

Infiltration of Lenticels of Potato Tubers by *Erwinia carotovora* pv. *carotovora* Under Hydrostatic Pressure in Relation to Bacterial Soft Rot

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ABSTRACT

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Aqueous suspensions of *Erwinia carotovora* pv. *carotovora* (Ecc), rhodamine dye, and india ink in water penetrated intact potato tubers that were submerged in them and subjected to hydrostatic pressures of 180–530 cm of water for 20 sec to 5 min. Stained tissues (usually located beneath or adjacent to lenticels) were more numerous in freshly harvested or warm (≥ 20 C) tubers than in stored or cold (4 C) tubers. The number of stained sites also increased as the concentration of Triton X-100, a nonionic surfactant, increased from 0.01 to 1% (w/v). When freshly harvested or commercially stored tubers were infiltrated with Ecc and incubated at 20 C in a mist chamber for 4 days, the severity of bacterial soft rot (surface area decayed) sometimes approached or equaled 100%. In contrast, severities seldom exceeded 50% in tubers that were submerged in suspensions of Ecc but not subjected to hydrostatic pressures resulting in infiltration. The high potential for soft rot associated with infiltration persisted for at least 4 days, whereas within that period, the increased potential associated with shallow immersion (5 cm) fell to levels that existed before inoculation.

Washing and fluming practices at potato packinghouses affect soft rot potential in washed potatoes (4,5). Populations of soft rot *Erwinia*,

concentration of a nonionic surfactant (Triton X-100), hydrostatic pressure on submerged tubers, and period of contact with water significantly affect soft rot potential expressed as disease severity after incubation in a mist chamber. Of these components, hydrostatic pressure (the pressure of water against tuber surfaces) would be the most difficult to manipulate as part of a control strategy for bacterial soft rot. Hydrostatic pressures result when tubers are submerged and are equal to immersion depths in pure water. In some packinghouse

systems, hydrostatic pressure is used to transport tubers from a collection sump below ground level to a packing line about 4 m above ground level.

High hydrostatic pressures may force water and bacteria suspended in water into potato lenticels, a process called infiltration. Although the permeability of lenticels to a fluorescein dye solution was correlated with susceptibility to *E. carotovora* pv. *atroseptica* (Eca) (2), the effect of infiltration on the potential for bacterial soft rot in potato tubers has not been documented. In tomato fruits, infiltration of stem scar tissues with *E. carotovora* pv. *carotovora* (Ecc) invariably led to bacterial soft rot (3). Both Eca and Ecc have been isolated from lenticels on potatoes from commercial storage but not from cortex tissues at least 2 mm below the periderm (15).

Potato tubers might become infiltrated during commercial production and handling practices. Flooding of potato fields has long been associated with preharvest and postharvest bacterial soft rot. During temporary flooding, lenticels may become infiltrated with bacteria; lenticels infiltrated with fluorescein were observed on tubers that had been submerged in a solution of that dye for 3.5 hr (2). Although the amount and duration of hydrostatic pressure that

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would cause infiltration of potato tubers submerged in water is unknown, commercial washing and fluming practices have been associated with an increased potential for bacterial soft rot (5,13,16,20). Moreover, lenticel infections increased when jet washers (1.4 kg/cm² water pressure) were used to clean tubers (12). Our objectives were to determine the levels of hydrostatic pressure and periods of exposure that would cause infiltration of freshly harvested tubers as well as those that had been in commercial storage facilities and the effect of infiltration on the soft rot potential of these tubers.

MATERIALS AND METHODS

General methods. Potato tubers selected for uniform size and absence of injury or disease were obtained from commercial storage facilities, commercial fields, or experimental plots. Specific details on cultivars, tuber age, and handling procedures are presented in the descriptions of the various treatments.

Inoculum of Ecc strain SR-38 was prepared from shake cultures as described previously (3,5). The concentration of cells in the suspensions, unless otherwise indicated, was 5×10^6 colony-forming units (cfu) per milliliter of tap water.

