Irrigation Water as a Source of Inoculum of Soft Rot Erwinias for Aerial Stem Rot of Potatoes

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ABSTRACT

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Seed pieces from a single seed lot of potato cultivar Russet Burbank were planted at two production areas in Oregon and Colorado in 1985 and 1986. Plots were established in fields irrigated from either surface- or well-water sources. Seed tubers, field soil, irrigation water, symptomless leaflets, and stems with aerial stem rot symptoms were assayed for the presence of soft rot erwinias. More than 95 and 90% of all strains recovered from Oregon and Colorado sources, respectively, were *Erwinia carotovora* subsp. *carotovora*. A total of 3,556 strains of *E. carotovora* were tested serologically against 21 different antisera by Ouchterlony agar double diffusion. In Oregon, seven different serogroups were detected in irrigation water first during the season, then on leaflets, and later in diseased stems. In Colorado, five different serogroups were detected in irrigation water before or at the same time they were detected on potato leaflets. However, only one plant developed aerial stem rot symptoms. In Oregon, 39% of the serogroups identified were common to irrigation water, leaflets, and diseased stems, whereas in Colorado 50% of the serogroups identified were common to irrigation water and leaflets. Contaminated water sources are a potential source of inoculum for aerial stem rot in Oregon.

Additional keyword: Erwinia chrysanthemi.

Aerial stem rot and blackleg of potatoes, caused by *Erwinia carotovora* subsp. *carotovora* and *E. c.* subsp. *atroseptica*, commonly occur in the center-pivot irrigated fields of the western United States. Symptoms caused by these soft rot erwinias range from general wilting of the foliage to a light brown to inky black coloration of the stems. *E. chrysanthemi* causes similar symptoms (22). Symptom expression, however, depends largely on environment, cultivar, and portion of the plant affected (21). According to the proposed terminology revision (22), blackleg describes infections that originate from the seed tuber whereas aerial stem rot describes infections that originate above ground. In Oregon, early-season blackleg is generally caused by *E. c. atroseptica*, whereas late-season blackleg and aerial stem rot usually are caused by *E. c. carotovora* (23). Aerial stem rot, however, is the predominant symptom observed. In contrast, blackleg caused by *E. c. carotovora* and *E. c. atroseptica* predominates in Colorado and aerial stem rot symptoms seldom are observed (18).

Previous studies (1,4) have focused on the seed tuber as an inoculum source for blackleg. Contaminated soil (24) and insects (17) are potential sources of inoculum for blackleg but also may be important sources for initiating aerial stem rot infections. Soft rot erwinias also have been recovered from rivers, oceans, aerosols, and rain (7,9,13). Surface water used for irrigation of potatoes has been sampled at many diverse locations within the United States and Scotland; it too is contaminated with these microorganisms (10,12,15). However, the importance of irrigation water as an inoculum source for aerial stem rot has not been determined.

Because *E. carotovora* is diverse serologically, the relative importance of various inoculum sources may be determined by tracing individual strains serologically. The serotyping scheme developed by De Boer et al (5), which allows the classification of *E. carotovora* strains into serogroups, has been used previously in inoculum-source studies (6,14,24). The objective of this research was to determine if irrigation water is important as an inoculum source for aerial stem rot of potatoes in the western United States.

MATERIALS AND METHODS

Field plots. Field plots were established in 1985 and 1986 in two potato production areas in Oregon and two in Colorado. Areas were located in Umatilla and Crook counties in Oregon and in Weld County and in three counties in the San Luis Valley in Colorado. Duplicate field plots were located within center-pivot irrigated commercial fields in each area. Field plots in each area were irrigated from either a surface-water source or a well-water source. Management practices were controlled by the grower and were considered standard for each area.

A single certified seed lot of potato cultivar Russet Burbank from Montana was planted the first week of April in Umatilla County and the third week of May in Crook and Weld counties and the San Luis Valley in both years. Seed tubers were warmed for 4 days at 22 C and cut into 40- to 55-g seed pieces. Seed pieces were spaced 23 cm apart in rows on 86-cm centers. Six observation plots, 7.5 m long and 4 or 6 rows wide, were established at each location.

