BLACKLEG AND SOFT ROT EPIDEMIOLOGY AS IT IS NOW UNDERSTOOD

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Introduction

Even though blackleg has been a problem since its discovery in Germany about 1900 it has not been until recently that we have begun to fully understand its epidemiology and thus be able to make a reasonably intelligent approach to its control. New research leading to development of new concepts or modifications of older ones has emerged rapidly and steadily since the mid 1960's. Sufficient data have been accumulated from numerous laboratories during the last 20 years to make it possible to formulate a tentative set of six general principles regarding blackleg and soft rot epidemiology which have a direct bearing on the control of the disease. These principles, while certainly subject to further modification, may serve as a basis for devising more effective control strategies.

Principle #1. Blackleg and soft rot bacteria are seedborne.

Studies in many parts of the world including Europe, the United States, and elsewhere have consistently shown that Erwinia is commonly associated with potato tubers. Bacteria can be found on the surface, in lenticels, in wounds or in the vascular bundles, often in high percentages of the seed tubers in some seedlots. This source of inoculum is a major factor in blackleg epidemiology and a major concern to potato seed certification agencies and potato producers.

It has also been established that the degree of contamination of potato seed tubers by Erwinia may vary considerably from season to season, from area to area and from lot to lot. To cite seedlots as the sole source of severe blackleg and soft rot problems without direct data establishing the actual degree of contamination is a mistake.

Principle #2. Blackleg and soft rot bacteria are transient in the soil.

Although still a somewhat controversial subject, the general experience of researchers around the world is that populations of Erwinia decline relatively rapidly in the soil to the point where they become undetectable by available techniques. Populations decline more rapidly in warm soils (hence in warmer climates) than in cool soils. Erwinia populations may decline from very high levels to undetectable numbers in only a few days at temperatures in the 20-25^{o} C range but they may be detectable in soils for several weeks when temperatures are 0-15^{o} C. Freezing and thawing also results in rapid population reductions. This principle is illustrated in Table 1 which summarizes one of many experiments on the survival of Erwinia in the soil.

It is certainly true that Erwinia has a soil phase. Cells are released into the soil from decaying seedpieces, from blackleg infected stems and possibly deposited from other sources, such as irrigation water, where they survive for varying periods depending upon the soil environment. Both soil temperature and soil moisture affect survival but temperature appears to be the major factor. Cool, moist conditions favor longer survival and thus favor contamination of tubers developing on adjacent plants. Warm dry conditions reduce the length of survival and so tend to reduce the levels of contamination in daughter tubers.

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Table 1. Survival of Erwinia carotovora subsp. atroseptica in field soil at six temperatures.

Temperature °C	Days after soil infestation 0	8	19	27	41	54	78
	Viable cells/gram of soil X 1000						
- 29	2060	1	<1	<1	0	0	0
0	2211	6225	4830	2678	1531	1689	2
4 - 10[1/]	7008	3848	2523	1143	87	98	<1
10 - 16[1/]	6204	4423	14	90	6	<1	0
16 - 21[1/]	9813	7	<1	0	0	0	0
21 - 27[1/]	9759	1	0	0	0	0	0

[1/] Diurnal cycle, 12 hours at each temperature.

Erwinia survives well in non-decomposed potato tissues such as tubers and stems and is fully capable of surviving from harvest (autumn) to planting (spring) in a given field in temperate climates. Thus, in areas where potatoes follow potatoes in a rotation or where other susceptible crops follow potatoes the "soil" may certainly be a source of inoculum. In warmer climates where susceptible crops are grown virutally the year around inoculum may be continuously present in the soil by virtue of the fact that crops are infected and bacteria released into the soil in a continual cycle.

Recent reports have indicated that Erwinia serogroups not associated with seed potatoes planted in a field may be isolated from the soil and infected plants. This may indicate that some strains of Erwinia are indeed soil borne in some localities or that there is an unrecognized source of inoculum, such as irrigation water, which is responsible for depositing the bacterial cells on the soil periodically where they survive sufficiently long to be recovered from soil samples. This area of blackleg/soft rot epidemiology is being investigated intensively and final answers should soon be forthcoming.

