Table 12 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Blackleg Symptom Development				Latent Stem Infection[4]			
			Percent infected	Strains recovered			Percent infected	Strains recovered		
				#Ecc	#Eca	Eca serogroup[5]		#Ecc	#Eca	Eca serogroup[5]
Aerosol Ecc	6.00	CR	0.0	-[6]	-	-	67	2	-	-
		NR	0.0	-	-	-	100	1	1	1XNR
		RB	0.0	-	-	-	33	1	-	-
		SA	0.0	-	-	-	75	3	-	-
		Average	0.0				68.8			
Rain Ecc	6.06	CR	0.0	-	-	-	0	-	-	-
		NR	0.0	-	-	-	0	-	-	-
		RB	0.0	-	-	-	50	-	2	1XNR
		SA	0.0	-	-	-	0	-	-	-
		Average	0.0				12.5			
Snow Ecc (NID)	5.80	CR	0.0	-	-	-	50	1	-	-
		NR	0.0	-	-	-	67	2	-	-
		RB	0.0	-	-	-	80	3	1	1XNR
		SA	0.0	-	-	-	40	1	1	-
		Average	0.0				59.3			

Continued next page

Table 12 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Blackleg Symptom Development				Latent Stem Infection[4]			
			Percent infected	Strains recovered #Ecc	#Eca	Eca serogroup[5]	Percent infected	Strains recovered #Ecc	#Eca	Eca serogroup[5]
Aerosol Eca	6.14	CR	0.0	-[6]	-	-	100	-	2	2XNR
		NR	20.0	-	2	2XNR	0	-	-	-
		RB	0.0	-	-	-	75	-	3	2XNR
		SA	0.0	-	-	-	40	-	2	2XNR
		Average	5.0				53.8			
Rain Eca	5.84	CR	0.0	-	-	-	-	-	-	-
		NR	0.0	-	-	-	-	-	-	-
		RB	0.0	-	-	-	40	-	2	2XNR
		SA	0.0	-	-	-	50	-	1	1XNR
		Average	0.0				45.0			
Snow Eca	5.92	CR	20.0	-	2	2XNID	0	-	-	-
		NR	0.0	-	-	-	-	-	-	-
		RB	0.0	-	-	-	75	-	3	3XNID
		SA	0.0	-	-	-	75	1	2	2XNID
		Average	5.0				50.0			

Continued next page

Table 12 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Blackleg Symptom Development: Percent infected	Strains recovered: #Ecc	#Eca	Eca serogroup[5]	Latent Stem Infection[4]: Percent infected	Strains recovered: #Ecc	#Eca	Eca serogroup[5]
Blackleg Eca (SKI)	6.22	CR	33.3	-[6]	2	2XSKI	67	-	2	2XSKI
		NR	40.0	-	4	4XSKI	-	-	-	-
		RB	0.0	-	-	-	80	-	4	3XSKI
		SA	0.0	-	-	-	40	-	2	2XSKI
		Average	18.3				62.3			
		Location Average	3.5				45.0			

[1] Original sources of strains used in the studies were aerosols and rain collected in Oregon and snow and a potato stem with typical blackleg symptoms from Colorado. Strain designations: Ecc = E. carotovora subsp. carotovora and Eca = E. carotovora subsp. atroseptica.

[2] Inoculum was applied in irrigation water seven times during the growing season in a total volume of 18 l per application. An additional 18 l of check water was applied to each plot after inoculation. Check water contained low natural populations of Erwinia, mostly Ecc.

[3] Cultivar designations: CR = Centennial Russet, NR = Norgold Russet, RB = Russet Burbank, SA = Sangre.

[4] Latent stem infection was detected by anaerobic enrichment sections of symptomless stems (see text).

Continued next page

Table 12 footnotes continued.

[5] Eca strains isolated were tested against Serogroup I (SKI) antiserum following the method of De Boer et al. (12). Results are reported as the number of strains X the serological reaction. Serological reactions are: NR = no reaction with Serogroup I, NID = a characteristic reaction of non-identity with Serogroup I and SKI = a reaction of identity with Serogroup I.

[6] " - " = not done or not applicable.

Table 13. Effect of Erwinia-contaminated irrigation water on infestation of potato tubers at two locations in Colorado. Seven E. carotovora strains were tested.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Tuber isolations (Periderm Peel Method)[4]				
			Presence of Erwinia (0 or 1)	Estimated cfu/g	Strains Recovered		
					# Ecc	# Eca	Eca serogroup[5]
Fort Collins							
Check	0.86	CR	0	0.00	-	-	-
		NR	1	0.00	2	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	25%	0.00			
Aerosol Ecc	6.00	CR	1	7.43	5	-	-
		NR	1	0.25	3	-	-
		RB	1	18.81	5	-	-
		SA	1	5.67	2	3	3XNID
		Average	100%	8.0			

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Table 13 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Tuber isolations (Periderm Peel Method)[4]				
			Presence of *Erwinia* (0 or 1)	Estimated cfu/g	Strains Recovered		
					# *Ecc*	# *Eca*	*Eca* serogroup[5]
Rain *Ecc*	6.06	CR	0	0.00	-	-	-
		NR	1	0.00	2	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	25%	0.0			
Snow *Ecc*	5.80	CR	0	0.00	-	-	-
		NR	0	0.00	-	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	0%	0.00			
Aerosol *Eca*	6.14	CR	0	0.00	-	-	-
		NR	1	0.00	-	2	2XNR
		RB	0	0.00	-	-	-
		SA	1	0.00	-	2	2XNR
		Average	50%	0.0			