Soil assays. At planting, 30 random soil samples 15- to 20-cm deep were taken at each location with a soil probe and analyzed for the presence of soft rot erwinias. About 8 g of soil was placed in a 40-ml vial, and pectate enrichment medium (PEM) (16) was added to fill the vial. The vials were incubated anaerobically for 4 days, and the enrichment medium was plated on crystal violet pectate (CVP) medium (2). Up to 10 *Erwinia*-like colonies per sample were purified by subculturing on CVP or nutrient agar (NA). Strains were stored on NA at 4 C for later characterization.

Seed tuber assays. Before planting, 10 symptomless seed tubers were randomly selected from each of 12 sacks of seed potatoes and tested for surface populations of soft rot erwinias. About 5 g of periderm was peeled from each group of 10 tubers, placed in 10 ml of sterile distilled water, agitated for 1 min, and allowed to stand at room temperature for 30 min. Aliquots (0.1 ml) were plated in

duplicate on CVP. In addition, a 1-ml aliquot was added to 29 ml of PEM, incubated anaerobically for 48 hr, and plated on duplicate plates of CVP. From each sample, up to 10 *Erwinia*-like colonies were selected, subcultured, and stored as described above for later characterization. In addition, approximately 50 tubers were incubated anaerobically according to the methods described by DeBoer and Kelman (6), except that the tubers were not injured. *E. carotovora* strains were isolated from soft rot pockets, purified, and stored as described above for later identification.

Water assays. Water used to irrigate plots was monitored periodically for soft rot erwinias during the growing season. Samples were collected in four 4-L sterile polypropylene jugs and returned to the laboratory for processing within 48 hr. Each 4-L sample was processed three different ways. In the direct plating method, 0.2-ml aliquots of water and 10-fold serial dilutions of surface-water samples were spread on triplicate plates of CVP. The number of colony-forming units (cfu) of pectolytic erwinias per milliliter of water was determined. In the direct enrichment method, a 50-ml aliquot was placed in a 100-ml sterile bottle, which was then filled with double-strength PEM and sealed with Parafilm or placed in a Gas Pak anaerobic chamber. After a 96-hr incubation at 22 C, a 0.2-ml aliquot was spread on CVP. In the Celite concentration and enrichment method, samples were passed through a Celite (diatomaceous earth) column filter to concentrate cells and facilitate detection of the bacteria (11). Soft rot erwinias were detected in the filtered concentrate after anaerobic enrichment using previously described methods (15). Up to five *Erwinia*-like colonies from each treatment were collected, purified, and stored on NA slants at 4 C.

Foliage assays. On each sampling date, leaflets were assayed for epiphytic populations of soft rot erwinias. Two leaves (Oregon in 1985 and Colorado in 1985 and 1986) or five leaves (Oregon in 1986) were collected from a middle row of each plot. The fourth leaf from the base of the plant was placed in a plastic bag, stored in a cooler, and processed within 24 hr. The terminal leaflet was removed and washed for 30 min in 50 ml of 0.13 M phosphate buffer (pH 7.2) on a rotary shaker at 125 rpm. Aliquots (0.1 ml) were spread on duplicate CVP plates. For leaflets that appeared chlorotic or decayed, 10-fold serial dilutions also were plated. For samples collected in Colorado, 50 ml of double-strength PEM was added to the buffer solution following washing. This enrichment was incubated anaerobically at room temperature for 4 days. Aliquots were plated on CVP, and up to five *Erwinia*-like colonies from each sample were purified and stored on NA slants for later identification.

Disease assessment and stem assays. Stems in 10 hills from a middle row of each plot were visually assessed for symptoms of aerial stem rot on each sampling date and the proportion of diseased stems was determined. Effect of irrigation source on incidence of aerial stem rot was based on the area under the disease progress curve (AUDPC) calculated by the methods of Shaner and Finney (25). Samples of symptomatic plants were collected beginning with the onset of disease. Up to five or three stems were taken from each plot in 1985 and 1986, respectively. Stems were rinsed with tap water and surface sterilized in 10% (v/v) commercial bleach solution for 3 min. A 1-cm segment of stem tissue in the region of incipient decay was macerated and placed in a test tube with 1 ml of sterile water. Tubes were vortexed, allowed to stand at 22 C for a minimum of 30 min, then gently vortexed again. A loopful of the suspension was streaked on CVP. Strains were purified and stored, as described above, for later characterization.

