with early-blight-type lesions was collected from potato fields in the Columbia Basin of Washington, in Rupert, ID, and near Bonner's Ferry in north Idaho in 2009 to 2011. In total, 940 small-spored *Alternaria* spp. and 600 large-spored isolates (putatively *A. solani*) were collected. Foliage was placed in plastic bags, sealed, and transported to a laboratory in Pullman, WA. Leaves were stored at 4°C until processed. Potato leaflets with lesions were surface disinfested by dipping in 70% ethanol for 3 to 5 s. Leaflets were blotted with paper towel and air dried. One to three lesions per leaf (one lesion per leaflet) were sampled. Lesion margins were excised and plated on a modified potato dextrose agar (mPDA; Difco Bactoagar at 20 g/liter, Difco PDA at 1 g/liter, and 95% ethanol at 6 ml/liter). Single-conidial isolates were obtained from single lesions from single leaflets and grown on mPDA at 21 to 23°C under constant light. Isolates were grown on mPDA for 7 to 10 days and stored on filter paper squares. Squares were placed in autoclaved coin envelopes and maintained at room temperature for future inoculation experiments.

Isolates were identified using morphological characteristics as well as through sequencing of glyceraldehyde 3 phosphate and Scar marker OPA 1-3 (Tyman et al. 2015).

Plant growth. Seed potato pieces were removed from cool storage and warmed to room temperature for 24 h prior to planting. Approximately three seed pieces were cut from each potato. One seed piece was planted approximately 6 cm deep into a round, plastic container (15.3 cm in diameter) filled with Sunshine number 1 (Sun Gro Horticulture, Agawam, MA) soilless planting media. Greenhouse temperatures were approximately 21°C during the day and 10°C at night. The photoperiod was at least 14 h from natural light. Russet Norkotah plants were maintained in the greenhouse during spring and summer for approximately 2.5 months after emergence in July and August 2012 and 2013 prior to leaf excision for detached-leaf assays. Alturas, Russet Burbank, Ranger Russet, Umatilla Russet, and Russet Norkotah potato plants (Table 1) were maintained for approximately 3.5 months post-emergence in July through September 2012 before inoculation.

Inoculum preparation. Two isolates of *A. arbusti*, two of *A. arborescens*, and one of *A. solani* were selected for inoculation from 200 isolates of *Alternaria* that were prescreened for pathogenicity on excised leaves of Russet Norkotah potato. The five isolates (Table 2) were pathogenic and were used to inoculate detached leaves and whole plants. The isolate of *A. solani* was used as a control. Inoculum was prepared by culturing single-spore isolates on mPDA for 13 days under 24-h lights at room temperature. Plates were gently scraped using a scalpel and spores were suspended in sterilized distilled H₂O. The suspension was filtered through three layers of cheesecloth and inoculum was standardized to 10³ spores/ml using a hemocytometer.

Detached-leaf assay. Potato leaflets from detached compound leaves were either not wounded or were wounded using a sterilized scalpel (one wound per leaflet). Wounds were approximately 10 mm long and the width of the blade edge. Excised leaves were sprayed with distilled water until runoff and then placed on moistened, clean paper towels on fiberglass screens in 5.5-cm-deep Pyrex baking pans. In all, 200 *Alternaria* isolates were used to prescreen for pathogenicity on potato. Of these 200 isolates, 5 isolates (2 isolates of *A. arbusti*, 2 of *A. arborescens*, and 1 of *A. solani*; Table 2) were selected for additional inoculation assays. The two *A. arborescens* isolates were selected based on mean infection frequency. Isolate aa10_312 exhibited moderate pathogenicity on nonwounded tissue and aa10_328 exhibited low

pathogenicity on nonwounded tissue (data not shown). Spore suspension (20 µl) was applied to a 1-cm² filter paper, which was placed so that conidia were in direct contact with either nonwounded or wounded tissue of the leaflets. Only one isolate was inoculated onto five leaflets (subsamples) per compound leaf, where leaflets remained attached to leaf. Whole leaves were placed into Pyrex pans and sealed into plastic bags. Pans were maintained under 24-h lights at 21 to 23°C on a laboratory benchtop. Filter paper squares were removed after 48 h and lesions were measured at 3, 5, and 7 days postinoculation.

