AN ABSTRACT OF THE THESIS OF

Marlys R. Cappaert for the degree of Master of Science in Botany and Plant Pathology presented on July 16, 1987.

Title: Irrigation Water and Plant Density Effects on the Epidemiology of Aerial Stem Rot of Potatoes.

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Field plots of cv. Russet Burbank potatoes from a single seedlot were established at four sites over two seasons (1985-86) in two locations in Oregon to determine the role of water-borne inoculum of Erwinia carotovora in plant infection. One site at each location was irrigated from a surface-water source and the other from a well-water source. Prior to planting, seed tubers and field soil were assayed for presence of Erwinia spp.. Populations of soft rot erwinias in water and on leaf surfaces, and the incidence of aerial stem rot were determined bimonthly from plant emergence until two weeks prior to regional harvest. Strains recovered from all sources were characterized biochemically, and Erwinia carotovora subsp. carotovora strains were typed serologically by Ouchterlony agar double diffusion.

Populations of soft rot erwinias were consistently higher in surface water compared to well water. Populations ranged from 0 to 524 and 0 to 25 cfu/ml in surface-water sources in 1985 and 1986, respectively. Detection of soft rot erwinias in well water usually required enrichment. Populations of soft rot erwinias on potato foliage were highest in midseason after row closure. Populations in plots irrigated with surface-water and well-water were similar and ranged from 0 to 5.90 log cfu/g and from 0 to 6.22 log cfu/g fresh weight in 1985 and 1986, respectively.

Final proportion of stems with aerial stem rot was consistently higher in well-water irrigated sites ranging from a low of 0.09 in the surface-water irrigated site in 1985 to a high of 0.51 in the well-water irrigated site in 1986. Over 90% of strains recovered from all sources were characterized as E. c. subsp. carotovora.

About 25% of the E. c. subsp. carotovora strains recovered from all sources were identified serologically. At all but two sites over two years some of the strains recovered from water sources were the same serologically as epiphytic strains and strains recovered from diseased stems. A majority of stains isolated from diseased stems differed serologically from water serogroups at all locations.

Field plots of potato cv. Russet Burbank were established at four sites in two years to determine the

effect of plant density and plant spacing on development of aerial stem rot. Plant densities were 13, 26, and 52 x 10^3 plants per hectare. The intermediate density had two treatments with different within-row and between-row spacing arrangements. Treatment effects were measured by onset of disease symptoms, final proportion of disease and area under the disease progress curve (AUDPC). In 1986, leaf area index was measured and throughout both seasons leaf wetness was monitored with a CR21X Campbell Scientific micrologger. Onset of aerial stem rot symptoms occurred earlier and final proportion of disease and AUDPC were greater in dense compared to sparse plantings. Larger differences in onset of disease and AUDPC occurred with a decrease in between-row spacings than in a decrease in within-row spacings. A linear regression model that used area under the leaf area index curve (AULAIC) for the four plant spacings as the independent variables accounted for 89-98% of the variation in AUDPC. Highest leaf area index values and longest average duration of leaf wetness preceded highest level of disease by two weeks.

Irrigation Water and Plant Density Effects on the Epidemiology of Aerial Stem Rot of Potatoes.

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IRRIGATION WATER AND PLANT DENSITY EFFECTS ON THE EPIDEMIOLOGY OF AERIAL STEM ROT OF POTATOES.

INTRODUCTION

Water is a regulating factor in disease epidemiology. It is important in the introduction and spread of inoculum in a crop as well as in creating microclimatic conditions conducive to infection and disease development. Aerial stem rot and blackleg of potatoes, caused by Erwinia carotovora subsp. carotovora and E. c. subsp. atroseptica, are a common occurence in overhead irrigated fields of the Pacific Northwest. Aerial stem rot, primarily caused by E. c. subsp. carotovora, however, is the predominant disease. Aerial infections occur when bacteria from external sources enter wounds or natural openings.

Soft rot erwinias have previously been regarded as seed-borne pathogens. Efforts to eliminate the pathogens were directed towards production of pathogen-free planting stock; however, seed stocks produced from pathogen-free material became readily recontaminated (Graham et al., 1976). Research was directed towards identifying sources of inoculum responsible for recontamination of pathogen-free seed stocks. Recently, soft rot erwinias have been found in association with insects, (Phillips and Kelman, 1982) aerosols, (Graham et al., 1977), soil, (Maher et al., 1986) and water (Jorge and Harrison, 1986). These

sources may logically result in aerial infections. Contaminated irrigation water has been implicated as an inoculum source (Jorge and Harrison, 1986). A classification scheme developed by De Boer et al. (1979), has allowed for rapid classification of bacterial strains into serogroups. The relationship between contaminated water sources and its role in aerial stem rot has not been investigated.

The effect of plant density on canopy microclimate is an important factor in disease epidemiology. Indirect effects of foliage density on disease development are related to microclimatic conditions created within the canopy (Burdon and Chilvers 1982). Overhead irrigation encourages a dense canopy which in turn creates conditions of high relative humidity, still air and long periods of leaf wetness (Rotem, 1969). Copious irrigation encourages lush canopy growth and productive yields. Yet these same dense canopies provide an ideal microclimate for the bacterial stem rot organism.

Soft rot erwinias are reported to have an epiphytic phase on symptomless potato foliage (Pérombelon, 1981) Recent work by Hirano and Upper (1983) suggested threshold populations for pathogenic epiphytes and subsequent disease development. Knowledge of such threshold populations may allow comparison for soft rot potential in distinct environments.

The objectives of this study were (1) to determine population size of water-borne inoculum of Erwinia spp. and its contribution to epiphytic populations and subsequent disease development and (2) to study the effect of plant density and microclimate on development of aerial stem rot.

CHAPTER ONE

Irrigation water as a source of inoculum of soft rot erwinias for aerial stem rot of potates.

ABSTRACT

Russet Burbank potatoes from one seedlot were planted at four locations in both 1985 and 1986. Prior to planting, seed tubers and field soil were assayed for the presence of Erwinia spp. After planting, irrigation water, leaflets and diseased stems were assayed bimonthly for soft rot erwinias. For both years, 92, 7 and 1% of the water strains were characterized as Erwinia carotovora subsp. carotovora, E. chrysanthemi, and E. c. subsp. atroseptica, respectively. Over 95% of strains recovered from all other sources were E. c. subsp. carotovora. A total of 2681 E. c. subsp. carotovora strains were tested serologically againist 20 different antisera by Ouchterlony agar double diffusion. In 1985, none of the soil or seed tuber strains were identified serologically; however, 34% of seed tuber strains and 92% of the soil strains from one location were identified in 1986. Strains were not recovered from soil at the second location in 1986. Serogroups IV, V, XVIII, and XXIX were present in irrigation water and were recovered from

diseased stems. One fourth of the strains were identified serologically and of these 15% were common to water, leaves, and diseased stems. Over two seasons there were a total of eight different serogroups that first appeared in water, secondly on leaflets and later in diseased stems. Contaminated water sources are a potential source of inoculum for plant infection.

INTRODUCTION

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 Pacific Northwest. Symptoms caused by these soft rot erwinias range from general wilting of the foliage to a light brown to inky black colored stem. E. chrysanthemi also causes similar symptoms (Pérombelon and Kelman, 1987). Symptom expression, however, largely depends on environment, the cultivar, and portion of plant affected (Pérombelon and Kelman, 1980). According to the proposed revision of terminology by Pérombelon and Kelman (1987), blackleg describes infections which originate from the seed tuber while aerial stem rot decribes infections which originate above ground. In the Pacific Northwest early season blackleg is generally caused by E. c. subsp. atroseptica, while late season blackleg and aerial symptoms are caused by E. c. subsp. carotovora (Powelson, 1980). Aerial stem rot, however, is the predominant symptom observed. Aerial symptoms occur when bacteria enter through wounds or natural openings; the infection may progress down the stem or remain localized. Aerial symptoms caused by E. c. subsp. carotovora have also been reported as bacterial toprot of potatoes in India (Shekhawat et al. 1976).

Previous studies (De Boer et al. 1978; Burr and Scroth, 1977) have focused on the seed tuber as an inoculum source of Erwinia spp. for blackleg. Soil, insects, and water have also been suggested as inoculum sources. These, however, may also be important sources for aerial infections. Cells of Erwinia spp. have been found in association with insects (Phillips and Kelman, 1982), aerosols (Graham et al., 1977), soil (Maher et al., 1986), and water (Jorge and Harrison, 1986). Insects, particularly Diptera, are capable of transporting viable cells for up to 1000 m from potato waste dumps or cull piles (Harrison et al., 1977; Phillips and Kelman, 1982; Kloepper et al., 1981). Soft rot erwinias are also dipersed in aerosols following rain impaction on diseased stems (Quinn et al., 1980; Graham et al., 1977). The bacteria have also been recovered from soil samples (De Boer et al., 1978; Maher et al., 1986; Powelson and Apple, 1984). In addition, Erwinia spp. have been recovered from rivers, oceans, aerosols, rain, and irrigation water (Jorge and Harrison, 1986). As early as 1959 researchers believed that Erwinia spp. may be present in water (Quinn, 1986). Techniques at that time, however, were not sensitive enough to detect the bacteria in water. The development of selective media (Cuppels and Kelman, 1974; Stewart, 1962) and enrichment techniques (Menely and Stanghellini 1976; Burr and Scroth, 1977) in the 1960's

and 1970's has now allowed their detection.

The importance of irrigation water as an inoculum source for aerial stem rot has not been determined. It is vital to establish a link between the presence of the pathogen in water and the initiation of disease in the field. A serotyping scheme developed by De Boer et al. (1979) allows for classifying bacterial strains into serogroups. E. c. subsp. carotovora is diverse serologically, so inoculum sources may be traced by identifying individual strains serologically . This method has been used previously in inoculum-source studies (De Boer, 1983; Powelson and Apple, 1984; Maher et al., 1986).

The objectives of this research were (1) to monitor the population size of soft rot erwinias in irrigation water (2) to examine subspecies and serogroup distribution in a surface-water source and a well-water source, on foliage, and in diseased stems, and (3) to determine if irrigation water is important as an inoculum source for aerial stem rot.

MATERIALS AND METHODS

Field plots. Field plots were established in 1985 and 1986 in two potato production areas in Oregon. Two sites were in Umatilla County near Hermiston and two were located in Crook County near Powell Butte. Plots were irrigated by center-pivot; one site at each location was irrigated from a surface-water source and one from a well-water source. Management practices were controlled by the grower.

A single seed lot of potato cv. Russet Burbank from Montana was planted the first week of April in Umatilla County and the third week of May in Crook County of both years. Seed tubers were warmed for four days at 22 C and cut into 40-55 g seed pieces. Seed pieces were spaced at 23 cm apart in rows on 68 cm centers. Plots were 7.5 m long and four or six rows wide. Plots were replicated six times at each site.

