Ecology and Epidemiology

Canopy Density and Microclimate Effects on the Development of Aerial Stem Rot of Potatoes

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ABSTRACT

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Field plots of potato cultivar Russet Burbank were established in four center-pivot irrigated fields in Oregon over 2 yr to evaluate canopy density and microclimate effects on the development of aerial stem rot caused by *Erwinia carotovora* subsp. *carotovora*. Plant densities were 13, 26, and 52×10^3 plants per hectare. Four treatments consisted of factorial combinations of within-row spacings of 23 or 46 cm and between-row spacings of 86 or 173 cm. Alteration in between-row spacings had a greater effect on disease onset and area under the disease progress curve (AUDPC) than did changes in within-row spacing. Area under the leaf area index curve (AULAIC) values were significantly higher ($P \leq 0.01$) with a decrease in either between- or within-row spacing. Disease onset in dense plantings occurred 5–34 days earlier than in sparse plantings. AUDPC values were significantly higher ($P \leq 0.01$) with 86 cm compared with 173 cm between-row spacings at four sites. Based on linear regression, AULAIC accounted for 95–99% of the variation in AUDPC. Plant density had no significant effect on epiphytic population size of soft rot erwinias, although some seasonal trends were noted. Populations of the epiphytes were not detected early in the season, but increased to peaks at mid- or late-season and generally declined by the end of the season. Average duration of leaf wetness was proportional to the leaf area index and periods of leaf wetness were of a longer duration in dense than in sparse plantings. Peak leaf area index values and longest periods of leaf wetness preceded extensive symptom development by 2 wk for all plant densities.

Additional keywords: epidemiology, epiphytic bacteria.

In the Pacific Northwest, potatoes are commonly grown under center-pivot irrigation. Frequent irrigations coupled with high rates of fertilizer application produce a lush canopy which promotes high relative humidity, still air, and long periods of leaf wetness (21). These conditions favor survival and reproduction of the soft rot erwinias and subsequent development of aerial stem rot of potatoes (18,17).

While water is critical for high tuber yields in this arid production area, it is also an essential component in the epidemiology of aerial stem rot caused by *Erwinia carotovora* subsp. *carotovora*. This soft rot erwinia is present in water used to irrigate potatoes, (2,8) and in soil (13,19). Recent reports indicate that the bacterium also is a resident on potato foliage (5,16). Leben (10) suggested that many phytopathogenic bacteria persist in an epiphytic phase on symptomless plants and disease may ensue when suitable environmental conditions develop. The objectives of this study were to determine the effects of plant density on the microclimate within the potato canopy, the population dynamics of soft rot erwinias on potato foliage, and the incidence of aerial stem rot.

MATERIALS AND METHODS

Field plots. Field plots of potato (*Solanum tuberosum* L. 'Russet Burbank') were established in two production areas in Oregon in 1985 and 1986. Two sites were located on a farm in