After treatment, tubers were incubated in a mist chamber at 20 C for 4 days (4,5,13). Some treatments included storage at 22 C in a humid chamber (15 min of water mist during 120 min), where tuber surfaces remained dry. Disease severity was rated by the Horsfall-Barratt system (5,10). These ratings were used in statistical analyses that were completed with the Statistical Analysis System (SAS Institute, Cary, NC) using the appropriate computer programs on the computing facilities at the University of Wisconsin, Madison.

Tubers were submerged in aqueous suspensions of bacteria or ink or dye solutions in a 19-L pressure-cooker and treated with air pressure to create the desired hydrostatic pressures. Tubers submerged in suspensions but not subjected to air pressure were exposed to about 5 cm of hydrostatic pressure, which equaled the average depth of submersion.

Treatments. Infiltration of lenticels with dye or ink. To determine the levels of hydrostatic pressure that would cause infiltration of lenticels on potatoes, tubers from various sources were submerged in aqueous solutions of rhodamine B dye (67 mg/L) or suspensions of india ink (100 g/L) and exposed to hydrostatic pressures for as long as 10 min. The tubers were removed, rinsed with tap water, and peeled. Stains on the inner surface of the peel (1 mm thick) were counted. The surface tension of some dye solutions or ink suspensions was reduced with Triton X-100 (Rohm and Haas, Philadelphia, PA), a nonionic

surfactant. Surface tensions of these solutions and suspensions were measured at air- and mineral oil-water interfaces with a Model 21 Surface Tensiometer (Fisher Scientific, Pittsburgh, PA).

The hydrostatic pressure needed to infiltrate stored tubers during a 10-min immersion period was determined with Russet Burbank tubers from a commercial storage facility in central Wisconsin (stored about 6 mo). Tubers initially at 4 C were warmed to room temperature (about 22 C), immersed in rhodamine dye containing 0, 0.01, 0.1, or 1% (w/v) Triton X-100, and exposed to pressures ranging from 5 to 530 cm of water.

The effect of tuber temperature at the time of immersion on the level of infiltration was examined. Russet Burbank tubers from commercial storage and tubers of two cultivars obtained from Florida (Red LaSoda and LaChipper, hand-harvested from plots near Hastings, FL, and stored at 4 C about 3 wk) were kept at 22 C in a humid chamber (>90% RH) for 24 hr. These tubers were paired with tubers at 4 C and treated with 180, 260, or 350 cm of pressure for 5 min. In a second series of tests, LaChipper tubers were stored at 22 or 32 C for 24 hr or at 22 C for 1.5, 3, or 4 hr. As in the previous tests, warmed tubers were paired with cold tubers, submerged in an india ink suspension + 0.2% (w/v) Triton X-100 and water, and exposed to a 350-cm hydrostatic pressure for 5 min. Tubers that were stored at 32 or 22 C for 24 hr had been enclosed in Kraft paper bags to retard moisture loss.

Pressure levels and exposure periods used to infiltrate tubers submerged in suspensions of Ecc were based on dye or ink submergence tests performed just before inoculation. An untreated sample of each tuber lot was moistened with water and incubated to determine the base-level disease severity associated with naturally occurring inocula and previous handling practices.

Infiltration with Ecc/4-day incubation. The effect on soft rot potential of infiltration of tubers with Ecc was examined with different samples of tubers. First, hand- and machine-harvested Superior tubers were treated for 5 min 3 days after harvest with two levels of inoculum (tap water or a suspension of Ecc), two levels of surfactant (with or without 0.1% Triton X-100), or two levels of hydrostatic pressure (5 or 180 cm), then incubated in the mist chamber. Both samples of tubers were from the same commercial field and collected the same day. The former, however, were removed from the soil about 18 hr before the latter because heavy rainfall stopped harvest operations and made it impossible to obtain both at the same time. Each treatment included five tubers. Infiltration by india ink began within 1 min in tubers treated with 180-cm hydrostatic pressure. Evidence of

infiltration was not observed in tubers immersed in india ink for 30 min without air pressure.