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Table 13 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Tuber isolations (Periderm Peel Method)[4]				
			Presence of *Erwinia* (0 or 1)	Estimated cfu/g	Strains Recovered		
					# *Ecc*	# *Eca*	*Eca* serogroup[5]
Rain *Eca*	5.84	CR	0	0.00	-	-	-
		NR	0	0.00	-	-	-
		RB	1	0.00	-	2	2XNR
		SA	1	0.00	-	2	1XNID,1XNR
		Average	50%	0.0			
Snow *Eca* (NID)	5.92	CR	1	3.75	3	2	2XNID
		NR	1	0.50	-	4	4XNID
		RB	1	0.00	-	1	1XNID
		SA	1	0.00	-	2	2XNID
		Average	100%	1.1			
Blackleg *Eca* (SKI)	6.22	CR	1	0.00	-	2	2XSKI
		NR	0	0.00	-	-	-
		RB	1	0.00	-	2	2XSKI
		SA	1	0.00	-	2	2XSKI
		Average	75%	0.00			
	Location	Average	53%	1.1			

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Table 13 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Tuber isolations (Periderm Peel Method)[4]				
			Presence of Erwinia (0 or 1)	Estimated cfu/g	Strains Recovered		
					# Ecc	# Eca	Eca serogroup[5]
Center							
Check	(-)0.15	CR	0	0.00	-	-	-
		NR	0	0.00	-	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	0%	0.0			
Aerosol Ecc	6.00	CR	0	0.00	-	-	-
		NR	1	0.00	2	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	25%	0.0			
Rain Ecc	6.06	CR	1	0.00	2	-	-
		NR	0	0.00	-	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	25%	0.0			

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Table 13 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Tuber isolations (Periderm Peel Method)[4]				
			Presence of *Erwinia* (0 or 1)	Estimated cfu/g	Strains Recovered		
					# *Ecc*	# *Eca*	*Eca* serogroup[5]
Snow *Ecc*	5.80	CR	0	0.00	-	-	-
		NR	0	0.00	-	-	-
		RB	0	0.00	-	-	-
		SA	0	0.00	-	-	-
		Average	0%	0.0			
Aerosol *Eca*	6.14	CR	1	13.50	0	5	5XNR
		NR	0	0.00	-	-	-
		RB	0	0.00	-	-	-
		SA	1	0.00	-	2	2XNR
		Average	50%	3.4			
Rain *Eca*	5.84	CR	0	0.00	-	-	-
		NR	1	0.00	-	2	2XNR
		RB	1	0.00	-	2	2XNR
		SA	0	0.00	-	-	-
		Average	50%	0.0			

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Table 13 continued.

Location and inoculum applied[1]	Inoculum concentration[2] Log_{10} cfu/ml	Cultivar inoculated[3]	Tuber isolations (Periderm Peel Method)[4]				
			Presence of *Erwinia* (0 or 1)	Estimated cfu/g	Strains Recovered		
					# *Ecc*	# *Eca*	*Eca* serogroup[5]
Snow *Eca*	5.92	CR	0	0.00	-	-	-
		NR	0	0.00	-	-	-
		RB	1	0.26	-	3	3XNID
		SA	1	0.00	1	1	1XNID
		Average	50%	0.1			
Blackleg *Eca* (SKI)	6.22	CR	1	0.25	-	3	3XSKI
		NR	0	0.00	-	-	-
		RB	0	0.00	-	-	-
		SA	1	0.99	-	5	4XSKI,1XNID
		Average	50%	0.3			
	Location Average		31%	0.5			

[1] Original sources of strains used in the studies were aerosols and rain collected in Oregon and snow and a potato stem with typical blackleg symptoms from Colorado. Strain designations: *Ecc* = *E. carotovora* subsp. *carotovora* and *Eca* = *E. carotovora* subsp. *atroseptica*.

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Table 13 footnotes continued.

[2] Inoculum was applied in irrigation water seven times during the growing season in a total volume of 18 l per application. An additional 18 l of check water was applied to each plot after inoculation. Check water contained natural low populations of Erwinia, mostly Ecc.

[3] Cultivar designations: CR = Centennial Russet, NR = Norgold Russet, RB = Russet Burbank, SA = Sangre.

[4] Erwinia presence (1) or absence (0) was determined by anaerobic enrichment of periderm peel suspensions used to estimate the colony forming units per gram (cfu/g) of tuber peel.

[5] Eca strains isolated were tested against Serogroup I (SKI) antiserum following the method of De Boer et al. (12). Results are reported as the number of strains X the serological reaction. Serological reactions: NR = no reaction with Serogroup I, NID = a characteristic reaction of non-identity with Serogroup I and SKI = a reaction of identity with Serogroup I.

[6] " - " = not done or not applicable.

Ecc snow strains to 81.3% for the Ecc aerosol strain. However, the strain isolated from the infested plant in the block inoculated with the Eca blackleg strain was an Ecc rather than an Eca strain.

The average incidence of latent plant infection in stems from blocks located at Center, CO ranged from 8.3% to 68.8% for the negative-check and Ecc aerosol strain, respectively. However, data for strains isolated show that all those from the block infested with the Ecc rain strain were Eca. One and two Eca strains were also isolated from stems in blocks inoculated with Eca aerosol and Ecc snow strains, respectively. The only Ecc strain isolated from stems in blocks inoculated with Eca strains was from those from the block inoculated with the Eca snow strain. Serological test data showed that all reactions of the Eca strains isolated from the plant stems were consistent with the reactions for the Eca strains applied in the irrigation water.

Isolation data from tubers (Table 13) show that applications of all Eca strains and both the Ecc aerosol and Ecc rain strains resulted in detectable levels of E. carotovora on daughter tubers. Viable cells were not recovered from tubers from plots treated with the Ecc snow strain at either Fort Collins or Center or those from the negative-check block at Center. Quantitative data show that an average of 8 cfu/g of tuber peel was present on surfaces of tubers harvested from the block treated with the Ecc aerosol strain at Fort Collins. However, three Eca strains were also recovered from tubers harvested from this plot in addition to 15 Ecc strains. Subspecies recovered from tubers generally matched those applied via irrigation water. However, Ecc strains were also recovered from tubers harvested from

plots treated with water containing Eca strains at both locations. Serological tests of Eca strains showed that serogroups different than those Eca strains applied via irrigation water were recovered only from tubers harvested from plots treated with the Eca rain strain in Fort Collins and the Eca blackleg strain at Center.