Biochemical and serological characterization. Soft rot erwinias were distinguished from one another based on biochemical properties. *E. c. atroseptica* differs from *E. c. carotovora* and *E. chrysanthemi* by production of acid from α-methyl glucoside, production of reducing substances from sucrose, and absence of growth at 36 C (8). *E. chrysanthemi* is separated from *E. c. carotovora* by phosphatase production or by indole production from tryptophan (8). All *E. carotovora* strains were tested with antisera produced against 21 serogroups using the Ouchterlony double diffusion technique (19). Immunodiffusion tests were conducted as previously described (24).

RESULTS

Water populations. Soft rot erwinias were recovered from both surface- and well-water sources in Oregon in 1985 and 1986 and in Colorado in 1985 (Table 1). Only surface-water sources yielded pectolytic erwinias in Colorado in 1986. Populations were higher in surface-water samples than in well-water samples at all sites. In Umatilla County, OR, mean populations in surface-water subsamples ranged from < 1 (detected by enrichment) to 108 cfu/ml in 1985 and < 1 to 18 cfu/ml in 1986. In Crook County, OR, in 1985, the highest surface-water population (575 cfu/ml) was measured in late August. Populations were lower in 1986 and ranged from nondetectable to 5 cfu/ml. Populations in surface-water samples collected in Colorado ranged from < 1 to 41 cfu/ml in Weld County and from 3 to 16 cfu/ml in San Luis Valley in 1985. In 1986, detection of soft rot erwinias in water was primarily through enrichment techniques and therefore could not be quantified. Soft rot erwinias seldom were recovered from well-water samples by direct plating and required enrichment techniques for detection at all locations.

E. c. carotovora was the predominant soft rot erwinia recovered from both surface and well water in Oregon and Colorado (Table 1). *E. chrysanthemi* also was present in Oregon surface-water samples but was not detected in Colorado samples. *E. c. atroseptica* rarely was recovered from either Oregon or Colorado

TABLE 1. Mean populations and relative percentages of *Erwinia carotovora* subsp. *carotovora* (Ecc), *E. c.* subsp. *atroseptica* (Eca), and *E. chrysanthemi* (Ech) in irrigation water in Oregon and Colorado

Location and year	Surface water				Well water			
	Mean cfu/ml[a]	Ecc (%)	Eca (%)	Ech (%)	Mean cfu/ml	Ecc (%)	Eca (%)	Ech (%)
Oregon								
Umatilla County								
1985	14.3	92.4	0	7.6	>1	100	0	0
1986	3.0	99.3	0	0	>1	100	0	0
Crook County								
1985	74.8	75.4	0	24.6	0.1	100	0	0
1986	1.6	99.1	0	0.9	>1	95.3	4.7	0
Colorado								
Weld County								
1985	10.8	100	0	0	>1	100	0	0
1986	>1	97.0	3.0	0	0	0	0	0
San Luis Valley								
1985	6.4	99.4	0.6	- 0	>1	66.5	33.5	0
1986	0.2	100	0	0	0	0	0	0

[a] Seasonal means determined by direct plating of nonfiltered water samples collected twice per month.

water samples.

Water strains. Only 30.7% of the 1,436 *E. carotovora* strains recovered from water could be identified serologically. Surface-water sources yielded more strains than did well-water sources (Table 2). In addition, strains from surface water were more diverse serologically than strains recovered from well water.

In Oregon, 15.2% of the water strains were classified as serogroup XXIX. In contrast, only 1.5% of the Colorado water strains were placed into this serogroup. Serogroup XVIII was the predominant strain found in Colorado water sources and represented 9.0% of the strains, whereas in Oregon, 5.3% of the strains were placed in this serogroup.