Soil assays. At planting, 30 random soil samples 15-20 cm deep were taken with a soil probe at all sites and analyzed for presence of soft rot erwinias. About 8 g soil were placed in a 40-ml vial, and pectate enrichment medium (PEM) (Meneley and Stanghellini, 1977) was added to fill the vial. The vials were sealed with a layer of parafilm. The samples were incubated for four days. The suspensions were plated directly or serially diluted

before being plated on crystal violet pectate (CVP) medium (Cuppels and Kelman, 1974). Plates were incubated at 22 C for 48 hr. Up to 10 Erwinia-like colonies per sample were purified and stored on nutrient agar (NA) at 4 C. All strains were characterized biochemically and serologically.

Seed tuber assays. Prior to planting, 10 symptomless tubers were randomly selected from each of 12 sacks of seed potatoes and tested for surface populations of Erwinia spp. About 5 g of periderm were peeled from each group of 10 tubers, placed in 10-ml sterile distilled water, and allowed to stand at room temperature for 30 min. Aliquots (0.1 ml) were plated on duplicate plates of CVP. Plates were read after 48 hr incubation at 22 C. In addition, 1 ml of the wash suspension was added to 29 ml double-strength PEM, incubated for 48 hr, and plated on duplicate plates of CVP. From each sample, up to 10 Erwinia-like colonies were selected, purified and stored on NA. All strains were biochemically and serologically characterized.

Water assays. Water used to irrigate plots was monitored for soft rot erwinias beginning at planting and thereafter twice per month. Surface-water samples were taken from a canal, and well-water samples from a spigot at the pump station. Surface-water samples were collected in four 4-liter sterile polyethylene jugs by submerging them below

the water surface. Well water samples were collected in four 4-liter jugs at pump stations adjacent to fields. Water samples were processed within 48 hrs. Each subsample (4-liter) was processed as follows: (1) Direct plating: 0.2 ml aliquots of water and serial dilutions of surface-water subsamples were spread on triplicate plates of CVP. (2) Direct enrichment: 50 ml of water from each 4-liter jug were placed in a 100-ml sterile bottle, which was then filled with double-strength PEM, and sealed with parafilm. After a 96-hr incubation at 22 C, a 0.2 ml aliquot was spread on CVP. (3) Celite filtration: Samples were processed through a Celite filter to facilitate detection of the bacteria (Hammerstrom and Ljutov, 1954). A buchner funnel with two Whatman # 1 filter papers was attached to a 2000-ml filter flask. Filtration was assisted with a water drawn vacuum. Before filtration began, a base layer of Celite was established by filtering 3-5 g of Celite suspended in 25 ml of sterile water through the filter. Each 4 liter subsample was thoroughly mixed with ca. 25 g of Celite and drawn through the filter. The Celite layer was then removed and resuspended in 100 ml of sterile water. Aliquots (0.2 ml) of the suspension were spread on triplicate plates of CVP. For surface-water subsamples, two 10-fold serial dilutions were similarly plated. (4) Celite enrichment: Celite suspensions were mixed with an equal volume of double-

strength PEM and incubated for 96 hr at 22 C. Aliquots of 0.2 ml were spread on duplicate plates of CVP. Up to five Erwinia-like colonies from each treatment were collected, purified and stored on NA slants at 4 C. By the direct plating and Celite-filtration procedures, number of colony forming units (cfu) of Erwinia spp. per ml of water were determined. All strains were characterized biochemically and serologically.

Epiphytic populations. On each sampling date, leaves were assayed for epiphytic populations of soft rot erwinias. Two (1985) or five leaves (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, weighed, 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 were also plated. Up to five Erwinia-like colonies were collected, purified and stored on NA slants for biochemical and serological characterization.

Stem isolations and disease assessment. Plants in 10 hills of a middle row of each plot were visually assessed for symptoms of aerial stem rot on each sampling date. Proportion of diseased stems in the ten hills was determined. Samples of symptomatic plants were collected

with the onset of disease. Up to five or three stems were taken from each plot in 1985 and 1986, respectively. Stem samples were stored in coolers and processed within 4 days. Stems were rinsed with tap water and then 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 sterile water. Tubes were vortexed and allowed to stand at room temperature for a minimum of 30 minutes. Tubes were then gentley vortexed again, and a loopful of the suspension was streaked on CVP. Purified Erwinia-like colonies were stored on NA slants. Strains were tested biochemically and typed serologically.

Biochemical and serological characterization. Soft rot erwinias were distinguished from one another based on biochemical properties. E. c. subsp. atroseptica differs from E. c. subsp. carotovora and E. chrysanthemi in its ability to produce acid from ã-methyl glucoside and absence of growth at 36 C (Graham, 1972). E. chrysanthemi is separated from the E. c. subsp. carotovora by phosphatase production. (Graham, 1972). All strains identified biochemically as E. c. subsp. carotovora were tested serologically using the Ouchterlony double diffusion technique (Ouchterlony, 1958). All E. c. subsp. carotovora strains were tested with antisera produced against 20 strains. Immunodiffusion tests were conducted

as previously described (Powelson and Apple, 1984).

RESULTS

Water populations. Soft rot erwinias were recovered from both surface and well water sources in 1985 and 1986 (Tables 1 and 2). Populations were consistently higher in surface water than in well water at both locations. In Umatilla County mean populations in surface water samples determined by direct counts in 1985 and 1986 were 14.3 and 3.0 cfu/ml, respectively (Table 1). In well-water samples, Erwinia spp. were detected with enrichment techniques on the first and final sampling dates in 1985 and on four sampling dates 1986. In 1986, populations were highest (0.2 cfu/ml) in mid-July. Populations of soft rot erwinias were higher and were detected more frequently in Crook County than in the Umatilla County (Table 2). In 1985, the highest surface water population (574.6 cfu/ml) was detected in late August. Populations were lower in 1986 and ranged from 0.1 to 4.6 cfu/ml. Soft rot erwinias were detected in well water samples primarily using enrichment techniques.

E. c. subsp. carotovora was the predominant soft rot erwinia recovered from water at both locations during 1985 and 1986 (Tables 3 and 4). In Umatilla County, 4% of the strains recovered from surface water samples for both years were E. chrysanthemi (Table 3). In Crook County, surface-water samples yielded E. c. subsp. carotovora and

TABLE 1. Mean populations of soft rot erwinias in surface- and well-water in Umatilla County, Oregon

Year and sampling date	Number of colony forming units/ml of water							
	Surface water				Well water			
	Direct[a]	Enriched[b]	Celite filtered[c]	Celite flitered enriched[d]	Direct	Enriched	Celite filtered	Celite filtered enriched
1985								
April 9	0.0	-[e]	0.1	+[f]	0.0	-	0.0	+
June 13	0.0	+	0.0	+	0.0	-	0.0	-
June 25	0.0	+	0.6	+	0.0	-	0.0	-
July 10	4.8	+	29.1	+	0.0	-	0.0	-
July 25	1.2	+	2.5	+	0.0	-	0.0	-
Aug 11	107.9	+	0.8	+	0.0	-	0.0	-
Aug 29	0.4	+	1.8	+	0.0	-	0.0	-
Sept 26	0.0	+	0.0	+	0.0	-	0.0	+
Mean	14.3		4.4		0.0		0.0	
1986								
April 18	0.0	+	0.0	+	0.0	-	0.0	-
June 13	0.0	-	0.0	+	0.0	-	0.0	-
June 30	2.5	+	1.8	+	0.0	+	0.0	-
July 16	0.4	+	0.6	+	0.0	+	0.2	+
July 30	0.0	+	0.0	+	0.0	-	0.0	+
Aug 12	0.0	+	0.0	+	0.0	-	0.0	+
Sept 4	17.9	+	3.7	+	0.0	-	0.0	-
Mean	3.0		0.9		0.0		0.0	

a Direct plating of nonfiltered water samples
b Nonfiltered water samples enriched
c Filter concentrated samples
d Filter concentrated samples enriched
e Soft rot erwinias not detected by enrichment procedures
f Soft rot erwinias detected by enrichment procedures

TABLE 2. Mean populations of soft rot erwinias in surface- and well-water in Crook County, Oregon

Year and sampling date	Number of colony forming units/ml of water							
	Surface water				Well water			
	Direct[a]	Enriched[b]	Celite filtered[c]	Celite filtered enriched[d]	Direct	Enriched	Celite filtered	Celite filtered enriched
1985								
May 23	0.0	-[e]	0.0	+[f]	0.0	-	0.0	-
June 28	0.0	+	0.0	+	0.0	-	0.0	+
July 15	18.7	+	0.5	+	0.0	-	0.0	-
July 30	0.0	+	97.5	+	0.0	+	0.0	+
Aug 14	0.0	+	0.1	+	0.0	+	0.0	+
Aug 26	574.6	+	232.0	+	0.0	-	0.0	-
Sept 10	4.6	+	1.7	+	0.8	+	0.1	+
Sept 25	0.4	+	0.0	+	0.0	+	0.0	+
Mean	74.8		41.5		0.1		0.0	
1986								
May 28	0.0	-	0.0	-	0.0	-	0.0	+
June 26	0.4	+	0.8	+	0.0	-	0.0	-
July 9	0.0	+	0.1	+	0.0	-	0.0	+
July 23	0.4	+	0.0	+	0.0	+	0.6	+
Aug 5	4.6	+	3.3	+	0.0	+	0.0	+
Aug 19	2.5	+	0.7	+	0.0	-	0.0	+
Aug 26	0.0	+	2.2	+	0.0	-	0.0	+
Sept 9	4.6	+	1.9	+	0.0	+	0.0	+
Mean	1.6		1.1		0.0		0.1	

a Direct plating of nonfiltered water samples
b Nonfiltered water samples enriched
c Filter concentrated samples
d Filter concentrated samples enriched
e Soft rot erwinias not detected by enrichment procedures
f Soft rot erwinias detected by enrichment procedures

TABLE 3. Relative percentages of *Erwinia carotovora* subsp. *carotovora*, *E. c.* subsp. *atroseptica* and *E. chrysanthemi* recovered from surface- and well-water sources in Umatilla County, Oregon in 1985 and 1986.

	Percent of strains					
	Surface water			Well water		
Year and sampling date	Ecc[a]	Eca[b]	Ech[c]	Ecc	Eca	Ech
1985						
April 9	100	0	0	100	0	0
June 13	89	0	11	-[d]	-	-
June 25	100	0	0	-	-	-
July 10	100	0	0	-	-	-
July 25	100	0	0	-	-	-
Aug 11	92	0	0	-	-	-
Aug 29	58	0	8	-	-	-
Sept 29	100	0	42	-	-	-
1986						
April 18	100	0	0	-	-	-
June 13	100	0	0	-	-	-
June 30	100	0	0	100	0	0
July 16	100	0	0	100	0	0
July 30	100	0	0	100	0	0
Aug 12	100	0	0	100	0	0
Sept 4	95	0	5	-	-	-

a *Erwinia carotovora* subsp. *carotovora*
b *E. c.* subsp. *atroseptica*
c *E. chrysanthemi*
d *Erwinia* spp. not detected

TABLE 4. Relative percentages of Erwinia carotovora subsp. carotovora, E. c. subsp. atroseptica and E. chrysanthemi recovered from surface- and well-water sources in Crook County, Oregon in 1985 and 1986.