Infiltration with Ecc/4-day dry storage followed by 4-day incubation. New-crop Russet Burbank tubers (commercially stored in central Wisconsin for about 1.5 mo) were infiltrated with 1×10^6 , 1×10^7 , or 1×10^8 cfu per milliliter. Half of each treatment of 20 tubers was dried for 2 hr and stored under high humidity (>90% RH) at 22 C for 4 days to determine if lesions might develop on infiltrated tubers during dry storage. A hydrostatic pressure of 530 cm applied for 5 min was used to infiltrate these tubers. A control group was submerged similarly but not exposed to air pressure. After a 4-day storage in the humid room, the dry tubers were examined carefully for active lesions. When none were found, the tubers were moistened gently with tap water and incubated in the mist chamber for an additional 4 days.

Infiltration with Ecc/incubation for different periods of time. The effect of infiltration on disease severity after less than a 4-day incubation period was examined with Red LaSoda and LaChipper tubers, with freshly hand-harvested Russet Burbank tubers produced in central Wisconsin (plants not vine-killed), and with new-crop, commercially stored Russet Burbank tubers. The Red LaSoda, LaChipper, and stored Russet Burbank tuber lots were described before. In all three tests, a control group of inoculated tubers was incubated for the full 4-day period. Disease severity in all treatments was evaluated at the end of that period (96 hr).

Red LaSoda and LaChipper tubers were submerged in a suspension of Ecc, exposed to hydrostatic pressures of 180 or 490 cm for 4 min, and placed in the mist chamber. Five-tuber samples of each cultivar were removed after 0, 2, 4, 9, 22, 33, 46, and 70 hr, then stored in the humid chamber. In the latter series, tubers appeared to be dry within about 2 hr (except at infected lenticels).

Fresh, hand-harvested Russet Burbank tubers (plants not vine-killed) were submerged in water and suspensions containing 5×10^4 or 5×10^6 cfu per milliliter of Ecc with hydrostatic pressures of 5 or 350 cm for 5 min. After incubation in the mist chamber for 16, 20, 24, or 28 hr, five-tuber samples were removed, air-dried for about 1 hr, placed in polyethylene bags, and stored at 20 C in the humid chamber. Tuber surfaces were dry when the bags were opened.

Commercially stored, new-crop Russet Burbank tubers were immersed in a suspension of Ecc for 5 min, removed, submerged in tap water for 20 sec with hydrostatic pressures of 5 or 530 cm, and incubated. Samples of five tubers were removed at 24, 41, and 48 hr, air-dried in the laboratory, and stored in the humid chamber at 22 C.

RESULTS

Treatments. *Infiltration with dye on ink.* The criterion for infiltration of potato tubers was the accumulation of dye or ink at sites in the white cortex tissue beneath the periderm. Most accumulations were associated with lenticels; however, infiltration of tissues was observed around some eyes and vascular tissue beginning at the stolons of freshly harvested tubers. More spots were observed on the stolon than on the bud ends of the tubers. Generally, fewer than 5% of the lenticels on a given tuber were penetrated. Dye accumulation at breaks in the periderm associated with mechanical harvest or other injuries were not observed in any of the tuber samples. However, dye and ink penetrated the surface layers of cells in fresh cuts and bruises (less than 1 hr old).