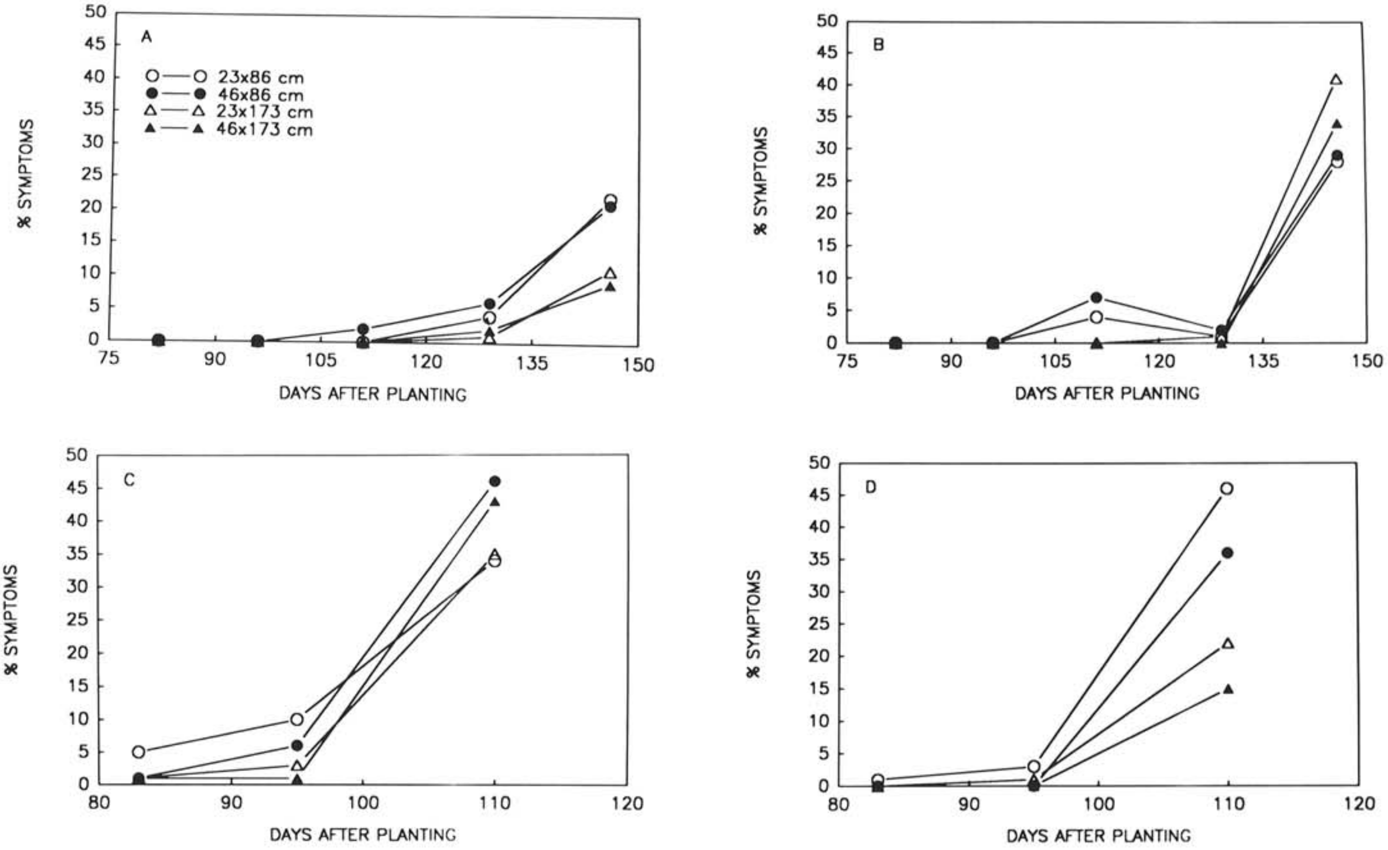

Fig. 1. Disease progress curves for aerial stem rot of potatoes at four plant spacings for four sites in Oregon in 1985. Treatments are within- and between-row spacings where ○ = 23 × 86 cm, ● = 46 × 86 cm, △ = 23 × 173 cm, ▲ = 46 × 173 cm. Each point is the mean of six replications. **A,** Umatilla County west; **B,** Umatilla County east; **C,** Crook County west; and **D,** Crook County east.

