Ecology and Epidemiology

Potato Blackleg in Progeny Plantings from Diseased and Symptomless Parent Plants

M. L. Powelson and J. D. Apple

Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331.
Technical Paper 7443 of the Oregon Agricultural Experiment Station. Supported in part by a grant from the Oregon Potato Commission.
Accepted for publication 29 July 1985.

ABSTRACT

Powelson, M. L., and Apple, J. D. 1986. Potato blackleg in progeny plantings from diseased and symptomless parent plants. Phytopathology 76: 56-60.

The incidence of potato stems with blackleg symptoms was studied in plots planted with seed tubers harvested from plants with or without blackleg symptoms. Plots at one location in 1982 and at two locations in 1983 were established with planting material from three different seedlots of early generation stocks of cultivar Russet Burbank. The incidence of stems with blackleg symptoms in plants from five of the six seedlots was significantly lower in progeny originating from symptomless parent plants than from parent plants with blackleg symptoms. However, average incidence of blackleg symptoms was high irrespective of the disease status of the parent plants (e.g., 85% in 1982 and 74.5% in 1983). *Erwinia carotovora* pv. *carotovora* was the principal pathogen associated with diseased progeny plants. However, both *E. c.* pv. *atroseptica* and *E. c.* pv. *carotovora* were isolated from diseased stems in the parent hills. Seed tubers from parent plants with or without blackleg symptoms were contaminated with *E. c.* pv. *carotovora* and *E. c.* pv. *atroseptica*. In one seedlot in both 1981 and 1982, a greater percentage of tubers from symptomatic parent plants was contaminated with *E. c.* pv. *atroseptica* than of tubers from symptomless parent plants. However, tubers from these parent plants with blackleg symptoms did not have signficantly more blackleg symptoms caused by *E. c.* pv. *atroseptica*.

Additional key words: irrigation, roguing, virus-tested stem-cut seed.

Blackleg of potatoes can occur wherever potatoes are grown. In general, disease incidence ranges from less than 2% of the stems in the temperate, nonirrigated regions (14) to as high as 75% of the stems in the sprinkler-irrigated fields of the Pacific Northwest (17). Traditionally, *Erwinia carotovora* pv. *atroseptica* has been regarded as the sole cause of blackleg particularly in cool, temperate, potato-producing regions of the world (12). But in warm, irrigated, potato-growing regions *E. c.* pv. *carotovora* is also associated with this disease (10,17,20).

In the past, it was generally thought that blackleg occurred primarily on plants grown from tubers harvested from plants with blackleg symptoms. In the 1950s, however, both Bonde (1) in Maine and Conroy (2) in New South Wales, Australia, reported no significant differences between the percentage of plants with blackleg symptoms grown from tubers produced by plants with blackleg symptoms or symptomless plants. In later studies, Pérombelon (11) in Scotland and DeBoer et al (4) in Wisconsin demonstrated that decaying mother tubers and not stem lesions

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

were a source of inoculum of *E. c.* pv. *atroseptica* and *E. c.* pv. *carotovora* for contamination of daughter tubers. Pérombelon (11) suggested that symptomless, but contaminated, daughter tubers could give rise to plants with blackleg.

Today, potato seed stocks are frequently derived from pathogen-tested stem cuttings. Although seed tubers may be initially free of *E. c.* pv. *carotovora* and *E. c.* pv. *atroseptica*, they are gradually recontaminated during seed increase and by the fifth multiplication may be extensively contaminated (15). Seed potatoes from the Oregon program for producing pathogen-tested stem cuttings are grown at cool, high-elevation sites in central, northeastern, and southern Oregon and may be planted commercially in the surrounding regions or at warm, low-elevation sites such as the Columbia Basin of Oregon and Washington.