Seed tuber and soil strains. In 1985 and 1986, 35 and 37% of the tubers, respectively, were contaminated with soft rot erwinias. *E. c. atroseptica* was not detected in 1985 but comprised 14% of the seed tuber strains in 1986. *E. chrysanthemi* was not detected. Soft rot erwinias were recovered from soil samples taken before planting at four of eight locations in 1985 and three of eight locations in 1986. Both *E. c. atroseptica* and *E. c. carotovora* were detected in both Oregon and Colorado soil samples. The former subspecies was found in soil samples from one location in Oregon in 1986 and from two of four locations in 1985 and 1986 in Colorado.

Thirty-seven percent of strains from seed tubers in 1985 were identified as serogroups XXIX or XXXVI, whereas 34% of the strains were identified as serogroups IV, V, and XXXI in 1986. All *E. c. atroseptica* strains were serogroup I. In Oregon, soil strains

TABLE 2. Serogroups represented among *Erwinia carotovora* strains recovered from irrigation water sources in Oregon and Colorado

	Number of strains															
	Umatilla County, OR				Crook County, OR				Weld County, CO				San Luis Valley, CO			
	Surface		Well		Surface		Well		Surface		Well		Surface		Well	
Serogroups[a]	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
I	...[b]	...	...	...	...	...	...	1	...	...	...	...	1	...	...	...
III	2	12	...	2	...	18	...	1	3	...	...	...	2	...	1	...
IV	1	1	...	...	...	...	...	...	1	...	...	...	2	...	...	...
V	12	14	...	...	...	1	...	...	...	1	...	...	3	...	...	...
VII	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
XI	1	6	...	...	...	4	...	...	...	...	...	...	...	...	...	...
XIV	2	12	...	7	...	...	...	...	...	...	...	...	...	...	...	...
XV	...	...	...	...	...	...	...	...	7	...	...	...	5	...	...	...
XVIII	18	17	...	2	5	...	16	...	15	3	2	...	9	1	...	...
XXVII	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...
XXVIII	9	...	...	...	...	...	...	...	...	2	...	...	1	...	...	...
XXIX	22	12	...	...	47	84	2	...	...	1	...	...	1	3	...	...
XXXI	...	1	...	2	...	...	...	1	...	...	...	...	...	...	...	...
XXXII	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
XXXIII	...	3	...	...	1	...	...	...	...	...	...	...	...	...	...	...
XXXV	1	1	...	...	...	2	3	...	2	...	...	...	4	...	...	...
XXXVI	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
XXXVII	...	...	...	...	...	...	1	3	...	...	...	...	...	...	...	...
XXXIX	...	...	...	...	...	6	...	7	...	...	...	...	...	...	...	...
XL	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...
Total tested	224	176	10	49	236	284	84	33	137	18	13	0	138	28	6	0

[a] Serogroups based on classification by De Boer et al (5).
[b] Not applicable because the serogroup was not recovered from the water.

TABLE 3. Serogroups represented among *Erwinia carotovora* strains recovered from potato leaflets in fields irrigated from surface- and well-water sources in Oregon and Colorado

	Number of strains															
	Umatilla County, OR				Crook County, OR				Weld County, CO				San Luis Valley, CO			
	Surface		Well		Surface		Well		Surface		Well		Surface		Well	
Serogroups[a]	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
I	...[b]	...	...	...	...	...	...	...	...	...	...	...	10	6	...	...
III	...	...	...	...	...	11	...	1	...	...	...	...	...	...	...	...
IV	1	5	12	4	...	...	...	...	...	...	...	...	...	...	...	...
V	13	10	...	3	...	4	...	...	...	...	...	...	14	...	4	...
VII	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...
XIV	4	12	2	7	...	...	...	...	...	...	...	...	...	...	...	...
XV	...	10	...	...	...	...	...	...	2	...	...	...	...	...	...	...
XVIII	2	17	1	...	1	...	...	...	...	4	...	...	8	...	...	...
XXVII	7	3	...	...	...	1	...	...	...	...	...	...	...	...	...	...
XXVIII	...	...	...	...	...	1	...	...	...	...	...	...	...	...	24	...
XXIX	2	2	8	...	19	3	1	...	...	...	...	...	...	6	35	...
XXXI	...	15	...	2	...	...	...	1	...	...	...	...	...	...	4	...
XXXII	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...
XXXV	...	1	...	3	...	...	...	...	...	...	...	...	...	...	...	...
XXXVI	...	8	...	...	...	1	...	...	...	...	...	...	...	...	...	...
XXXVII	8	9	3	3	...	...	...	3	...	...	...	...	...	...	...	...
XXXVIII	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...
XXXIX	...	12	...	...	...	4	...	...	...	...	...	...	...	...	...	...
Total tested	107	299	117	92	120	114	26	32	71	20	0	5	146	40	92	34