Laboratory space was limited and did not allow for replications of isolates within each trial. Therefore, repeated trials were used as replications, with the first and second trials 2 weeks apart in July 2012 and the third trial in August 2013, giving three replications of five subsamples (leaflets) for each of the five isolates.

Whole-plant assay. Pathogenicity of the five selected isolates used in the detached-leaf assays (Table 2) was also tested on whole plants to validate the inoculated detached-leaf assays. Norkotah potato plants were grown in a greenhouse environment for 2 months postemergence in July and August 2013 at 12-h mean temperatures of 21°C during the day and 10°C at night. A spore suspension for each isolate was prepared and standardized to 10³ spores/ml as above. Potato leaflets were abraded using a heavy-duty scouring pad (3M, St. Paul, MN). Wounded leaflets were sprayed with distilled water until runoff using a hand sprayer. Filter paper squares were dipped into the spore suspension and then placed on the wounded leaf. Each isolate was inoculated onto one leaflet on one leaf on each of four plants. Each of the four plants was a replicate in a randomized complete block design, where the plant was the block. Whole plants were sealed in clear plastic bags. Plants were maintained at approximately 21 to 23°C for 7 days under constant light. Bags and the filter paper were removed after 48 h. Lesions were measured at 3, 5, and 7 days postinoculation. The whole-plant assay was repeated a week later.

Experimental design and analysis. Infection frequency for each replicate was calculated as the mean incidence of infection of the five subsamples. Lesion area was calculated from lesion diameter measurements diameter 1 (d_1) and diameter 2 (d_2) using the formula $A = d_1 \times d_2$, where d_1 and d_2 were perpendicular to each other. Mean lesion area of the five subsamples was then used to calculate the area under the lesion expansion curve (AULEC), which integrates lesion area over time (Shaner and Finney 1977). AULEC was calculated as follows:

$$AULEC = \sum_{i=1}^n \left[\frac{(y_i - y_{i+1})}{2} \right] (t_{i+1} - t_i)$$

where y_i is lesion area in square millimeters at time t_i . Mean infection frequency (MIF) and AULEC were measures of pathogen aggressiveness.

Table 2. Isolate, collection year, *Alternaria* spp., and collection area of the five isolates selected for pathogenicity and aggressiveness assays on detached leaves and whole plants^a

Isolate	Year collected	Species	Collection area
aa09_157	2009	<i>Alternaria arbusti</i>	Bonnerr's Ferry, ID
aa11_80	2011	<i>A. arbusti</i>	Bonnerr's Ferry, ID
aa10_312	2010	<i>A. arborescens</i>	Rupert, ID
aa10_328	2010	<i>A. arborescens</i>	Rupert, ID
as10_315	2010	<i>A. solani</i>	Rupert, ID

^a Isolates were selected based on preliminary pathogenicity assays.

Table 1. Maturity and early blight resistance of five potato cultivars

Cultivar	Maturity	Early blight resistance	Reference
Alturas	Late	Resistance	Novy et al. 2003
Russet Norkotah	Early to medium	Susceptible	Johanson et al. 1988
Ranger Russet	Late	Moderately resistant	Pavek et al. 1992
Russet Burbank	Late to very late	None noted	Rykboost et al. 1990
Umatilla Russet	Medium to late	Moderately susceptible	Mosley et al. 2000

A treatment was an inoculation by a species on wounded or non-wounded potato leaflets. Data for MIF and AULEC were analyzed by analysis of variance using PROC GLM in SAS statistical software (ver. 9.2; SAS Institute Inc., Cary NC). Trials were used as replications for detached-leaf assays. For the whole-plant assays, plants were used for replications of the treatments (isolates) and repeated. No significant differences in MIF or AULEC were observed between isolates within species among the three trials. Therefore, isolates within a species were combined.

AULEC of *Alternaria* isolates on detached leaves were regressed on the AULEC of isolates on whole plants. Regression compared AULEC from the third trial on detached leaves to AULEC on whole-plant trials because the detached leaves were excised from plants of identical age, seed source, and location as the whole-plants trial.