Symptoms produced by soft rot erwinias in the field can be quite diverse. An inky black wet rot of the stem, commonly termed blackleg, is the most widely recognized symptom, but in some cases, the rot remains localized in the belowground stem and foliar wilting and leaf chlorosis are the only apparent aboveground symptoms. Frequently, a wet rot of the stem occurs with little or no discoloration of the tissues. This has been called stem soft rot (17). "Blackleg" is used in this paper to describe all the field symptoms caused by the soft rot erwinias.

The major objective of this research was to determine if potato plants with blackleg symptoms in early generation parent seed stocks are a good predictor of subsequent disease incidence. Our approach was to determine: the soft rot erwinia associated with blackleg symptoms in two seed potato regions in Oregon, the frequency of daughter tubers contaminated with soft rot erwinia, the disease incidence in progeny from parent plants with or without blackleg symptoms, and the soft rot erwinia associated with these symptomatic plants.

MATERIALS AND METHODS

Seed fields. In 1981 and 1982, stems and tubers were collected from 15 to 25 hills each of potato plants (*Solanum tuberosum* L.) with and without blackleg symptoms in three seed fields of potato cultivar Russet Burbank. Hills with symptomatic plants were identified and flagged in late August, while those with only healthy appearing stems were selected during sampling in early September. All the stems in each hill were harvested in September and visually assessed for disease symptoms. All symptomatic stems in 1981 and at least one symptomatic stem from each hill in 1982 were returned to the laboratory for isolation and characterization of strains of *E. carotovora*.

Tubers from each hill were hand harvested, and firm symptomless tubers from each hill were separated into two lots, placed in brown paper bags, and stored at 7 C until the following spring. One lot was reserved for planting while the other was assayed for the presence of *E. carotovora*.

A total of six seed fields were sampled in 1981 and 1982. The source of the seed planted in these fields was either Generation I or Generation II virus-tested stem-cut seed. One of the fields in 1981 and two of the fields in 1982 were located in Wallowa County, OR. These seed fields, elevation about 1,265 m, were irrigated with solid-set sprinklers. The other three seed fields were located in Crook County, OR. These seed fields, elevation about 945 m, were irrigated with center-pivot sprinklers.

Progeny plots. Tubers from seedlots representing parent plants with and without blackleg symptoms were hand cut into seed pieces weighing 42–57 g. The cutting knife was surface sterilized with 0.25% sodium hypochlorite before cutting tubers from each hill. After cutting, seed pieces were placed at 13 C for 6 days for suberization.

In 1982, plots were established in a randomized block design at the Central Oregon Experiment Station in Crook County on 18 May. Plots consisted of 15–25 sampling units; each sampling unit represented progeny from a single parent hill and consisted of two to eight hills. Each sampling unit was separated from other progeny hills within the row by a single hill of cultivar Red Pontiac. The entire experimental plot was bordered on all sides by a single row of Oregon nuclear seed of cultivar Russet Burbank. Seed pieces were spaced 23 cm apart in rows on 86 cm centers. The plots were located in a solid-set sprinkler-irrigated field that had been cropped to winter wheat in 1981 and to potatoes in 1980.

In 1983, plots were established in a randomized block design at the Central Oregon Experiment Station in Crook County on 17 May and in a commercial field in the Columbia Basin near Hermiston in Umatilla County on 27 April. Plots consisted of 15 and 10 sampling units at the Crook County and Umatilla County sites, respectively. Each sampling unit represented progeny from a single parent hill and consisted of two to eight hills. Each unit was separated from other progeny hills within the sampling unit by a single hill of cultivar Red Pontiac. Seeding rate was the same as the 1982 trial. The Crook County plots were located in a solid-set sprinkler-irrigated field that had been cropped to winter wheat in 1982 and potatoes in 1981. Water from the Deschutes River was used to irrigate the plots. The Umatilla County plots were irrigated with center pivot-sprinklers and the field was last cropped to potatoes in 1981. Winter wheat was grown in 1982. The source of the irrigation water was the Columbia River. Cultural and fertility practices for all plots were similar to those used commercially in the respective production areas.