Principle #3. Blackleg and soft rot bacteria can be eliminated from seed potatoes by procedures such as stem cutting and meristem culture.

Since a major source of Erwinia inoculum is the seed tuber, the logical approach to breaking the disease cycle is to eliminate tuber contamination. Experience from several programs has shown that stocks derived from bacteriologically tested stem cuttings or meristem cultures are free from Erwinia contamination. These methods provide relatively easy means to eliminate seedborne inoculum as a factor in blackleg and soft rot epidemiology and an effective method of disease control, provided that rapid recontamination of clean stocks can be effectively prevented.

Principle #4. Blackleg expression is highly dependent upon many factors. The pathogens can, therefore, be latent in potato seed when conditions do not favor disease development.

Since expression of typical blackleg symptoms may not occur in the field except under certain conditions, contamination of seed lots may not be detected by normal field inspections or visual tuber examination.

Among the numerous factors which affect the amount and type blackleg or soft rot expression are: 1) the organism(s) involved, 2) environmental conditions, 3) cultural practices and 4) the number of bacterial cells per tuber or seedpiece.

Three distinctly different bacteria are known to cause blackleg and soft rot. Erwinia carotovora subsp. carotovora (ECC) and Erwinia carotovora subsp. atroseptica (ECA) are widely distributed throughout the world while Erwinia chrysanthemi (Ech) has been reported from only a few areas (none in the United States). Studies have shown that each of the three organisms produces infection under different conditions. Table 2 shows that ECA is most active under cool conditions and hence is responsible for virtually all of the blackleg expression in cold climates.

Table 2. Effect of inoculating Erwinia-free potato seed tubers with two subspecies of Erwinia carotovora on postemergence blackleg expression under controlled soil moisture and temperature conditions. [1]

	Percent of plants showing postemergence blackleg[2] Soil temperature (day/night) (°C)			
Inoculum	18/7	24/13	29/18	35/24
E. atroseptica	8.3	66.6	16.7	0.0
E. carotovora	0.0	16.7	25.0	25.0
Control	0.0	0.0	0.0	0.0

[1] Soil moisture kept constant at 90% field capacity.

[2] Based on 12 plants per treatment.

ECA activity declines as temperatures increase between approximately 18 and 25° C and no disease expression may occur at higher temperatures. ECC on the other hand is not active at low temperatures and produces most disease at 20-30°C. Ech is active at still higher temperatures and has only been reported from very warm areas. Potato seed contaminated with predominantly ECC, for example, may produce virtually no symptoms when planted in a cool area (or early in the season when temperatures are low) but may cause considerable infection when planted in a warm area (or later in the season).

Environmental conditions affect blackleg/soft rot expression considerably as the above discussion suggests. Generally, experience in Colorado indicates that more total loss due to Erwinia infection occurs in warm climates (or warm seasons) than in cool climates (or cool seasons). This may not be apparent to the general observer since in warm areas much of the loss may occur as seedpiece decay or very early blackleg expression in the shoots before emergence of sprouts. This results primarily in stand reduction with little obvious blackleg infection even though total loss may be high. Cooler conditions may favor more typical blackleg but much less stand loss. The resulting total loss may be much lower but more readily identified resulting in the impression of greater infection. This principle is strikingly illustrated in Table 3 which shows the effect of location (temperature) on total loss due to Erwinia. The data show that greater total loss occurred in the warmer areas and that more stand loss (not easily diagnosed as caused by Erwinia) and less typical blackleg expression occurred as temperatures increased.

Table 3. Influence of soil temperature on blackleg expression in one potato seed lot planted at three locations in Colorado.

Location	Mean soil temperature[3/] °C	Percent blackleg		
		Preemergence[1/]	Postemergence	Total
Rio Grande County	10.9	5.5 a[2/]	8.5 b	14.0 b
Weld County	17.8	15.9 b	14.7 a	30.6 a
Morgan County	21.1	20.5 b	5.8 b	26.3 a

[1/] Includes seedpiece decay and preemergence shoot infection.