Infiltration occurred more readily when Triton X-100 was added to dye solutions. Russet Burbank tubers at 22 C were immersed in rhodamine dye solutions containing 0–1% Triton X-100 and exposed to hydrostatic pressures of 230–530 cm for 10 min. After treatment with 530 cm of pressure, tubers in each solution were infiltrated. After the 490-cm treatment, only tubers in the 0.01, 0.1, and 1% Triton X-100 solutions were infiltrated, whereas after the 230-cm treatment, only those in the 1% Triton X-100 treatment were infiltrated. Unadjusted surface tensions at the air-water interface were 65, 36, 34, and 34 dynes/cm² for the 0, 0.01, 0.1, and 1% Triton X-100-rhodamine solutions, respectively, in contrast to 76 dynes/cm² for distilled water. Surface tensions measured at the oil-water interface for 0.01, 0.1, and 1% Triton X-100 in water and water alone were 10, 5, 3, and 48 dynes/cm², respectively.

Red LaSoda and LaChipper tubers that had been stored at 4 C for about 3 wk after harvest were infiltrated more easily than commercially cured Russet Burbank tubers that had been stored for nearly 9 mo (Table 1). Increased hydrostatic pressure and reduced surface tension were correlated with increased infiltration, whereas a low pulp temperature (4 C) at the time of treatment was associated with decreased infiltration. When Triton X-100 was in the dye solution, each of the Red LaSoda and two of the three LaChipper tubers exposed to the 180-cm pressure for 5 min were infiltrated at one or more points. However, when Triton X-100 was absent, none of the tubers were infiltrated. Fewer infiltration sites were observed in the cool tubers. In subsequent tests with LaChipper tubers, a 350-cm hydrostatic pressure and a suspension of india ink, tubers removed from cold storage 1.5–24 hr before treatment and held at 22 C were infiltrated in as many areas as those stored at 32 C for 24 hr. However, significantly fewer penetration points (1.3 vs. 18.4 per tuber) were

observed in tubers that had been removed from cold storage (4 C) just before treatment. Moreover, in peels of the latter, ink particles were restricted to relatively tiny pinpoint areas, whereas in tubers stored at 32 C, the ink particles had infiltrated much larger areas (up to 8 mm in diameter).

Infiltration with Ecc/4-day incubation. Nearly the entire surface of infiltrated, freshly harvested Superior tubers became diseased during incubation, whereas less than 40% of that of the noninfiltrated

tubers was affected (Table 2). When Triton X-100 was added to the suspension of Ecc, the entire surface of each hand-harvested tuber in both hydrostatic pressure treatments was soft-rotted. Moreover, immersion of tubers in an aqueous solution of this surfactant without suspended cells of Ecc increased disease severities well above base levels, not only in this test but also in tests reported previously (5). Skinned areas on machine-harvested tubers were relatively free of decay, evidence that wound

Table 1. Number of potato tuber lenticels in three cultivars penetrated by rhodamine dye in relation to tuber temperature, presence of a surfactant, and hydrostatic pressure on the tubers^a

Hydrostatic pressure (cm of water)	Surfactant ^b	Cultivar (tuber temperature [C])					
		Red LaSoda ^c		Russet Burbank ^d		LaChipper ^c	
		4	22	4	22	4	22
180	+	0	2	0	0	0	3
260	–	0	0	0	0	0	0
350	+	2	7	0	14	1	25
350	–	0	4	0	5	0	7

^a Average of three tubers submerged in a solution of rhodamine (67 mg/L) for 5 min. Individual spots of dye in the inner white tissues of peel (periderm) were counted as penetration points.

^b Triton X-100, 0.1% (w/v), in water, + = surfactant added and – = not added.

^c Treated within 3 wk of harvest.

^d Treated about 8 mo after harvest.

Table 2. Severity of bacterial soft rot after immersion of Superior potato tubers in water or suspensions of *Erwinia carotovora* pv. *carotovora* in relation to harvesting procedure, hydrostatic pressure, and presence of a surfactant^{a,b}

Inoculum ^c	Surfactant ^d	Percentage of surface area decayed after indicated hydrostatic pressure (cm of water)			
		Machine-harvested		Hand-harvested	
		4	180	5	180
+	+	82 ^e	96	100	100
+	–	38	83	36	96
–	+	43	63	30	86
–	–	15	34	22	63

^a Freshly harvested tubers immersed with hydrostatic pressure for 5 min, then incubated in mist chamber for 4 days at 20 C.