Disease readings were made biweekly or monthly beginning 10 wk after planting. Each stem in each hill was visually evaluated for blackleg symptoms. At each date, 10–30 symptomatic stems were returned to the laboratory for isolation and characterization of strains of *E. carotovora*.

Plant and tuber isolations. For isolations from symptomatic stems, pieces of stem tissue, dissected from the advancing margin of the rot, were suspended in 1 ml of sterile distilled water. After 30 min of incubation at 22 C, the suspension was agitated and an aliquot streaked onto crystal violet pectate (CVP) medium (3). After 40–48 hr of incubation at 22 C, colonies resembling typical *E. carotovora* were subcultured on fresh CVP medium. Single colonies were then transferred to nutrient agar slants for maintenance.

The tuber incubation method (6) was used on at least one tuber from each hill to assay for the presence of *E. carotovora*. Ten lenticels per tuber were punctured with sterile toothpicks. Tubers were individually wrapped in moist paper toweling and incubated at 24 C for 4 days in plastic bags. After incubation, isolations were made from decayed tissues on CVP medium. In total, 462 and 503 tubers were assayed from the 1981 and 1982 seed fields, respectively.

Soil and water isolations. In the 1983 progeny trials, 10 soil samples were collected at planting and biweekly during the season at both locations. Soil samples were taken with a standard 2.54-cm-diameter tubular soil sampler inserted to a depth of 20 cm. Each soil sample was placed in individual plastic bags and stored at 5 C until processed.

At biweekly intervals beginning in June, 10 water samples were collected from the irrigation water as it was applied to the field. Each water sample was placed in 200-ml plastic bottles and returned to the laboratory where it was processed immediately.

About 4 g of soil was placed in a 40-ml vial, then enrichment pectate medium (9) was added to fill the vial. With the water samples 20 ml of water was added to a 40-ml vial, then 20 ml of enrichment pectate medium was added. In both instances, the vials were capped with Parafilm, incubated at 22 C for 2 days, then serially diluted in sterile water and plated on CVP medium to determine the presence of *E. carotovora*. Cultures were purified by streaking on CVP and stored on nutrient agar slants. Biochemical tests were performed on all strains.

Characterization of strains of *E. carotovora*. Strains of *E. c.* pv. *atroseptica* were distinguished from strains of *E. c.* pv. *carotovora* by acid production from α-methyl glucoside (16), absence of growth at 36 C, and production of reducing substances from sucrose following the procedures of Stowell (21). To distinguish *E. c.* pv. *carotovora* from *E. chrysanthemi*, phosphatase production was tested by using the procedure described by De Boer et al (5). All strains were tested for ability to cause soft rot of a potato tuber slice.

TABLE 1. Strains of *Erwinia carotovora* pv. *carotovora* (Ecc) and *E. carotovora* pv. *atroseptica* (Eca) associated with blackleg symptoms in three Russet Burbank seed potato fields in 1981 and 1982

	Strains isolated (%)			
	Crook County[b]		Wallowa County[b]	
Year and seedlot[a]	Ecc	Eca	Ecc	Eca
1981				
Seedlot 1	...	...	53	47
Seedlot 2	38	62	...	...
Seedlot 3	90	10	...	...
1982				
Seedlot 1	...	...	32	68
Seedlot 2	...	...	23	77
Seedlot 3	62	38	...	...

[a]Seedlots 1 and 2 in 1981 were grown from Generation I, virus-tested stem-cut seed; seedlot 3 in 1981 and seedlots 1, 2, and 3 in 1982 were grown from Generation II virus-tested stem-cut seed.
[b]Oregon.