	Percent of strains					
	Surface water			Well water		
Year and sampling date	Ecc[a]	Eca[b]	Ech[c]	Ecc	Eca	Ech
1985						
May 23	100	0	0	-[d]	-	-
June 28	100	0	0	100	0	0
July 15	89	0	11	-	-	-
July 30	66	0	34	0	0	0
Aug 14	50	0	50	100	0	0
Aug 26	12	0	88	-	-	-
Sept 10	90	0	10	100	0	0
Sept 25	96	0	4	100	0	0
1986						
May 29	-	-	-	100	0	0
June 26	94	0	4	-	-	-
July 9	100	0	0	100	0	0
July 23	100	0	0	100	0	0
Aug 5	100	0	0	100	0	0
Aug 19	100	0	0	67	33	0
Aug 26	100	0	0	100	0	0
Sept 9	100	0	0	100	0	0

a Erwinia carotovora subsp. carotovora
b E. c. subsp. atroseptica
c E. chrysanthemi
d Erwinia spp. not detected

E. chrysanthemi in both years (Table 4). E. c. subsp. carotovora was prevalent in early and late season. E. chrysanthemi was recovered primarily in midseason and represented 28% of the strains in 1985. In contrast, six of the eight surface-water samples in 1986 yielded only E. c. subsp. carotovora while E. chrysanthemi was recovered on one date and represented less than 1% of the strains. In well water samples, E. c. subsp. carotovora was the predominant soft rot erwinia recovered in both years. E. c. subsp. atroseptica was recovered from one well-water sample in 1986.

Seed tuber and soil populations. Surface populations of soft rot erwinias on seed tubers ranged from 0 to 8 x 10^3 cfu/g of periderm in 1985 and 37% of the tubers were contaminated with these bacteria. In 1986, 35% of tuber samples yielded Erwinia spp., and populations ranged from 0 to 3 x 10^3 cfu/ml.

E. c. subsp. carotovora was detected in soil samples by enrichment in the surface-water irrigated plots in Umatilla County in 1986 and in both Crook County plots in 1985.

Disease incidence. The proportion of stems with aerial stem rot symptoms at the final sampling date was consistently higher in fields irrigated with well water than those irrigated with surface water. In Umatilla County, disease incidence on the final sampling date was

22 and 44% in surface water irrigated plots compared to 28 and 51% in well water irrigated plots in 1985 and 1986, respectively. In Crook County, final proportion of disease was 0.34 and 0.05 in the surface-water irrigated plots in 1985 and 1986, respectively. In the well-water irrigated plots final disease incidence was 46 and 35% in 1985 and 1986, respectively.

Seed tuber and soil strains. None of the seed tuber strains were identified serologically in 1985 whereas 34% of the strains were identified as serogroups IV and V in 1986. In 1986, soil strains from Umatilla County surface water irrigated plots were the only ones identified serologically; 92% of identified strains were serogroups III and IV.

Water strains. A total of 1095 E. c. subsp. carotovora strains were recovered from water sources. Of those, 28% were identified serologically (Table 5). In Umatilla County, 32 and 45% of surface water strains were identified serologically in 1985 and 1986, respectively. None of the strains recovered from well water in Umatilla County in 1985 were identified whereas in 1986 12% of the 49 well water strains were identified serologically. In Crook County 23 and 41% of the surface water strains were identified serologically in 1985 and 1986, and 27% and 38% of strains recovered from well water were identified in 1985 and 1986, respectively.

TABLE 5. Serogroups represented among Erwinia carotovora subsp. carotovora strains recovered from surface- and well-water sources in Umatilla and Crook Counties, Oregon

	Number of strains							
	Umatilla County				Crook County			
	1985		1986		1985		1986	
Serogroups[a]	Surface	Well	Surface	Well	Surface	Well	Surface	Well
III	2	---[b]	12	2	---	---	18	1
IV	1	---	1	---	---	---	---	---
V	12	---	14	---	---	---	1	---
VII	2	---	---	---	---	---	---	---
XI	1	---	6	---	---	---	4	---
XIV	2	---	12	7	---	---	---	---
XVIII	18	---	17	2	5	16	---	---
XXVII	---	---	---	---	1	---	---	---
XXVIII	9	---	---	---	---	---	---	---
XXIX	22	---	12	2	47	2	84	---
XXXI	---	---	1	---	---	---	---	1
XXXII	---	---	---	---	---	---	1	---
XXXIII	---	---	3	---	1	---	---	---
XXXV	1	---	1	---	---	3	2	---
XXXVI	2	---	---	---	---	---	---	---
XXXVII	---	---	---	---	---	1	---	3
XXXIX	---	---	---	---	---	---	6	7
XL	---	---	---	---	1	---	---	---
No. of strains tested	224	10	176	49	236	84	284	32

a Serogroups based on classification by De Boer et al. 1979.
b Not applicable, as serogroup not recovered from water samples

A majority of Umatilla County surface water strains were classified into three serogroups. In 1985, 72% of the serologically identified strains were serogroups V, XVIII or XXIX. In 1986, these same three serogroups represented 54% of the identified strains. Additionally, in 1986 serogroup III accounted for 15% of identified strains. In 1986, serogroups III, XIV, XVIII and XXIX represented 100% of the identified strains from well water.

In Crook County, 78 and 75% of the serologically identified surface water strains were serogroup XXIX in 1985 and 1986, respectively (Table 5). The remaining identified strains were spread among four and six additional serogroups in 1985 and 1986. In well water samples in 1985, 70% of the identified strains were XVIII. In 1986, serogroup XXXIX was the most frequently recovered serogroup and represented 50% of the serologically identified strains.

Epiphytic strains. A total of 907 epiphytic strains were tested serologically. A higher percentage of epiphytic strains were serologically identified in plots irrigated with surface water (29%) than in plots irrigated with well water (23%) (Table 6). Additionally, strains recovered from foliage in surface-water irrigated plots were more diverse serologically. In Umatilla County, 14 different serogroups were identified in surface-water irrigated

TABLE 6. Serogroups represented among *Erwinia carotovora* subsp. *carotovora* strains recovered from potato leaflets in fields irrigated from surface- and well-water sources in Umatilla and Crook Counties, Oregon

	Number of strains							
	Umatilla County				Crook County			
	1985		1986		1985		1986	
Serogroups[a]	Surface	Well	Surface	Well	Surface	Well	Surface	Well
III	---[b]	---	---	---	---	---	11	1
IV	1	12	5	4	---	---	---	---
V	13	---	10	3	---	---	4	---
VII	---	---	---	1	---	---	---	---
XIV	4	2	12	7	---	---	---	---
XV	---	---	10	---	---	---	---	---
XVIII	2	1	17	---	1	---	---	---
XXVII	7	---	3	---	---	---	1	---
XXVIII	---	---	---	---	---	---	1	---
XXIX	2	8	2	---	19	1	3	---
XXXI	---	---	15	2	---	---	---	1
XXXII	---	---	1	---	---	---	---	---
XXXV	---	---	1	3	---	---	---	---
XXXVI	---	---	8	---	---	---	1	---
XXXVII	8	3	9	3	---	---	---	3
XXXVIII	---	---	1	---	---	---	---	---
XXXIX	---	---	12	---	---	---	4	---
No. of strains tested	107	117	299	92	120	26	114	32

a Serogroups based on classification by De Boer et al. 1979.
b Not applicable, as serogroup not recovered from foliage

plots whereas nine different serogroups were found as epiphytes in well-water irrigated plots. In Crook County eight and four serogroups were recovered from foliage in surface- and well-water irrigated plots, respectively.

In Umatilla County surface-water irrigated plots, the same serogroups recovered from foliage in 1985 were also identified in 1986 (Table 6). In 1985, 35 and 27% of identified strains were serogroups V and XXXVII, respectively. In 1986, 10% of identified strains belonged to serogroups XIV, XVIII, XXXI and XXXIX. In the well-water irrigated plots serogroups IV, XIV and XXXVII were common in both years. In 1985 serogroup IV accounted for 46% of identified strains whereas serogroup XIV was the most frequently identified strain in 1986 (Table 6).

In Crook County in 1985, serogroups XVIII and XXIX were recovered from foliage in surface-water irrigated plots; however, 95% were serogroup XXIX (Table 6). In 1986, the most frequently isolated serogroup was serogroup III which represented 44% of the serologically identified strains. In the well-water irrigated field in 1985, only serogroup XXIX was identified. In contrast serogroups III, XXXI, and XXXVII were recovered in 1986.

Diseased stem strains. A total of 614 strains recovered from diseased stems were tested serologically and of these 20% were identified. Strains recovered from diseased stems in surface- and well-water irrigated plots in

Umatilla County were represented by 11 and 6 serogroups, respectively (Table 7). In Crook County of the 11 serogroups recovered from diseased stems in surface-water irrigated plot 40 and 63% of the identified strains in 1985 and 1986, respectively were serogroups XVIII and XXXIX. In the well-water irrigated plot, 21% of the strains from diseased stems were identified serologically. A majority of strains were serogroup XXVII and XXXVII in 1985 and 1986, respectively.

In Crook County, serogroups XXVIII, XXXVI and XXXVII were recovered from diseased stems in the surface-water irrigated plot in both years. Identified strains were divided equally among six and three additional serogroups in 1985 and 1986, respectively.

Several serogroups were common to water and diseased stems (Table 8). Similarities ranged from 0% in the 1985 and 1986 well-water irrigated plots to 18 and 5% in the 1985 and 1986 surface-water irrigated plots, respectively, in Umatilla County. In Crook County, in 1985 1 and 5% of the serologically identified stem strains were common to water in the surface- and well-water irrigated plots, respectively. In 1986 similarities were 10 and 15% in the surface- and well-water irrigated plots, respectively.

Progression of inoculum. Some serogroups were isolated sequentially over the season from water, leaflets, and diseased stems. Five serogroups were common to water and

TABLE 7. Serogroups represented among Erwinia carotovora subsp. 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			
	1985		1986		1985		1986	
Serogroups[a]	Surface	Well	Surface	Well	Surface	Well	Surface	Well
III	---[b]	---	---	---	---	1	---	---
IV	2	---	---	1	---	1	---	---
V	2	---	2	---	---	6	1	---
VII	2	---	1	---	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	---	---	1	2	---
XXXI	---	---	---	---	1	9	---	---
XXXV	---	---	---	2	1	1	---	---
XXXVI	---	---	1	---	5	---	2	1
XXXVII	---	2	---	8	1	1	2	1
XXXIX	---	---	12	---	---	---	2	2
No. of strains tested	81	87	58	87	122	83	50	46

a Serogroups based on classification by De Boer et al. 1979.
b Not applicable, as serogroup not recovered from diseased stems

TABLE 8. Percentages of *Erwinia carotovora* subsp. *carotovora* strains isolated from potato plants with aerial stem rot symptoms that were serologically characterized the same as water serogroups, or untyped strains

Year and location	Water source	Percent	
		Water strains	Untyped strains
1985			
Umatilla	Surface	18	75
	Well	0	87
Crook	Surface	1	67
	Well	5	83
1986			
Umatilla	Surface	5	67
	Well	0	83
Crook	Surface	10	78
	Well	15	74

stems with three of these also recovered from leaflets in the surface water irrigated plot in Umatilla County in 1985. All five serogroups were found in the water prior to being isolated from diseased stems. Serogroups V and XVIII were found at each sampling date in the water, whereas IV was recovered from water only once. Serogroups VII and XI were found in water and later in diseased stems but were never recovered from leaflets. In 1986, serogroups XXIX and V were the only two serogroups present in water, on leaves and in diseased stems. Serogroup V was also recovered from tubers prior to planting in 1986, however, all isolations were made from plants with aerial symptoms. Serogroup XXVIII was the only identified surface-water strain found in diseased stems in Crook County in 1985. In the well-water irrigated plot serogroups XVIII, XXIX and XXXVII were recovered from water prior to being recovered from diseased stems. In 1986, serogroup XXXIX was recovered from water throughout the season as well as from stems at the end of the season in both surface- and well-water irrigated plots.