Results

Detached-leaf assays on Russet Norkotah. Mean infection frequency on nonwounded tissue was significantly greater ($P < 0.05$) for *A. solani* than for *A. arborescens* and *A. arbusti* in all three trials (Table 3). A significant interaction ($P < 0.05$) was observed between species and wounding, which was due to an increased MIF on wounded leaflets inoculated with *A. arbusti*. A significant interaction

Table 3. Mean infection frequency on nonwounded and wounded detached leaves of Russet Norkotah inoculated with three *Alternaria* spp. in three trials^a

<i>Alternaria</i> spp.	Nonwounded	Wounded	<i>P</i> value
<i>Alternaria arborescens</i>	0.83 a	0.7 a	0.09
<i>A. arbusti</i>	0.33 a*	0.6 a	0.008
<i>A. solani</i>	0.08 b	1.0 a	0.38
<i>P</i> value	0.0072	0.24	...

^a Values with the same letters within a column are not significantly different at $P \geq 0.05$. An asterisk (*) indicates that values are significantly different than the wounded at $P < 0.05$.

Table 4. Area under the lesion expansion curve on nonwounded and wounded Russet Norkotah leaves in two trials and wounded whole Russet Norkotah plants inoculated with *Alternaria* spp. in two trials^a

<i>Alternaria</i> spp.	Detached-leaf assay			Whole plant
	Nonwounded	Wounded	<i>P</i> value	Wounded
<i>Alternaria arborescens</i>	50 a*	211 a	0.01	345 a
<i>A. arbusti</i>	8 a*	64 a	0.0047	294 a
<i>A. solani</i>	716 b	499 b	0.55	404 a
<i>P</i> value	0.0002	0.001	...	0.34

^a Values with the same letters within a column are not significantly different at $P \geq 0.05$. An asterisk (*) indicates that values are significantly different than the wounded at $P < 0.05$.

was not observed ($P > 0.05$) between the MIF and wounding of tissue inoculated with *A. arborescens* or *A. solani*.

AULEC of trial 1 was significantly greater than for trials 2 and 3. However, in all three trials, AULEC was significantly greater when tissues were inoculated with *A. solani* than with *A. arborescens* or *A. arbusti* regardless of wounding and did not significantly differ between *A. arborescens* and *A. arbusti* (Table 4). A significant interaction was observed ($P < 0.05$) between species and wounding, which was due to an increased AULEC on wounded than nonwounded leaflets inoculated with *A. arborescens* and *A. arbusti*.

Whole-plant assay. AULEC did not differ significantly among the three *Alternaria* spp. on whole plants (Table 4). However, AULEC of isolates on leaves of whole plants significantly increased as AULEC on detached leaves increased when analysis was conducted on the third trial ($P = 0.03$; Fig. 1). When all trials were combined, an association was found between AULEC values obtained from whole plants and detached leaves ($P = 0.07$) (data not shown). *A. solani* was the most aggressive on whole plants and *A. arbusti* isolates were the least aggressive.

Detached-leaf assay on Russet potato cultivars. The MIF was significantly greater ($P < 0.05$) on Umatilla Russet than Russet Burbank when inoculated with *A. arborescens* or *A. arbusti* (Table 5); mean infection frequency did not differ significantly on Umatilla Russet, Ranger Russet, Russet Norkotah, and Alturas when inoculated with *A. arborescens*. A significant difference in MIF was not observed between Umatilla Russet and Ranger Russet when inoculated with *A. arbusti* but MIF on Umatilla Russet was significantly greater than on Russet Norkotah and Alturas. A significant difference was not observed among cultivars when inoculated with *A. solani*. Mean infection frequency on Russet Norkotah and Russet Burbank was significantly greater when inoculated with *A. solani* than *A. arborescens* or *A. arbusti* and no significant difference was observed among the species of *Alternaria* on Umatilla, Ranger, or Alturas.

AULEC of *Alternaria* spp. varied significantly among potato cultivars (Table 6). AULEC did not differ significantly among cultivars when inoculated with *A. arborescens* but was significantly greater ($P < 0.05$) on Umatilla Russet than on Alturas and Russet Burbank when inoculated with *A. solani* or *A. arbusti*. AULEC was significantly greater on leaflets inoculated with *A. solani* than with *A. arborescens* or *A. arbusti* on each of the cultivars except Alturas. A significant difference in AULEC was not observed when Umatilla Russet, Ranger Russet, Russet Norkotah, or Russet Burbank was inoculated with *A. arborescens* or *A. arbusti*.