Data clearly show that inoculum applied via irrigation water can invade stems and may cause typical blackleg symptoms. They also show that the inoculum can contaminate daughter tubers.

Laboratory Studies

Activity of Aerosolized Erwinia carotovora as Cloud Condensation Nuclei

Results of preliminary studies (Figure 7) show that E. carotovora cells are only slightly less efficient CCN than ammonium sulfate particles when relative comparisons are made. The three E. carotovora strains tested became hydrated and functioned as CCN under the environmental conditions present during the simulated ascent. Activation of E. carotovora strains appeared to occur at the same thermodynamic point as ammonium sulfate. Data on pressure (Figure 8) and temperature (°C) (Figure 9) versus elapsed time show that little variation occurred among the four simulated ascents. Therefore, selection of the time when relative humidity reached 100% as t=0 was appropriate. This served as a common reference point for each ascent and made relative comparisons among the four simulated ascents possible.

Survival of Erwinia carotovora in Snow

The estimated detection limit for samples processed by membrane filtration was $\geq 6.1 \times 10^{-4}$ and $\geq 9.1 \times 10^{-4}$ viable cells per ml for experiments 1 and 2, respectively.

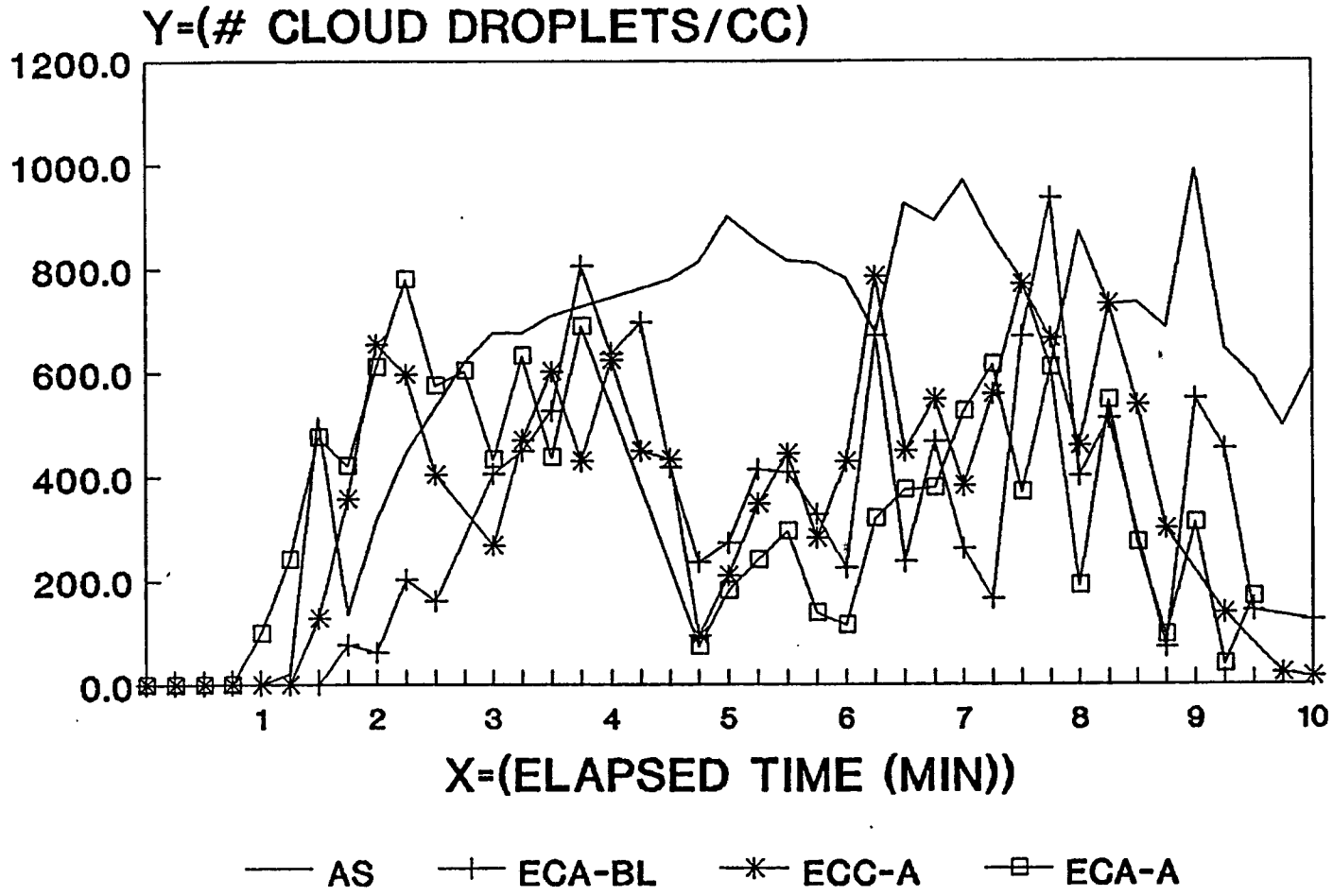

Figure 7. Relationship of cloud droplet (activated CCN) concentration (cm^{-3}) to elapsed time during four simulated air parcel ascents. The starting time (X=0) corresponds to the point at which relative humidity reached 100% in the air parcel. Aerosols tested as CCN during ascents were: AS = ammonium sulfate; ECA-BL = E. carotovora subsp. atroseptica (blackleg strain); ECC-A = E. c. subsp. carotovora (aerosol strain); and, ECA-A = E. c. subsp. atroseptica (aerosol strain).