DISCUSSION

Water can be a critical factor in development of aerial stem rot and is a potential inoculum source for plant infection. E. c. subsp. carotovora was the predominant pathogen in irrigation water, on foliage and in diseased stems. One fourth of the strains from all sources in both years were identified serologically, and of those 15% were common to water, leaves and diseased stems. At surface-water irrigated locations, 35% of identified strains from diseased stems were common serologically to the strains recovered from water. At locations where plots were irrigated with well-water, 20% of serologically identified strains isolated from diseased stems were similar to serogroups recovered from water. Populations of E. c. subsp. carotovora were consistently higher and a larger percentage of stem strains were serologically similar to water strains in the surface-water irrigated plots. Disease incidence, however, was consistently higher in well-water irrigated plots than in surface-water irrigated plots. In Umatilla County disease incidence was 15% higher in well-water than in surface-water irrigated plots in 1985. A similar trend was observed in 1986. In Crook County the amount of disease was 21% higher in well than in surface-water irrigated plots. Water sources may contribute some inoculum,

however, other factors are vital to disease development.

The populations of soft rot erwinias in surface water peaked from mid-July to mid-August which coincided with lush potato-canopy growth, and a conducive microclimate for epiphytic growth and survival of the bacteria (Chapter 2). These high populations preceded the development of disease symptoms by about two weeks (Chapter 2).

Populations of soft rot erwinias in water were higher and the bacteria were more consistently recovered in Crook County than in Umatilla County. Surface-water populations were higher than well-water populations, although well-water populations were higher than previously reported (McCarter-Zorner et al., 1984). McCarter-Zorner et al. (1984) have shown well-water to be relatively free of Erwinia spp.. In Crook County, soft rot erwinias were detected more frequently in well-water than in Umatilla County well-water. Well depth in Crook County was 35 m and in Umatilla County well-water was from a comingling of wells averaging 300 m in depth.

Determinations of bacterial populations from water samples indicated a relative abundance of Erwinia spp. which is indicative of its ubiquitous nature. Generally, the highest populations occurred in the warmest months. In Colorado, Erwinia spp. populations in flowing surface water reached 144 cfu/ml at one site in July (Jorge and Harrison, 1986). Mean populations over 18 months ranged

from 24.13 cfu/ml at on site to 5.57 cfu/ml at another site. In southern Scotland streams, populations in 1981 peaked in July and reached 192 cfu/ml. Detection techniques are limited by the tremendous volume of the sampling source. Problems of detection may explain why surface water populations were so much higher in 1985 than in 1986; however, Erwinia spp. were still detected throughout both seasons.

Surface waters used for irrigation in Oregon are fed by major river systems. In Umatilla County, water originates from the Columbia River which is fed by the Snake River. Large acreages of agricultural operations occur along these two rivers. In Crook County, irrigation canals are fed by the Deschutes River which originates in the Cascades mountains. Jorge and Harrison (1986) in Colorado found Erwinia spp. in streams year-round and suggested two explanations: a periodic (or constant) introduction of bacterial cells from external sources such as precipitation or agricultural operations, or possibly sites where Erwinia spp. are resident and cells are periodically released.

The predominance of E. c. subsp. carotovora in Oregon water sources is not surprising. Previous studies indicate that E. c. subsp. carotovora to be the predominant soft rot erwinia in water (McCarter-Zorner, 1984; Jorge and Harrison, 1986; Franc et al., 1986).

Because E. c. subsp. carotovora predominates in irrigation sources (Jorge and Harrison, 1986), and is also the primary soft rot erwinia involved in the recontamimation of seed stocks (Pérombelon, 1980), water may be an important inoculum source for aerial stem rot. In this study 80% of the bacterial soft rot symptoms were aerial infections and 99% of these were caused by E. c. subsp. carotovora. E. c. subsp. carotovora was also the predominant soft rot erwinia associated with potato foliage and diseased stems. E. chrysanthemi was also recovered periodically from water samples, from potato foliage and from diseased stems. E. c. subsp. atroseptica was only detected in one water sample and never detected on foliage or in stems with aerial symptoms.

In addition to serving as an inoculum source, contaminated water must be considered as a potential source for soil infestation (Powelson and Apple, 1984). Populations of soft rot erwinias in soil are extremely low or non-detectable outside the growing season (De Boer, 1979). Soilborne populations of soft rot erwinias may be below detection limits during the winter months or they may not survive. Detection of Erwinia spp. in soil prior to planting was infrequent in this study. E. c. subsp. carotovora, however, has been recovered from soil samples throughout the growing season in Oregon and Wisconsin (Powelson and Apple, 1986; Maher et al., 1986). Soil may

become contaminated with soft rot erwinias via irrigation water or alternatively the application of water may create an environment favorable for reproduction of resident populations of this bacterium. Soil may also be a source of inoculum for aerial infections. By mid to late season the foliage comes in contact with the soil where soil-borne inoculum may infect aerial portions of the plant.

In this study there was a progression over the season of similar serogroups in water, on foliage and in diseased stems. Cells of the soft rot erwinias can be deposited on the foliage and to the soil surface by irrigation. If the bacteria remain on the foliage and increase in numbers they may infect the plant. In previous studies (De Boer, 1983; Maher et al., 1986; Powelson and Apple, 1984) both seedborne and soilborne inoculum have been shown to cause plant infection under field conditions, but the majority of disease was due to unknown inoculum sources. De Boer (1983) found seed tubers to be predominantly contaminated with serogroup III whereas epiphytic strains early in the season were comprised of serogroups XVIII and XXVII. Serogroup III was isolated from foliage late in the season. De Boer suggested that there were two E. c. subsp. carotovora populations; an early season population originating from external sources and a late season population originating from the seed tuber. Late season epiphytic strains may also originate from sources other

than the tuber. We have shown that serogroups of E. c. subsp. carotovora present as epiphytes are the same serogroups as those in irrigation water.

Seventeen different serogroups were identified from a variety of sources. In pathogenicity tests all of these produced soft rot symptoms in the aerial portions of potato plants under greenhouse conditions (Cappaert and Powelson, 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 (Stanghellini et al., 1977). Serogroup XXIX was the most frequently isolated serogroup from any source in this study. It has also been isolated from soils, foliage, diseased stems, and water (Maher et al., 1986; Franc et al., 1986; DeBoer 1983) and is clearly well adapted to survive in many environments. Other serogroups such as XVIII, which was found as the most predominant early-season epiphyte in British Columbia (De Boer, 1983), was found only on one occasion as an epiphyte in Crook County, though it was recovered from the water source. Serogroups XXXIX and XXIX were frequently recovered from leaflets in Crook County and were also found in water sources. They may be better adapted to this environment.

Water may serve as an inoculum source for plant infection. The ample populations of Erwinia spp. in the

environment suggest controlling inoculum sources may not be feasible. Additional studies (Chapter 2) have indicated elements other than size of initial inoculum source may be more important to the development of the Erwinia-caused diseases. Management factors, such as frequency and duration of irrigation, may play a more important role. Further work in defining these factors is needed to manage aerial stem rot effectively.

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CHAPTER TWO

Canopy density and microclimate effects on the development of aerial stem rot of potates.

ABSTRACT

Field plots were established at two different sites at each of two locations in Oregon in 1985 and 1986. Russet Burbank potatoes were planted at two within-row and two between-row plant spacings. Plant densities were 13, 26, and 52 x 10^3 plants per hectare. Leaf area index, epiphytic populations of soft rot erwinias, and disease incidence were determined bimonthly beginning at row closure. Leaf wetness was monitored continuously throughout both growing seasons.

There were no significant differences ($p=0.05$) among treatments in epiphytic populations although some seasonal trends were noted. Epiphytes were non-detectable early in the season, tended to have a midseason peak, and declined at the end of the season. In 1986 for all plant densities, largest leaf area index values and longest periods of leaf wetness preceded the highest incidence of disease by two weeks. Onset of aerial stem rot symptoms occurred earlier and final proportion of disease was greater in dense compared to sparse plantings in both

years. Area under the disease progress curve (AUDPC) and area under the leaf area index curve (AULAIC) were significantly greater ($p=0.05$) in the dense compared to the sparse plantings. Mean AULAIC values at one location were 357.6 and 137.9 in plots with the most dense and least dense plant populations, and mean AUDPC values were 18.5 and 4.7, respectively. At the second location, mean AULAIC values were 216.1 and 100.6 for the most dense and least dense plant spacings, and corresponding AUDPC values were 6.45 and 0.79, respectively. AUDPC and AULAIC were positively correlated ($p=0.05$) at three of the four sites.

INTRODUCTION

In the Pacific Northwest potatoes are commonly grown under center-pivot irrigation. Overhead irrigation encourages lush plant growth which creates conditions of high relative humidity, still air, and long periods of leaf wetness in the canopy (Rotem, 1969). Aerial stem rot and blackleg can be severe in fields subjected to this type of irrigation (Powelson, 1980).

Plant density is an important factor in disease epidemiology. It can have both direct and indirect effects on disease development (Burdon and Chilvers 1982). Direct effects involve physical proximity of inoculum to the host in space or time. Host density, which affects the microclimate within the plant canopy, largely determines the rate of evaporation of water from within the canopy (Rotem, 1969). The impact of alteration in host density on changes in the microclimate is regarded as an indirect effect.

The soft rot erwinias are present in water used to irrigate potatoes, (Chapter 1; Jorge and Harrison, 1986) on seed tubers (Burr and Scroth, 1977) and in the soil (De Boer et. al 1978). Recent reports indicate that these bacteria are residents on potato foliage (De Boer, 1983; Pérombelon, 1981) and that there may be threshold populations for pathogenic epiphytes and subsequent

disease development (Hirano and Upper, 1983). An earlier hypothesis by Leben (1965) suggests that phytopathogenic bacteria may have an epiphytic phase on symptomless plants and disease may ensue when conditions are suitable.