^b Probabilities for effects of inoculum surfactant, hydrostatic pressure, and harvest procedure were 0.0001, 0.0024, and 0.0663, respectively. Interactions were not significant.

^c Suspension containing 5×10^6 cfu per milliliter; + = inoculated and – = not inoculated.

^d Triton X-100, 0.1% (w/v); + = suspension of bacteria and – = water alone.

^e Each value is the average of five tubers.

Table 3. Severity of bacterial soft rot after immersion of Russet Burbank potato tubers in suspensions of *Erwinia carotovora* pv. *carotovora* in relation to hydrostatic pressure, inoculum concentration, and storage regime^{a,b,c}

Inoculum concentration (cfu/ml)	Hydrostatic pressure (cm of water)	Percentage of surface area decayed after indicated storage regime	
		4 Days wet	4 Days dry/4 days wet
1×10^8	5	58 ^d	3
	530	100	63
1×10^7	5	26	4
	530	91	43
1×10^6	5	19	3
	530	66	38

^a Tubers from commercial storage (about 2 mo from harvest to treatment).

^b Tubers were immersed with hydrostatic pressure for 5 min, then incubated in mist chamber for 4 days at 20 C or stored dry in humid room (>90% RH) at 20 C for 4 days followed by rewetting and incubation for 4 days.

^c Probabilities for effects of inoculum concentration, storage, hydrostatic pressure, and interaction of storage \times inoculum concentration were 0.0049, 0.0001, 0.0001, and 0.0154, respectively. Probabilities for effects of remaining interactions were not significant.

^d Each value is the average of five tubers.

healing had begun and the tissues were either nonporous, nonsusceptible, or both.

Infiltration with *Ecc*/4-day dry storage followed by 4-day incubation. Lesions were not observed on any of the tubers that were not infiltrated or infiltrated with suspensions containing 1×10^6 – 1×10^8 cfu per milliliter of *Ecc* and stored at 22 C in a humid chamber. However, when these tubers were moistened with water and incubated, substantial disease developed on infiltrated but not on noninfiltrated tubers (Table 3). The disease severity for the latter, regardless of inoculum concentration, was near the 2% base level determined for this tuber lot. Therefore, the increased potential for bacterial soft rot in potato tubers associated with immersion in suspensions of *Ecc* persisted for 4 days only in the infiltrated tubers.

Infiltration with *Ecc*/incubation for different periods of time. Infiltrated tubers became diseased much earlier than noninfiltrated tubers. In the first of a series of treatments that simulated the slow drying of wet tubers after washing, lesions were observed on tubers that had been incubated for only 9 hr and then dried (Table 4). However, the contents of all these early lesions were dry when the tubers were examined 85 hr later. Dried soft rot lesions have been called hard rots

(12,20). Hard rots were observed on 33 and 60% of the noninfiltrated (180 cm of water) and infiltrated (490 cm of water) tubers, respectively. None of the tubers incubated for 0, 2, or 4 hr had hard rots. Some of the lesions on the tubers sampled at 22 hr were still moist 74 hr later; they probably expanded while the dried tubers were held in the humid chamber. Host tissues surrounding these lesions were relatively free of discoloration. This type of lesion is hereafter called self-sustained. After 22 hr of incubation, three times as many self-sustained lesions had developed in the infiltrated as in the noninfiltrated tubers. After 46 hr, most lesions in the infiltrated tubers were self-sustained, whereas most lesions in the noninfiltrated tubers were hard rots. After 69 hr, lesions in both groups of tubers were mostly self-sustained.

