Special Report

Blackleg and Other Potato Diseases Caused by Soft Rot Erwinias: Proposal for Revision of Terminology

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The bacterial disease of the potato plant caused by *Erwinia carotovora* subsp. *atroseptica* commonly induces a typical black rot of the stem base and thus is usually designated as potato blackleg disease (9). The symptoms expressed can vary widely, however, depending on prevailing environmental conditions (24). Because potato cultivation has been mainly restricted to temperate regions where the common pathogen is *E. c.* subsp. *atroseptica*, the term "blackleg bacteria" is often used colloquially as a synonym of *E. c.* subsp. *atroseptica*. We now know, however, that two other soft rot erwinias, *E. c.* subsp. *carotovora* and *E. chrysanthemi*, can infect the potato plant in the field and can cause symptoms similar to those associated with *E. c.* subsp. *atroseptica* infection, including basal stem rot (3,5,11,14,19,25,30–32). Each of these bacteria may also infect tubers in storage, causing decay, or in the field, resulting in nonemergence (blanking) if the seed tubers rot early in the growing season.

In his initial in-depth examination of *E. carotovora*, Dye (6) concluded that the nomenspecies *E. atroseptica* should be designated as a variety of *E. carotovora*. Subsequently, the substitution of "pathovar" for the term "var." (*E. c.* var. *atroseptica* and *E. c.* var. *carotovora*) was proposed by Dye (6) in order to maintain consistency with the other changes in nomenclature of phytopathogenic bacteria. The designation of "subspecies" has been accepted as a valid equivalent for "var." in the approved lists of bacterial names (29), however, and Lelliott and Dickey (12) have accepted this terminology in their section on *Erwinia* in the last edition of *Bergey's Manual*. Thus, to minimize confusion, we suggest that the term "subspecies" be accepted now as the preferred usage for the subspecific groups in *E. carotovora*.

Several common names have been used to refer to infection of potatoes by soft rot erwinias in the field and in storage. For example, the terms "blackleg" and "soft rot" usually describe stem and tuber infections, respectively, but are sometimes applied indiscriminately to all symptoms irrespective of the part of the plant affected. More recently, names such as postemergence blackleg (1), bacterial wilt (11,14), bacterial top rot (27), and bacterial stem rot (22,25,31) have been used to describe stem infection by any of the three erwinias. In some cases, "blackleg" is reserved to describe symptoms on the plant caused by *E. c.* subsp. *atroseptica* alone and "soft rot" is applied only when the disease is caused by *E. c.* subsp. *carotovora* or *E. chrysanthemi*. As a result, a confusing range of names is now used to describe the infection by soft rot erwinias.

Infection of potatoes by soft rot erwinias is of great concern to the potato industry in general and to potato seed production and certification agencies in particular. We propose a revised terminology based on recent studies on the biology of soft rot erwinias that infect potatoes in different climates.

The pathogens

The three soft rot erwinias associated with potatoes—*E. c.* subsp. *carotovora*, *E. c.* subsp. *atroseptica*, and *E. chrysanthemi*—have a geographic/climatic distribution that reflects the ranges of their different hosts as well as their growth characteristics at different temperatures (23). *E. c.* subsp. *atroseptica* is restricted mostly to potatoes in temperate regions where the crop has been grown most extensively and the strains isolated belong usually to one serogroup (serogroup I) (4,17). It is notable that less than two decades ago, *E. c.* subsp. *atroseptica* was the only pathogen commonly associated with stem infection (blackleg) in the field. Although this pathogen can cause disease in hot climates in crops grown from contaminated seed usually imported from temperate regions, its survival in soil and on progeny tubers in hot climates is poor, and seed tuber contamination tends to disappear after one or two generations. In contrast, *E. c.* subsp. *carotovora* has a worldwide distribution in both temperate and tropical zones and is pathogenic to a wide range of plants. Unlike *E. c.* subsp. *atroseptica*, the strains of *E. c.* subsp. *carotovora* include a large number of different serogroups (4). Furthermore, *E. c.* subsp. *carotovora* can survive in many environments, including soil, rivers, lakes, and even oceans (18). *E. chrysanthemi* is also widely distributed in tropical, subtropical, and warm temperate zones, where it is a pathogen of many crops as well as those grown in glasshouses in temperate regions. Recently, this pathogen has been found on potato seed in some cool temperate regions (Japan, Switzerland, Netherlands, and France), where it has also caused stem rot under field conditions (11,31,32; V. M. Lumb and M. C. M. Pérombelon, *unpublished*). It has also been determined as a cause of stem rot in Oregon and Washington in the United States (M. Powelson, *personal communication*).