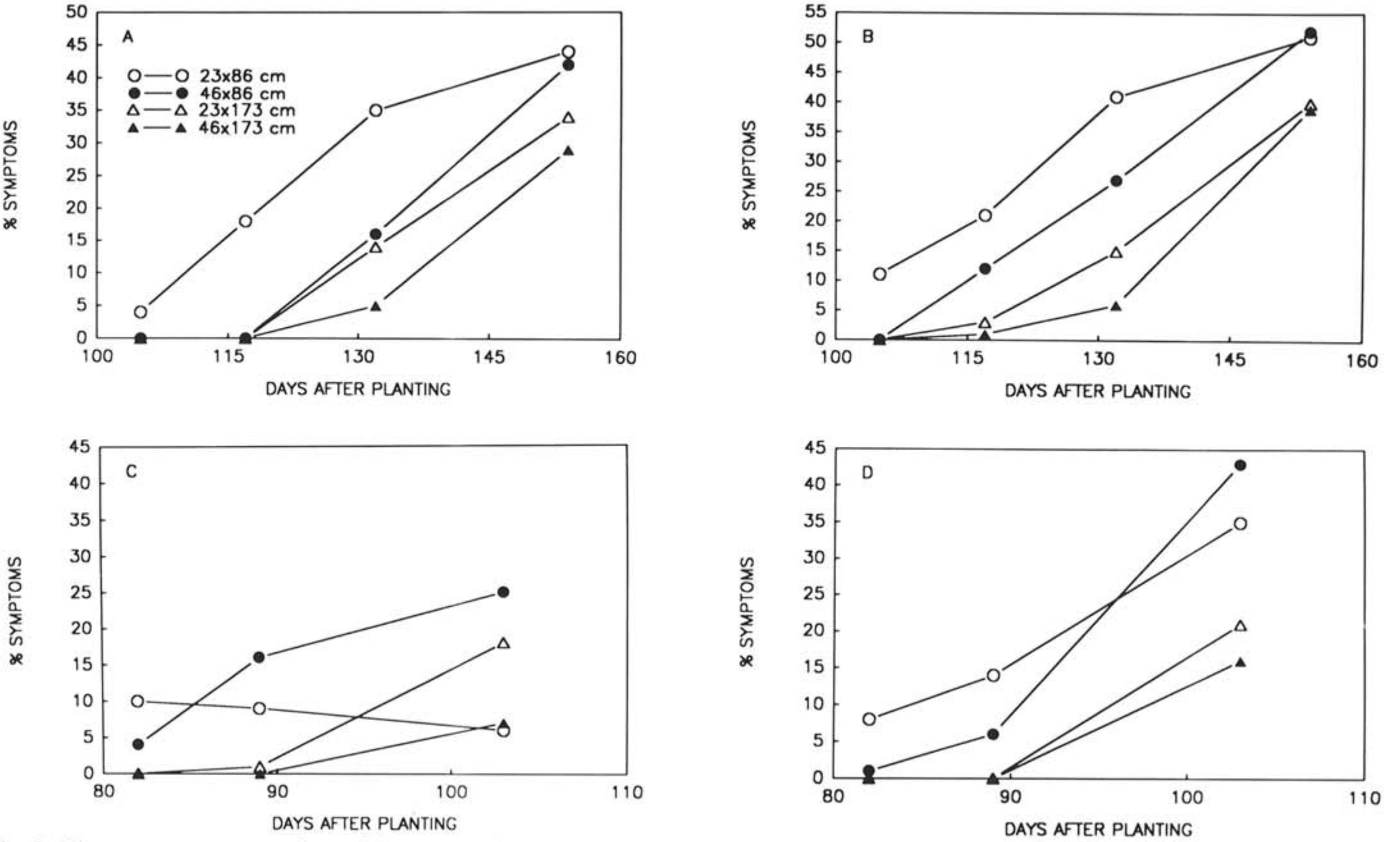

Fig. 2. Disease progress curves for aerial stem rot of potatoes at four plant spacings for four sites in Oregon in 1986. Treatments are within- and between-row spacings where ○ = 23 × 86 cm, ● = 46 × 86 cm, △ = 23 × 173 cm, ▲ = 46 × 173 cm. Each point is the mean of six replications. **A,** Umatilla County west; **B,** Umatilla County east; **C,** Crook County west; and **D,** Crook County east.

Umatilla County (east and west) and another two sites on a farm in Crook County (east and west). Field plots were planted during the first week of April in Umatilla County and during the third week of May in Crook County in both years. Each year, seed tubers from a single seedlot grown and certified in Montana were held for 4 days at 22 C and then cut into seed pieces weighing 40–55 g. After cutting, seed pieces were kept at 13 C for 6 days to allow for suberization. Treatments consisted of factorial combinations of within-row spacings of 23 or 46 cm and between-row spacings of 86 or 173 cm. Plant densities were about 13, 26, and 52×10^3 plants per hectare. Two of the four treatments contained 26×10^3 plants per hectare in two different spacing arrangements. Plots were four or six rows wide and 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 assessments were made twice a month beginning at plant emergence. The central 10 hills of a middle row in each plot were evaluated visually for symptoms of aerial stem rot. The first date on which aerial stem rot symptoms were observed for each treatment was considered disease onset. Disease progress curves were generated for each treatment based on the mean proportion of stems affected. Treatment comparisons were based on date of disease onset and area under the disease progress curve (AUDPC) (23).

Epiphytic populations. Potato leaflets were assayed for epiphytic populations of soft rot erwinias every 2 wk beginning at row closure. Two (1985) and five (1986) leaves were randomly sampled from a middle row of each plot. Early in the season the fourth leaf from the base of the plant was collected; as the season progressed and the lower leaves had senesced, the first intact leaf from the base of the plant was sampled. Sampled leaves were placed in a plastic bag, stored in a portable cooler, and processed within 24 hr. The terminal leaflet was removed, weighed, and 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 spread on duplicate plates of crystal violet pectate (CVP) medium (4). Tenfold serial dilutions were plated similarly for leaflets that appeared chlorotic or decayed. Epiphytic populations of soft rot erwinias were based on the number of colony-forming units (cfu) per gram fresh weight of leaflet tissue. Bacterial populations were expressed $\log_{10}(X+1)$, where X was the number of colony-forming units per gram fresh weight of leaflet tissue.

Canopy measurement. In 1986, an individual stem was taken from one hill in a row outside the disease assessment area in each plot at three of the four sites. At the fourth site (Crook County west) all stems from one hill in each plot were collected. Leaves were stripped from the stem, placed in a plastic bag, and stored in portable coolers. Within 24 hr, leaf area was measured with a LiCor LI-3000 leaf area meter (Lambda Instruments Corp., Lincoln, NE). Leaf area index (LAI) was determined as ([cm^2 of leaf tissue per stem][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 same procedure used for AUDPC.

Environmental data. Leaf wetness was measured with a Campbell Scientific 21X micrologger (Campbell Scientific Inc., Logan, UT) at the west site in Umatilla County in 1985 and at one site in both counties in 1986. Leaf wetness sensors were attached to ring stands (one per treatment in 1985 and two per treatment in 1986) and maintained near the center of the canopy. Sensors sampled at 30-min intervals and wetness duration was computed

TABLE 1. Effect of plant spacing on the onset of aerial stem soft rot of potatoes in five locations in Oregon; three in 1985 and two 1986

Location and year	Between-row 86 cm	Between-row 173 cm	Within-row 23 cm	Within-row 46 cm	LSD[a]
Umatilla Co. 1985					
East	114	123**[b,c]	136	132 ns[d]	9.0
West	142	132**	139	135 ns	8.0
Crook Co. 1985					
West	93	99 ns	94	98 ns	5.0
Umatilla Co. 1986					
East	113	131**	120	124 ns	7.0
Crook Co. 1986					
West	86	101**	93	94 ns	4.0

[a] Least significant difference ($P = 0.05$).
[b] Days after planting.
[c] Means differ significantly at $P = 0.01$ (**) by Fisher's protected least significant difference.
[d] Means do not differ significantly at $P = 0.05$ by Fisher's protected least significant difference.