TABLE 2. Potato tuber contamination with *Erwinia carotovora* pv. *carotovora* (Ecc) and *E. carotovora* pv. *atroseptica* (Eca) in three seedlots of cultivar Russet Burbank harvested from plants with and without blackleg symptoms in Oregon in 1981 and 1982

	Tuber contamination (%)					
Parent disease status and	1981			1982		
seedlot	Ecc	Eca	Total	Ecc	Eca	Total
Blackleg parents						
Seedlot 1[a]	2.5	1.3	3.8	1.2	4.9	6.2
Seedlot 2	9.6	19.2	28.7	6.0	0	6.0
Seedlot 3	3.4	6.7	10.1	50.0	30.2	80.2
Average	5.2	9.1	14.2	19.1	11.7	30.8
Symptomless parents						
Seedlot 1	3.5	0	3.5	2.2	5.4	7.6
Seedlot 2	6.6	1.9***[b]	8.5***	2.7	0	2.7
Seedlot 3	2.8	2.8	5.6	19.3***	7.2***	26.5***
Average	4.3	1.6	5.9	8.1	4.2	12.3

[a]Seedlots 1 and 2 in 1981 were grown from Generation I virus-tested stem-cut seed; seedlot 3 in 1981 and seedlots 1, 2, and 3 in 1982 were grown from Generation II virus-tested stem-cut seed.
[b]Asterisks indicate means for seedlots from symptomless parents are significantly different ($P<0.001$) from corresponding means for seedlots from blackleg parents as determined by a Student's *t*-test.

RESULTS

E. c. pv. *carotovora* was associated with stems with blackleg symptoms in the seed fields studied in Crook County (Table 1). In 1981 and 1982, respectively, 71 and 62% of the strains isolated from diseased stems at this location were characterized as *E. c.* pv. *carotovora*. However, stems in seedlot 2 in 1981 were more often infected with *E. c.* pv. *atroseptica* than with *E. c.* pv. *carotovora*. At the Wallowa County site, both *E. c.* pv. *atroseptica* and *E. c.* pv. *carotovora* were isolated with similar frequency from diseased stems in 1981 whereas in 1982, 73% of the strains were characterized as *E. c.* pv. *atroseptica*. *E. chrysanthemi* was not recovered from any of the stems sampled.

Seed tubers harvested from plants with or without blackleg symptoms were contaminated with soft rot erwinia (Table 2). None of the tubers were contaminated with detectable levels of *E. chrysanthemi*. In seedlot 2 in 1981 and seedlot 3 in 1982 there was significantly more ($P<0.001$) tubers from plants with blackleg symptoms contaminated with *E. c.* pv. *atroseptica* than from symptomless plants. Both of these seedlots plus seedlot 3 in 1981 were grown on the same farm in Crook County. Only with seedlot 3 in 1982 was there a significantly higher percentage ($P<0.001$) of the daughter tubers from parent plants with blackleg symptoms contaminated with *E. c.* pv. *carotovora* compared with tubers from symptomless parent plants. Similar significant differences were observed for the total percentage of tubers contaminated with *E. c.* pv. *atroseptica* and *E. c.* pv. *carotovora*.

A soft rot of the stem was the predominant "blackleg" symptom observed in the progeny plots throughout the season. Blackleg was first observed in all plots about 12 wk after planting in 1982 and 1983 (Table 3). At the end of the season the average incidence of stems with blackleg symptoms at Crook County in 1982 was 92.8% in plots originating from tubers from parent plants with symptoms compared with 74.6% in plots planted with tubers from symptomless parent plants. Similar differences were observed at both sites in 1983. For all three seedlots in 1982 and seedlots 1 and 2 at both locations in 1983, the incidence of stems with blackleg symptoms was significantly lower (Table 3) in progeny originating from tubers harvested from healthy appearing plants than in progeny from symptomatic parent plants. However, the difference in the incidence of blackleg in progeny plantings originating from parent plants with blackleg symptoms versus symptomless-parent plants averaged only 18.2% in 1982 and 19.3 and 10.2% at the Crook County and Umatilla County sites, respectively, in 1983. Furthermore, the percentage of stems with blackleg symptoms at both a cool, short-season site (Crook County; 902 degree days [base 10 C] after planting) and a warm, long-season site (Umatilla County; 1,441 degree days) did not differ significantly.