Disease development

Seed tubers are commonly contaminated by more than one soft rot erwinia (17,20,21). The bacteria multiply as the mother tubers decay and subsequently move into the stem through the vascular system, where they can remain quiescent for a long time. Infection may also occur from invasion of mother tubers and roots by soft rot erwinias in the soil (17). The plants may appear to be healthy and free from external symptoms, but under certain conditions, the bacteria in the vascular system can become active and cause disease. More than one species or subspecies of *Erwinia* can be present in apparently healthy as well as in diseased stems; this is more common under warm than under cool conditions (14,16). Temperature is the main factor affecting pathogenesis by different soft rot erwinias and determining which organism will predominate. Recent studies in Israel (14) showed that when more than one soft rot erwinia is present, *E. c.* subsp. *atroseptica* tends to predominate in rotting mother tubers and in diseased stems at temperatures < 25 C but that *E. c.* subsp. *carotovora* and *E. chrysanthemi* prevail at higher temperatures. A wet rot may develop under prolonged wet conditions when aerial parts of the stem are wounded and leaves are broken, followed by a soft rot erwinia infection from sources external to the crop as well as from strains introduced on the seed (25–27). Infection of stems can occur at points where vines come in contact with the soil between the hills and at breaks or wounds on the stem. Generally, *E. c.* subsp. *carotovora* is the causal agent, since it is the most prevalent *Erwinia* sp. in irrigation water, on insects, and in aerosols (8,18,24).

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Symptoms

Symptoms caused by soft rot erwinias on potatoes vary depending on the environment, the specific pathogen(s), the cultivar, the part of the plant affected, and the progress of the disease (24,28). Early decay of the seed tuber or seed piece or death of the eyes and sprouts before or at emergence results in nonemergence. Although soft rot erwinias are often the causal agents, other pectolytic bacteria (*Clostridium* and *Bacillus* spp.) as well as certain fungi (*Rhizoctonia solani, Polyscytalum pustulans*, and *Fusarium* spp.) can also be implicated (15,24). After harvest, infection of tubers in storage or in transit may result in a soft rot that frequently spreads to neighboring tubers. Other pectolytic bacteria, such as *Clostridium* spp., *Bacillus* spp., and *Pseudomonas marginalis*, or other pectolytic fluorescent pseudomonads (2,7,15) may be involved and may be the primary cause of decay at the high temperatures that can exist in storage in hot climates (27). Sometimes, an arrested sunken soft rot lesion known as lenticellular hard rot or pit rot may develop on harvested tubers that have been covered with a film of water for a period of time and then become dry (13). Thus, the species of *Erwinia* involved in tuber decay cannot be identified solely on the basis of visible symptoms.

Symptoms caused by the different soft rot erwinias on plants may vary not only from one climatic region to another but also within a region according to local and annual variations in weather conditions. Symptoms on stems, leaf petioles, and leaves may appear at any time between emergence and harvest; often, only one stem of a plant is affected. The color of the lesion may range from black to brown or yellow, depending on the temperature and the pathogen. Stem rot is usually associated with extended periods of rain, heavy dews, and high relative humidity. Under dry conditions, in contrast, the bacteria are restricted to the vascular system, which may be discolored at the stem base. Wilting of leaves and desiccation of the stem may develop; occasionally, the first visible symptom is desiccation of leaf margins. These symptoms can also occur in different combinations and variations. Under certain field conditions, symptoms caused by the three soft rot erwinias may be indistinguishable. For example, the typical black basal stem rot that *E. c.* subsp. *atroseptica* can induce in cool temperate regions can also be caused by *E. c.* subsp. *carotovora* and *E. chrysanthemi* under hot, damp conditions similar to those in the lowland tropical region of Peru (5). Similarly, almost identical symptoms are caused by *E. c.* subsp. *atroseptica* and *E. chrysanthemi* late in the spring growing season in Israel, when the temperature is high and relative humidity is low (14). Again, the specific soft rot erwinia involved cannot be identified on the basis of visible symptoms.