TABLE 2. Interactions of plant spacing on the onset of aerial stem rot of potatoes in three locations in Oregon; one in 1985 and two in 1986

Plant spacing	Crook Co. (East) 1985	Crook Co. (East) 1986	Umatilla Co. (West) 1986
23-cm within-row			
86-cm between-row	93[a]	83	109
173-cm between-row	108	103	139
46-cm within-row			
86-cm between-row	110	90	132
173-cm between-row	110	103	143
$\text{LSD}_{(.05)}$ (within × between)	7	4	10

[a]Days after planting.

TABLE 3. Effect of plant spacing on area under the disease progress curve for aerial stem rot of potatoes in six locations in Oregon; four in 1985 and two 1986

Location and year	Between-row 86 cm	Between-row 173 cm	Within-row 23 cm	Within-row 46 cm	LSD[a]
Umatilla Co. 1985					
East	3.8	3.3 ns[b]	3.6	3.5 ns	1.7
West	2.8	1.0**[c]	1.7	2.1 ns	0.8
Crook Co. 1985					
East	3.4	1.3**	3.0	1.8**	0.7
West	5.3	3.6*	4.8	4.1 ns	3.5
Umatilla Co. 1986					
East	16.3	6.0**	13.4	8.9 ns	28.9
Crook Co. 1986					
West	5.4	0.9**	3.5	2.8 ns	13.6

[a]Least significant difference ($P = 0.05$).
[b]Means do not differ significantly at $P = 0.05$ by Fisher's protected least significant difference.
[c]Means differ significantly at $P = 0.01$ (**) and $P = 0.05$ (*) by Fisher's protected least significant difference, respectively.

TABLE 4. Interactions of plant spacing on area under the disease progress curve for aerial stem rot of potatoes in two locations in Oregon in 1986

Plant spacings	Crook Co. (East)	Umatilla Co. (West)
23-cm within-row		
86-cm between-row	7.3	16.1
173-cm between-row	1.5	6.2
46-cm within-row		
86-cm between-row	3.9	6.7
173-cm between-row	1.1	3.9
$\text{LSD}_{(.05)}$ (within × between)	2.0	3.1

as the percentage of the intervals that the sensor was wet.

Analyses. Date of disease onset, AUDPC, and AULAIC were assessed by analysis of variance, and treatment means were compared by Fisher's protected least significant difference procedure. Regression coefficients were determined for AUDPC and AULAIC by fitting a simple linear regression model to these variables.

RESULTS

Disease incidence. Onset of aerial stem rot symptoms was earlier in the dense (23 × 86 cm) compared with the sparse (86 × 173 cm) plantings (Fig. 1A–D and Fig. 2A–D). In 1985 and 1986, respectively, disease onset occurred 5–24 and 17–34 days earlier in the dense compared with the sparse plant populations. In addition to plant density, planting arrangement had an effect on date of disease onset. At five locations there were no significant interactions of between × within-row spacing. At these locations, date of disease onset was significantly ($P \leq 0.01$) earlier in 86-cm rows as compared with 173-cm rows (Table 1). Within-row spacing, however, had little effect on date of disease onset. Although there were significant ($P \leq 0.05$) interactions of between- × within-row spacing at three locations, the trend was for symptoms of aerial stem rot to occur earlier in plots with either 86-cm between-row or 23-cm within-row spacings (Table 2).

AUDPC values were significantly larger ($P \leq 0.05$) in the dense as compared with the sparse plantings at all but the 1985 Umatilla County east location (data not shown). AUDPC values were significantly larger ($P \leq 0.05$) for 86-cm compared with the 173-cm between-row spacing at three locations in 1985 and two locations in 1986 (Table 3). AUDPC values were significantly greater ($P \leq 0.01$) for 23-cm compared with 46-cm within-row spacing only at the Crook County east site in 1985. At the two sites with significant ($P \leq 0.05$) interactions of between- × within-row spacings, AUDPC values were consistently higher in the 86-cm between-row and the 23-cm within-row spacings (Table 4).

Canopy density. The largest LAI values were recorded approximately 75–100 days after planting. LAI values were always higher in the dense than in the sparse plant populations with values for the intermediate plant populations generally falling in between these extremes (Fig. 3A–D).

AULAIC values were significantly greater ($P \leq 0.01$) in the 86-cm as compared with 173-cm between-row spacing as well as the 23-cm compared with 46-cm within-row spacing for all locations in 1986 (Table 5). AULAIC values were positively correlated with AUDPC values at all sites (Fig. 4). Regression coefficients were 0.98, 0.95, 0.99, and 0.98 at Umatilla west, Umatilla east, Crook west, and Crook east, respectively.

Epiphytic populations. Size of epiphytic populations of soft rot erwinias depended on sampling time. Leaflets sampled following an irrigation harbored higher populations than leaflets sampled before an irrigation. Although there were no significant differences in size of epiphytic populations among plant densities, some seasonal trends were observed (Fig. 5A–D and 6A–D). Early in the season, epiphytic populations were nondetectable. As the season progressed, populations increased in size with a peak occurring either at midseason or late in the season. By the end of the season populations generally decreased to a low or nondetectable level.