Inoculum concentration had a significant impact on disease severity after infiltration but not after shallow-immersion treatment of freshly harvested Russet Burbank tubers incubated for 96 hr (Table 5). A 100-fold reduction in inoculum concentration led to an 8-hr delay in the development of disease, whereas infiltration advanced development by more than 8 hr. In this test and in the following test, disease severity ratings included only self-sustained or active lesions. Only one such lesion was

observed in the noninfiltrated tubers incubated for less than 96 hr (on a tuber removed from the mist chamber 28 hr after immersion in 5×10^6 cfu per milliliter). None of the tubers that had been removed from the mist chamber after 16 hr had self-sustained lesions, and only those infiltrated with the suspension containing 5×10^6 cfu per milliliter had hard rots.

Many infiltrated tubers in this experiment had an unusual symptom development. In addition to lesions associated with lenticels, the vascular ring area of some tubers was soft-rotted beginning at the stolon end and extending toward the bud end of the tuber. Firm tissues were located both inside and outside the decayed area and the outer tissues could be broken off in chunks. Ink-infiltration patterns in some of these tubers were consistent with infiltration of vascular tissues through the stolon. Thus, during infiltration of some tubers with soft rot *Erwinia*, bacteria presumably were forced through the stolon into the vascular ring area of the tuber. The vascular-ring soft rot symptom was not observed in tubers that were either not inoculated or inoculated by shallow immersion.

Infiltration had a similar effect on development of self-sustained lesions in Russet Burbank tubers from commercial storage. Infiltration of submerged tubers was observed after a relatively short (20-sec) exposure to 530 cm of water. Prior contamination of tuber surfaces with *Ecc* followed by immersion in tap water and exposure to hydrostatic pressures of 5 or 530 cm of water for 20 sec led to disease severities as high as 46%. After 96 hr of incubation, disease severities in the shallow-immersion and infiltration treatments were similar (37 and 39%, respectively). Corresponding values after the shorter incubation periods were 0–4, 1–19, and 11–46%, for 24, 41, and 48 hr, respectively.

DISCUSSION

When tubers are infiltrated with soft rot *Erwinia*, populations of these bacteria become located in living tissues usually in or immediately beneath lenticels. The unbroken periderm is nearly impervious to water; therefore, most penetration occurs through wounds and lenticels (1,2). Accumulations of dye or ink observed in our experiments and reported previously (2) would only occur in tissues with relatively large intercellular spaces. Such spaces occur in the lenticel, phelloderm, and cortex tissues (1,8). Most dye accumulations were in the peel (average thickness about 1 mm) rather than the underlying tissues; therefore, they were probably located in phelloderm and outer cortex tissues as well as in the lenticel.

The effect of infiltration on the soft rot potential of potato tubers was manifested

Table 4. Severity of bacterial soft rot after immersion of potato tubers in a suspension of *Erwinia carotovora* pv. *carotovora*^a in relation to period of incubation,^b hydrostatic pressure, and cultivar^{c,d}

Hydrostatic pressure (cm of water)	Cultivar	Percentage of surface area decayed after indicated incubation period (hr)				
		22	33	46	70	96
180	Red LaSoda	3 ^e	13	9	26	17
	LaChipper	4	4	15	17	13
490	Red LaSoda	9	43	82	82	85
	LaChipper	4	22	13	39	22

^a Immersed in 5×10^6 cfu per milliliter of tap water with hydrostatic pressure for 5 min.

^b Stored at 20 C in continuous mist of water, removed at given time, and stored in high humidity (>90% RH) at 20 C until 96 hr after inoculation.

^c Freshly harvested from experimental plots near Hastings, FL (about 3 wk from harvest to treatment).

^d Probability for effects of duration, hydrostatic pressure, cultivar, and interaction of cultivar \times hydrostatic pressure was 0.0001. Probabilities for remaining interactions were not significant.

^e Each value is the average of seven tubers evaluated 96 hr after inoculation.