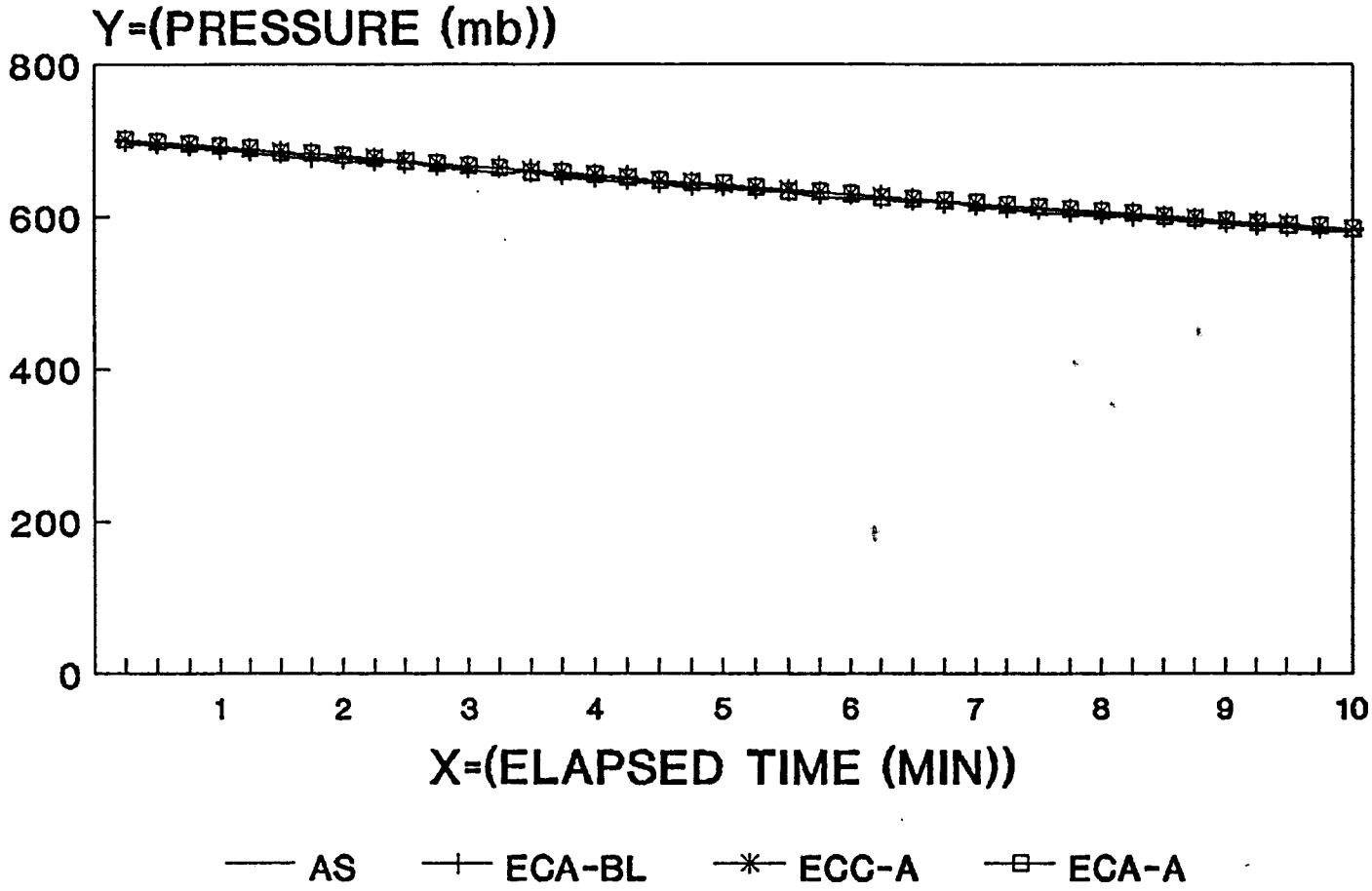

Figure 8. Relationship of pressure (mb) to elapsed time (minutes) during four simulated air parcel ascents. The starting time (X=0) corresponds to the point at which relative humidity reached 100% in the air parcel. Aerosols tested as CCN during ascents were: AS = ammonium sulfate; ECA-BL = E. carotovora subsp. atroseptica (blackleg strain); ECC-A = E. c. subsp. carotovora (aerosol strain); and, ECA-A = E. c. subsp. atroseptica (aerosol strain).