Leaf wetness. Two trends were evident in duration of leaf wetness. First, leaf wetness was of a longer duration in the dense compared with the sparse populations. Second, the average duration of leaf wetness increased as the canopy developed and then decreased as plants senesced and the canopy disintegrated (Table 6). There was a clear difference in average duration of leaf wetness between the two between-row plant spacings. Average duration of leaf wetness was 6.6 and 4.7 hr in 1985 and 5.6 and 4.4 hr in 1986 for the 86- and 173-cm between-row spacings, respectively, in Umatilla County. In Crook County in 1986, aver-

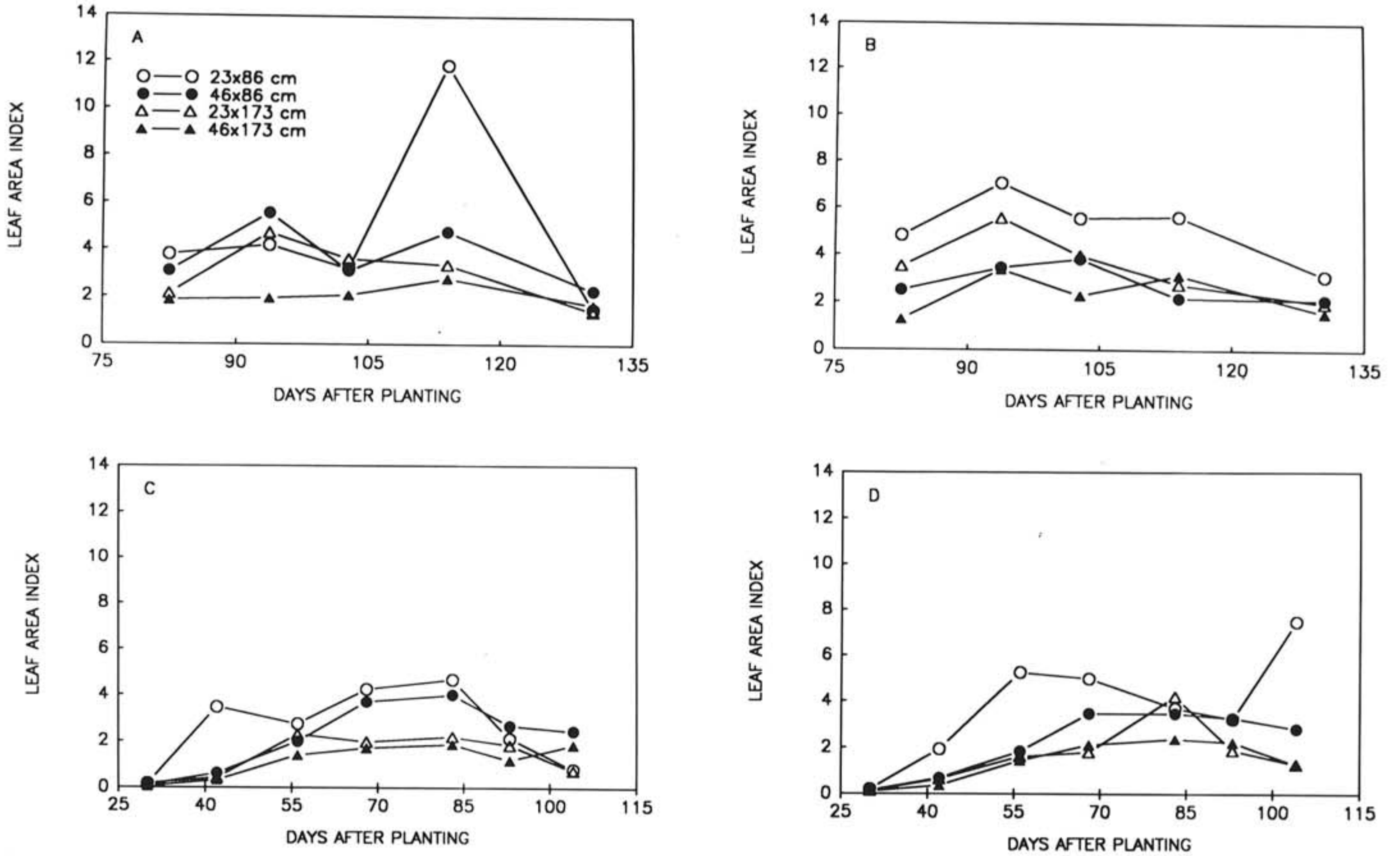

Fig. 3. Leaf area index values for potatoes at four plant spacings for four sites in Oregon in 1986. Treatments are within- and between-row spacings where ○ = 23 × 86 cm, ● = 46 × 86 cm, △ = 23 × 173 cm, ▲ = 46 × 173 cm. Each point is the mean of six replications. **A,** Umatilla County west; **B,** Umatilla County east; **C,** Crook County west; and **D,** Crook County east.

age duration of leaf wetness was 5.4 and 4.9 hr for the 86- and 173-cm between-row spacings, respectively. Effect of within-row spacings on leaf wetness was negligible at both locations.

DISCUSSION

Alteration in plant density affected the total leaf area, the environment within the canopy, and the incidence of aerial stem rot of potatoes. In the dense plantings, AULAIC values were larger, periods of leaf wetness were longer, disease was observed earlier, and AUDPC values were higher compared with the intermediate and sparse plant densities. Furthermore, with an increase in AULAIC values there was a corresponding increase in AUDPC values. The effect, however, of planting density was due to between-row rather than within-row spacing. Increases in between-row spacing left an open canopy where foliage was exposed to the drying effects of wind and sun.