Table 5. Severity of bacterial soft rot after immersion of hand-harvested Russet Burbank potato tubers in water or suspensions of *Erwinia carotovora* pv. *carotovora*^a in relation to period of incubation,^b hydrostatic pressure, and inoculum concentration

Inoculum concentration (cfu/ml)	Hydrostatic pressure (cm of water)	Percentage of surface area decayed after indicated incubation period (hr)			
		20	24	28	96
Tap water	5	0 ^c	0	0	13
	350	0	0	0	22
5×10^4	5	0	0	0	13
	350	0	0	3	58
5×10^6	5	0	0	0	13
	350	8	3	22	95

^a Immersed in water or suspension with hydrostatic pressure for 5 min.

^b Stored at 20 C in continuous mist of water, removed at given time, dried for 2 hr in the laboratory, then stored in polyethylene bags at 20 C until 96 hr after inoculation.

^c Each value is the average of five tubers evaluated 96 hr after inoculation.

in three ways. First, disease severity after a 4-day incubation was increased to levels well above those associated with tubers immersed in suspensions of Ecc but not infiltrated. However, bacterial soft rot did not inevitably occur after infiltration, even with inoculum concentrations as high as 1×10^8 cfu per milliliter and storage in high humidity; a progressive decay occurred only when tubers were covered with a film of water for 20–24 hr after infiltration. When cells of Eca were injected into dry tubers that were stored aerobically, De Boer and Kelman (7) concluded that a concentration of more than 10^9 cells per injection site would be required to initiate lesions in 50% of aerobic tubers. In contrast, one cell could initiate a lesion in anaerobic tissue with a 5-day incubation period (14). Because inoculum concentrations of 10^8 cfu per milliliter or more in packinghouse water systems are unlikely, the major contributing factor to bacterial soft rot in uninjured potatoes in commercial operations is the continuous presence of a water film covering the entire surface of the tuber. The water film prevents adequate gas exchange and tuber tissues become anaerobic within 2.5 hr at 21 C (6). Ruehle's (18) recommendations on drying for control of bacterial soft rot are probably more important for infiltrated tubers than for tubers inoculated by shallow immersion.

The second effect of infiltration on the soft rot potential of potato tubers was that the increased soft rot potential associated with infiltration persisted over time. During humid storage of dry tubers, bacteria in living tissues of the tuber apparently not only remained viable but were also capable of initiating lesions. There was no apparent host response to the bacteria under these conditions. On the other hand, bacteria on the surface of lenticels either became isolated from susceptible tissues or were reduced in number, because after a 4-day humid storage period, disease severity levels in noninfiltrated tubers were similar to the base level determined for the tuber lot. Pérombelon (15) reported that the number of soft rot *Erwinia* in lenticels of commercially stored tubers remained relatively constant over several months of winter storage, whereas those on the periderm decreased rapidly. Therefore, it is likely that the bacteria in lenticels on noninfiltrated tubers were either isolated from potentially susceptible tissues by changes in the outer tissue layers or the outer tissues became more resistant to bacterial soft rot because of a decrease in tissue water potential associated with drying (11).

The third effect of infiltration was enhancement of the rate of lesion development. Large lesions capable of continued development under dry, aerobic conditions developed in infiltrated tubers after relatively short incubation periods (20–24 hr). Self-sustained lesions

occur when activity of bacteria in the lesion and the extent of tissue damage lead to an anaerobic environment at the margin of the lesion (14). This internal condition prevents host resistance responses (7,8). Lesions not large enough to continue to expand are walled off by the host (8) and become hard rots (12,20). Factors that interact with duration of wet storage in the creation of self-sustained lesions include time to the onset of tissue maceration, tissue susceptibility, amount of tissues initially attacked, and number or virulence of bacteria deposited in tissues. In infiltrated tubers, bacteria (possibly high populations) are positioned among a relatively large number of host cells several cell layers below the relatively resistant outer periderm layer. Self-sustained lesions are threats to tubers in consumer packages as well as commercial storages. Bacteria in water ooze released in the decay process not only provide fresh inoculum for adjacent tubers but may also release the free water needed to cause these tubers to become anaerobic. Conversely, other than an adverse appearance, hard rots are relatively nonthreatening unless exposure to free water or mechanical damage allows the bacteria in them to become active.