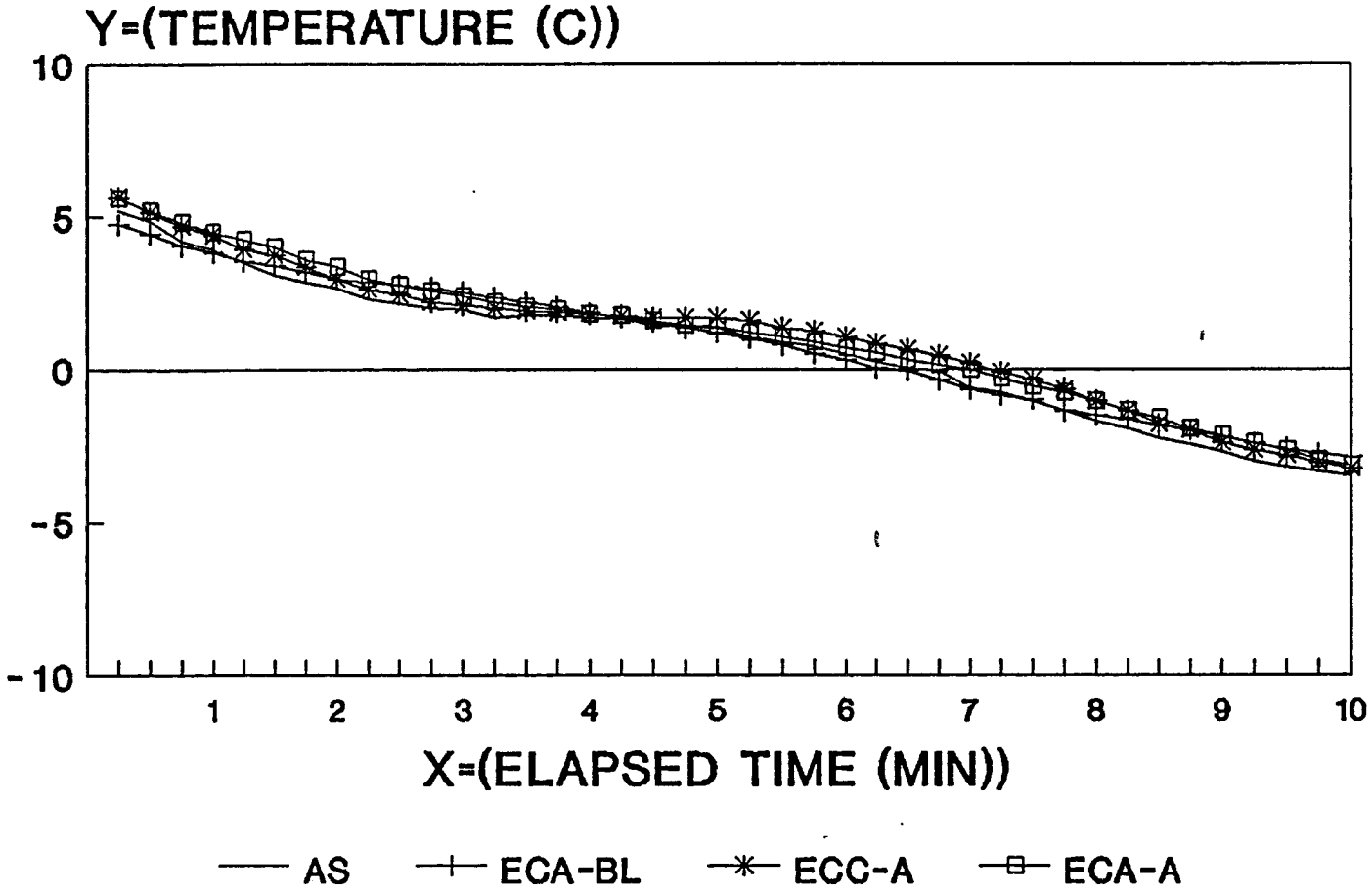

Figure 9. Relationship of temperature (°C) to elapsed time (minutes) during four simulated air parcel ascents. The starting time (X=0) corresponds to the point at which relative humidity reached 100% in the air parcel. Aerosols tested as CCN during ascents were: AS = ammonium sulfate; ECA-BL = E. carotovora subsp. atroseptica (blackleg strain); ECC-A = E. c. subsp. carotovora (aerosol strain); and, ECA-A = E. c. subsp. atroseptica (aerosol strain).

Data from experiment 1 showed that initial populations of Ecc (strain C19) and Eca (strain J10) were 560 and 1028 cfu/ml of melted snow, respectively. Although populations declined rapidly during storage at -30°C, viable cells were recovered for as long as 28 d, the longest time tested. Calculated half-life values were 0.4 d and 5.6 d for Ecc and Eca, respectively.

Initial populations in experiment 2 were 491 and 367 cfu/ml of melted snow for Ecc (serogroup XXIX) and Eca (strain J10), respectively. Viable cells were recovered from Ecc-inoculated snow samples after 233 d storage at -15 to -20°C but not after 707 d, the longest time tested. Viable Eca cells were recovered after 105 d but not after 233 d. Calculated half-life values were 14.2 d and 3.8 d for Ecc (serogroup XXIX) and Eca (strain J10), respectively.

Replication of Erwinia carotovora in Natural Surface Water

The results are shown in Table 14. When data for the four E. carotovora strains are compared by combining all water sources except deionized water, the Eca serogroup I blackleg strain (strain #1) did not appear to replicate and was undetectable after 72 hr. In contrast, the Eca non-serogroup I strain isolated from snow (strain #2) showed increased numbers 32 hr and 72 hr after inoculation. However, populations declined from that point and were undetectable by 127 hr.

The non-XXIX serogroup Ecc strain (strain #3) isolated from water also showed a large population increase by 32 hr but declined sharply by 72 hr and viable cells were undetectable at 127 hr. The Ecc serogroup XXIX strain (strain #4) showed increased cell numbers by 16 hr and reached a peak population at 32 hr. Populations of this strain

Table 14. Replication of four Erwinia carotovora strains in natural surface and deionized water.

Water source	Erwinia strain[1]	Time Interval Tested (hr) and Estimated Average cfu/ml Recovered									
		0	1	2	4	8	16	32	72	127	337
Combined[2]	1	26.3	43.8	31.3	11.3	16.3	21.3	30.0	0.0	0.0	0.0
Combined[2]	2	20.0	7.5	13.8	7.5	6.3	85.0	623.7	1791.0	0.0	0.0
Combined[2]	3	45.0	32.5	35.0	28.8	31.3	71.3	862.5	25.0	0.0	0.0
Combined[2]	4	53.8	57.5	43.8	32.5	30.0	423.7	1532.0	207.5	7.5	3.8
Rio Grande	Combined	40.0	42.5	30.0	25.0	18.8	21.3	5.0	1.3	0.0	ND[3]
South Platte	Combined	27.5	35.0	40.0	31.3	43.8	536.2	481.2	103.7	0.0	ND
Ocean	Combined	35.0	30.0	30.0	7.5	3.8	0.0	0.0	0.0	0.0	0.0
Ocean + Sea Weed	Combined	42.5	33.8	23.8	16.3	17.5	43.8	2562.0	1918.0	7.5	3.8
Deionized	Combined	28.8	31.3	41.3	21.3	23.8	96.3	2501.0	378.7	0.0	ND

[1] 1 = Eca blackleg strain serogroup I; 2 = Eca snow strain non-serogroup I; 3 = Ecc rain strain non-serogroup XXIX; 4 = Ecc aerosol strain serogroup XXIX.

[2] Averages are for natural surface water only and do not include data for deionized water. Assay sensitivity was $\geq$ 1.25 cfu/ml.

[3] ND = assay not done.

persisted and viable cells were still detected 337 hr after inoculation.

When comparisons were made among water sources by combining data for the four E. carotovora strains it was found that the starting populations (0 hr) in Colorado River water averaged 40 cfu/ml (range 20-65 cfu/ml). Average populations began to decline between 1 hr and 2 hr after inoculation and reached undetectable levels (assay sensitivity ca 1.25 cfu/ml) by 127 hr. Populations in the South Platte River water ranged from 27.5 - 43.8 cfu/ml during the first 8 hr, increased to 536.2 cfu/ml at 16 hr after inoculation then declined to undetectable levels by 127 hr. The population increase that occurred between 8 hr and 16 hr indicated that Erwinia replication is possible in South Platte River and that populations ca 19 times the original may occur within 16 hr after inoculation.