Discussion

A. solani was the most aggressive of the three *Alternaria* spp. tested. When tissue was wounded, MIF and AULEC for *A. arborescens* and *A. arbusti* increased significantly. Thus, wounding of plant tissue is an important factor for severe disease symptoms to develop. The importance of wounding has been demonstrated with *Alternaria*

Fig. 1. Third trial regression line for area under the lesion expansion curve (AULEC) of *Alternaria solani* (As), *A. arborescens* (Aa), and *A. arbusti* (Aab) inoculated on detached Russet Norkotah leaves to the AULEC of isolates inoculated on whole Russet Norkotah plants.

spp. infection on other crops. On *Amaranth hybridus*, *Alternaria tenuissima* infection on wounded leaves increased symptom development (Blodgett and Swart 2002) and, on blueberry, a higher incidence of *Alternaria* spp. infection occurred on berries with stem scars (Cappellini and Ceronis 1977). Wounding of potato leaves in commercial fields occurs frequently through wind carrying soil particles, insects, windburn, or machinery. In the Columbia Basin of Washington, dust storms frequently occur (Sharratt and Lauer 2006) and damage to potato foliage is not uncommon. Aggressiveness of *A. solani* did not increase on wounded tissue as it did for *A. arborescens* and *A. arbusti* because wounds may not be necessary for severe infection. Lesions caused by foliar pathogens such as *A. solani* or *Colletotrichum coccodes* could provide additional openings into host tissue, where *A. arborescens* and *A. arbusti* then act as secondary invaders (Rotem 1994; Tymon et al. 2015).

AULEC was greater on leaves inoculated with *A. arborescens* than with *A. arbusti*, which may be a result of toxin production. *A. arborescens* as well as *A. solani* produce nonhost and host-specific toxins (Rotem 1994). *A. arborescens* produces high levels of pectin methyl lyase, which break down the waxy cuticles; tenuazonic acid, which prevents the synthesis of proteins; and tentoxin, which inhibits photophosphorylation (Rotem 1994; Thomma 2003). In contrast, *A. arbusti* clusters within the infectoria clade (Lawrence et al. 2013). Host-specific toxin production is not known to occur by members of the *A. infectoria* clade (Andersen and Thrane 1996; Logrieco et al. 1990) although it is suspected that phytotoxic metabolites are produced by some members (Kumar and Rao 1979). Disease establishment does not require nonhost-specific and host-specific toxins. However, they do increase disease symptoms (Fry 2007) and are thought to facilitate colonization by killing cells prior to fungal invasion (Kumar and Rao 1979). Additionally, the lack of significance observed for AULEC between *A. arborescens* and *A. arbusti* on nonwounded leaves of Russet Norkotah contrasted with the significance on wounded leaves illustrates the influence that host defenses of intact leaves have on overall aggressiveness of *Alternaria* spp. (Olanya et al. 2009).

Resistance is directly associated with cultivar maturity (Boiteux et al. 1995; Douglas and Pavek 1972; Pelletier and Fry 1989). Cultivars that mature early, such as 'Norchip', tend to be more susceptible due to earlier senescence than late-maturing cultivars (Johanson and Thurston 1990; Pelletier and Fry 1989). However, some early-maturing cultivars do exhibit early blight resistance (Boiteux et al.

1995). In this study, a significant cultivar effect was observed on fully expanded and green, excised leaves. All three species of *Alternaria* were most aggressive on Umatilla Russet and least aggressive on Russet Burbank. A comparison of these two cultivars should be made in a field study to confirm these results. Regardless, the decreased susceptibility of certain potato cultivars could be exploited to reduce the number of fungicide applications, which are currently the common management strategy in the Columbia Basin.

AULEC of *Alternaria* isolates tested on whole plants were reflective of results obtained from the detached-leaf assays, although this has not been the case in other studies (Odilbekov et al. 2014). A correlation between field and whole-plant assays with detached-leaf assays was not found in a previous study. It was also determined that a higher level of resistance to infection was exhibited in detached-leaf assays (Odilbekov et al. 2014). In this study, *A. arborescens* and *A. arbusti* exhibited increased resistance in the detached-leaf assay. Although detached-leaf assays may not be suitable for assessing field resistance of a cultivar, they can be used to gauge an isolate's aggressiveness. Overall, *A. arbusti* isolates were the least aggressive among the three *Alternaria* isolates and *A. solani* was the most aggressive, regardless of assay type. A positive relationship was observed when the AULEC of *Alternaria* isolates on whole plants was regressed against the AULEC on detached leaves, indicating that the detached-leaf assay has the potential to robustly predict the response of whole plants to infection.