TABLE 3. Seasonal incidence of blackleg symptoms in potato stems of plants grown at two Oregon locations in 1982 and in 1983 from three seedlots of cultivar Russet Burbank which originated from parent plants with or without blackleg symptoms

	Stems with symptoms (%)								
	1982		1983						
	Crook County		Crook County			Umatilla County			
Source and seedlot	93[a]	108	74	94	118	72	83	105	147
Blackleg parents									
Seedlot 1[b]	0.4	92.7	0	30.4	87.0	0	17.9	51.3	79.5
Seedlot 2	0.8	95.6	0.3	33.1	78.5	0	27.1	55.0	79.6
Seedlot 3	1.0	90.2	0	44.5	82.4	8.3	18.8	55.2	84.2
Average		92.8			82.6				81.1
Symptomless parents									
Seedlot 1	0.4	82.7**[c]	0	30.9	53.2***	4.7	21.4	41.5	60.2**
Seedlot 2	1.6	82.0***	0	28.9	55.2***	0	14.7	43.9	67.9†
Seedlot 3	1.8	59.2***	0	42.9	81.7	0	32.0	60.6	84.5
Average		74.6***			63.4***				70.9**

[a]Days from planting.
[b]Seedlots 1 and 2 in 1981 were grown from Generation I virus-tested stem-cut seed; seedlot 3 in 1981 and seedlots 1, 2, and 3 in 1982 were grown from Generation II virus-tested stem-cut seed.
[c]Asterisks indicate means for seedlots from symptomless parents are significantly different from corresponding mean for seedlots from blackleg parents as determined by a Student's *t*-test. † = $P<0.10$; ** = $P<0.01$ and *** = $P<0.001$.

In the 1982 progeny trials, both *E. c.* pv. *carotovora* and *E. c.* pv. *atroseptica* were recovered from symptomatic stems (Table 4). However, 91% of the strains were characterized as *E. c.* pv. *carotovora*. The predominant soft rot erwinia isolated from symptomatic stems was also *E. c.* pv. *carotovora* at both locations in 1983. *E. chrysanthemi* was not isolated from symptomatic stems. Plants grown from seed tubers from parent plants with blackleg symptoms caused by *E. c.* pv. *atroseptica* did not have significantly more blackleg symptoms caused by *E. c.* pv. *atroseptica* than did parent plants without symptoms.

At the Crook County and Umatilla County plots, respectively, *E. c.* pv. *carotovora* was recovered from 58 and 47% of the soil samples. Neither *E. c.* pv. *atroseptica* nor *E. chrysanthemi* was recovered from the soil samples. Irrigation water at both locations was contaminated only with *E. c.* pv. *carotovora*. At the Crook County and Umatilla County plots, respectively, 67 and 45% of the water samples yielded this soft rot erwinia.

TABLE 4. Strains of *Erwinia carotovora* pv. *carotovora* (Ecc) and *E. carotovora* pv. *atroseptica* (Eca) associated with blackleg symptoms in cultivar Russet Burbank potato plants at two locations in Oregon

Source and seedlot	Number of strains					
	1982		1983			
	Crook County[a]		Crook County[a]		Umatilla County[a]	
	Ecc	Eca	Ecc	Eca	Ecc	Eca
Blackleg parents						
Seedlot 1[b]	9	3	12	0	23	1
Seedlot 2	8	2	17	0	17	0
Seedlot 3	10	0	12	0	20	0
Subtotal	27	5	41	0	60	1
Symptomless parents						
Seedlot 1	13	0	13	0	14	0
Seedlot 2	33	1	15	0	25	0
Seedlot 3	5	1	14	0	21	0
Subtotal	51	2	42	0	60	0
Totals	78	7	83	0	120	1

[a]Oregon.
[b]Seedlots 1 and 2 in 1981 were grown from Generation I virus-tested stem-cut seed; seedlot 3 in 1981 and seedlots 1, 2, and 3 in 1982 were grown from Generation II virus-tested stem-cut seed.