Data for ocean water showed that average populations for the E. carotovora four strains decreased rapidly and were undetectable 16 hr after inoculation. However, when sea weed was added to the water, average populations increased to 2562 cfu/ml 32 hr after inoculation. This population was ca 60 times higher than the original average population of 42.5 cfu/ml. Viable cells could still be detected 337 hr after inoculation.

Data for deionized water also showed an average population increase over time. The increase appeared to start at ca 16 hr and populations comparable to those for the ocean water plus sea weed were found at 32 hr after inoculation. However, populations decreased more quickly in the deionized water than in ocean water plus sea weed and were undetectable by 127 hr.

DISCUSSION

Results of surveys made along the Oregon coast showed that viable E. carotovora cells were routinely isolated from ocean water, rain water, and, with some difficulty, from aerosols. No attempts were made to quantify cells present in ocean water or rain water samples. However, it is possible to estimate the average "most probable number" (MPN) of viable E. carotovora cells present in samples collected during the survey by comparing the ratio of the number of 50 ml direct enrichments which did not yield E. carotovora to the total number of enrichments made for each water source using the methods of Cochran (9). Such estimates show that 1.39×10^{-2} cfu/ml and 1.06×10^{-2} cfu/ml were present in ocean water and rain water samples, respectively. The fact that these studies showed E. carotovora was recovered from ocean water collected at sites ranging from Alaska to the west coast of central Mexico, up to 3.2 km away from shore in Oregon, the northern coast of the Dominican Republic and the Arabian sea, suggests the ocean is a limitless natural source of E. carotovora cells even though the estimated population per unit volume of water is not high. This becomes even more significant if cell replication in ocean water is possible as laboratory studies suggested (Table 14).

Characterization of strains isolated from Oregon samples (ocean water, rain and aerosols) showed that both Ecc and Eca were recovered

from all sources. Seven Ecc serogroups found in ocean water were also recovered from rain (Table 2). The single Ecc serogroup, serogroup XXIX, recovered from aerosols, was also found in ocean and rain water. Characterization of Eca strains isolated from ocean water, rain and aerosols also showed a high degree of similarity among strains. Their growth characteristics and serological reactions showed that they differed from the properties normally associated with Eca strains isolated from infected potatoes. Eca strains isolated during the Oregon surveys were tentatively identified as "sugar-beet strains" [E. carotovora subsp. betavasculorum (75)] based on the fact that they grew in culture at 36°C and did not belong to serogroups I and XVIII (M.L. Powelson, Oregon State University, personal communication, August, 1984).

Results from highly specific serological tests and the simultaneous recovery of Eca strains with unusual properties from all sources strongly suggest a common source of cells exists on the Oregon coast. Although this evidence is circumstantial, it appears highly probable that E. carotovora cells are cycled through storm systems on the Oregon coast. Cells appear to be entering the clouds from some source and are deposited with precipitation. The ocean is the most logical source of E. carotovora cells found in storm systems since it represents a seemingly infinite supply of cells, and contains both Ecc and Eca strains with characteristics identical to those recovered from precipitation. However, in order for the ocean to serve as a major source of cells for both local and long distance transport of E. carotovora in the atmosphere, the cells must be transferred from the water into the air and become aerosolized. Under unstable atmospheric

conditions E. carotovora aerosols can be carried to great heights in the atmosphere and would be dispersed for greater distances than previously thought (61) prior to deposition.

Bursting bubbles, present in the ocean surf, are known to be an efficient mechanism which not only produces bacterial aerosols (water-to-air transfer of cells) but also physically concentrates cells into jet droplets. At least 10 to 20 times the numbers of cells found in ocean water have been found in jet droplets (3, 4, 5).

Furthermore, regions of brightness (radiance) variation have often been observed in visible and near-infrared satellite images of cloud-free, coastal regions (15). Studies off the coast of southern California in the fall of 1980 (38) and 1982 (15) showed a positive relationship between marine aerosol particle concentration and satellite-detected radiance. Therefore, it appears that relatively high concentrations of marine aerosols can commonly be found along coastal regions, presumably, due to the presence of an efficient aerosolization mechanism. Thus, based on the facts that (1) significant numbers of E. carotovora cells are present in ocean water, (2) an efficient mechanism for aerosol generation is present along the coast, (3) the aerosolization mechanism can concentrate cells suspended in water, and (4) satellite imagery shows that relatively high concentrations of marine aerosols occurred in coastal regions, the ocean probably contributes large numbers of particles to the atmospheric aerosol. It is also likely that E. carotovora cells comprise a sizeable portion of that aerosol based upon the fact that they are commonly present in the ocean in significant numbers.

Aerosol particles capable of initiating water droplet formation in the atmosphere at relatively low water vapor supersaturations (typically less than 10%) are termed cloud condensation nuclei (CCN) (69). Oceans are believed to be the most significant source of atmospheric CCN which consist primarily of ammonium sulfate, ammonium chloride and sodium chloride aerosols (69). Little is known about the presence, relative abundance and significance of organic substances in the atmosphere (69). However, cloud chamber studies reported here (Figure 7) showed that aerosolized Ecc and Eca cells are also probably efficient CCN. They were activated at cloud water supersaturations comparable to those for ammonium sulfate, another efficient CCN, and will readily form cloud droplets. Other bacteria (both gram-positive and gram-negative) have been shown by others to act as CCN in laboratory studies (46). However, these cells were lyophilized prior to testing and were not tested during simulated cloud ascents as was done in the studies reported in this dissertation.