Symptoms of wilting and desiccation (14) can also be confused with symptoms of bacterial wilt (*Pseudomonas solanacearum*), black scurf (*R. solani*) when roots and basal portions of stems are girdled, ring rot (*Corynebacterium sepedonicum*), and Fusarium (10) and Verticillium wilts (26). When crops are simultaneously infected with one or more of these pathogens as well as with soft rot erwinias, ascribing symptoms to a particular disease or to a single *Erwinia* species or subspecies is difficult.

Terminology

There is a strong case for the concept that different soft rot erwinias actually cause only one disease when the inoculum source is the seed tuber. Symptoms caused by the three soft rot erwinias are often indistinguishable, the biology of infection is similar, more than one soft rot erwinia can be present in a diseased plant, and the bacteria are very similar physiologically. An analogy can be drawn with the Fusarium and Verticillium wilts of potato that also are caused by more than one *Fusarium* and *Verticillium* species (10,26). If this view is accepted, one name only could be used to describe all manifestations of the disease. On this basis, retaining as much of the old terminology as possible would be wise, and for this reason the name "blackleg" is proposed to define all symptoms resulting from infections by any of the three soft rot erwinias and originating from the rotting mother tubers. Although specifically describing a black basal stem rot, the name has also been used for a long time to describe nonrotting symptoms caused by *E. c.* subsp. *atroseptica*. Because the name "blackleg" is likely to be retained at least colloquially, introduction of another name may increase the confusion. Finally, the name "blackleg" has already been advocated by Harrison and Nielsen (9) to describe the disease of potato stems caused by either *E. c.* subsp. *carotovora* or *E. c.* subsp. *atroseptica*. Our proposal is to extend its use to apply also to the disease caused by *E. chrysanthemi*.

An exception could be made in the case of the rot affecting aerial stems caused by direct infections; this is common and can be very severe in fields subjected to frequent overhead irrigation during periods of high temperatures (25). When extensive, these symptoms may superficially be confused with those of blackleg developing under wet conditions, except that in the former, the stem rot rarely extends to the point of attachment to the mother tuber. However, because seed contamination by the soft rot erwinias may not be a direct or primary contributing factor and

Table 1. Terminology of potato diseases caused by the soft rot erwinias: *Erwinia carotovora* subsp. *carotovora*, *E. c.* subsp. *atroseptica*, and *E. chrysanthemi*

In the field		In storage or transit	
Term	**Explanation**	**Term**	**Explanation**
Nonemergence or blanking	Caused by decay of seed tuber or early sprout death below ground	Tuber soft rot	Can lead to soft rot pocket characterized by cream to tan color and soft, granular consistency, with brown to black pigments often developing at margins of decayed tissue
Blackleg	Infections originating from seed tubers; symptoms variable, ranging from black or dark brown basal stem rot to wilting leaves and plant desiccation only	Lenticellular hard rot or pit rot	Sunken, hard, dry, brown to black spots at point where lenticels became infected and decay was arrested at early stage
Aerial stem rot	Tan, brown, or black decay lesion initiated on exposed stem and not originating at point of attachment to seed piece or tuber, as with blackleg		
Stolon end rot	Affects progeny tubers of blackleg plants; usually results in decay of central portion of tuber		
Tuber soft rot of progeny tubers	Can lead to soft rot pocket characterized by cream to tan color and soft, granular consistency, with brown to black pigments often developing at margins of decayed tissue		

because infection is initiated above ground from external sources, this disease should be distinguished from "blackleg." We propose the name "aerial stem rot." The low economic importance of aerial stem rot relative to blackleg in most regions where seed crops are usually lightly or not irrigated and harvested early further justifies this distinction; otherwise, seed health status would be a meaningless concept.