Peak LAI values preceded maximum symptom expression by 2 wk. As LAI increased there was a corresponding increase in the incidence of aerial stem rot at all but one location. At that location (Crook County west) there was a high incidence of blackleg; hence, effects of plant spacing on aerial stem rot were not observed. There was, nonetheless, a correlation between AUDPC and AULAIC at that location because onset of aerial stem rot symptoms occurred at least 1 wk earlier in the dense compared with the sparse population.

Several researchers have demonstrated a positive relationship between plant density and amount of disease (3,20,22,26). In each of these studies, disease increased with an increase in host plant density and changes in host plant density were hypothesized to affect the microclimate within the canopy. Crandell et al (3) found that the effects of increasing plant density were to reduce air movement, increase relative humidity, and reduce temperatures within the canopy. Dense canopies also reduced the amount of solar radiation reaching leaf surfaces (22).

In this study, the average duration of leaf wetness in the canopy increased as LAI increased and peaked at midseason when leaf area was at its greatest. In addition, longer periods of leaf wetness occurred earlier in the season in the dense than in the sparse plantings. In some plots at midseason, however, periods of leaf wetness were longer in sparse than in the dense plantings. Sensors placed deep within the dense canopies may not have detected brief irrigation events or periods of dew. Sensors in the sparse plantings, however, were more exposed and may have detected these subtle wetting periods of lesser intensities and duration.

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 has been shown to be a critical factor in initiation of infections and infection efficiency for several patho-systems. In greenhouse studies on downy mildew of grape, infection efficiency increased rapidly when corresponding leaf wetness duration went from 0–2 hr to 4–5 hr. Increases were not so dramatic as leaf wetness duration increased to 15 hr (9). Prolonged periods of leaf wetness were associated with a high incidence of grey mold of snap beans (7) and white mold of snap beans (1). Population increases of *Erwinia amylovora* and *Pseudomonas syringae* pv. *tomato* have been linked to periods of high moisture and dew. Infection of pear by *E. amylovora* was enhanced by wet, humid conditions (25). In a Georgia field study, epiphytic populations of *P. s. tomato* increased with periods of high moisture until temperatures became limiting (24).

TABLE 5. Effect of plant spacing on area under the leaf area index curve for potatoes in four locations in Oregon in 1986

Location	Between-row		Within-row		LSD[a]
	86 cm	173 cm	23 cm	46 cm	
Umatilla Co.					
East	290.0	179.8**[b]	280.0	189.7**	58.9
West	294.5	161.1**	283.0	172.7**	78.1
Crook Co.					
East	213.5	127.5**	195.6	145.3**	41.9
West	173.6	99.4**	146.8	126.2**	28.1

[a] Least significant difference ($P = 0.05$).

[b] **Means differ significantly at $P = 0.01$ by Fisher's protected least significant difference.

Survival and reproduction of the soft rot erwinias on foliage are favored when the leaf surfaces are wet, but populations will rapidly decline as the leaf surface dries (15). Leben and Daft (11) 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 nondetectable to 673,000 cfu/g fresh weight, and detection of these bacteria on leaf surfaces was related to the presence of water on foliage. On sampling dates in midseason when no epiphytes were detected, corresponding leaf wetness values were low. For example, in Umatilla County in 1985, epiphytic populations were nondetectable 97 days after planting, although the bacteria had been detected on an earlier sampling date (Fig. 5A). Average length of leaf wetness for the 48-hr period before sampling was 9 hr in all four treatments. Soft rot erwinias may not have survived this dry foliage period or populations may have been too small to detect.

In the potato growing regions of the Pacific Northwest, rainfall is a rare occurrence during the summer months; therefore, microclimatic conditions within a potato canopy depend on irrigation practices. Dense canopies and a favorable microenvironment created by overhead irrigation have been associated with an increased incidence and severity of foliar diseases of many important crops (21). In the Columbia Basin of Oregon and in central Oregon, a crop of Russet Burbank potatoes receives between 700 and 1,300 mm of water per growing season. Because of the low water holding capacity of many of the soils in these areas, the fields are irrigated every 18–48 hr with an average of 8 mm depth with each application. With frequent irrigations, soil surfaces and foliage deep within the canopy may remain wet for long periods. Under conducive environmental conditions, the potato's resistance to soft rot may be altered. With potato tubers, decay will occur under conditions of oxygen depletion (6,14). The accumulation of CO_2 or the presence of free water on the tuber surface are enough to induce anaerobic conditions, and in the presence of the pathogen, decay may be initiated (12). The same effect could be important in the development of aerial stem rot, especially in fields irrigated frequently by overhead sprinklers.