The ability of E. carotovora cells to function as CCN may account for their presence in precipitation and their apparent ability to cycle through storms on the west coast and farther inland. Because bacterial CCN will form cloud droplets at low supersaturation of water vapor (i.e., slightly greater than 100% relative humidity) this may provide a mechanism for cells to survive for the prolonged periods of time necessary for long distance transport in the atmosphere to occur by protecting them from desiccation. Furthermore, observations made during cloud chamber studies showed that haze particles were visible in the CSU DCC during simulated ascents. This showed that hydration of cells was occurring at relative humidities considerably less than 100%.

It was estimated that this phenomenon may have been occurring at relative humidities less than 85%. The formation of haze indicates that E. carotovora cells are hydrophilic and will start to hydrate, and thus be protected from desiccation, even before clouds form. The ability of E. carotovora cells to become hydrated while aerosolized may be a key factor in their ability to survive for sufficiently long periods of time to allow for transport and subsequent deposition in precipitation at locations considerably greater distances from their sources than may be possible for non-hydrated cells. Data from in this study suggest that this may account for the deposition of viable E. carotovora cells as far inland as Colorado.

When the MPN was calculated for E. carotovora populations present in melted snow collected in Colorado, it was found that ca 4.87×10^{-5} cfu/ml were present. Populations for ocean and rain water collected on the Oregon coast were estimated to be at least 218 times greater than those found in snow. This again supports the hypothesis that the ocean probably serves as the source of E. carotovora aerosols. In the absence of intermediate sources of E. carotovora cells to replenish the numbers in the clouds, factors such as dilution, deposition of cells in precipitation at intermediate sites and cell death during transport, would be expected to markedly decrease populations measured in precipitation collected as far inland as Colorado versus populations measured in precipitation on the coast. This was the case in these studies. It was, however, not possible using the experimental approach employed for this study, to demonstrate conclusively that the source of viable cells recovered from snow in the Colorado mountains was aerosols generated from the Pacific Ocean.

Use of weather records to track storm systems and determine characteristics of storm systems important for long distance transport would potentially provide important information to support or refute the hypothesis that long distance atmospheric transport is occurring. However, to do this, comparisons among storm systems known to have produced precipitation from which E. carotovora was and was not isolated would need to be made. Tracing such storm systems was beyond the scope of this study since so few Erwinia-positive snow collections were made for which the date of storm passage was known with certainty. However, at least one Erwinia-positive snow collection, made on March 10, 1986, was deposited by an organized storm system known to have originated off the coast of California. All rime-ice samples were negative for E. carotovora. However, none of the rime-ice samples were collected when positive snow collections were made. Therefore, it is likely that collection of rime-ice samples did not coincide with an Erwinia-positive storm system.

Regardless of these problems, considerable circumstantial evidence exists for long distance transport of E. carotovora. For example, all snow samples were collected at times of the year (winter) when no other source of cells was known to exist. Also, the pattern of sites from which E. carotovora-positive snow samples were collected suggests a common source of cells existed.

For example, the single E. carotovora-positive snow sample found at the Mount Werner (MTW) Storm Peak Laboratory (SPL) site was collected in January, 1984. Snow samples collected at Cameron Pass (CAM), Gore Pass (GOR) and Rabbit Ears Pass (REP) at the same time all yielded the organism as well. Furthermore, characterization of strains

recovered from snow showed that Eca, which was only isolated during a two-month period during the entire snow survey (i.e., January and February 1984), was simultaneously isolated from snow samples collected at CAM, REP and MTW. Snow samples collected from CAM, GOR and REP during December, 1983 were all negative indicating that the organism was not present prior to the January 1984 collection and assays of foliage (329 g), decaying wood (79 g), soil (1.92 kg) and snow (8.15 l) samples collected at MTW prior to January 1984 (assays were made during November 1983) as well as assays of 5.39 kg of soil samples collected at MTW after January 1984 all failed to show that E. carotovora was present at this site. This, again, supports the conclusion that a large influx of E. carotovora occurred over a relatively large geographical area; apparently from a storm prior to the January 1984 collection.

The general pattern of sites from which Erwinia-positive snow samples were collected during the entire survey period also suggests that large influxes of cells can occur. Ten snow collections were made during the course of the study in which two or more sites were sampled on the same date. From four of these collections snow samples from two or more sites were found to be contaminated with E. carotovora. Therefore, in cases where comparisons were possible, 40% of the snow collections showed that E. carotovora occurred simultaneously in samples from more than one site which were often widely separated. These results show that when a positive snow sample is collected from a given site there is a tendency for samples collected at other sites to be positive as well. This suggests a broader source of viable E. carotovora than can be explained by contamination from local sources.

Simultaneous deposition of E. carotovora with snowfall at several sites would explain the patterns observed.

Characterization of strains recovered from snow showed that atypical Eca strains, similar to those isolated from ocean water, rain water and aerosols on the Oregon coast were also found in Colorado. Strains with these characteristics were not previously known to occur in Colorado. However, the only months when this Eca strain was recovered from snow in Colorado were January and February, 1984. This pattern suggests that some factor associated with long distance transport or survival in snow may select against Eca cells since they were recovered more frequently from samples collected during Oregon surveys than in the Colorado mountains. Four of six Ecc serogroups recovered from snow in Colorado, excluding results for a seventh serogroup (CC603) recovered from snow but not tested for among the strains recovered from Oregon samples, were also found in ocean and rain water and in aerosol samples collected on the Oregon coast (Table 2). Six of seven Ecc serogroups found in the mountain snow pack were also found in surface water in Colorado (Tables 6, 8, 9 and 10). Therefore, comparisons of strain characteristics show strong similarities among those recovered from the Oregon coast, Colorado snow and flowing surface water in Colorado. Four serogroups, XXVIII, XXIX, XXXIV, and CC651, recovered from samples collected on the Oregon coast were also recovered from Colorado snow and flowing surface water. This suggests that cells present on the west coast can be transported to Colorado where they subsequently find their way into streams, presumably via run-off.