The soft rot erwinias can also infect tubers in the field, causing a tuber soft rot. Although the same term is used to describe tuber decay in storage and in transit, the context would make clear where the problem arises. Rotting of the seed tuber or of the sprouts before emergence can cause nonemergence. This is an economically important disease in some countries, especially when cut seed are used and the field surface is irrigated. However, nonemergence can also be caused by several other bacterial and fungal pathogens, either by rotting the seed tuber or by killing the sprouts. A special case is the tuber soft rot that affects progeny tubers of blackleg plants. This merits a name of its own, and the old name "stolon end rot" is descriptive and appropriate.

The proposed nomenclature of potato diseases caused by *E. c.* subsp. *carotovora, E. c.* subsp. *atroseptica*, and *E. chrysanthemi,* singly or in any combination, is summarized in Table 1. As indicated previously, certain symptoms could also be attributed to other causes.

Finally, acceptance of the proposed terminology and the principles on which it is based implies that visual inspection of seed crops for blackleg symptoms should not be the main criterion when assessing certification status of seed potatoes. The progeny tubers (the future seed) may be and often are contaminated by soft rot erwinias other than the one usually responsible for disease in a given region or country but which could be pathogenic when the tubers are grown under different climatic conditions. Furthermore, it should be emphasized that primary reliance on blackleg symptoms to indicate whether seed tubers carry latent infections by soft rot erwinias in seed certification inspections may be misleading. Seed contamination level by the pathogens together with environmental and physiological factors affecting host resistance are more important than blackleg incidence in the parental crop in determining disease level in the daughter crop (1,19). A more appropriate estimation of potential for blackleg to develop from a given seed lot could be obtained by determining the population numbers of the different soft rot erwinias present. In addition, other factors such as the status of bruising and conditions favoring wound healing after harvest need to be considered. Work to that end is in progress in several countries.