Irrigation management may be the key to control of aerial stem rot. An integrated approach to manage this disease while

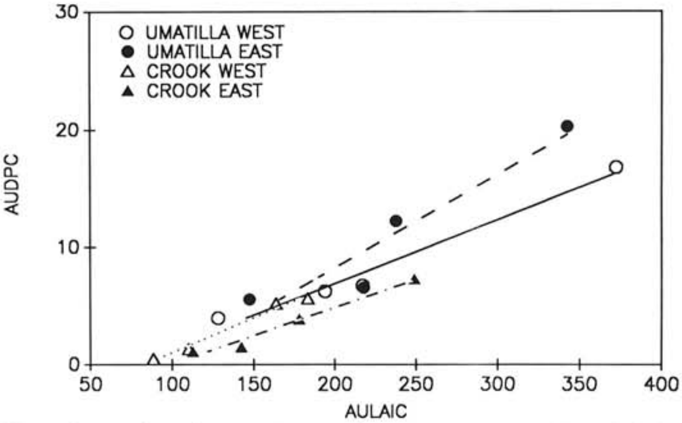

Fig. 4. Regression of area under the disease progress curve (AUDPC)(y) on area under the leaf area index curve (AULAIC)(x) for four plant spacings at three plant densities at four sites in Oregon in 1986. The line of the regression and regression coefficients are: $y = -4.514 + 0.05476x$, $R^2 = 0.98$ (Umatilla west); $y = -2 + 0.07988x$, $R^2 = 0.95$ (Umatilla east); $y = -4.847 + 0.05855x$, $R^2 = 0.99$ (Crook west); $y = -4.7344 + 0.04790x$, $R^2 = 0.98$. The regression coefficients for all locations are highly significant ($P \leq 0.01$).

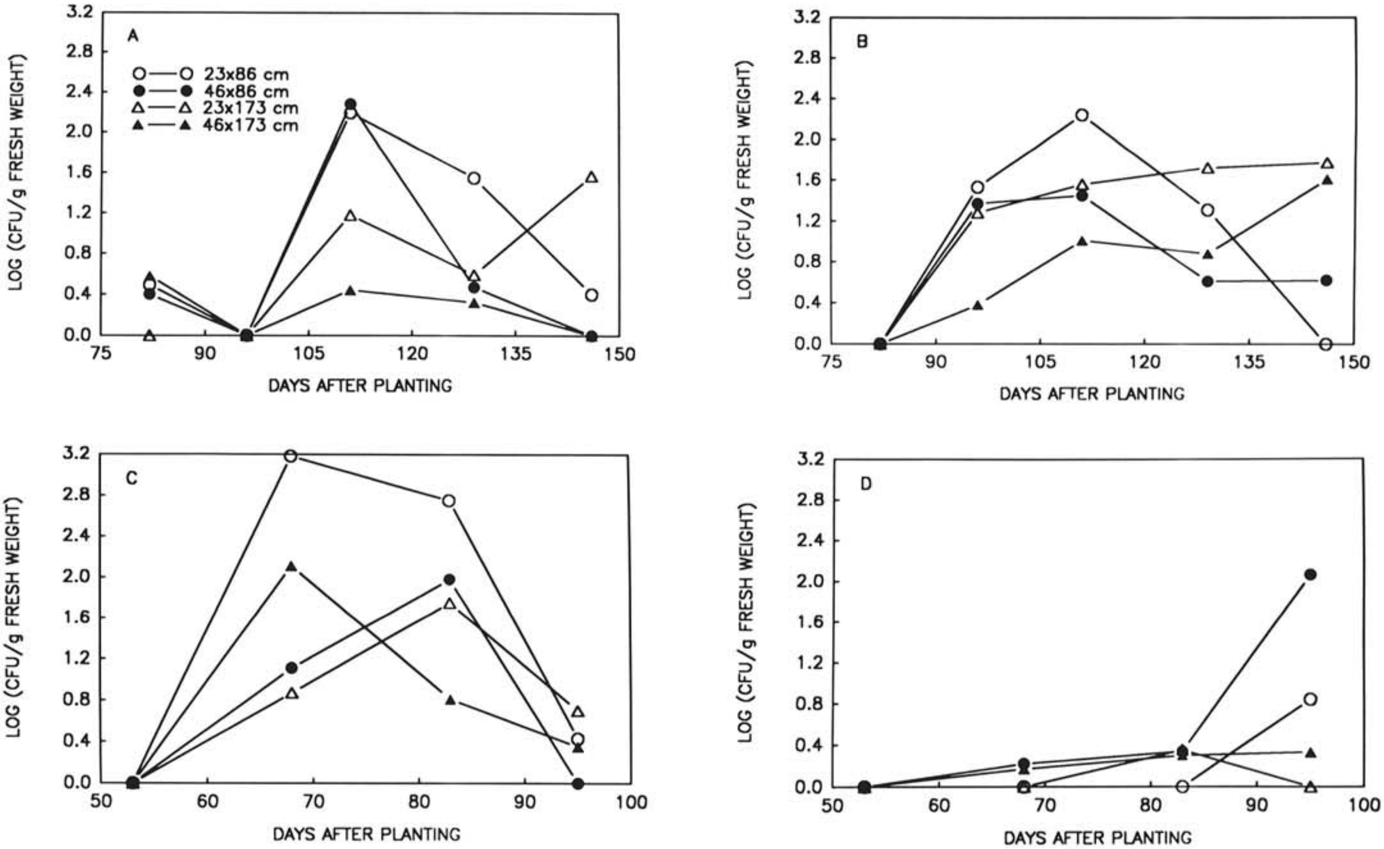

Fig. 5. Epiphytic populations of soft rot erwinias on potato foliage at four sites in Oregon in 1985. Treatments are within- and between-row spacings where ○ = 23 × 86 cm, ● = 46 × 86 cm, △ = 23 × 173 cm, ▲ = 46 × 173 cm. Each point is the mean of two leaflets averaged over six replications. **A,** Umatilla County west; **B,** Umatilla County east; **C,** Crook County west; **D,** Crook County east.