Results of serogrouping Ecc strains isolated from flowing surface water showed that in the three rivers sampled (ARK, SPR and RGR, respectively), eight of 10, five of five and five of seven serogroups isolated from the two sample sites located nearest to the headwaters of each stream were also recovered from at least one downstream site (Tables 8, 9 and 10). Studies also showed that E. carotovora populations in water increased as it flowed downstream. These results are similar to those reported from other studies (39, 51) which showed a positive correlation between E. carotovora populations and water temperature thus implying, that cells were replicating in surface water. Survey results reported here (Figures 2 and 3) not only suggest cells can replicate in flowing surface water but showed that, in addition to temperature, other factors associated with sites, are also important. Such factors may be nutritional status and perhaps others which need to be considered in addition to temperature. For example, replication occurred in SPR but not in RGR water in laboratory studies (Table 14) when temperature was controlled and therefore not a variable. RGR water used in the study was collected at a relatively pristine site near Del Norte, CO in a sparsely populated area. In contrast, SPR water was collected at a site downstream from Denver, CO and would be expected to have a much greater biological oxygen demand due to dissolved and suspended organic matter capable of supporting bacterial growth. Populations were greater for SPR site 4 than for site 6 (Figure 3) possibly due to greater nutrient availability at site 4 when the water leaves a large metropolitan area like Denver in contrast to site 6 located further downstream. Factors such as this could account for the significant statistical interactions ($P \leq 0.05$)

between season and site measured for ARK and SPR which both pass through more populated areas than the RGR. Results for RGR which flows through only sparsely populated areas showed E. carotovora populations increased as water flowed downstream and all sites responded to seasonal effects in a similar manner [P (interaction) = 0.619].

Thus, results of serological tests and population studies showed that it may not only be possible for cells present in water near the head of the stream to be carried downstream to agricultural areas but also that replication probably occurs. It is likely that viable E. carotovora cells transported to Colorado and deposited in snow, although initially in very low numbers, have an opportunity to replicate in flowing surface water thereby markedly increasing their numbers prior to reaching agricultural areas where water is subsequently used for irrigation of susceptible crops.

Results of field studies clearly showed that Ecc (Serogroup XXIX) recovered from ocean water, aerosols and rain water on the Oregon coast and from snow and surface water collected in Colorado, will invade potato stems (Figure 4) and will become established on the surface of daughter tubers (Figure 6). Also, the atypical Eca strain (non-serogroup I) isolated from Oregon coastal samples and Colorado snow was capable of invading stems (Figure 5) and infesting tubers (Figure 6) when present in water used to irrigate healthy plants. Atypical Eca strains recovered from aerosols or snow also caused typical blackleg symptoms indistinguishable from those caused by a known Eca blackleg strain (serogroup I) in the field (Table 12). Thus, results from field studies using Kochs postulates (1) showed that application of cells to healthy plants via contaminated irrigation water was an efficient means

for infesting healthy tubers and re-establishing the disease cycle and also that Ecc and Eca strains recovered from the Oregon coast and from snow and surface water in Colorado are pathogenic to potatoes (Tables 12 and 13).

Data gathered during this study strongly suggest that E. carotovora cells present in the Pacific Ocean become aerosolized by bursting bubbles and are present as atmospheric aerosols. Aerosolized cells can become hydrated, thus protected from desiccation and radiation, and can travel with storm systems to the Rocky mountains where they are subsequently deposited into the snow pack. Once in the snow pack, cells can persist for prolonged periods of time and will be present in the run-off. Cells find their way to surface water when snow melts, travel downstream with flowing water and eventually reach potatoes via irrigation water where they can establish infections. Data suggest that E. carotovora cells can replicate in flowing surface water resulting in populations greater than that found in ocean water.

CONCLUSIONS

The results of these studies justify the following conclusions:

1. Viable E. carotovora cells are present in storm systems originating off the west coast of the United States. The ocean is a likely source of viable cells in the atmosphere since E. carotovora is easily recovered from ocean water and efficient mechanisms are known which can account for the aerosolization of bacterial cells from water.
2. Atmospheric transport of viable E. carotovora cells as far inland as Colorado is possible. The ability of E. carotovora cells to function as cloud condensation nuclei may account for their ability to survive atmospheric transport and be deposited with precipitation.
3. Viable cells deposited in precipitation in Colorado enter streams as snow melts and run-off occurs. Flowing surface water can serve as a means to transport viable cells to agricultural areas. Cells may also replicate in surface water while travelling downstream. This would increase their numbers, thus, overcome the dilution effects of water which could render numbers too low to be of any significance when applied to potatoes via irrigation water.
4. E. carotovora cells isolated from ocean water, rain water, aerosols, snow and surface water (i.e., throughout the proposed transport process) are pathogenic to potato tubers and stems.
5. Irrigation of healthy potatoes with E. carotovora contaminated

irrigation water is an efficient method for reintroduction of E. carotovora into Erwinia-free stocks.

Areas for Further Study

Evidence for atmospheric transport, presented here, is largely circumstantial. Valuable information could be added if clouds were sampled directly using aircraft. This would allow larger volumes of cloud water to be collected in a more timely manner than was possible in this study. It would also determine if viable cells could be recovered directly from clouds. Studies to determine if a dispersion gradient exists from the coastal areas to sites located progressively farther inland would also help to identify, more precisely, the source of E. carotovora cells. Storm systems originating in the Gulf of Mexico and the Atlantic Ocean should also be studied as sources of E. carotovora inoculum for Colorado and other areas of the world.

Additional cloud chamber tests are needed to document CCN activity of aerosolized E. carotovora cells as well as their ability to function as ice nuclei (IN). Their CCN and IN spectra need to be determined over a wide range of environmental conditions to more fully determine the possible roles these characteristics play in cell survival during long distance transport. The ability of a range of E. carotovora strains to survive over a range of simulated atmospheric conditions needs to be determined as well.

It has not been conclusively demonstrated that cells deposited in streams near the headwaters will survive transport in water to agricultural areas which are often long distances away. It is not known for certain if cells can replicate in surface streams even though data suggest that they can. Tracer studies using stable drug-

resistant bacterial strains seeded into surface water and their presence monitored at various distances downstream may provide this information. Such studies should be undertaken.

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