[a] Serogroups based on classification by De Boer et al (5).
[b] Not applicable because the serogroups was not recovered from the foliage.

were identified as serogroups III and V, whereas serogroups I, IV, V, XI, XVIII, XXIX, and XXXV were recovered from Colorado soil samples.

Epiphytic strains. *E. c. carotovora* was the predominant soft rot erwinia recovered from foliage at all locations. In Oregon, *E. chrysanthemi* represented < 1% of the epiphytic soft rot erwinias in 1985 and 1986, whereas *E. c. atroseptica* was not recovered. In contrast, *E. chrysanthemi* was not recovered as an epiphyte in Colorado; however, *E. c. atroseptica* represented 12 and 18% of the epiphytic soft rot erwinias in the San Luis Valley in 1985 and 1986, respectively. A total of 1,325 epiphytic strains of *E. carotovora* were tested serologically and 26.4% could be identified. In Oregon, a higher proportion of these strains was serologically identified from plots irrigated with surface water (29.4%) than from plots irrigated with well water (20.6%) (Table 3). The opposite was true in Colorado where 13.5% of the strains from surface-water-irrigated plots and 51.1% of those from well-water-irrigated plots were identified serologically. Strains recovered from foliage in surface-water-irrigated plots also were more diverse serologically than strains recovered from foliage in well-water-irrigated plots. Serogroups V, XIV, XVIII, XXIX, and XXXVII were recovered from symptomless leaves in Oregon more frequently than other serogroups, whereas serogroups I, V, XXVIII, and XXIX were found most frequently in Colorado.

Diseased stem strains. *E. c. carotovora* was recovered consistently from diseased stems in Oregon and Colorado. *E. chrysanthemi* was recovered from < 1% of diseased stems in Umatilla County, OR, in 1985 and was not recovered from diseased stems in Colorado. *E. c. atroseptica* was not isolated from potatoes with aerial stem rot symptoms.

A total of 614 *E. carotovora* strains recovered from diseased stems in Oregon was tested serologically and of these 19.9% could be identified (Table 4). Serogroups most frequently recovered from diseased stems were V, XVIII, XXVII, XXXI, XXXVII, and XXXIX. In Colorado, only one stem was observed with aerial stem rot, and the recovered *E. c. carotovora* strain was not identifiable serologically.

Seven serogroups (IV, V, XIV, XVIII, XXIX, XXXVII, XXXIX) were common to water, foliage, and diseased stems in Oregon. Sixty-one percent of the foliage serogroups were the same as water serogroups, and 64 and 39% of the stem serogroups were the same as foliage and water serogroups, respectively. In Colorado, five (V, XV XVIII, XXVIII, XXIX) of eight serogroups recovered from irrigation water also were recovered from symptomless leaflets simultaneously or after they were detected in water.

Disease incidence. Only one stem was found with aerial stem rot symptoms in Colorado during the two seasons. Although aerial stem rot developed at all locations in Oregon, there were no differences in disease incidence, as measured by AUDPC, between plots irrigated with well water and surface water at each location. In Umatilla County, AUDPC values for surface-water-irrigated and well-water-irrigated plots were 2.4 and 3.5 in 1985 and 16.1 and 20.3 in 1986, respectively. In Crook County, AUDPC values in the surface-water-irrigated and well-water-irrigated plots were 6.3 and 4.3 in 1985 and 5.6 and 7.3 in 1986, respectively.