Water becomes the critical factor in balancing potato production and disease. Symptoms of aerial soft rot and blackleg may increase as the microclimate within the potato canopy and in the soil surrounding the seed piece becomes conducive for bacterial survival and growth. Irrigation encourages lush canopy growth and productive yields; yet dense canopies and moist soils may provide an ideal microclimate for reproduction of the bacterial soft rot organism and disease development. Soft rot has been reported to progress rapidly under somewhat anerobic conditions due to a decrease of host plant resistance to the bacteria. This effect could be important in fields irrigated by overhead sprinklers.

The objectives of the study were to determine if changes in plant density affect the size of epiphytic populations of the soft rot erwinias and development of aerial stem rot. Our approach was to alter plant density to achieve differences in the canopy density per unit area and in the microclimate within the canopy.

MATERIALS AND METHODS

Field plots. Field plots of potato cv. 'Russet Burbank' were established in four center-pivot irrigated fields in Oregon in 1985 and 1986. Two sites were in Umatilla County (west and east) and two sites were located in Crook County (west and east). Experiments were planted the first week of April in Umatilla County and the third week of May in Crook County of both years. Seed tubers from a single seed lot grown and certified in Montana the previous year were warmed for 4 days at 22 C and cut in seed pieces weighing 40-55 g. After cutting, seed pieces were placed at 13 C for 6 days for suberization. Treatments consisted of within-row spacings of 23 or 46 cm and spacing between rows of 86 or 173 cm. Plant densities ranged from 13 to 52 x 10^3 plants per hectare. Two of the four treatments contained 26 x 10^3 plants per hectare in two different spacing arrangements. Each treatment consisted of four or six rows that were 7.5 m long. Treatments were arranged in a randomized block design and replicated six times. Cultural practices for all sites were similar to those used commercially in the respective production areas.

Disease assessment. Disease readings were taken twice a month beginning at plant emergence. Plants in 10 hills of

a middle row of each plot were visually evaluated for presence of blackleg and aerial stem rot symptoms. Proportion of plants with blackleg of aerial stem rot symptoms for 10 hills was determined. Effects of plant density and plant spacing on incidence of aerial stem rot were evaluated by three methods. Treatment comparisons were based on date of disease onset, final proportion disease, and area under the disease progress curve (AUDPC). The latter was calculated with the methods of Shanner and Finney (1977).

Epiphytic populations. Potato leaves were sampled beginning at row closure and every two weeks thereafter. Two (1985) and five (1986) leaves were sampled from a middle row of each plot. Early in the season the fourth leaf from the base of the plant was collected and as the season progressed and the lower leaves had senesced, the first intact leaf from the base of the plant was sampled. Leaves were placed in a plastic bag, stored in a cooler and processed within 24 hr. The terminal leaflet was removed, weighed, washed in 50 ml of 0.13 M phosphate buffer (pH 7.2) on a rotary shaker for 30 min. at 125 rpm. Aliquots (0.01 ml) were transferred to duplicate plates of crystal violet pectate (CVP) medium (Cuppels and Kelman, 1974). With leaflets that appeared chlorotic or decayed, 10-fold serial dilutions were similarly plated. Populations of soft rot erwinias were based on the number

of colony forming units (cfu) per gram fresh weight of leaflet tissue. Bacterial populations are expressed as log-transformed values (eg;$\log_{10}$ (x+1)).

Canopy measurement. In 1986, an individual plant was taken from the outside row of each plot at three of the four sites. At the fourth site (Crook County west) all plants from one hill in each plot were collected. Leaves were stripped from the stem, placed in a plastic bag, and stored in coolers until processed. Within 24-hrs, leaf area was measured with a LiCor LI-3000 area meter (Lambda Instruments Corp., P.O. Box 4423, 4423 Superior St., Linclon, NB 68504). Leaf Area Index (LAI) was determined as [(cm^2 of leaf tissue)(average number of stems/hill)(number of hills/plot area)] for each of the four plant spacings. Area under the leaf area index curve (AULAIC) was calculated following the method of Shanner and Finney (1977) for AUDPC.

Environmental data. Leaf wetness was measured at one site at each location with a Campbell Scientific 21X micrologger (Campbell Scientific Inc., Logan UT). Leaf wetness sensors were attached to rings on ringstands, (one per treatment in 1985 and two per treatment in 1986) and placed at the approximate spherical center of the canopy. At half hour intervals leaf wetness values were recorded as a percentage of the interval that the sensor was wet.

Data analyses. Treatment differences in onset of disease,

final proportion of disease, AUDPC and AULAIC were assessed by analysis of variance, and means were separated by Fisher's protected least significant difference (FPLSD). Correlation coefficients were determined for disease and plant spacing by fitting AUDPC and AULAIC to a simple linear regression model.

RESULTS

Disease incidence. Onset of disease symptoms was earlier and final proportion of disease was higher in the most dense plantings compared to the least dense plantings at all sites in both years (Fig. 1a-d and Fig. 2a-d). In 1985, disease onset occurred 6-25 days earlier in the most dense compared to the most sparse plant populations. In the Umatilla County east site, onset of symptoms occurred 18 days earlier in treatments with 86-cm between-row spacing than in treatments with 173-cm between-row spacing (Fig. 1b). In the Umatilla County west site and the Crook County east site, final proportion of disease was at least 10% higher in plots with 86-cm between-row spacings than with the 173-cm between-row spacings (Figs. 1a and 1d). At Crook County west site the highest disease incidence was in the 86-cm between-row treatments on the first two sampling dates but by the final sampling date there were little differences among treatments (Fig 1c.).

At all sites in 1986 onset of symptoms occurred 7 to 27 days earlier in the dense plantings compared to the sparse plantings (Fig. 2a-d). Final proportion of disease averaged 0.43 in treatments with 86-cm between-rows and 0.31 in treatments with 173-cm between-rows in the Umatilla County west site (Fig. 2a). In the

Fig. 1. Disease progress curves for aerial stem rot of potatoes at four plant spacings for four sites in Oregon in 1985. Treatments are within and between row spacings, where □ =23x86 cm, + =46x86 cm, ◊ =23x173 cm, △=46x173 cm. Each point is the mean of six replications. A) Umatilla County west; B) Umatilla County east; C) Crook County west; D) Crook County east.

Figure 1

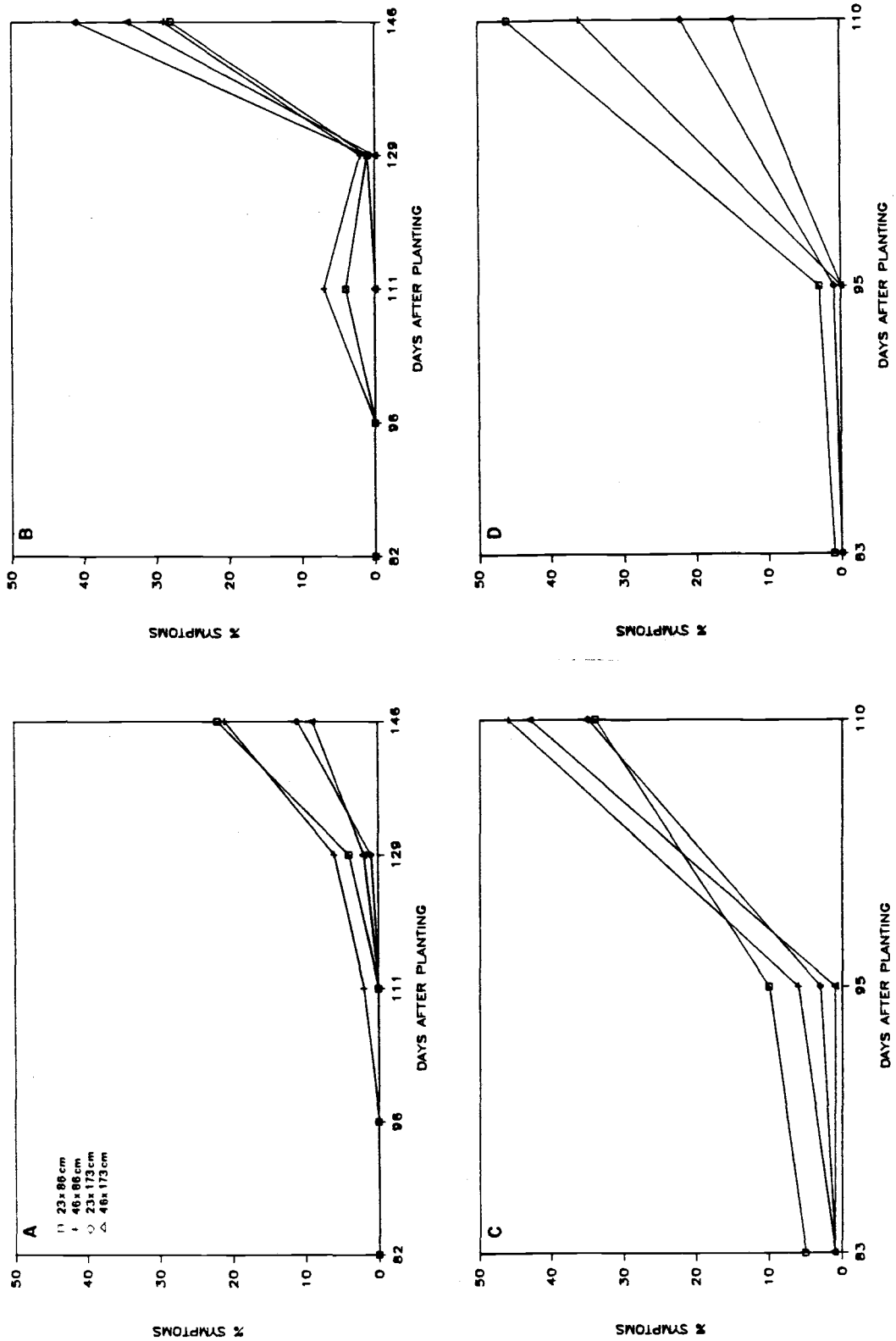
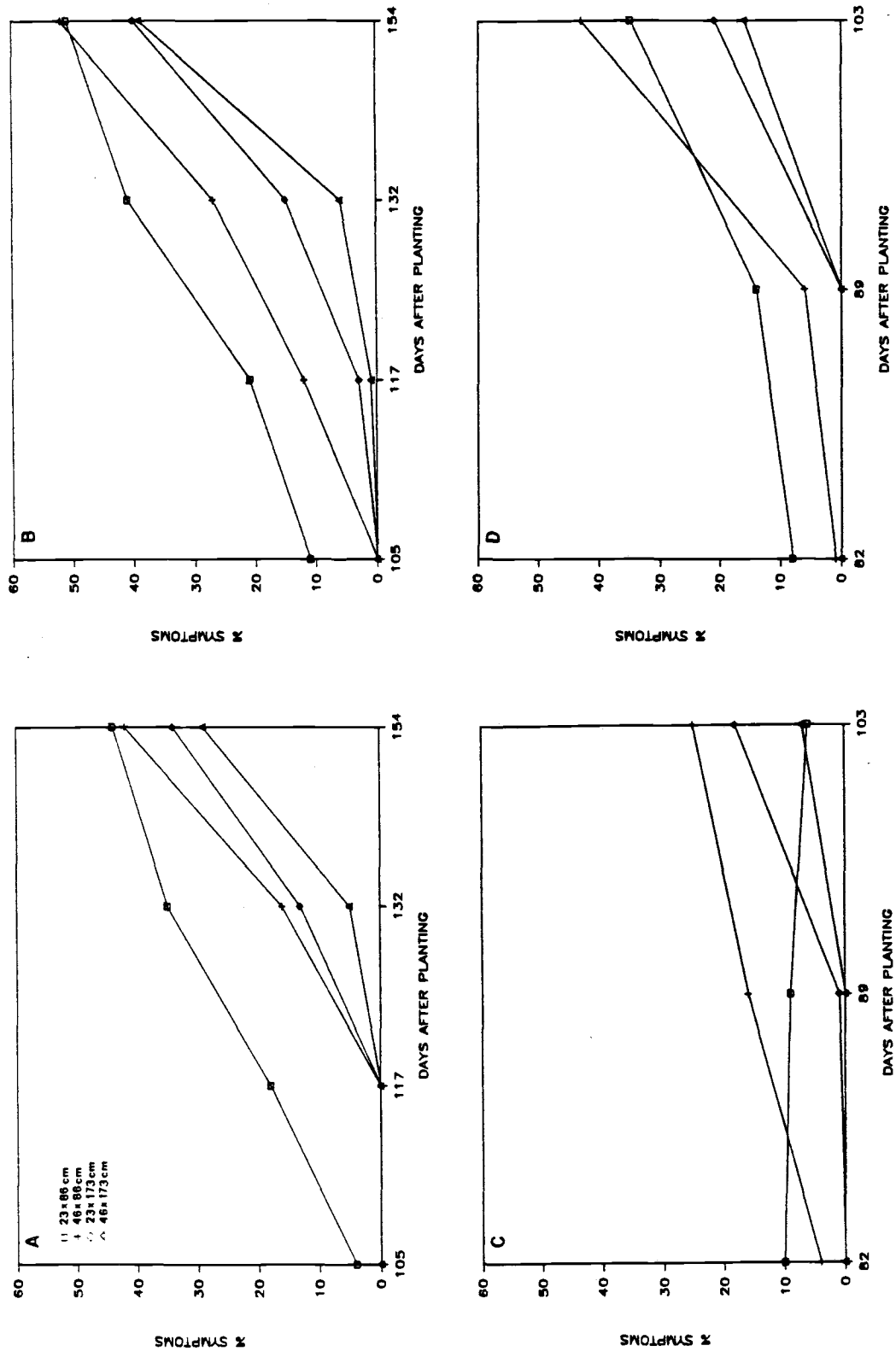