DISCUSSION

Earlier reports (1,2) suggest there is no correlation between the presence or absence of blackleg symptoms in parent plants and the incidence of disease in progeny plantings. These early studies were conducted with seed tubers that had been increased through a nonlimited generation seed increase program in which a high percentage of tubers are frequently contaminated with soft rot erwinia. Today, many seed programs employ a limited generation scheme based on stem-cut sources or the recycling of pathogen-tested tubers. Seed stocks derived from stem cuttings may become contaminated with *E. c.* pv. *carotovora* and *E. c.* pv. *atroseptica*, but are generally not extensively contaminated until later on in their multiplication (15). In this study, the incidence of stems with blackleg symptoms was very high (Table 3); however, the percentage of seed tubers contaminated with *E. c.* pv. *carotovora* and *E. c.* pv. *atroseptica* was low for all seedlots but seedlot 3 in 1982 (Table 2). The high incidence of seed tuber contamination in seedlot 3 in 1982 may explain, in part, why no significant difference in blackleg incidence was observed in progeny plantings originating from symptomless and blackleg-affected parent plants.

The total amount of disease observed in this study, however, cannot be attributed solely to tuberborne inoculum. *E. c.* pv. *carotovora* was the predominant soft rot erwinia associated with disease symptoms in the progeny trials and was isolated frequently from diseased stems in the seed fields. Soilborne strains of *E. c.* pv. *carotovora* have been reported to cause plant infection under field conditions (8,18) and in this study, *E. c.* pv. *carotovora* was isolated frequently from soil samples collected during the 1983 growing season. In addition, inoculum of *E. c.* pv. *carotovora* was introduced into the potato crop in irrigation water that originated from surface water sources. This inoculum may be effective in plant infection during the current season (19). Finally, plants produced from the nuclear seed stocks may have served as a source of inoculum. Nuclear seed potatoes from Oregon's limited generation scheme have been contaminated *E. c.* pv. *atroseptica* and *E. c.* pv. *carotovora* (M. L. Powelson, *unpublished*). However, the frequency of tuber contamination has been less than 2%.

In general, more losses due to blackleg occur in warm than in cool regions (14). Harrison (7) suggested that this may be true when seed potatoes produced in cool regions, where chances for higher levels of seed tuber contamination by *E. c.* pv. *atroseptica* and *E. c.* pv. *carotovora* are greater, are planted in warmer areas. In the current study, seed tubers were produced at relatively cool, high elevation sites, and the percentage of tubers contaminated with soft rot erwinia was low in five of the six seedlots. A blackleg problem may depend more upon whether or not fields are irrigated and if water contaminated with *E. c.* pv. *carotovora* is applied. Blackleg expression is favored by prolonged wet conditions after plant emergence (14), and in Oregon, overhead irrigation frequently creates wet conditions in the canopy. The frequent application of irrigation water may explain, in part, the high incidence of blackleg expression in the progeny trials. Pérombelon (13) suggested that if crops in cool nonirrigated seed-producing areas were subjected to a similar irrigation regime as found in hot, irrigated situations, disease incidence would be equally high.

With Oregon's certification program the visual identification of blackleg symptoms in some classes of seed is used as an indicator of the presence of *E. carotovora* in seed stocks. Roguing of plants with blackleg symptoms, which is done two or more times during the growing season, is practiced routinely in many seedlots regardless of origin of the seedlot. Removal of diseased plants and their daughter tubers in early generation material will significantly reduce the incidence of blackleg in the next generation (Table 3). However, despite the roguing of plants with blackleg symptoms in seed fields, the amount of disease expressed in the sprinkler-irrigated commercial fields in Oregon remains high. A better understanding of environmental relationships involved in disease initiation and expression under irrigated conditions is essential if successful disease management strategies are to be developed.