TABLE 4. Serogroups represented among *Erwinia carotovora* strains isolated from diseased stems in fields irrigated from surface- and well-water sources in Umatilla and Crook counties, Oregon

	Number of strains							
	Umatilla County				Crook County			
	Surface		Well		Surface		Well	
Serogroups[a]	1985	1986	1985	1986	1985	1986	1985	1986
III	...[b]	...	...	...	...	...	1	...
IV	2	...	...	1	...	...	1	...
V	2	2	...	...	...	1	6	...
VII	2	2	...	...	2	...	...	1
XI	1	...	...	...	1	...	...	...
XIV	...	...	2	2	1	...	1	2
XV	...	2	...	1	...	...	...	1
XVIII	8	...	1	...	...	...	2	...
XXVII	3	...	6	1	2	...	2	...
XXVIII	...	...	...	...	1	2	...	...
XXIX	...	1	...	...	...	2	1	...
XXI	...	...	...	...	1	...	9	...
XXXV	...	...	...	2	1	...	1	...
XXXVI	...	1	...	...	5	2	...	1
XXXVII	...	...	2	8	1	2	1	1
XXXVII	...	...	...	...	...	...	...	...
XXXIX	...	12	...	...	...	2	...	2
Total	81	58	87	87	122	50	83	46

[a] Serogroups based on classification by De Boer et al (5).
[b] Not applicable because the serogroup was not recovered from the diseased stem.

DISCUSSION

Water is a potential inoculum source of *E. c. carotovora* for aerial stem rot of potatoes. *E. c. carotovora* has been reported to be the predominant soft rot erwinia in water sources used for irrigation (7,13,15), in soil (24), in aerosols (7), and in the recontamination of potato seed stocks (20). This subspecies was the primary pectolytic erwinia recovered from irrigation water and foliage in Oregon and Colorado and from diseased stems in Oregon. *E. chrysanthemi* also was recovered periodically from water samples, foliage, and diseased stems in Oregon. Although *E. c. atroseptica* was detected on seed tubers, in soil, and in water samples from both Oregon and Colorado, and on potato foliage in Colorado, it was not recovered from plants with aerial stem rot symptoms.

Twenty-one serogroups were identified from a variety of sources. Representative strains within each serogroup were pathogenic in the aerial portions of potato plants in studies under greenhouse conditions (Cappaert, Powelson, Franc, and Harrison, *unpublished*). No one serogroup was unique to a particular source or location. The predominance of any one serogroup over another may depend on the host environment rather than inoculum source (26). Serogroups XVIII and XXIX were the most frequently isolated serogroups in this study. Other studies (6,7,14,24) have found serogroup XXIX in soil, water, foliage, and diseased stems; this serogroup is clearly well adapted to survive in many environments. Serogroup XVIII, the predominant early-season epiphyte recovered in British Columbia (6), also was found as an epiphyte in Oregon and Colorado and was frequently recovered from diseased stems in Oregon.

Both seedborne and soilborne inocula of *E. carotovora* colonize host tissue under field conditions (6,14,24). In British Columbia, early-season epiphytic strains of soft rot erwinias are serologically different from those found on seed tubers (6). The late-season epiphytic serogroups, however, are the same as those recovered from seed tubers. DeBoer suggested that there were two *E. c. carotovora* populations: an early-season population originating from external sources, and a late-season population originating from the seed tuber. We have shown that some serogroups that were present as epiphytes in Oregon and Colorado and in diseased stems in Oregon were the same serogroups as those in irrigation water and were different from seed tuber and soil serogroups. Populations of soft rot erwinias in water sources peaked from mid-July to mid-August in our study, which coincided with lush canopy development and a conducive microclimate for epiphytic growth and survival of the bacteria (Cappaert and Powelson, *unpublished*). If the bacteria remain on the foliage and increase in numbers, they eventually may infect the plant.

Plots irrigated with surface water did not differ from plots irrigated with well water in the amount of aerial stem soft rot, despite higher populations of soft rot erwinias in surface water than in well water. Furthermore, disease incidence was much higher in Oregon plots than in Colorado plots. Factors such as irrigation frequency and amount, and canopy size may explain some of the variation in disease incidence between Oregon and Colorado plots. In Oregon, fields are irrigated more frequently, a greater amount of water is applied per growing season, and the

vines are larger than in Colorado. Each of these factors may help to create a microclimate favorable for disease development. Further work in defining these factors is needed if aerial stem soft rot is to be managed effectively.

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