A
B
C
D
23x86cm
46x86cm
23x173cm
46x173cm
% SYMPTOMS
DAYS AFTER PLANTING
0
10
20
30
40
50
82
96
111
129
146
83
95
110

Fig. 2. Disease progress curves for aerial stem rot of potatoes at four plant spacings for four sites in Oregon in 1986. Treatments are within and between row spacings, where □ =23x86 cm, + =46x86 cm, ◊ =23x173 cm, △=46x173 cm. Each point is the mean of six replications. A) Umatilla County west; B) Umatilla County east; C) Crook County west; D) Crook County east.

Figure 2


A
B
C
D
% SYMPTOMS
DAYS AFTER PLANTING
0
10
20
30
40
50
60
105
117
132
154
82
89
103

Umatilla County east site the final proportion of disease was 0.52 and 0.39 in the 86 cm and 173 cm between-row treatments, respectively (Fig. 2b). Incidence of aerial stem rot was lower in the most dense planting than in the sparse planting in the Crook County west site. In the most dense planting there was a high incidence (32.5%) of blackleg and plants died prematurely. In the Crook County east site final proportion of stems with symptoms averaged 0.39 and 0.18 in treatments with 86 cm and 173 cm between-row spacings, respectively.

AUDPC values were significantly ($p=0.05$) greater in the most dense plantings than in the least dense plantings at all sites but the 1985 Umatilla County east site (Table 9). Significantly higher ($p=0.05$) means were observed in 86 between-row spacings compared to the 173 between-row spacing treatments at three of the four sites in 1985. In 1986, significant differences ($p=0.05$) occurred in the 23 x 86 cm spaced treatment compared to all other treatments in three of the four sites. Differences between the 86-cm between-row spacings versus the 173-cm between-row spacings were observed in both the Umatilla and Crook County east sites. In the Crook County west site AUDPC values were significantly ($p=0.05$) greater in the dense planting and the other three plant spacing treatments (Table 9).

TABLE 9. Effect of plant spacing on area under the disease progress curve (AUDPC) for aerial stem rot of potatoes in Umatilla and Crook Counties, Oregon in 1985 and 1986

	Mean AUDPC[a,b]							
	1985				1986			
	Umatilla		Crook		Umatilla		Crook	
Plant Spacing[c]	West	East	West	East	West	East	West	East
23x86 cm	2.44 x	3.55 x	6.32 x	4.34 x	16.81 x	20.28 x	5.61 x	7.29 x
46x86 cm	3.15 x	4.16 x	4.31 xy	2.44 xy	6.72 y	12.25 y	5.18 x	3.85 y
23x173 cm	0.94 y	3.75 x	3.27 y	1.60 yz	6.24 y	6.56 yz	1.32 x	1.49 z
46x173 cm	1.00 y	2.91 x	3.83 y	1.06 z	3.92 y	5.53 z	0.47 z	1.10 z
LSD p=0.05	1.10	2.70	2.99	0.99	3.06	6.18	4.54	1.98

a based on methods of Shanner and Finney, 1977.
b based on average of six replications
c first and second numbers represent within-row and between-row spacings, respectively
d means followed by the same letter do not differ significantly at p=0.05 by Fischer's protected least significant difference

Canopy density. Highest leaf area index (LAI) values were recorded approximately 100 and 75 days after planting in the Umatilla County and Crook County sites, respectively. LAI values were always higher in the dense than in the sparse plant populations. The intermediate plant populations generally fell in between (Fig. 3).

Individual plants in the sparse planting grew both larger and more vigouously than plants in the dense planting. This growth compensation was corroborated by LAI values. In the treatment with 13,000 plants/ha, LAI values were not 4-times lower than the treatment with 52,000 plants/ha.

AULAIC was significantly ($p=0.05$) greater in the most dense plantings than in the sparse plantings at all sites in 1986 (Table 10). In the intermediate plant densities, mean AULAIC was always larger in plots with 86-cm between-rows than in plots with 173-cm between rows (Table 10).

AULAIC was positively correlated with AUDPC. The coefficient of determination (R^2) values were significant in Crook County east ($R^2=0.98$, $p=0.05$) and west plots ($R^2=0.98$, $p=0.05$). In Umatilla County, R^2 values were 0.92 and 0.89 in west and east plots, respectively. Corresponding significance levels for Umatilla County were $p=0.05$ and $p=0.10$ (Fig. 4).

Epiphytic populations. Size of epiphytic populations of soft rot erwinias was dependent on sampling time.

Fig. 3. Leaf area index values for potatoes at four plant spacings at four sites in Oregon in 1986. Treatments are with and between row spacings, □ =23x86 cm, + =46x86 cm, ◇ =46x173cm, △ =86x173 cm. Each point is the mean of six replications. A) Umatilla County west; B) Umatilla County east; C) Crook County west; D) Crook County east.

Figure 3

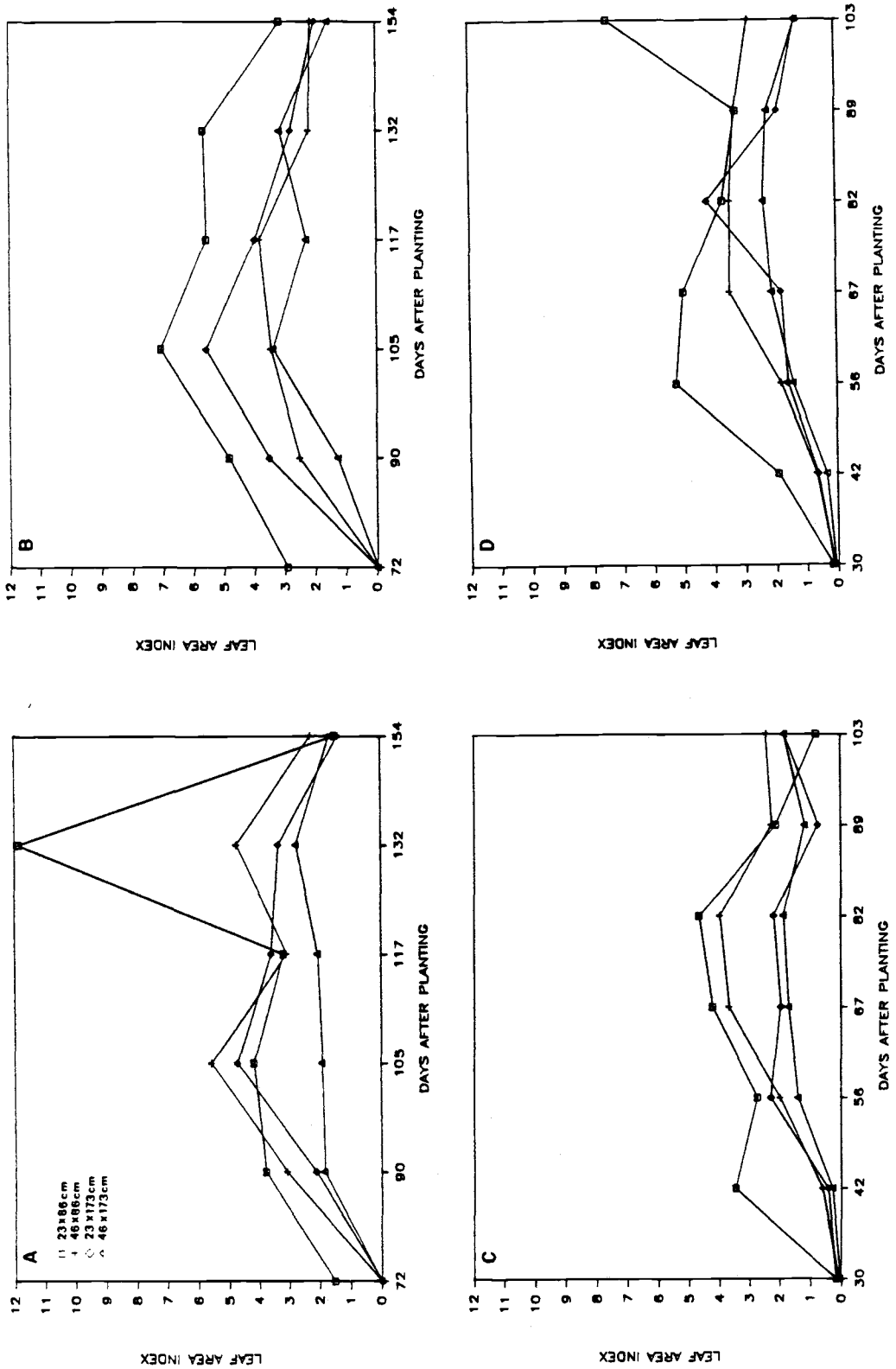

A
B
C
D
23x86cm
46x86cm
23x173cm
46x173cm
LEAF AREA INDEX
DAYS AFTER PLANTING
0
1
2
3
4
5
6
7
8
9
10
11
12
72
90
105
117
132
154
30
42
56
67
82
89
103