The effects of infiltration on the soft rot potential appeared to be entirely associated with the location of the bacteria in tuber tissues. Populations of soft rot *Erwinia* in tuber peels were not detectably (at least fivefold to 10-fold) increased by infiltration compared with those resulting from shallow-immersion inoculation (J. A. Bartz, unpublished). In addition, evidence of tissue damage in tubers stored dry that might be associated with the infiltration of tissues with bacteria or water per se was never observed.

The likelihood that tubers will be infiltrated during commercial handling depends on many factors. The most important are level of hydrostatic pressure, period of immersion in water, lenticel porosity, and surface tension of the water. Packinghouse design and/or management practices may also contribute to infiltration. When tubers are flumed long distances or pumped upward several meters, conditions are highly favorable for infiltration. The depth of immersion in water is directly correlated with hydrostatic pressure; a pressure of 180 cm of water occurs when tubers are submerged to that depth (180 cm). Therefore, infiltration is enhanced in deep dump tanks and when tubers remain submerged in water for several minutes or more.

The likelihood of infiltration was increased with decreases in surface tension measured at the oil-water interface (17). Thus, the wetting of suberized surfaces by a surfactant appears to be more important than reduction of surface tension of water

interfacing with air in the lenticels. Increased bacterial soft rot occurred in tubers that were treated with suspensions of Ecc or water containing surfactant whether hydrostatic pressure was applied or not. This was observed previously and may be related to the effect of Triton X-100 on tuber tissues (5). The influence of other surfactants, including potato wash water additives, in this regard is not known. However, the apparent virulence of several isolates of *E. chrysanthemi* pv. *zeae* to sweet corn was enhanced by addition of Tween 40, another surfactant, to suspensions of those bacteria (9). Some Florida isolates of Ecc were pathogenic to sweet corn plants when Tween 20 was in the suspension (0.9%, w/v) (19) but not when it was absent (J. A. Bartz, unpublished). Infiltration of uncured tubers (cultivars Superior and Atlantic) that were immersed in a suspension of Ecc (1×10^6 cfu per milliliter) either mixed with india ink or alone plus 0.1% Triton X-100 led to active soft rot lesions in dry tubers stored aerobically at 20 C (J. A. Bartz, unpublished). Whether other soaps or wetting agents would behave similarly is not known. However, addition of these types of materials to water handling systems at packinghouses for purposes of improved cleaning of tuber surfaces may increase soft rot hazards.

The relative porosity of lenticels on tubers is another component of the potential for infiltration. Adams (2) first noticed that lenticel porosity decreased with increased tuber age. We observed that higher hydrostatic pressures were required to infiltrate stored tubers than freshly harvested tubers. In addition, lenticels on warm tubers were more easily infiltrated than those on cold tubers. However, as noted previously, handling of cold tubers is more likely to cause bruise injury, which in turn results in an increase in bacterial soft rot (4). Finally, lenticels on tubers of certain cultivars may be more prone to infiltration than those of other cultivars (2).

A prediction of whether lenticels are infiltrated during various commercial handling practices cannot be made without additional information. The amount of injury and lenticel porosity on various types of tubers along with values for surface tension of water, period of immersion, and hydrostatic pressures that normally occur in commercial handling are needed. In the meantime, practices that might lead to infiltration should be avoided because infiltrated tubers are so difficult to handle safely. Lesions can appear within 11 hr if infiltrated tubers become wet or damaged. If the period of free moisture is extended another 9 hr, lesions may become self-sustained and, as a result, impervious to drying. Moreover, the high soft rot potential of infiltrated tubers appears to persist during storage.

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