[2/] Means within a column with a common letter do not differ significantly at $P=0.05$.

[3/] Means represent the entire growing season from planting (May) to harvest (September).

This type of environment/disease interaction explains how a single seedlot may perform very differently when planted in different locations or at different times of the year. This variation has been attributed to the presence or absence of soil borne inoculum in the past.

The amount of inoculum present in seed tubers may also markedly affect disease expression. Generally, as the inoculum load increases the amount of seedpiece decay increases and the amount of typical blackleg decreases. This is due to the fact that heavily contaminated seedpieces often decay before a shoot is produced thus no blackleg expression is possible.

Generally speaking, typical blackleg expression is favored by cool soil temperatures at planting which allow shoots to emerge before the seedpiece decays followed by warm temperatures which seem to favor invasion of the stems and blackleg expression.

Cultural practices such as seed handling, seed treatment for control of fungus infections and nutrition, especially nitrogen levels all may affect the amount and the type of disease expression caused by *Erwinia*.

Since expression of *Erwinia* infection is so variable and it can be latent in seed it is difficult to predict the probable performance of a given seedlot without utilizing direct tuber assays to determine the degree of contamination prior to planting.

Principle #5. Blackleg/soft rot expression in the field may not accurately reflect the state of health of the seed produced by the crop.

A common question asked by growers around the world is - "why do we see so much blackleg in our fields when we are careful to buy certified seed with low blackleg readings."

While the answer to this question may range from the contamination of the seed during cutting and handling to infection of the growing crop by contaminated water, a probable explanation in many, if not most, cases is that field blackleg readings do not accurately reflect the degree of contamination of the seed produced by the crop.

It has already been pointed out that: (1) the length of the soil phase of the pathogen is markedly affected by soil temperature and (2) that more total disease occurs under warm than under cool temperature conditions. Since the bacteria depend to a large extent upon the soil phase (i.e., movement of the bacteria from infected plants to healthy daughter tubers on adjacent plants via the soil water) for contamination of developing tubers on adjacent plants and thus for successful perpetuation from crop to crop in or on the seed, it is clear that disease expression and the degree of contamination of the seed tubers produced by the crop may not be closely related.

Warm conditions which favor disease expression may also limit the survival and movement of bacterial cells in the soil especially if dry conditions accompany the warm weather. Cold wet conditions, however, which tend to reduce the amount of disease expression may favor survival and movement of the bacteria in the soil and thus result in greater contamination of tubers produced by the crop.

It has often been observed, as illustrated by data in Table 4, that potato seed produced in a cold wet climate produces a high incidence of blackleg and soft rot when planted in a warm area but that seed produced in the warmer area and replanted often produces crops with considerably lower disease incidence.

Table 4. Relationship between blackleg field readings and the performance of seed produced by the crop - cv Kennebec, San Luis Valley, Colorado.

	Season	
	1969[1/]	1970[1/]
% stand	96.6	91.9
% blackleg	55.9	0.7

[1/] 1969 was favorable for blackleg expression. The temperature was considerably warmer than usual in early spring. 1970 was a normal year with cooler spring temperatures.

This is frustrating to certification agencies and producers as well and illustrates the need to determine the state of health of the seed tubers themselves rather than the state of health of the crop which produced them to be sure of the potential performance of the seed.

Principle #6. There are numerous sources of blackleg and soft rot bacteria other than the seed which can result in recontamination of clean stocks or significant increases in the amount of contamination (and hence disease) in stocks with initially low disease potential.

Extensive research during the past few years has focused on studies of sources of Erwinia inoculum (other than seed tubers) which might account for the contamination of seed stocks and blackleg and soft rot infection in growing crops.

A number of sources of bacteria and means of dispersal of bacterial cells have been discovered. Several of these have a high potential for widespread contamination of potatoes by Erwinia.

Cutting and handling equipment, especially mechanical seed cutters, have been shown to be universally contaminated with Erwinia (Tables 5 & 6) and capable of spreading infection to large numbers of cut seedpieces.