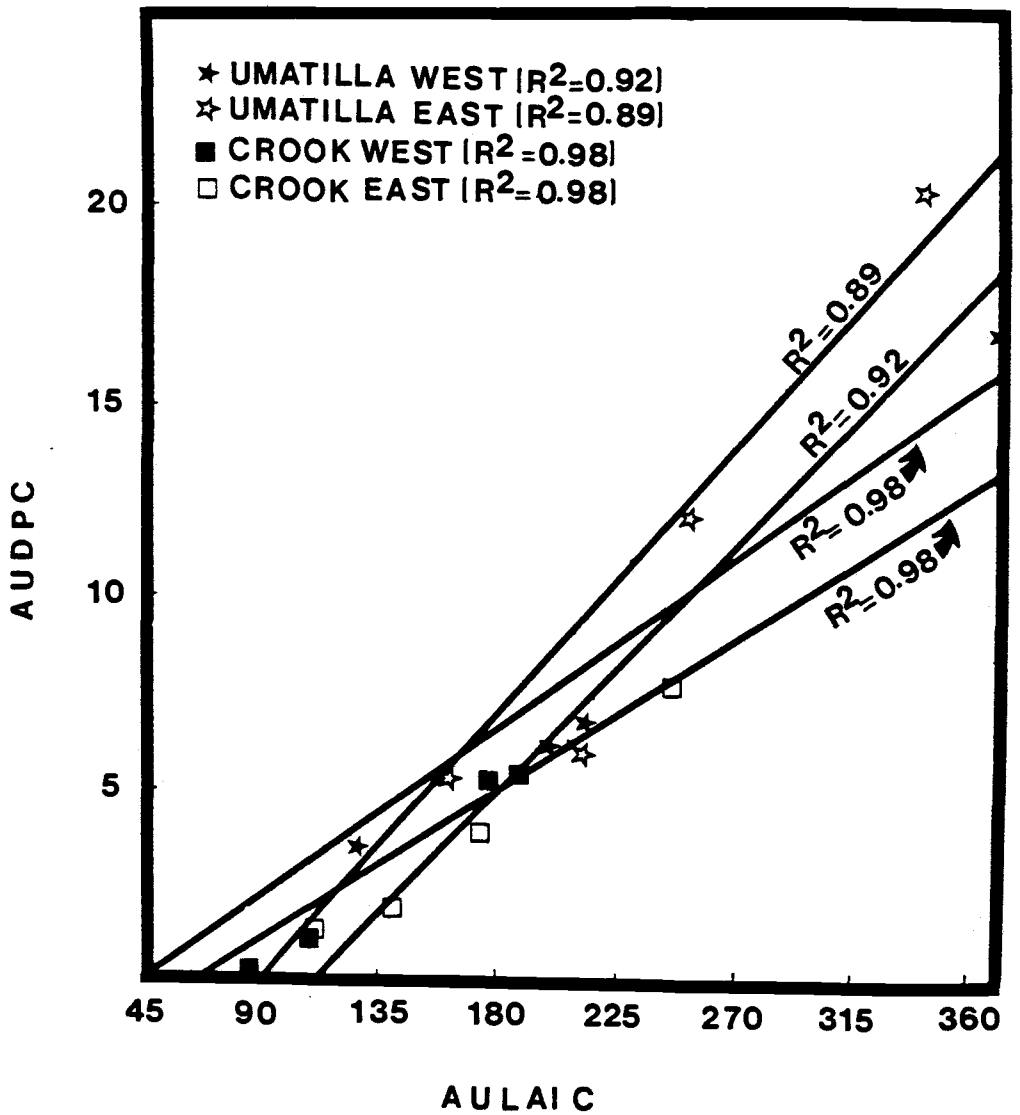
TABLE 10. Effect of plant spacing on area under the leaf area index curve (AULAIC) for potatoes in Umatilla and Crook Counties, Oregon in 1986

	Mean AULAIC[ab]			
	1986			
	Umatilla		Crook	
Plant spacing[c]	West	East	West	East
23x86 cm	371.9x[d]	342.2x	183.4x	248.9x
46x86 cm	217.1 y	237.7 y	163.8x	178.0 y
23x173 cm	194.0 y	217.8 yz	110.2 y	142.4 yz
46x173 cm	128.2 y	147.6 z	88.6 y	112.7 z
LSD p=0.05	110.5	83.3	39.7	59.3

[a] based on methods of Shanner and Finney, 1977.
[b] based on the average of six replications
[c] first and second numbers represent within-row and between-row spacings, respectively
[d] means followed by the same letter do not differ significantly at p=0.05 by Fischer's protected least significant difference

Fig. 4. Relationship between area under the disease progress curve (AUDPC) and area under the leaf area index curve (AULAIC) for four plant spacings at four plant densities at four sites in Oregon in 1986.

Figure 4


UMATILLA WEST (R2=0.92)
UMATILLA EAST (R2=0.89)
CROOK WEST (R2=0.98)
CROOK EAST (R2=0.98)
R2=0.89
R2=0.92
R2=0.98
R2=0.98
AUDPC
20
15
10
5
45
90
135
180
225
270
315
360
AULAIC

Leaflets sampled just after an irrigation event harbored higher populations than leaflets sampled prior to irrigation. Although there were no significant differences among treatments in size of epiphytic populations, some seasonal trends were noted. Early in the season, epiphytic populations were non-detectable. Epiphytic populations tended to have a midseason peak at some sites and then they declined by the end of the season (Figs. 5 and 6). Epiphytic populations were highest 111 days after planting in both Umatilla County sites in 1985. In the Crook County west site epiphytic populations peaked 68 days after planting (2.14 $\log_{10}$ cfu/g). Crook County east site populations increased through the end of the season with the highest number recorded at the end of the season (2.06 $\log_{10}$ cfu/g).

In Umatilla County in 1986, epiphytic soft rot erwinias were first detected 90 days after planting. In the west site highest populations (2.77 $\log_{10}$ cfu/g) were recorded 154 days after planting and at the east site highest populations (0.85 log10 cfu/g) occurred on the final sampling date. (Fig 6a and b). In Crook County, peaks in epiphytic populations occurred 68 and 83 days after planting in west and east sites, respectively.

Leaf Wetness. Two trends were evident in duration of leaf wetness. First, duration of leaf wetness was longer in plots with the dense plant populations than in the sparse

Fig. 5. Epiphytic populations of soft rot erwinias on potato foliage at four sites in Oregon in 1985. Treatments are between and within row spacings, where, □ =23x46 cm, + =46x86 cm, ◊ =23x173cm, △ =46x173 cm. Each point is the mean of two leaflets averaged over six replications. A) Umatilla County west; B) Umatilla County east; C) Crook County west; D) Crook County east.