LITERATURE CITED

1. Bonde, R. 1950. Factors affecting potato blackleg and seed piece decay. Maine Agric. Exp. Stn. Bull. 482. 31 pp.
2. Conroy, R. J. 1952. Blackleg of potatoes in New South Wales. The question of seed treatment. Agric. Gaz. 63:534-536.
3. Cuppels, D., and Kelman, A. 1974. Evaluation of selective media for isolation of soft rot bacteria from soil and plant tissue. Phytopathology 64:468-475.
4. De Boer, S. H., Cuppels, D. A., and Kelman, A. 1978. Pectolytic *Erwinia* spp. in the root zone of potato plants in relation to infestation of daughter tubers. Phytopathology 68:1784-1790.
5. De Boer, S. H., Copeman, R. J., and Vruggink, H. 1979. Serogroups of *Erwinia carotovora* potato strains determined with diffusible somatic antigens. Phytopathology 69:316-319.
6. De Boer, S. H., and Kelman, A. 1975. Evaluation of procedures for detection of pectolytic *Erwinia* spp. on potato tubers. Am. Potato J. 52:117-123.
7. Harrison, M. D. 1983. Blackleg and soft rot epidemiology as it is now understood. Pages 41-48 in: Proc. 1983 Washington Potato Conf. and Trade Fair. 1-3 February 1983, Moses Lake.
8. Maher, E., Kelman, A., and De Boer, S. H. 1981. Infestation of potato tubers by *Erwinia carotovora* from soil. (Abstr.) Phytopathology 71:892.
9. Meneley, J. C., and Stanghellini, M. E. 1976. Isolation of soft-rot *Erwinia* spp. from agricultural soils using an enrichment technique. Phytopathology 66:367-370.
10. Molina, J. J., and Harrison, M. D. 1977. The role of *Erwinia carotovora* in the epidemiology of potato blackleg. I. Relationship of *E. carotovora* var. *carotovora* and *E. carotovora* var. *atroseptica* in potato blackleg in Colorado. Am. Potato J. 54:587-591.

11. Pérombelon, M. C. M. 1974. The role of seed tuber in the contamination by *Erwinia carotovora* of potato crops in Scotland. Potato Res. 18:205-215.
12. Pérombelon, M. C. M. 1982. The impaired host and soft rot bacteria. Pages 55-69 in: M. S. Mount and G. H. Lacy, eds. Phytopathogenic Prokaryotes. Vol. 2. Academic Press, New York.
13. Pérombelon, M. C. M. 1985. The blackleg problem as it affects seed potato exports. Proc. Int. Conf. on Potato Blackleg Disease. 26-29 June 1984, Edinburgh, Scotland. (In press).
14. Pérombelon, M. C. M., and Kelman, A. 1980. Ecology of the soft rot erwinias. Annu. Rev. Phytopathol. 18:361-387.
15. Pérombelon, M. C. M., Lowe, R., and Ballantine, E. 1976. Contamination by *Erwinia carotovora* of potato seed stocks in the process of multiplication. Potato Res. 19:335-347.
16. Phillips, J. A., and Kelman, A. 1982. Direct fluorescent antibody stain procedure applied to insect transmission of *Erwinia carotovora*. Phytopathology 72:898-901.
17. Powelson, M. L. 1980. Seasonal incidence and cause of blackleg and a stem soft rot of potatoes in Oregon. Am. Potato J. 57:301-306.
18. Powelson, M. L., and Apple, J. D. 1984. Soil and seed tubers as sources of inoculum of *Erwinia carotovora* pv. *carotovora* for stem soft rot of potatoes. Phytopathology 74:429-432.
19. Powelson, M. L., and Apple, J. D. 1984. Water as a source of inoculum in stem soft rot of potato. (Abstr.) Phytopathology 74:1100.
20. Stanghellini, M. E., and Meneley, J. C. 1975. Identification of soft rot *Erwinia* associated with blackleg of potato in Arizona. Phytopathology 65:86-87.
21. Stowell, L. J. 1982. The correlation of certain quantitative characters with the virulence of *Erwinia carotovora*. Ph.D. thesis. University of Arizona, Tucson. 49 pp.