A. arborescens and *A. arbusti* are likely less important pathogens in the field than *A. solani*, although *A. arborescens* is an aggressive pathogen on potato when leaves are wounded. This is supported by the increase in mean infection frequency and aggressiveness of *A. arborescens* isolates on nonwounded and wounded tissue. In contrast, whereas *A. arbusti* is capable of infecting wounded potato foliage, the comparatively diminished AULEC suggests that it is not as effective in colonizing host tissue as *A. arborescens* or *A. solani*.

A. arbusti on potato may not be a new pathogen. There is extensive morphological plasticity of *A. arborescens* and *A. arbusti* and they may overlap in morphological characteristics (Simmons 2007). Therefore, it is possible that *A. arbusti* was misidentified as *A. alternata* in the past. Two key features differentiate *A. arbusti* from *A. arborescens*. Young conidial chains of *A. arbusti* are not branched, although branching can occur on secondary conidiophores and older primary conidiophores (Simmons 1993), and a conidium of *A. arbusti* typically produces one to five cells at the apical end to form a secondary conidiophore (Simmons 1993).

Alternatively, the pathogenicity of *A. arbusti* on potato may be a result of a newly emerging pathogen due to either an expansion in host range or a change in virulence, possibly through horizontal gene transfer (Stukenbrock and McDonald 2008). Geographically, pear and cherry are grown in close proximity to potato in central Washington, increasing the potential for local adaptation of *A. arbusti* to potato. Horizontal gene transfer of virulence genes between *A. arborescens* and *A. arbusti* may be responsible for the ability of potato to serve as a new host and is the proposed mechanism through which *A. arborescens* acquired host-specific toxin genes (Akagi et al. 2009; Hu et al. 2012).

A. arbusti, which has not been previously known to cause disease in potato, was only mildly aggressive in this study, even when wounding had occurred on leaf tissue. This suggests that *A. arbusti*

Table 5. Mean infection frequency on wounded leaves of five potato cultivars inoculated with three *Alternaria* spp.^a

Cultivar	<i>Alternaria arborescens</i>	<i>A. arbusti</i>	<i>A. solani</i>	P value
Umatilla Russet	0.6 a	0.8 a	1 a	0.2432
Ranger Russet	0.4 ab	0.5 ab	1 a	0.281
Norkotah Russet	0.3 ab*	0.3 bc*	0.9 a	0.0188
Russet Alturas	0.2 ab	0.1 bc	0.7 a	0.054
Russet Burbank	0 b*	0 c*	0.8 a	<0.001
P value	0.11	0.0052	0.35	...

^a Values with the same letters within a column are not significantly different at $P \geq 0.05$. An asterisk (*) indicates that values are significantly different than for *A. solani* (across a row) at $P < 0.05$.

Table 6. Area under the lesion expansion curve on wounded leaves of Russet cultivars inoculated with three *Alternaria* spp.^a

Cultivar	<i>Alternaria arborescens</i>	<i>A. arbusti</i>	<i>A. solani</i>	P value
Umatilla Russet	125 a*	80 a*	1,488 a	0.0063
Ranger Russet	105 a*	44 ab*	625 ab	0.019
Norkotah Russet	142 a*	32 ab*	604 ab	0.0334
Russet Alturas	13 a	3 b	43 b	0.1104
Russet Burbank	0 a*	0 b*	135 b	0.001
P value	0.4535	0.1679	0.1422	...

^a Values with the same letters within a column are not significantly different at $P \geq 0.05$. An asterisk (*) indicates that values are significantly different than for *A. solani* (across a row) at $P < 0.05$.

is a minor pathogen that contributes little to disease symptoms in the field. No pathogenicity studies have been performed using *A. arbusti* to determine whether it is actually a pathogen on pear and cherry or merely a saprophyte. The host range of this fungus needs to be determined to assess potential impacts that it may have on orchards, especially those located in close proximity to potato fields, as in the Pacific Northwest.

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