Figure 5

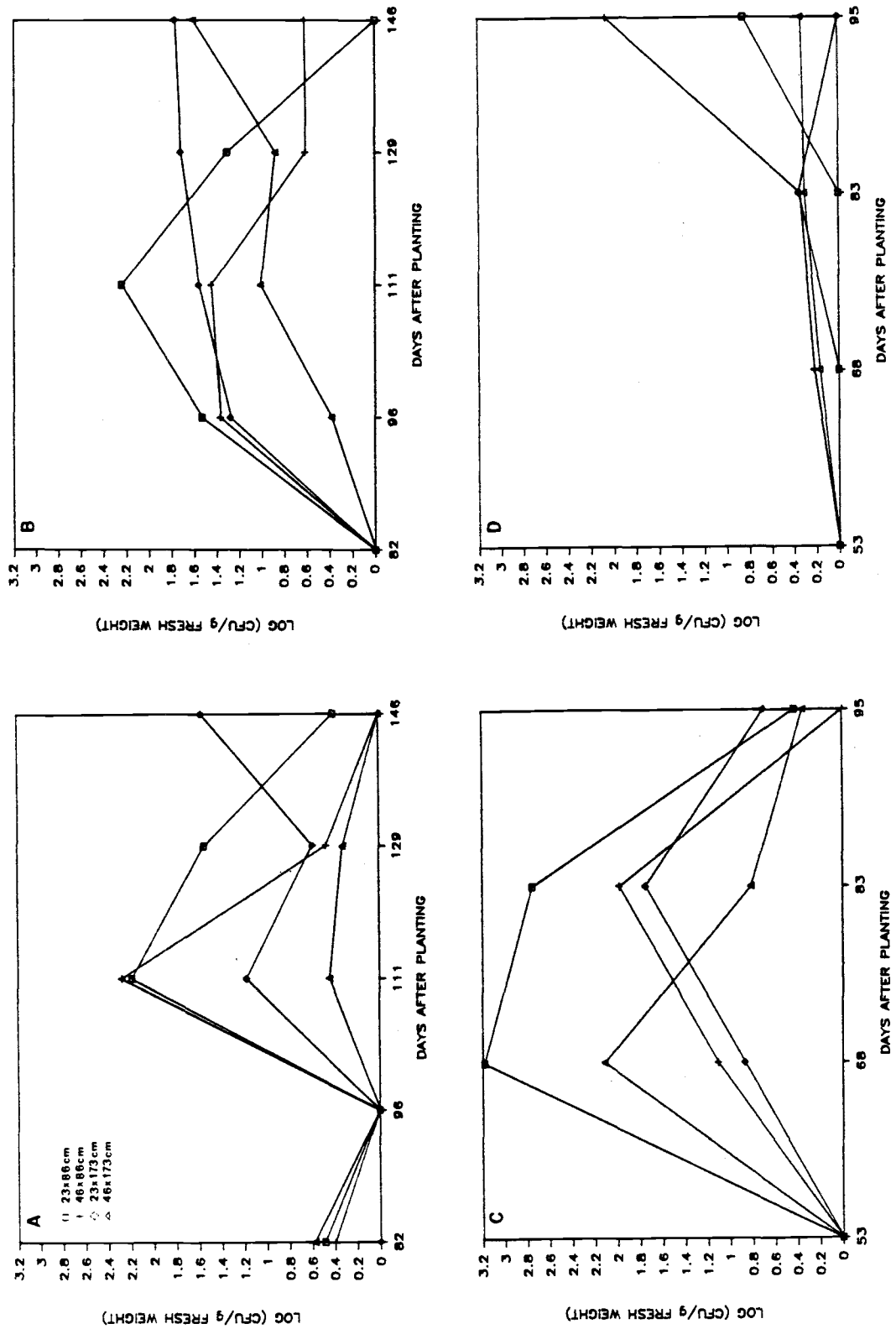
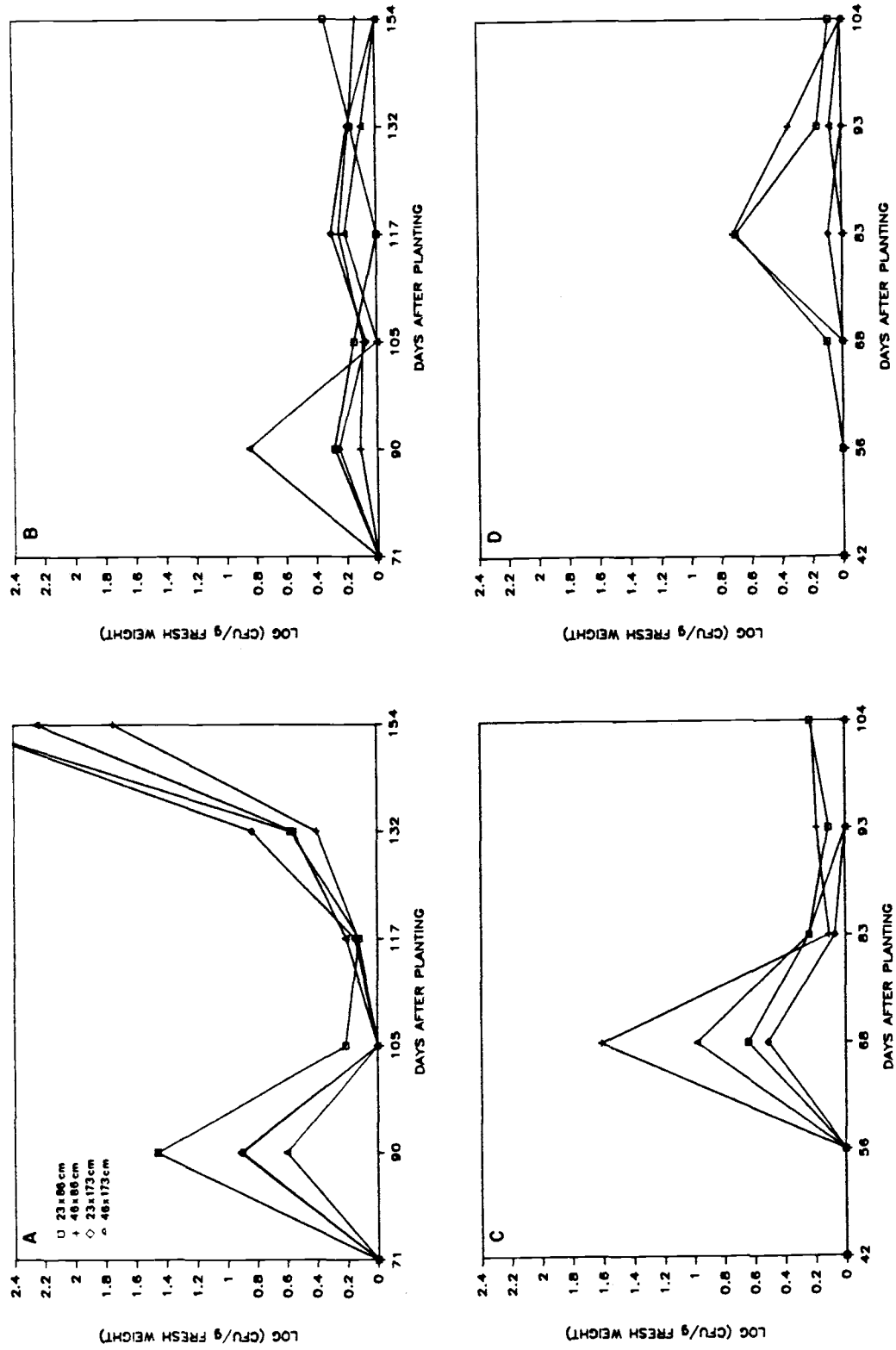

A
B
C
D
23x86cm
46x86cm
23x173cm
46x173cm
LOG (CFU/g FRESH WEIGHT)
DAYS AFTER PLANTING
0
82
96
111
129
146
53
68
83
95

Fig. 6. Epiphytic populations of soft rot erwinias on potato foliage at four sites in Oregon in 1986. Treatments are between and within row spacings, where, □ =23x86 cm, + =46x86 cm, ◇ =23x173 cm, △ =46x173 cm. Each point is the mean of five leaflets averaged over six replications. A) Umatilla County west; B) Umatilla County east; C) Crook County west; D) Crook County east.

Figure 6


A
B
C
D
□ 23x86cm
+ 46x86cm
◇ 23x173cm
△ 46x173cm
LOG (CFU/g FRESH WEIGHT)
DAYS AFTER PLANTING
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
42
56
68
83
93
104
71
90
105
117
132
154

plantings and secondly, average duration of leaf wetness increased as the season progressed and then decreased as plants senesced. In Umatilla county in 1986, mean length of leaf wetness ranged from 5.4 to 4.9 hours in the most dense and least dense plantings, respectively (Table 11). There was a clear difference in average duration of leaf wetness among the plant spacings with 86-cm and 173-cm between-rows. Average duration of leaf wetness was 5.6 and 4.4 hrs for the 86-cm and 173-cm between-row spacings, respectively. In Crook County the longest duration of leaf wetness periods occurred between 57-69 days after planting, where it averaged 7.3 and 6.7 hours for treatments with 86- and 173-cm between-rows, respectively (Table 11). Similar trends were observed in 1985.

TABLE 11. Effect of plant spacings on average duration of leaf wetness in potatoes in Umatilla and Crook Counties, Oregon in 1986

Location and days after planting	Average duration of leaf wetness (hr)[a]			
	23x86cm[b]	46x86cm	23x173cm	46x173cm
Umatilla County				
72-91	3.9	4.7	3.2	4.9
91-105	5.0	5.5	4.5	3.8
106-118	6.4	5.5	5.2	5.2
119-132	6.5	7.5	3.5	5.2
133-155	5.3	5.8	3.1	4.9
Mean	5.4	5.8	3.9	4.9
Crook County				
29-32	2.5	2.8	2.2	2.2
33-43	3.3	3.5	2.0	3.7
44-56	3.7	4.3	2.4	3.9
57-69	6.1	8.4	2.8	10.7
70-84	5.9	8.7	2.6	4.2
85-91	4.7	7.3	5.4	5.4
92-103	7.6	6.9	6.9	14.3
Mean	4.8	6.0	3.5	6.3

a Based on the two sensor per treatment
b First and second numbers represent within-row and between-row spacings, respectively

DISCUSSION

Changes in host density had an effect on canopy density, associated microenvironmental conditions within the canopy, and development of aerial stem rot of potatoes. Onset of disease occurred earlier and final proportion of disease was higher in dense plantings compared to the intermediate and sparse plantings. There was also a positive relationship between AUDPC and AULAIC. In 1986, the highest LAI values preceded the highest amount of disease by 2 wks. As LAI increased there was a corresponding increase in amount of aerial stem rot at all but one site. At that site (Crook County west) there was a high incidence of blackleg and plants died prematurely; hence, effects of plant spacing on aerial stem rot were not observed. There was a positive correlation, however, between AUDPC and AULAIC at that site because onset of symptoms occurred at least one week eariler in the dense plantings. In addition, between-row spacings had greater effect on date of disease onset, final proportion of disease, AUDPC and AULAIC than did within-row spacings. These trends were consistent regardless of location (Chapter 1).

Several researchers have demonstrated an increase in disease with an increase in plant host density (Crandell, 1971; Hoes and Huang, 1985; Schmidt and daSilva, 1986;

Porter et al., 1987; Strandberg and White, 1978; Berger, 1975; Grimes, 1986 and Williams, 1975). These studies suggested that changes in host plant density affect the microclimate within the canopy. Crandell (1971) found that the effects of increasing plant density was to reduce air movement, increase relative humidity, and reduce temperatures within the canopy. Dense canopies will also reduce the amount of solar radiation reaching leaf surfaces (Schmidt and daSilva, 1986).

In this study, the canopy microclimate was assessed by measuring the duration of leaf wetness. Measurements of length of leaf wetness demonstrated that there was an increase in the average duration of leaf wetness as LAI increased. This trend was apparent earlier in the season in the dense plantings than in the sparse plantings. Prolonged periods of leaf wetness may be associated with the development of aerial stem rot as the soft rot erwinias may have a competitive advantage in these microenvironments. Duration of leaf wetness is an important factor in the development of several diseases. Prolonged leaf wetness was associated with grey mold of snap beans (Johnson and Powelson, 1983) and white mold of snap beans (Abawi and Grogan, 1975). Soft rot of potato tubers occurs when free water covers the tuber surface and anerobic conditions prevail (Wiggington, 1973; Maher and Kelman, 1983). Soft rot erwinia are reported to have an

epiphytic phase on potato leaflets (Perombelon, 1978; De Boer, 1983). Their survival and reproduction are favored when the leaf surfaces are wet. In contrast, populations will decrease dramatically as the leaf surface dries (Perombelon, 1978). Variation in epiphytic populations from leaf to leaf can be extreme. Leben and Daft (1967) found growth of microbial epiphytes was directly related to the amount of rainfall and the length of time leaves remained wet. In this study, populations of soft rot erwinias on individual leaflets ranged from non-detectable to 673,000 cfu/g fresh weight. Detection of these bacteria on leaf surfaces was related to the presence of water on foliage following irrigation. On sampling dates in midseason when no epiphytes were detected, corresponding leaf wetness values were low. Leaf wetness values were calculated for the 48 hr period surrounding sampling times. For example, in Umatilla County in 1985, epiphytic populations were non-detectable 97 days after planting, although the bacteria had been detected on an earlier sampling date (Fig. 5a). Average leaf wetness for the 48-hr period prior to sampling was 0 hr in all four treatments. Soft rot erwinias may not have survived the dry foliage periods.

Altering plant spacing allowed comparisons of microclimatic conditions on disease development, though changing plant density may not be economically feasible in

potatoes. Plant spacing practices must be compatible with crop growth and yields. In a study of plant spacing, Strandberg and White (1978) agreed with the conclusion of Berger (1975) that an increase plant density increased incidence and severity of foliar diseases of celery. They subsequently manipulated plant spacing and configurations by standards acceptable to growers, and within those constraints, there were no differences in levels of disease.

In the Pacific Northwest rainfall is a rare occurrence during the summer months; therefore, microclimatic conditions rely heavily on irrigation practices. Dense canopies and a favorable microenvironment created by overhead irrigation have been associated in increased incidence and severity of foliar diseases of many important crops (Rotem, 1969). Therefore irrigation management may be the key to disease control. With frequent irrigations such as occurs in potatoes in the Pacific Northwest, soil surfaces and foliage deep within the canopy may remain wet for long periods. An integrated approach must be developed to control aerial stem rot while maintaining high yields. This approach may include amount of water applied through irrigation as well as the frequency and timing of applications. Future research, then, may be aimed at management of agronomic

practices such as irrigation frequency and canopy development to control aerial stem rot of potatoes.

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