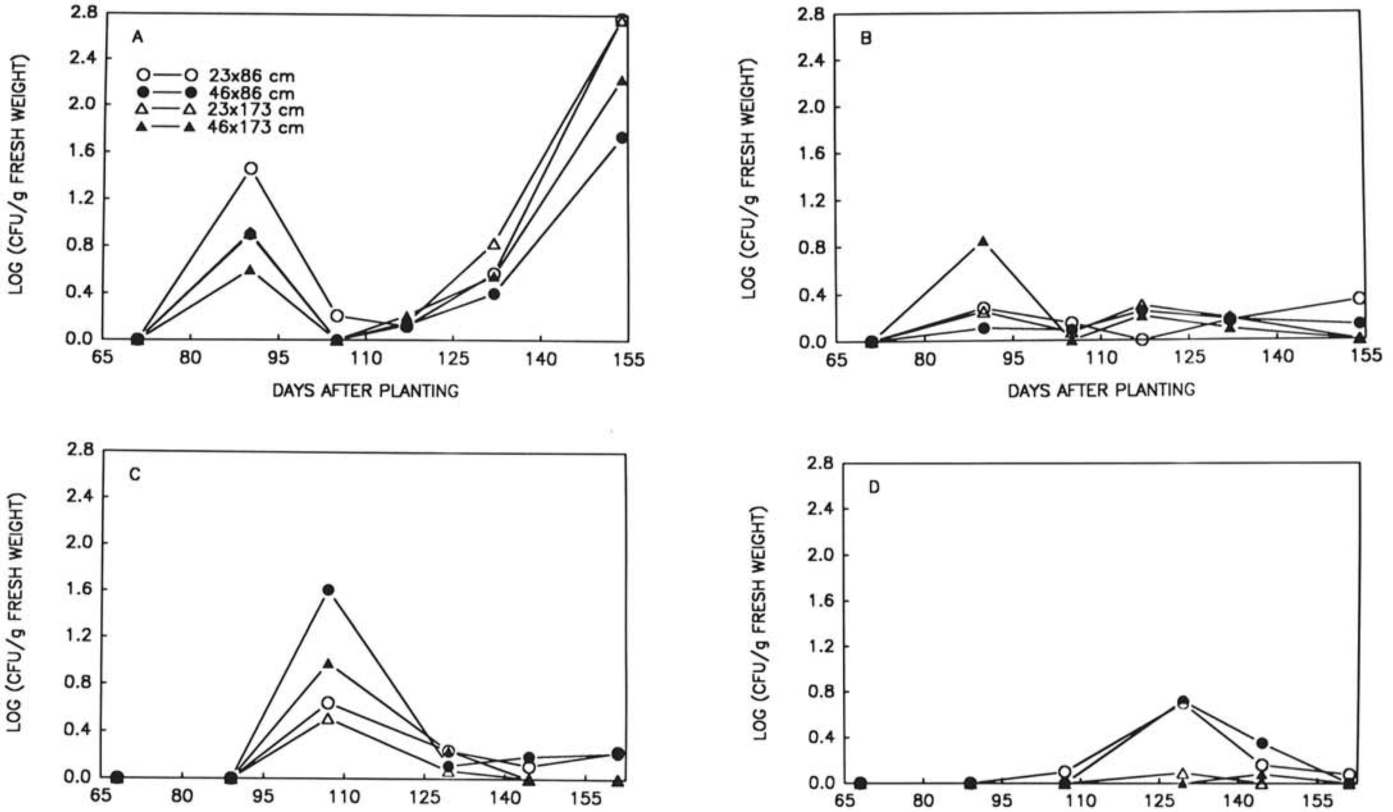

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TABLE 6. Effect of plant arrangement on average duration of leaf wetness in potatoes in Umatilla County in 1985 and Crook and Umatilla counties in 1986

Year, location and days after planting	Average duration of leaf wetness (hr)[a]			
	23 × 86 cm[b]	46 × 86 cm	23 × 173 cm	46 × 173 cm
1985				
Umatilla County				
68–82	6.6	...[c]	5.1	4.6
83–96	2.5	4.6	1.6	1.4
97–111	7.8	3.2	6.4	3.9
112–129	8.0	10.0	7.5	5.6
130–146	8.3	8.8	5.8	5.2
Mean	6.6	6.6	5.3	4.1
1986				
Umatilla County				
72–91	3.9	4.7	3.2	4.9
92–105	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	2.4
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 one sensor per treatment in 1985 and two sensors per treatment in 1986.

[b] First and second numbers represent within-row and between-row spacings, respectively.

[c] Data not available for this time period.

maintaining high yields may include controlling amount of water applied through irrigation, the frequency and timing of applications, planting arrangements, and rates of fertilizers as they affect canopy development.

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