Table 5. Contamination of mechanical potato seed cutters by Erwinia carotovora - Colorado 1975.

Machine part	% of machines contaminated
Cutting blades	100
Splitter disks	100
Rollers	100
Conveyor belt	100

Table 6. Contamination of seedpieces cut on mechanical seed cutters by Erwinia carotovora - Colorado 1975.

Machine number	% of seedpieces contaminated
1	100
2	65
3	50
4	--
5	50
6	100

Contamination of cutting blades on the machines is often very high. As many as 264,000 cells per square inch have been counted on blades on machines in Colorado. Disinfection of this machinery is extremely difficult and the potential for spreading Erwinia from a low percentage of contaminated tubers in a lot to a high percentage of seedpieces cut on the machine is high.

Large numbers of insect species (mostly flies) have been shown to carry viable Erwinia cells and to be able to transmit the organism to injured potatoes in the field. Flies acquire the bacteria from numerous sources especially potato cull piles and are able to carry the organism to injured plants located at least several hundred feet away from the inoculum source. There is no evidence to suggest that insects produce widespread recontamination of high percentages of plants in a field but they do introduce low levels of contamination into clean stocks which can be rapidly increased in the cutting and handling operations.

Airborne Erwinia cells (aerosols) produced from infected crops by overhead sprinklers, rainfall or mechanical vine beating are known to survive for sufficient periods to be carried considerable distances by air currents and deposited on potato plants. This source of inoculum represents a potential means of widespread recontamination but it is much more dangerous in cool rainy climates than in dry warm areas since the survival of Erwinia in the air is favored by these conditions. Even in warm dry areas, however, efficient survival and movement at night or during other favorable periods presents a significant threat of contamination.

Erwinia inoculum has been shown to be associated with the roots of a wide range of weed species and crop plants. While there is no good evidence that this association contributes to long term survival in the soil environment, the presence of weed hosts may extend to some extent the survival time of Erwinia cells in the soil and thus contribute to the blackleg/soft rot problem.

The recent discovery that surface water from a wide variety of sources (Table 7) is commonly contaminated with Erwinia has added still another dimension to blackleg and soft rot epidemiology. Populations of from less than 1 to over 100 cells per ml have been found in numerous sources of irrigation water or potential irrigation water from 12 states. Contamination has been found during every month of the year in streams sampled on a regular basis. The use of contaminated water for irrigation insures that a dilute suspension of Erwinia inoculum is applied to the potatoes one is trying to protect from contamination. This creates a difficult problem and one which must be considered carefully in the production of potatoes, especially seed potatoes, in irrigated regions. Since there is no conclusive evidence to suggest that subterranean (well) water is contaminated, the use of this water source, especially for irrigation of seed crops, may significantly reduce the threat of Erwinia contamination.

Table 7. Association of Erwinia carotovora with water sources in the United States.

Sources	Number sampled	%yielding Erwinia
Rivers	26	92
Creeks	14	79
Reservoirs	3	33
Sea	12	75

Conclusions

The epidemiology of potato blackleg and soft rot is obviously very complex. Effective control of the disease requires a knowledge of the many factors which affect it and a willingness to implement a number of simultaneous approaches to control.

The myriad of sources of inoculum and means of dispersal provide formidable challenges to the potato producers which often may seen insurmountable.

States which have implemented blackleg control programs including stem cuttings, rapid multiplication and other approaches to control have generally been pleased with the results. Although recontamination has occurred, sometimes quite rapidly, the general performance of the stocks has often proven superior to regular stocks over a period of several years. True, it has not been possible to totally eliminate Erwinia as a factor in potato production but good progress has been made towards reducing losses caused by the pathogen. With the information currently available which has been summarized in this paper it should be possible to make intelligent informed management decisions which will help individual growers minimize losses.

As more data become available some of the current concepts may be modified but certainly our ability to cope with the Erwinia problem and thus benefit the entire potato industry will be increased by each new discovery.

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