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LITERATURE CITED

1. Aleck, J. R., and Harrison, M. D. 1978. The influence of inoculum density and environment on the development of potato blackleg. Am. Potato J. 55:479-494.
2. Campos, E., Maher, E. A., and Kelman, A. 1982. Relationship of pectolytic clostridia and *Erwinia carotovora* strains to decay of potato tubers in storage. Plant Dis. 66:543-546.
3. Cother, E. J. 1980. Bacterial seed tuber decay in irrigated sandy soils of New South Wales. Potato Res. 23:75-84.
4. De Boer, S. H., Copeman, R. J., and Vruggink, H. 1979. Serogroups of *Erwinia carotovora* potato strains determined with diffusible somatic antigens. Phytopathology 69:316-319.
5. De Lindo, L., French, E. R., and Kelman, A. 1978. *Erwinia* spp. pathogenic to potatoes in Peru. (Abstr.) Am. Potato J. 55:383.
6. Dye, D. W. 1981. A numerical taxonomic study of the genus *Erwinia*. N.Z. J. Agric. Res. 24:223-229.
7. Folsom, D., and Friedman, B. A. 1959. *Pseudomonas fluorescens* in relation to certain diseases of potato tubers in Maine. Am. Potato J. 36:90-97.
8. Harrison, M. D., and Brewer, J. W. 1982. Field dispersal of soft rot bacteria. Pages 31-53 in: Phytopathogenic Prokaryotes. Vol. 2. M. S. Mount and G. H. Lacy, eds. Academic Press, New York. 506 pp.
9. Harrison, M. D., and Nielsen, L. W. 1981. Blackleg, bacterial soft rot. Pages 27-29 in: Compendium of Potato Diseases. W. J. Hooker, ed. American Phytopathological Society, St. Paul, MN. 125 pp.
10. Huguelet, J. E., and Hooker, W. J. 1981. Fusarium wilts. Pages 60-62 in: Compendium of Potato Diseases. W. J. Hooker, ed. American Phytopathological Society, St. Paul, MN. 125 pp.
11. Jäggi, W., and Winiger, F. A. 1979. Schwartzbeinigkeit und bakterielle Welke bei Kartoffeln. Mitt. Schweiz. Landwirtsch. 27:207-216.
12. Lelliott, R. A., and Dickey, R. S. 1984. Genus VII. *Erwinia*. Pages 469-476 in: Bergey's Manual of Systematic Bacteriology. Vol. 1. N. R. Krieg and J. G. Holt, eds. Williams & Wilkins, Baltimore, MD.
13. Logan, C. 1965. Bacterial hard rot of potato. Eur. Potato J. 7:45-56.
14. Lumb, V. M., Pérombelon, M. C. M., and Zutra, D. 1986. Studies of a wilt disease of the potato plant in Israel caused by *Erwinia chrysanthemi*. Plant Pathol. 35:196-202.
15. Lund, B. M. 1979. Bacterial soft-rot of potatoes. Pages 14-49 in: Plant Pathogens. D. W. Lovelock, ed. Society for Applied Bacteriology Technical Series 12. Academic Press, London. 121 pp.
16. Maas Geesteranus, H. P. 1972. Natrot en zwartbenighied bij aardappelen. Bedrijfsontwikkeling 3:941-945.
17. Maher, E. A., De Boer, S. H., and Kelman, A. 1986. Serogroups of *Erwinia carotovora* involved in systemic infection of potato plants and infestation of daughter tubers. Am. Potato J. 63:1-12.
18. McCarter-Zorner, N. J., Franc, G. D., Harrison, M. D., Michaud, J. E., Quinn, C. E., Sells, A. I., and Graham, D. C. 1984. Soft rot *Erwinia* bacteria in surface and underground waters in southern Scotland and Colorado, United States. J. Appl. Bacteriol. 57:95-105.
19. Molina, J. J., and Harrison, M. D. 1977. The role of *Erwinia carotovora* in the epidemiology of potato blackleg. I. Relationship of *E. carotovora* var. *carotovora* and *E. carotovora* var. *atroseptica* to potato blackleg in Colorado. Am. Potato J. 54:587-591.
20. Nielsen, L. W. 1978. *Erwinia* species in the lenticels of certified seed potatoes. Am. Potato J. 55:671-676.
21. Pérombelon, M. C. M. 1972. The extent and survival of contamination of potato stocks in Scotland by *Erwinia carotovora* var. *carotovora* and *E. carotovora* var. *atroseptica*. Ann. Appl. Biol. 71:111-117.
22. Pérombelon, M. C. M. 1982. The impaired host and soft rot bacteria. Pages 55-69 in: Phytopathogenic Prokaryotes. M. S. Mount and G. H. Lacy, eds. Vol. 2. Academic Press, New York. 506 pp.
23. Pérombelon, M. C. M. 1986. Pathogenesis by pectolytic erwinias. Proc. Int. Conf. Plant Pathog. Bact. 6th. In press.
24. Pérombelon, M. C. M., and Kelman, A. 1980. Ecology of the soft rot erwinias. Annu. Rev. Phytopathol. 18:361-387.
25. Powelson, M. 1980. Seasonal incidence and cause of blackleg and a stem soft rot of potatoes in Oregon. Am. Potato J. 57:301-306.
26. Rich, A. E. 1981. Verticillium wilt. Pages 62-63 in: Compendium of Potato Diseases. W. J. Hooker, ed. American Phytopathological Society, St. Paul, MN. 125 pp.
27. Shekhawat, G. S., Nagaich, B. B., Rajpal, R., and Kishore, V. 1976. Bacterial top rot: A new disease of potato. Potato Res. 17:241-247.
28. Sivasithamparam, K. 1982. Blackleg, a confusing disease. J. Agric. Dep. Agric. West. Aust. 1:17-18.
29. Skerman, V. B. D., McGowan, V., and Sneath, P. H. A. 1980. Approved lists of bacterial names. Int. J. Syst. Bacteriol. 30:225-420.
30. Stanghellini, M. E., and Meneley, J. C. 1975. Identification of soft-rot *Erwinia* associated with blackleg of potato in Arizona. Phytopathology 65:86-87.
31. Tanii, A., and Baba, T. 1971. Bacterial plant disease in Hokkaido. II. Bacterial stem rot of potato plant caused by *Erwinia chrysanthemi* Burkholder *et al. (Pectobacterium carotovorum* var. *chrysanthemi*). Hokkaido Prefect. Agric. Exp. Stn. Bull. 24:1-10.
32. Tominaga, T., and Ogasawara, K. 1979. Bacterial stem rot of potato caused by *Erwinia chrysanthemi*. Ann. Phytopathol. Soc. Jpn. 45:474-477.